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Developing Drought- and Low N-Tolerant Maize

Proceedings of a Symposium

March 25-29, 1996, CIMMYT, El Batán, Mexico

G.O. Edmeades, M. Bänziger,
H.R. Mickelson, and C.B. Peña-Valdivia
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CIMMYT is an internationally funded, nonprofit scientific research and training organization. Headquartered in Mexico, the Center works with agricultural research institutions worldwide to improve the productivity and sustainability of maize and wheat systems for poor farmers in developing countries. It is one of 16 similar centers supported by the Consultative Group on International Agricultural Research (CGIAR). The CGIAR comprises over 50 partner countries, international and regional organizations, and private foundations. It is co-sponsored by the Food and Agriculture Organization (FAO) of the United Nations, the International Bank for Reconstruction and Development (World Bank), the United Nations Development Programme (UNDP), and the United Nations Environment Programme (UNEP).

Financial support for CIMMYT's research agenda currently comes from many sources, including the governments of Australia, Austria, Belgium, Canada, China, Denmark, France, Germany, India, Iran, Italy, Japan, the Republic of Korea, Mexico, the Netherlands, Norway, the Philippines, Spain, Switzerland, the United Kingdom, and the USA, and from the European Union, the Ford Foundation, the Inter-American Development Bank, the Kellogg Foundation, the OPEC Fund for International Development, the Rockefeller Foundation, the Sasakawa Africa Association, UNDP, and the World Bank.

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Abstract: Proceedings of a symposium hosted at CIMMYT in 1996, this publication describes the incidence and intensity of drought and low nitrogen conditions for maize in the tropics, the physiology of drought tolerance and the identification of secondary traits, breeding for drought tolerance, the performance of maize under low nitrogen conditions and breeding for tolerance, general considerations for stress breeding, designs and software for experiments in stressed environments, germplasm sources of drought tolerance, and modeling and geographic information system studies.

AGROVOC Descriptors: Zea mays; Maize; Plant breeding; Selection; Injurious factors; Nitrogen; Resistance to injurious factors; Stress; Drought resistance; Plant physiology; Plant production; Crop losses; Simulation models; Computer software; Latin America; Africa; Tropical zones; Research projects

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Foreword:

Food Security and Stress Tolerant Maize

Prof. Timothy G. Reeves
Director General, International Maize and Wheat Improvement Center (CIMMYT)

Food security is a pressing concern for the world today. Even if available food energy were evenly distributed within each country — which it is not — 33 countries would not be able to assure the minimum necessary food energy (2,200 calories per person per day) for their populations. Over 800 million people in the developing world — fully one-fifth of its inhabitants — are food insecure, more than 180 million preschool children are malnourished, and many hundreds of millions of people suffer from diseases of hunger and malnutrition.

A particular area of concern is sub-Saharan Africa, where food security is rapidly deteriorating. The number of undernourished people in that region almost doubled in the two decades since the early 1970s, reaching 175 million, or nearly four-tenths of the populace. Africa must increase crop yields by 3.3% annually for the next 30 years just to keep pace with its population, and it must do so in a way that counteracts the current rapid degradation of its natural resources. Diets in sub-Saharan Africa are based primarily on maize, and the demand for this crop as a human foodstuff (rather than an ingredient in animal feed) is expected to rise more than 2% annually in the region over the next decade.

Research for Marginal Areas is Vital
One key to sustainably addressing this demand in sub-Saharan Africa and elsewhere in developing countries will be improved maize production technology for marginal lands. Much maize in sub-Saharan Africa is sown in areas typified by infertile soils and the threat of creeping desertification or periodic, severe droughts. Farmers squeeze meager harvests out of holdings which have shrunk and lost productivity; fallows have been abandoned in favor of intensive, multiple cropping year round. Worldwide, the relegation of maize to ever-more marginal cropping circumstances represents a continual hardship for millions of farmers.

Stress Breeding for Maize
A major effort to help maize farmers in less-favored areas began in 1990 when CIMMYT, with support from UNDP and in concert with a global network of colleagues, accelerated its development of new, stress resistant maize and related breeding techniques. Aimed at the major constraints of harsh cropping environments — insects, drought, low nitrogen and acid soil conditions — this new maize technology not only fosters food security, but also provides significant environmental payoffs, including the more efficient use of water and nitrogen and a reduced need for potentially harmful chemicals. The technology comes enclosed in a seed, that most traditional and convenient of packages, but research results also include important insights on improved, resource conserving strategies for marginal cropping zones. Most importantly, farmers who use the new seed and techniques will have better harvests in difficult years without paying any yield “penalty” under favorable circumstances — a “win-win” situation.

The project concluded in 1996 and has been a fruitful source of experimental seed and breeding methodologies. Now that the methods are well-proven, the urgent aim — and certainly the thrust of future maize stress research — must be to ensure that stress tolerant maize reaches farmers’ fields, especially in sub-Saharan Africa. Three new CIMMYT initiatives are designed to help accomplish this:

- One launched in 1996 will support efforts of researchers in the Southern Africa Development Community (SADC) to develop locally adapted drought and low nitrogen tolerant maize cultivars. Financed by the Swiss Development Cooperation (SDC),

this innovative partnership complements current activities of CIMMYT in the region and is fully integrated with the existing maize and wheat improvement research network for SADC.
- A second project, to begin in late 1997 with support from UNDP, the International Fund for Agricultural Development (IFAD), and the Swedish International Development Cooperation Agency (SIDA), will expand the development of stress tolerant cultivars into Eastern, Western, and Central Africa. Coordinated by the CIMMYT regional office in Kenya and the International Institute for Tropical Agriculture (IITA), Nigeria, this project will focus on resistance to insect pests and to the parasitic weed *Striga* spp., in addition to drought and low soil fertility.
- As of mid-1997 CIMMYT began to assist the national programs of Kenya and Zimbabwe in the use of biotechnology tools in maize breeding for drought tolerance and insect resistance. This undertaking, which is financed by the General Directorate, International Cooperation, of the government of the Netherlands (DGIS), brings high-tech expertise available at the CIMMYT Applied Biotechnology Center to bear on the very immediate threat of famine faced by farmers in sub-Saharan Africa, and will build on the more conventional approaches described above.

Sharing Knowledge

As part of the original UNDP project, CIMMYT organized and hosted two international conferences in which researchers assessed progress and set new directions. The first was *Insect Resistant Maize: Recent Advances and Utilization*, held from 27 November to 3 December, 1994. Involving approximately 80 participants and 60 scientific papers, this event is covered in a 300-page proceedings of the same title (Dr. John A. Mihm, ed.) that was printed in May, 1997, and distributed to some 500 cooperators and key libraries worldwide. Copies are available from CIMMYT.

The second, *Developing Drought- and Low Nitrogen-Tolerant Maize*, took place from 25 to 29 March, 1996, and is reported in the present publication. The meeting attracted 121 participants and featured a program of 36 oral presentations and 65 posters. From the discussions, it is apparent that effective selection methodologies for tolerances to drought and low nitrogen conditions do exist. In special consultation sessions with developing country representatives attending the conference, it was also concluded that CIMMYT can best serve research partners by establishing regional breeding programs focused on improvement of regionally-adapted germplasm. Finally, participants concurred that networks are an acceptable mechanism for regional collaboration, provided all participants are treated as equals in their planning and execution.

The Future

The success of efforts to reach farmers with useful technologies such as drought- and low nitrogen-tolerant maize and related cropping techniques will depend very much on the continued availability of funding for public sector agricultural research. Breeding under controlled moisture and fertility conditions, for example, requires considerable resources. There will be relatively few offerings from the private sector for marginal regions, where the promise of large profits is scant. Their most significant contribution, perhaps, will be that of increasing productivity in favored areas, which helps reduce the pressure for opening still more fragile lands, such as tropical forest margins, to agricultural production.

CIMMYT is helping research partners in developing countries to obtain additional funding for this work and, through networking, to use current resources more effectively. The information in this proceedings, which covers a range of topics from drought and low nitrogen stress incidence for maize in the tropics through to related biotech applications, modeling, and geographic information system studies, is intended to add to their effectiveness and provide a useful reference for years to come. Because of our interest in getting this material as quickly as possible to readers who can use it, we decided not to translate the Spanish language papers; rather, we have provided English abstracts which contain salient information about the aims, methods, and outcomes of the research described. We hope this proceedings will serve your needs, and welcome your comments and questions about the research it covers.

Acknowledgments

We would like to thank UNDP for its long-standing financial support to maize research at CIMMYT, especially that related to tolerance to drought and low nitrogen, and to host-plant resistance to insects. In particular we thank UNDP for financial support for the symposium and these proceedings. We wish to acknowledge also the support of Rockefeller Foundation, East Africa, who funded the attendance of three participants; the foundations of FAPEMIG of Brazil and DANAC of Venezuela, who provided travel scholarships for two attendees; CIBA Seeds and MAHYICO of India who provided tickets for a further three participants; and SIDA, Sweden, and the ARC-Grain Crops Institute, South Africa, who supported attendance of two southern African attendees. Various projects affiliated with CIMMYT supported attendance of participants, and we thank the East African Cereals Project, the Maize and Wheat Research Network of southern Africa, the Ghana Grains Development Project, and the Programa Regional de Maíz of Central America and the Caribbean. Considerable financial and logistical help to participants was provided by our colleagues in CIMMYT's regional programs, and we thank them.

Our sincere thanks go to Mrs. Esperanza Calderón for her untiring efforts before and during the symposium as secretary to the whole process, and for her good humor and innovative support throughout. During the conference Dr. Anne Elings provided invaluable help during our consultation with national program participants over future research priorities. We thank Dr. Richard Wedderburn and Ing. Alejandro Lopez for their able assistance during the visit to Tlaltizapán Field Station, and at the conference dinner. Excellent logistical support before and during the conference was provided by Linda Ainsworth, Laura Rodríguez and Rey Lugo, Gilberto Hernandez, Miriam Sanchez, Elsa Espinosa, Rodolfo Rojano and Francisco Cervantes. We are grateful to Carmen Espinosa for her assistance with visas for participants, and to Hugo Alvarez and Ing. Eduardo de la Rosa for their assistance with poster boards and purchases. To Maria Garay, Enrique Cosilion, Luis Baños and Guillermo López and their staff we give special thanks for excellent food, accommodation, transport and travel services at CIMMYT for participants. We thank those participants who willingly assisted by chairing sessions or serving on panels. We were much encouraged by comments and suggestions by Prof. Tim Reeves, Director General, CIMMYT, and Dr. Delbert Hess, Director of CIMMYT's Maize Program, while planning and holding this conference.

The dedicated efforts of editors David Hodson and Mike Listman in preparing the symposium materials for publication are greatly appreciated, as well as the professional design of Eliot Sánchez and Miguel Mellado and the layout of Juan José Joven, Marcelo Ortíz and Antonio Luna.

Finally, we thank all participants who willingly shared data and experiences and made the week enjoyable and memorable. We trust that these proceedings do justice to their dedication.

Gregory Edmeades, CIMMYT
Marianne Bänziger, CIMMYT
Harold Mickelson, CIMMYT
Cecilia Peña-Valdivia, Colegio de Postgraduados, Montecillos

Opening Comments

D.C. Hess, Director, Maize Program, CIMMYT

I would like to welcome the distinguished participants of this conference, who comprise a broad representation of the world's experts on the improvement of maize for drought and low nitrogen tolerance. We at CIMMYT, and especially those of us in the Maize Program, are pleased to have you here.
Research on tolerance to deficits of water and N is of particular importance to CIMMYT's Maize Program and to the clients that it serves. Drought and low N are common features of maize-growing environments in the developing world. Maize is often grown in less-favored areas because better land is reserved for higher-value crops. Where farmers know that drought is highly probable, they will usually not risk capital losses by applying fertilizer, even if it is available. Thus, these stresses often occur together in the tropics. High mean precipitation can often mask water shortages from poor rainfall distribution or shallow soils. These factors, combined with limited resources and adverse government policies, result in declining sustainability as soil and water resources become depleted. Improved germplasm will not solve all of the problems; however, results presented by scientists, many of whom are present today, leave little doubt that improved germplasm, when coupled with sound sustainable cropping systems, can go a long way in increasing food security in many parts of the developing world. CIMMYT's Maize Program continues to allocate considerable resources to the development of drought-and low- N tolerant germplasm, primarily because the problems are important and the traits difficult to improve. This calls for a well-coordinated and effective effort by CIMMYT in partnership with national programs.

Work on tolerance to drought was initiated at CIMMYT in 1975. The scientists who have made significant contributions to the work here include Drs. Ken Fischer, Elmer Johnson, Peter Goldsworthy, Shivaji Pandey, Greg Edmeades, Jorge Bolaños, Renee Lafitte, Marianne Bänziger, David Beck, Scott Chapman and Anne Elings. You will visit the CIMMYT experiment station at Tlaltizapán, the primary location at which the research has been conducted and where the timing and severity of water stress can be controlled, a factor eesential to the success of this research. CIMMYT research on low N tolerance began in 1985. Renee Lafitte and Marianne Bänziger have led the work, which was done mostly at the Poza Rica station where long-term low nitrogen blocks have been established. Recent results suggest there are linkages between low N tolerance and drought tolerance -- an exciting finding.

I would like to thank national program cooperators who have tested germplasm in collaboration with CIMMYT and provided necessary feedback on research directions. I would like to single out the contributions of Dr. Alejandro Ortega C., INIFAP, Mexico, who has consistently provided valuable data, advice and assistance in the Sonoran Desert under hot and difficult field conditions. During the latter part of the Symposium, we will be consulting with all of you to better define the future of collaborative drought and low N research at CIMMYT. We welcome and thank you in advance for your input.

The CIMMYT Maize Program helps the poor in developing countries by increasing the productivity of resources committed to maize, while protecting natural resources. This is accomplished through the preservation, improvement, and dissemination of genetic resources; the development of environmentally compatible crop management practices; the provision of research methodologies and information; and through training and consulting. The research on drought and low N tolerance is entirely consistent with Maize Program goals. Finally, I would like to recognize Greg Edmeades, Marianne Bänziger, Anne Elings and other CIMMYT staff for assistance in bringing this symposium to fruition. The results will speak volumes for the worthwhileness and thoroughness of their efforts.

Characterizing Patterns of Water Deficit and Nitrogen Stress in Maize Growing Regions of the Tropics

J.W. White, Natural Resources Group, CIMMYT, México
and A. Elings, Maize Program, CIMMYT

Abstract

Water and nitrogen deficits frequently reduce maize production in tropical regions, but it is difficult to assign precise values to their impact or to subdivide regions experiencing water deficit into well-defined categories. Nonetheless, there are clear benefits to obtaining such information. Assessments of impact are crucial to priority setting, while classification of patterns of water deficit can improve targeting of research both in crop improvement and crop management. Simple classifications using subjective evaluations or analyses of monthly weather data are useful, but there is strong demand for more quantitative approaches. Process-based crop growth models show much promise for integrating effects of diverse environmental and agronomic factors, but such models are very data intensive. This paper examines three facets of use of models for characterizing patterns of water deficit and nitrogen stress for maize growing regions of the tropics. The water deficit index (WDI) of the CERES-Maize model was found to show promise as an indicator of seasonal variation in water deficit. Similarly, the nitrogen stress index (NSI) of the model appears useful for nitrogen deficit. The model predicted that water deficits show much stronger seasonal variation than nitrogen stress and that varying N-fertilization levels has relatively little impact on variation in WDI. Thus, WDI shows strong spatial and temporal variation, while NSI shows mainly spatial variation. The daily weather data required by simulation models are seldom available for large numbers of sites, so researchers have developed "weather generators" that create simulated weather data based on monthly means, which are easily interpolated over geographic regions. Although the two generators examined, WGEN and SIMMETEO, provided weather data that gave mean yields similar to those obtained from observed weather data, they did not capture expected associations between date of onset of growing seasons and total seasonal precipitation. Thus, data from weather generators may not be suitable for use with models simulating detailed mechanisms of adaptation to water deficit.

Water and nitrogen deficits in maize production regions show large spatial and temporal variation. Although researchers can incorporate an intuitive understanding of this variation in their research strategies, more objective and quantitative characterizations are desirable. These should help clarify discussions of possible mechanisms of adaptation or strategies for agronomic management of stresses and assist prioritization of research. The latter point is gaining in relevance as providers of research support increasingly expect that potential research results be quantified in economic terms (Antle and Wagenet, 1995). Although characterizations can focus on specific locations, most research has a regional focus, which implies definition of agroecological zones. In the remainder of this paper, we will emphasize approaches for defining zones that incorporate information on water and nitrogen stresses.

Approaches for characterizing stress can include tabulation of expert opinion, cluster analysis of climate or soils data, analyses with simulation models, and spatial analyses using geographical information systems (GIS). The approaches are often complementary, allowing strengths and weaknesses to be balanced (Table 1). Thus, surveys of experts usually provide subjective estimates of the effects of stresses, but experts can help guide simulation modeling to assure that models are applied using realistic cropping practices and that model outputs are realistic.

The megaenvironment classification developed by the CIMMYT Maize Program (1988) demonstrates the utility of expert opinion. However, the zones described do not permit quantifying the impact of water or nitrogen stress on production nor do they indicate how patterns of stress vary within or across regions.

Corbett (in press) classified maize production zones in Kenya using multivariate cluster analysis of climate and elevation data followed by consultation with maize researchers. Preliminary zones were defined using monthly data for maximum and minimum temperatures and precipitation plus altitude. The limits for these zones were then adjusted to create a final classification system that would be similar to the previous systems used by KARI, and would capture important new information. The new zonification indicated a need to shift regional priorities for maize breeding. It was also used to guide stratified surveys of farms and villages for a more detailed database on maize production (Hassan et al., in press). However, the approach still did not quantify potential yield levels or patterns of water or nitrogen deficit.

Simulation models have been used to characterize production potential over regions; e.g., Lal et al. (1993) used the BEANGRO model interfaced to a GIS system to map potential yield of common bean over Puerto Rico, Rötter (1993) used the WOFOST model to examine biophysical limits to maize production in Kenya, and Woopereis (1993) examined regional variation in rainfed rice yields for the Tarlac Province, Philippines using ORYZA1-DSTRESS-PADDY. Models are also being integrated with multiple-goal linear programming to create flexible tools for reconciling different objectives of participants in classification exercises (van Keulen, 1993). While these approaches show promise, they require extensive data. A typical “minimum data set” for application of simulation models includes daily weather data (maximum and minimum temperature, solar radiation and precipitation), details of cropping practices (cultivar, planting date, row spacing and population density, fertilizer, and irrigation dates and amounts), and a description of the soil profile.

Table 1. Example of approaches for defining agroecological zones, including indication of their reliability, cost, reproducibility and degree of quantification. The number of asterisks indicates a range from low (one) to high (five).

Approach	Reliability	Cost	Reproducible	Degree of quantification
Expert opinion	**	**	*	*
Cluster analysis of monthly weather data	**	**	***	**
Cluster analysis + expert opinion	***	***	**	***
Cluster analysis of crop simulation results	****	****	***	*****
Cluster analysis of simulation results + expert opinion	*****	*****	**	****

This paper examines the potential of simulation models to quantify temporal and spatial variation in water deficit and nitrogen stress for tropical maize production. The CERES-Maize model is used throughout (Jones and Kiniry, 1986; Hoogenboom et al., 1994; W. Bowen, personal communication, Nov., 1995) because it is widely known. Emphasis is given to three issues. Can models quantify water deficits in a manner that is more useful than simple ratios of actual to potential evapotranspiration? Can models quantify nitrogen stress and if so, how does N stress interact with water deficit patterns? Are daily weather data “generated” by statistical analyses of monthly data an adequate substitute for observed daily data?

Implicit throughout these discussions is the assumption that models such as CERES-Maize simulate maize growth and development in a sufficiently realistic fashion to produce useful results. Although CERES-Maize has been tested in diverse environments, it is known not to include certain basic responses to stress such as lengthening of the anthesis-silking interval (ASI). Further model development and field testing must accompany any attempts to apply models to characterization studies involving stress near flowering.

Materials and Methods

All simulations were conducted with the model CERES-Maize v. 3.10 (95.0) (Hoogenboom et al., 1994; W. Bowen, personal communication, Nov., 1995). Daily weather data were obtained from experiment stations or from the Global Daily Summary database (National Climatic Data Center, Asheville, North Carolina). Where data for solar radiation were not available, the SIMMETEO weather generator (Geng et al., 1986) was used to estimate daily values. Monthly means required as input for SIMMETEO were obtained from the FAO agroclimatological reports (FAO, 1984; FAO, 1985; FAO, 1987).

For simulations of maize at Gainesville, Florida, initial conditions and cropping practices were used as provided in sample data sets of CERES-Maize. Briefly, these were a 26 Feb. 1982 planting with 7.2 plants / m^2 of cultivar. McCurdy 84aa and providing either 116 kg N / ha over three dates (low-N treatment) or 400 kg N / ha over six dates. In simulations for Palmira, Colombia, Nakhon Saw, Thailand, Kitale, Kenya, Harare, Zimbabwe and Natal, Brazil, initial conditions and management were inferred from various sources. Planting dates were assigned based either on dates used for nearby sites of international maize trials or on the date of onset of the growing season. The growing season was considered to have started when a site received more than 30 mm of rainfall within a 10 day period. Planting arrangements were 5 plants m^{-2} with 0.76 m row spacing. Nitrogen fertilizer was applied only at planting and was either 0 or 90 kg N / ha.

Simulations were started 30 to 50 days prior to planting to permit soil moisture in the upper horizons in the profile to equilibrate. The default limits of soil depth and soil moisture depletion provided with CERES-Maize were used for automatic irrigation to obtain fully-irrigated treatments.

Results and Discussion

Characterizing patterns of water deficit

Patterns of water deficit vary both with weather and soil conditions. Simple water balance models, which only compare precipitation and potential evapotranspiration, will not respond to effects of growth stage or variation in soil moisture on actual evapotranspiration. Simulation models such as CERES-Maize do account for these effects and furthermore, can provide various levels of detail in their outputs. These include potential and actual evapotranspiration, plant transpiration, and summary statistics of water deficit level, as illustrated in Figure 1 for a maize crop grown at Gainesville, Florida.

A common index is simply the ratio of actual to potential evapotranspiration (ET ratio) (Fig. 1B). The water deficit index (WDI) calculated by CERES-Maize has the further advantage of indicating whether transpiration was limited by water uptake capacity of the crop by accounting for variation in soil moisture availability in relation to root distribution in the soil profile. A value of zero means that no deficit occurred, and a value of one means that for that day, none of the demand for water was met. The WDI and the ET ratio describe essentially identical information except during early crop growth (Fig. 1B). However, WDI indicates a low level of stress during early crop growth (15 to 22 days after planting), while the ET ratio indicates considerable stress. This discrepancy is because WDI accounts for effects of reduced plant size on transpiration, but use of the ET ratio implies that a crop has a closed canopy throughout its growth cycle. WDI thus appears more suitable than the ET ratio for characterizing water deficit patterns in an annual crop such as maize.

To examine variation in stress patterns over multiple seasons, WDI can be estimated for each season and compared. Overlaying graphs of variation in WDI quickly results in a

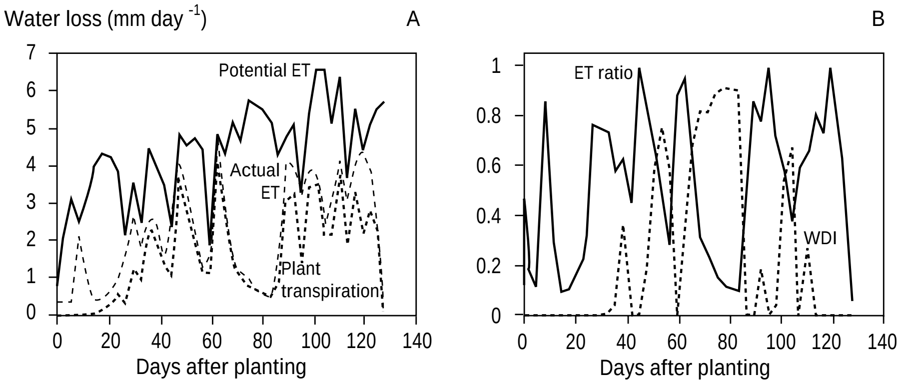

Figure 1. Variation in the crop water balance of a maize crop grown under rainfed, low nitrogen conditions at Gainesville, Florida (Bennett et al., 1989) and as simulated by CERES-Maize. A. Transpiration, actual evapotranspiration (ET) and potential evapotranspiration. B. Water deficit index (WDI) calculated by CERES-Maize and the ratio of actual to potential evapotranspiration (ET ratio).

confusion of lines that is difficult to interpret (Fig. 2A). A useful strategy to synthesize data on WDI over time is to simply graph lines indicating when WDI exceeded a critical level. Fig. 2B illustrates this for 16 years of data for simulations of a maize crop grown at Palmira, Colombia, arbitrarily assuming a critical level of 0.25.

Characterizing interactions of water deficit and nitrogen stress

The ability of simulation models to account for different agronomic practices and growing conditions makes them suitable for comparing the relative importance of water and nitrogen deficits assuming different management practices. For 16 seasons at Palmira, Colombia, applying 0 or 90 kg / ha of nitrogen at planting and using irrigated or rainfed conditions, CERES-Maize predicted that fertilizing a rainfed crop would provide greater yields than irrigation without N fertilizer (Fig. 3). However, rainfed systems would show much greater season-to-season variation.

An alternate perspective is to use the nitrogen stress index (NSI) calculated by CERES-Maize as an index of N deficit during the growth a crop. NSI is calculated by determining whether the N demand on a given day can be satisfied by the pool of readily available soil N. As with WDI, a value of zero for NSI indicates no stress and a value of one, maximum stress. Variation in NSI over seasons (Fig. 4) was much less pronounced than for WDI (Fig. 2A) for similar conditions. Furthermore, different levels of N seem to have relatively small effects on the pattern of water deficit as indicated by WDI (Fig. 5). Thus, where risk due to variable precipitation is a major concern, emphasis can be given to patterns of water deficit with less concern over confounding effects of N availability. This conclusion is counter-intuitive since it seems to violate the widely held belief that there are strong interactions between water deficit and N stress. This discrepancy is explained by several factors. First is that an interaction effect on yield may occur without there being a difference in the pattern of stress. The example in Figure 3 suggests an interaction for yield: if the effects of irrigation and nitrogen were additive, the expected yield for irrigation with 90 kg N / ha would be approximately 5800 kg / ha; the actual value is 5350 kg / ha. Nonetheless, the same simulations produced the data for variation in WDI that are shown in Figure 5. A more mechanistic explanation is that water deficits may induce N deficits by reducing the availability of soil N. Thus, under water deficit conditions, the overriding determinant of stress patterns will be water availability. Tolerance to water deficit and to N stress in maize also may involve similar mechanisms through stress signals and reduction in leaf area expansion (see Lafitte et al., 1997).

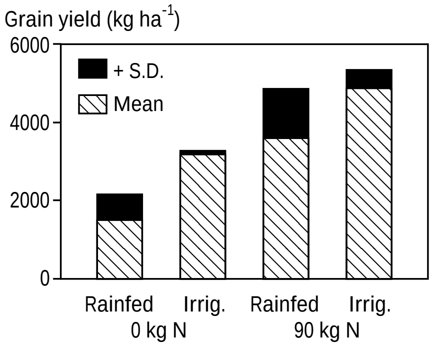

Figure 3. Variation in grain yield for simulations of cv. Suwan-1 for 16 seasons at Palmira, Colombia, assuming irrigated or rainfed conditions and 0 or 90 kg N/ha fertilization at planting. Shaded portions indicate plus one standard deviation above the mean. Numbers within open bars are mean yields (corresponding to height of the bars).

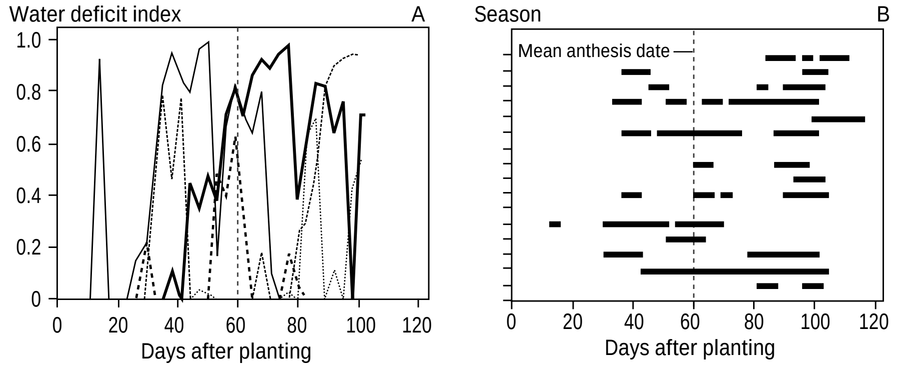

Figure 2. Variation in the water deficit index (WDI) for simulations of cv. Suwan-1 at Palmira, Colombia assuming rainfed conditions and 90 kg N/ha at planting. A. WDI as absolute values over five seasons. B. periods during the growing season when WDI values exceeded 0.25 for 16 individual seasons.

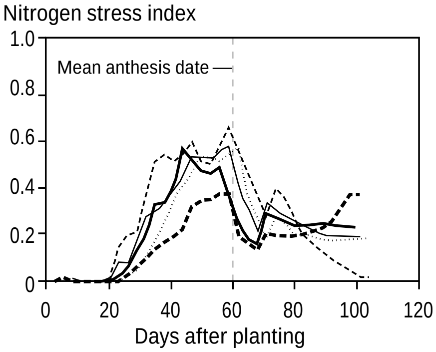

Figure 4. Variation in nitrogen stress index for simulations of cv. Suwan-1 for five seasons at Palmira, Colombia, assuming rainfed conditions and no N fertilization.

Using generated weather data as a substitute for observed data

If it is accepted that simulation models show promise for characterizing patterns of water deficit and nitrogen stress, perhaps the most pressing issue is how to obtain the extensive meteorological and soil data that models require. For weather data, various strategies have been developed for "generating" daily weather data from monthly means and statistical descriptors of patterns of variation. Two weather generators are provided in the DSSAT3 modeling package, the Richardson (1985) and SIMMETEO (Geng et al., 1986) generators.

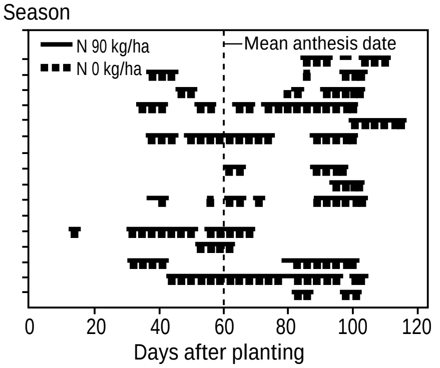

Fig. 5. Periods during the growing season when the water deficit index (WDI) exceeded 0.25 for simulations of cv. Suwan-1 at Palmira, Colombia, assuming rainfed conditions and 0 or 90 kg N/ha at planting and using data for 16 individual seasons.

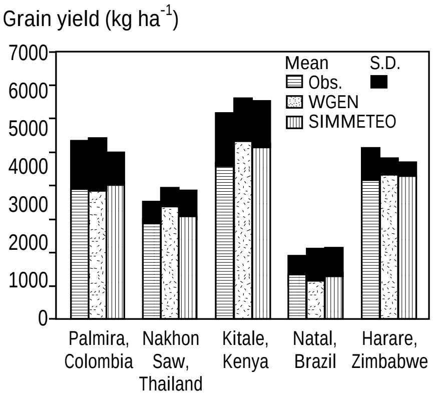

Figure 6. Means and standard deviation of grain yield for simulations of cv. Suwan-1 for 10 seasons at five locations and using either observed daily weather data or data generated by the WGEN and SIMMETEO generators of DSSAT3. Shaded portions indicate plus one standard deviation above the mean.

To test the efficiency of the generators, simulated grain yields and variation in yields were compared for 10 years of observed or generated weather data over five sites (Fig. 6). Values for simulated yields from the generators were generally close to those obtained using observed weather data. However, the generated data still might fail to reproduce patterns of weather variation that would become important as simulation of different adaptive mechanisms is improved in the models (see Elings et al., 1997).

One such pattern is the relation between time of onset of the rainy season and the total precipitation during the season. For summer monsoon rains, later onset may be associated with decreasing total precipitation. A short-day photoperiod response might permit a crop to reduce its growth cycle with very late plantings, thus adjusting the length of the growth cycle to the expected available precipitation. Observed data from F. Madero, Durango, Mexico showed the expected negative association between onset of the season and total precipitation (Fig. 7), but generated weather data showed no relation. In contrast, for Harare, Zimbabwe, no relation was noted with observed data (r = 0.20, NS), but the generated data indicated that a late onset was associated with greater precipitation ($r = 0.55$, $P < 0.05$). Thus, while weather generators may have utility for examining spatial variation in grain yield, they may be inadequate for characterizing variation in weather patterns that would influence specific adaptation mechanisms.

Conclusions

The described simulation experiments support the thesis that models such as CERES-Maize may be valuable tools for characterizing patterns of water deficit and nitrogen stress in maize production areas. Specific points that emerged from the study were:

- WDI appears more useful for characterizing variation in moisture deficit levels than the more frequently used ratio of

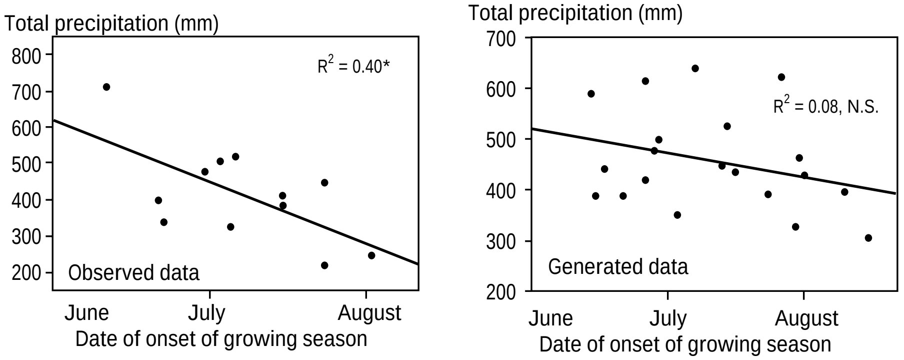

Figure 7. Relationship between date of onset of growing season and total precipitation received at Francisco Madero, Durango, Mexico. Observed data are for 12 years and generated data for 20 years as generated by the WGEN generator of DSSAT3.

actual to potential evapotranspiration.

- Seasonal variation in WDI did not vary greatly with nitrogen regime. If these results are confirmed for a wider range of conditions, emphasis in studies of risk may focus on water deficit patterns and consider patterns of N stress variation as a secondary issue.
- While weather generators may be adequate for broad studies of variation in grain yield under water deficit, they may fail to reproduce variations in precipitation patterns that will become of greater interest as maize models incorporate more detailed sub-routines that simulate effects of adaptation mechanisms.

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Incidencia de la Sequía en la Producción de Maíz en Sudamérica y la Necesidad de un Trabajo Colaborativo

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Abstract

The area sown to maize in South America fluctuates around 18 million hectares, with an average yield of 2.21 t/ha. Some 15% of this area is usually affected by drought. Basically two types of maize are planted in the region: hard dent (MD) in the lowland tropical zone and floury morocho (MA) in the Andean region (at altitudes above 2200 m). The effect of drought stress varies for each county and type of maize. For MD, 28% of Bolivia's maize area experiences frequent drought stress; in Argentina, Brazil, Colombia, Ecuador, Peru and Venezuela, the area with drought stress ranges from 15 to 22%. Chile and Paraguay do not show any problems with drought. For MA, two-thirds of the area planted in Bolivia and Peru is subject to frequent drought stress; frequent drought stress occurs in Ecuador on 19% and in Colombia on 38% of cultivated area. The wide distribution of drought makes this an ideal target for collaborative work among research organizations that work in the areas affected; the exchange of germplasm, knowledge, and experiences would foster more rapid and efficient progress. With regard to germplasm, CIMMYT coordinates research networks for drought and for acid soils which can be utilized by collaborating countries.

Introducción

El área sembrada con maíz en Sudamérica es de 17.35 millones de ha con un rendimiento promedio de 2.2 t/ha, que es menor al de otras regiones en vías de desarrollo (2.4 t/ha) y al de los países en desarrollo (6.9 t/ha) (CIMMYT 1994). Por otro lado, también para Sudamérica se reporta uno de los rendimientos más altos en el mundo (Chile 8.3 t/ha); aunque, existen países como Ecuador donde el rendimiento promedio es solo 1.1 t/ha. Indudablemente, la gran variabilidad observada en la productividad de maíz en Sudamérica es consecuencia de una serie de factores socioeconómicos, ecológicos y tecnológicos que inciden en el desarrollo del cultivo. Estos factores han determinado que podamos diferenciar dos tipos de maíz como los más difundidos en nuestra región: Maíz dentado y duro de trópico bajo (MD) y maíz amiláceo y morocho de la zona andina (MA). El MD incluye maíces de granos amarillos y blancos cultivados en todos los países de Sudamérica a altitudes menores a 1500 msnm, el uso del maíz amarillo es principalmente para alimentación animal mientras que el maíz blanco es para consumo humano y generalmente responden a un tipo de agricultura de intercambio. El MA incluye granos de diversas coloraciones de acuerdo con el uso al que se destine en cada región de un país, ya que es principalmente utilizado para consumo humano directo, se siembra básicamente en Bolivia, Colombia, Ecuador y Perú a altitudes mayores a 2200 msnm, generalmente responde a un tipo de economía de autoconsumo. En relación con los daños por el estrés de sequía el MA es más afectado (entre 19 y 66% del área sembrada es afectada por algún tipo de estrés) mientras que para el MD el porcentaje varía entre 0 y 28%.

Indudablemente la sequía es un problema que afecta la producción de maíz, sin embargo es difícil cuantificar el daño real, para tener una aproximación se ha recurrido a la información disponible en el CIMMYT y a los datos proporcionados por los coordinadores de los programas nacionales. Por ser la sequía un factor climático aleatorio, la búsqueda y obtención de individuos con mayor tolerancia es un reto para los científicos interesados en solucionar esta importante limitación de la producción de maíz.

Al referirnos al estudio realizado por CIMMYT (1988) en relación con el estrés por sequía, A significa muy rara ocurrencia de estrés, B algunas veces con estrés, C estrés frecuente y D usualmente bajo algún tipo de estrés.

Los resultados experimentales que se presentan y los rubros de investigación que se vienen ejecutando en la región tienen por finalidad demostrar nuestro interés por contribuir a la solución de los problemas de la producción maicera y motivarnos a incrementar nuestra colaboración para convertir esta meta en un ideal común de quienes estamos involucrados en el quehacer maicero.

Areas Afectadas por la Sequía

Argentina

En Argentina se sembró, promedio del quinquenio 1986-90, 2.71 millones de ha de maíz en 9 regiones geográficas. Existen problemas de estrés hídrico en 2.46 millones de ha distribuidas en seis de las nueve regiones. Se calcula una merma en la producción del 30% por efecto de la sequía y la periodicidad de ocurrencia es de uno cada dos años, calculándose una pérdida anual de 18.58 millones de dólares (Eyherabide, 1993). Para el área típica argentina (Región IV), donde se siembran 653,000 ha de maíz, se ha calculado que 34% de la variabilidad en el rendimiento puede ser explicada por variaciones en la precipitación (Oyarzábal et al., 1980). La precipitación promedio en esta área es de 944 mm. Aunque la mayor frecuencia de lluvias es en verano, también en esta época se tiene la mayor evapotranspiración, la que genera déficit hídrico principalmente entre diciembre y enero, periodo en el que coinciden la pre y post-floración. Lo anterior, puede generar pérdidas del rendimiento de hasta 50% (Celiz et al., 1995).

Bolivia

El área sembrada con maíz en Bolivia durante 1992-93 fue de 287 140 ha, con un rendimiento de 1.75 t/ha (Claure, 1996, comunicación personal). Como resultado del creciente mercado nacional e internacional, derivado del incremento de la actividad avícola, la tendencia de los últimos 3 años ha sido el incremento tanto en el área sembrada (de 200 000 a casi 300 000 ha) como de la productividad (de 1.25 a 1.75 t/ha) (Avila, 1993).

El MD se siembra principalmente en los departamentos de Santa Cruz y Tarija. En Santa Cruz se sembraron 84 390 ha con un rendimiento de 2.9 t/ha y fluctuaciones entre 1.46 t/ha en 1990 y 2.26 t/ha en 1989, es el área de mayor desarrollo agropecuario de Bolivia y presenta clima tropical con temperatura media anual de 20.7ºC y precipitación de 818 mm por año (promedio de 1981 a 1992) (Claure, 1996, comunicación personal). Aquí, la distribución y cantidad de lluvia en noviembre es fundamental para la siembra, la de diciembre afecta el desarrollo vegetativo, la de enero y febrero está directamente relacionada con el rendimiento y la de marzo determina el llenado del grano. En promedio, la precipitación de noviembre entre 1981 y 1991 fue 80 mm y fluctuó entre 49 y 100 mm, 115 mm en diciembre con mayor variabilidad que el mes anterior, entre 28 y 280 mm, y entre enero y febrero fluctuó desde 140 hasta 252 mm, finalmente, en marzo fue de 100 mm y mostró la más alta variabilidad, desde 15 en 1989 hasta 221 mm en 1981. Aunque, además de la distribución y cantidad de lluvia existen otros factores agroclimáticos que afectan el rendimiento, específicamente en 1990 la caída del rendimiento puede explicarse por la escasa precipitación (534 mm) en todo el año y particularmente en enero y febrero.

En el departamento de Tarija se siembran 40 900 ha con maíces amarillos dentados y cristalinos principalmente, con rendimiento promedio de 1.65 t/ha. Las zonas maiceras están localizadas en 3 provincias; Cercado (Valle Central) con temperatura media de 17.9ºC y 606 mm precipitación anual y 538 mm en la época de siembra del maíz (noviembre-marzo), Valle Central de Tarija que incluye 50% de la superficie total aprovechable y sólo 15% posee riego (Cabrera et al., 1995);

O’connor con temperatura de 19.7ºC, y 1014 mm y 829 mm de precipitación media anual y entre noviembre y marzo, respectivamente. Además, en la provincia del Gran Chaco hay otras dos zonas: Yacuiba y Villamontes.

El MA se siembra principalmente en los departamentos de Chuquisaca y Cochabamba. En Chuquisaca se siembran 70 150 ha de maíz con un rendimiento de 1.22 t / ha. El área maicera en Chuquisaca está principalmente en 3 provincias: Tonina a 2 100 msnm con temperatura media de 17.3ºC y 619 mm de precipitación anual, Zadañez a 2 500 msnm con temperatura media de 16ºC y 560 mm de precipitación anual y Luis Calvo donde se puede diferenciar una zona de transición (Muyupampa) a 1 110 msnm con 24.1ºC y 699 mm de precipitación anual y la zona del Chaco Chuquisaqueño a 340 msnm con 24.4ºC y 500 mm de precipitación. En el Departamento de Cochabamba se siembran 38 000 ha de MA con un rendimiento promedio de 1.06 t / ha. La temperatura y precipitación media anual es 16.5ºC y 610 mm al año. Cochabamba representa a los valles interandinos donde se calcula que está 60% del área afectada por efecto de la sequía (INE, 1994).

De acuerdo con esta información la superficie afectada por la sequía se calcula de la siguiente manera: 52% para la zona de Santa Cruz, 59% para la de Chuquisaca y 41% para la de Tarija y afecta a 12 987, 20 940 y 4 352 productores, respectivamente (Claure, 1996, comunicación personal).

Brasil

En Brasil se siembran 12.64 millones de ha de maíz con un rendimiento promedio de 2 t / ha (CIMMYT, 1994). En Brasil el maíz se produce en cinco regiones con características agroecológicas y de producción muy diferentes. 1) En la región norte, que abarca siete estados con clima cálido y húmedo, se produce 2.5% del total del maíz, se siembra entre octubre y diciembre, a altitudes que oscilan entre 0 y 200 msnm y la sequía no es un problema pues recibe una precipitación anual de 1 500 a 3 000 mm. 2) En la región noreste, que abarca 9 estados con clima seco y altas temperaturas, se cosecha 5.3% del total, se siembra entre noviembre y mayo a altitudes entre 0 y 1 200 msnm y la sequía es un factor negativo importante pues presenta precipitación de 300 a 500 mm. El área afectada por estrés de sequía es aproximadamente 1.5 millones de ha. 3) La región sureste contribuye con 28% de la producción e incluye 4 estados con clima extremoso, nueve meses fríos y tres meses con altas temperaturas, y precipitación entre 800 y 1 500 mm. La siembra se realiza a altitudes entre 0 y 1 300 m, entre octubre y noviembre y es usual que se presenten períodos cortos de sequía, que afectan aproximadamente 38 000 ha. 4). La región centro-oeste aporta 17% de la producción, abarca 3 estados donde la siembra se realiza durante octubre y noviembre, la precipitación es de 800 a 1300 mm, y es frecuente la incidencia de altas temperaturas durante la floración, aquí 208 000 ha presentan problemas de estrés por sequía. 5) Finalmente, la región sur es la más importante productora de maíz con 47% de la producción total. Abarca tres estados con buenas condiciones para la producción, con veranos de días calurosos y noches frescas, con precipitación entre 800 y 1 500 mm y zonas de cultivo con altitudes de 0 a 1 100 m. El daño producido por sequía es aproximadamente de 151 000 ha.

En conclusión, el estrés por sequía afecta 14.8% del área maicera de Brasil, equivalente a 1.9 millones de ha y la pérdida alcanza 3.7 millones de t (Santos, 1996, comunicación personal).

Colombia

En Colombia en el quinquenio 1991-95 se sembraron en promedio 700 000 ha de maíz. El maíz se cultiva prácticamente en todo el país, desde el nivel del mar hasta los 2 600 m, con temperaturas desde 4°C en el altiplano Cundi-Boyacense hasta los 35°C el la costa Atlántica y con precipitaciones desde 30 mm anuales en la Guajira hasta 10 m en el Urabá Chocoano. Es el cereal más importante para la alimentación humana y animal, aproximadamente 62% se consume como alimento en diferentes preparaciones de acuerdo con la región y el resto se usa para fabricar alimentos procesados y balanceados. Aproximadamente, 75% de la producción total corresponde a casi 85% del área en la que se realizan prácticas agrícolas tradicionales. Las importaciones de maíz han ido en aumento, pasando de 14 000 t en 1991 a 1.2 millones de t en 1995 (LENGUA, 1996, comunicación personal).

En Colombia, las estaciones secas y las inundaciones, causan periódicamente pérdidas considerables en la producción agrícola. La estación seca en Colombia y en especial en la región Caribe (toda la costa Atlántica) se presenta desde enero hasta marzo y con menor intensidad entre julio y septiembre. Otras regiones con estaciones secas marcadas son la parte del valle alto del Magdalena, altiplano Santandereano, Dagua, Villa de Leiva y Ráquira, además el departamento del Cauca y los Llanos Orientales (Marín, 1992).

La Región Andina (sobre los 1 500 msnm) es la principal zona productora con 49 % del área total. El rendimiento promedios es 1.5 t/ha, con fluctuaciones entre 1.1 y 1.9 t/ha. Los MA, de período vegetativo largo (3.5-4 meses a la floración) se siembran en altitudes superiores a 2 200 m, especialmente en los departamentos de Cundinamarca, Boyacá, Santanderes y Nariño, y cubren 40% del área maicera andina. Los MD (2.5-3 meses a la floración) ocupan el 60% restante, a altitudes entre 1 500 y 2 200 m, en los departamentos de Antioquía, Santanderes y la zona cafetera colombiana. La región Andina presenta variaciones en el régimen pluviométrico con valores de 800 mm (Nariño, Cundinamarca y Boyacá) a 1 850 mm en zonas de clima frío húmedo; en general, aquí no se dispone de riego (Navas et al., 1995). En los Valles interandinos (Valle del Cauca, Valle del Patía, Alto y Medio Magdalena) se cultiva 10% del área maicera total, con MD blanco y amarillo principalmente y rendimiento promedio de 2 t/ha.

La Costa Atlántica (región Caribe) es una de las regiones de mayor producción de maíz en Colombia con 25 % del área total, sobresalen los departamentos de Córdoba, Sucre, Bolívar, Atlántico, Magdalena y Cesar, donde se sembraron 107 400 ha en 1992 (FENALCE, 1994), contribuyó con 215 000 t a la producción Nacional (Navas et al., 1995). El régimen pluviométrico de la región es muy variable con 300 mm anuales en el norte de la península de la Guajira hasta 2 500 mm anuales en la Sierra nevada de Santa Marta y al sur del departamento del Cesar. Los estudios sobre patrones de precipitación indican a la mala distribución más que a la cantidad de precipitación la causante de períodos secos en etapas críticas del desarrollo del maíz en estas zonas (Terán, 1994).

En la Orinoquía Colombiana (departamentos del Meta, Arauca y Guaviare) el área sembrada con maíz representa 12% del total, tanto en el sistema tradicional como en el tecnificado, con rendimientos promedio de 1 y 2 t/ha, respectivamente. Esta área se localiza principalmente en el pie de monte y vegas de los ríos, con precipitaciones superiores a 1 800 mm (Navas et al., 1995).

De acuerdo con la información consignada por CIMMYT (1988) 57.3% del área sembrada en Colombia (caribe húmedo, climas medios húmedos de la región cafetera y regiones del clima frío húmedo) no tiene problemas de estrés, 27.3% corresponde a la categoría B, algunas veces con estrés, 13.6% presenta estrés frecuente (caribe seco, alto y medio Magdalena, regiones secas de la zona cafetera y climas fríos secos de Cundinamarca, Boyacá, Nariño y los Santanderes y 1.7% está usualmente bajo estrés y corresponde a la alta Guajira (300 mm anuales) y zonas de los departamentos del Atlántico, Bolívar y Cesar.

Ecuador

En el Ecuador se sembraron, entre 1986-90 un promedio de 468 347 ha de maíz por año con un rendimiento de 1 t/ha (Caviedes, 1991). El área sembrada con MD (260 605 ha) esta localizada principalmente en la costa y algunos valles interandinos. En 1994 se sembraron 170 000 ha en las provincias de Manabí y Guayas (Costa) y los valles interandinos de Loja (Reyes, 1996, comunicación personal). La principal característica de estas áreas es la gran variabilidad en la distribución de las lluvias tanto entre años como entre meses. Más de 90% del área maicera de esta región se siembra entre enero y mayo y durante estos meses, en el periodo 1983-1994, la precipitación en la provincia de Manabí sobrepasó los 1 000 mm en algunos años y en otros no llegó a 400 mm. Aún más importante es la precipitación durante febrero y marzo, época en la que el maíz está en floración. El menor rendimiento promedio obtenido en ese periodo (1983-1994) fue de 1.07 t/ha en 1988, el año con menor precipitación desde enero hasta mayo, pero especialmente en marzo (25 mm).

El MA se siembra en la región andina a altitudes mayores a 2 200 m, cubre un área de 206 710 ha y su rendimiento promedio es 0.7 t/ha. De esta área 86% se dedica a la producción de maíz como grano seco, obteniéndose muy bajos rendimientos (0.5 t/ha) y 14% se destina a la producción de choclo, obteniéndose rendimientos mayores (1.8 t/ha). El MA se siembra básicamente en suelos que no disponen de riego, en consecuencia depende de la precipitación que es bastante errática, hecho que se complica con el largo período vegetativo de los maíces que se siembran en estas áreas (3.5-4.5 meses a la floración).

De acuerdo con la información consignada en el CIMMYT (1988) 34% del área (la zona productora cercana a Pichilingue) recibe 2740 mm por año y la temperatura promedio es 24.3ºC, consecuentemente el cultivo de maíz se desarrolla sin mayores problemas; pero, 66% del área (Portoviejo, Machala y Valles interandinos de Loja) corresponde a las categorías de estrés B y D, es decir, los daños son frecuentes. La precipitación promedio en esta área es de 500 mm por año y la temperatura media anual de 24.6ºC. Para el caso de MA el 59% del área maicera corresponde a la categoría B y está ubicada al norte de Quito hasta la frontera con Colombia y una zona productora al sur de Quito y norte de Cuenca; la zona productora de maíz ubicada al sur de Quito abarca 29% del área y corresponde a la categoría C.

Perú

En el Perú se sembraron 379 000 ha de maíz con un rendimiento aproximado de 1.8 t/ha, en el período 1970-89 (Narro, 1991). El MD se siembra en dos regiones geográficas tropicales (costa y selva) con intervalos de precipitación muy amplios. La costa es una franja de tierra ubicada en forma paralela al Océano Pacífico y se caracteriza porque no hay precipitación a lo largo del año, en consecuencia toda la agricultura se desarrolla con alguna forma de irrigación. La costa peruana es el lugar ideal para realizar estudios de tolerancia a sequía justamente por esta característica. En la Costa se sembraron 89 000 ha de maíz con un rendimiento promedio de 3.6 t/ha, toda la producción es utilizada en la elaboración de alimentos para animales, principalmente aves. En la selva se sembraron 83 000 ha de MD con un rendimiento promedio de 1.8 t/ha, la producción se dedica también para la alimentación animal, aquí el estrés por sequía es una de las causas del bajo rendimiento. Del área maicera de la selva, 60% se encuentra en la zona tropical nororiental en los departamentos de San Martín, Cajamarca y Amazonas. En estas áreas la temperatura es de 25ºC y la precipitación anual alrededor de 1 000 mm, de la que más de la mitad se presenta en la época del cultivo del maíz, aunque con gran variación entre los meses; el área restante de la selva no tiene problemas de sequía. Por ejemplo, para el departamento de Loreto donde está 12.6% del área maicera de la selva, para el período 1980-93 la precipitación fue de 2 921 mm por año y 1 380 mm para la época de siembra de maíz (julio-octubre).

El MA se sembró en 207 000 ha con un rendimiento promedio de 1 t/ha. Es un cultivo ampliamente distribuido en todos los departamentos de la Sierra (Cordillera de los Andes), se siembra en pequeñas extensiones generalmente menores a una ha por agricultor y principalmente sin posibilidades de irrigación, la cosecha se utiliza para el autoconsumo. Aproximadamente, 52% del área se siembra en la sierra norte donde predomina el consumo del grano seco y sólo 15% de ésta área se dedica a la producción de choclo, la cosecha de las parcelas con riego se dedica al mercado. Así, la mayor área se cultiva en temporal o secano, por lo que la precipitación es uno de los factores determinantes del desarrollo del cultivo. La época de siembra del maíz coincide con el establecimiento de las lluvias. Tradicionalmente la siembra en la sierra norte se realizaba en octubre, en la última década, el inicio tardío de las lluvias ha generado un retraso y ahora se siembra hasta noviembre, con lo que se ha incrementado el riesgo de daños por heladas. De alguna manera, la introgresión de germoplasma precoz en el germoplasma local de largo período vegetativo (8-9 meses) está ayudando al agricultor a controlar los efectos negativos del estrés por sequía en pre-siembra y siembra, siendo más difícil encontrar alternativas para solucionar el estrés que se presenta durante la floración. La cantidad de lluvia en febrero es mayor que la de enero; así que, el maíz que se siembre a mediados de noviembre y florezca en febrero, es el que tendrá mayor probabilidad de producir buenos rendimientos, por otro lado los cultivares precoces (7 meses) tendrán mayores posibilidades para una mayor producción que aquellos que normalmente siembra el agricultor (9 meses). Además, las labores culturales tendientes a retener más tiempo el agua de lluvia, tales como dar dirección y profundidad adecuada a los surcos, establecer cultivos asociados, etc., ayudarían a disminuir los daños por el estrés de sequía.

El CIMMYT (1988) indica que para Perú existen 355 000 ha sembradas con maíz: 205 000 con MD y 150,000 con MA. Del MD total 44% se sembró en la costa, donde toda la agricultura se desarrolla exclusivamente con riego, y correspondió a la categoría D de estrés por sequía; 31% se sembró en selva baja, ubicada en la cuenca amazónica a menos de 100 msnm donde la precipitación es suficiente para el cultivo de maíz, y 20% estuvo localizado en la selva media a altitudes menores a 500 m con precipitaciones erráticas por lo que se generan problemas de estrés hídrico, la zona corresponde a la categoría B. Respecto a MA, 77% está clasificado en la categoría C y 23% en la categoría D.

Investigaciones Recientes Realizadas en Sudamérica

Recientemente se realizaron cinco ensayos de las Variedades Experimentales de la Red Sequía (DEVT) precoces y tardías, se incluyeron 12 y 20 cultivares, respectivamente, y los sitios fueron: 1) Jipijapa, Portoviejo, Ecuador, 2) Portoviejo, Ecuador, 3) Chiclayo, Perú, 4) Mairana, Santa Cruz, Bolivia y 5) Ivoperenda, Bolivia. El rendimiento promedio dentro de cada grupo y entre grupos fluctuó notablemente, desde poco menos de 1 t hasta más de 6 t, en dependencia del nivel de estrés y de la longitud del periodo de estrés en cada etapa de desarrollo. Además, dentro de cada grupo hubo cultivares sobresalientes, este fue el caso del precoz Pool 18 Sequía C_3, y los tardíos Golden Valley 89DTP1 y Across 89DTP1 que con estrés hídrico drástico (en Jipijapa, Portoviejo, Ecuador) tuvieron rendimientos mayores a la tonelada. Así, en Chiclayo, Perú únicamente con la aplicación de tres riegos (presiembra, 40 días después de la siembra y tres semanas después de la floración) hubo cultivares con rendimiento mayor de 1 t, estos fueron los más tardíos, de ambos grupos (precoces y tardíos). En contraste, en Mairana, Santa Cruz e Ivoperenda, Bolivia, con estrés severo los cultivares con mayor rendimiento fueron los más precoces de ambos grupos.

En la III Reunión de Coordinadores Sudamericanos del Programa de Maíz realizada en Palmira Colombia, en enero de 1995, se decidió evaluar en condiciones de estrés de sequía los cuatro topcroses entre líneas S_1 x variedad (dos amarillos: (SA3+SA5)*SA4, SA4*SA3 y dos blancos: (SA7+SA8)*SA6 y SA6*SA8, que incluyen más de 500 mestizos) para seleccionar las mejores líneas y formar cultivares experimentales que se han venido utilizando en el programa de maíz para suelos ácidos de CIMMYT, Cali, Colombia. Los ensayos han sido conducidos en coordinación con los programas nacionales de Bolivia, Colombia, Ecuador y Perú. Los resultados son muy alentadores pues se han detectado mestizos con rendimiento 71 y 86% superior al promedio de los ensayos y en todos los casos el rendimiento del mejor mestizo fue mayor al rendimiento del mejor testigo local.

Individualmente, en cada país también se están realizando trabajos en los programas nacionales. En Argentina, Celiz et al. (1995) evaluó el comportamiento de 14 líneas endocriadas de maíz en condiciones de estrés hídrico y observó disminución de la biomasa vegetativa y del rendimiento y aunque no disminuyó el número de mazorcas sí disminuyó el número de granos por mazorca y en consecuencia el peso de la mazorca.

En Bolivia se seleccionó al ‘Pool 18’ como material básico para desarrollar una variedad tolerante a la sequía, se utilizó una combinación de selección masal estratificada y de medios hermanos, se tomaron como principales criterios de selección la sincronización de la floración masculina-femenina y el rendimiento en condiciones de estrés (Díaz et al., 1995); actualmente, se dispone de las progenies que serán evaluadas a partir de 1996.

En Brasil, el CNPMS formó un dialelo con poblaciones precoces para evaluarlo en condiciones de estrés por sequía y básicamente explotar el mecanismo de escape basado en el corto período vegetativo de los materiales. Se han evaluado 20 ensayos de los que se espera obtener información útil para la región.

En Ecuador se hizo un estudio de estabilidad de cultivares de maíz durante tres años, en 8 localidades de

Manabí donde se sembraron y cultivaron con precipitación natural (Alarcón y Reyes, 1995). Se observó que el rendimiento estuvo íntimamente asociado con la prolificidad y que 'INIAP 542' posee buen rendimiento en la mayoría de los ambientes, principalmente en aquellos con problemas de sequía. 'INIAP 542' es una variedad de grano amarillo liberada por INIAP en 1994 y proviene del 'Pool 26 Selección Sequía'.

Con MA se ha realizado menos investigación en la región, Terrazas et al. (1995) han iniciado en Bolivia un proyecto de selección de hermanos completos con la variedad Pairumani Compuesto 18.

Finalmente, al reconocer el arduo trabajo realizado en la búsqueda de metodologías y en la obtención de cultivares tolerantes al estrés de sequía, queda la invitación para continuar trabajando en forma conjunta a fin de evaluar nuestros materiales en tantas localidades como sea posible, de esta forma podrá avanzarse en el mejoramiento contra el estrés por sequía y por otros factores. En las evaluaciones es conveniente considerar al rendimiento de grano, como el carácter de selección principal, tanto con estrés como sin él, pero también es conveniente incluir el ASI, la producción y calidad de las mazorcas y el vigor de las plantas. Por otro lado, se recomienda incrementar la densidad de siembra de las progenies al menos en 50%, en el material de crianza, como factor de presión para la expresión de la capacidad de sobrevivencia y producción de la planta. De la ejecución de un buen trabajo de campo dependerá la eficiencia y eficacia de nuestros programas de mejoramiento.

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Patterns in Spatial Rainfall Forecasts as Affected by the *El Niño*/Southern Oscillation

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Abstract

The El Niño*/Southern Oscillation (ENSO) climate pattern in the southern Pacific is known to affect global rainfall patterns with direct impacts on agriculture and fishing industries. Previously, a long-term historical database of monthly rainfall for stations around the world was analyzed. For each station and Southern Oscillation Index (SOI) phase, the probabilities of obtaining amounts of seasonal rainfall relative to the median at the station were calculated. These data were interpolated so that for each SOI phase determined over two months, rainfall forecasts are made for the coming three-month period. In this paper, we further interpret those results and look for relationships among locations. A consistently negative SOI in May/June is one of the strongest signals. It forecasts only a 10 to 30% chance of achieving median rainfall (i.e., high probability of drought) for July to September in eastern Australia, south Asia, south-east Asia, west Africa, Central America and northern Brazil. This same signal predicts greater than median rainfall in the USA, central Asia and the Southern Cone of South America. Another strong signal during the same period is a consistently positive SOI, and it often forecasts virtually the opposite situation. Knowing the SOI phase prior to planting, the likelihood of receiving a good, average or poor season can be forecast. On a global basis, this knowledge has application for decision-making on-farm and in marketing and policy formation.*

Background: What is the SOI?

The southern oscillation index (SOI) is a function of sea-level air pressure at Papeete, Tahiti and Darwin, Australia, and indicates differences in atmospheric conditions over the southeastern Pacific Ocean compared to those over Australia (Troup, 1965). The index is normally interpreted on a monthly or seasonal basis, although it can be recomputed each day as:

$$SOI = (PA(Tahiti) - PA(Darwin))/SD \times 10$$

where

PA = pressure anomaly (monthly mean - long-term mean)
SD = standard deviation of the difference

El Niño events are associated with high sea temperatures in the eastern Pacific and result in extremely low (negative) SOI values. In *El Niño* years, there is a high probability of below average rainfall for many regions of the world. At the same time, some regions will have a high probability of receiving more than their average rainfall. Southern Oscillation Index values have been correlated with future seasonal rainfall in some regions (e.g., McBride and Nicholls, 1983; for other examples see Stone and Auliciems, 1992), though the SOI signal is complex so correlations with it are 'noisy'. General circulation models concentrate on predicting when an *El Niño* event will occur and how long it will persist, but cannot estimate the potential rainfall.

In Australia, the SOI has been exploited in a forecasting system based on association of monthly SOI 'phases' with the probability distribution of subsequent seasonal rainfall at a location as observed in the historical record (Stone and Auliciems, 1992). The value of this technology was truly realized when rainfall probability forecasts based on SOI phases were associated with consequent adjustments in agricultural decision-making (Hammer and Nicholls, 1996). Given that the SOI phase methodology is exploited only in the Australian agricultural community, the work of Stone et al. (1996a) is reproduced here as part of this paper.

Five SOI phases were developed by pattern analysis (principal component and clustering) based on SOI values going back to 1882 (Stone and Auliciems, 1992). These are defined (Stone et al. 1996b) as:

	SOI trend	Avg. for current month	SOI cf. previous month
Phase 1:	Consistently negative SOI	-12.2	+2.3
Phase 2:	Consistently positive SOI	+9.5	-1.7
Phase 3:	Rapidly falling SOI	-9.9	-12.7
Phase 4:	Rapidly rising SOI	+6.6	+11.0
Phase 5:	SOI consistently near zero	-1.7	-1.3

A common application of these phases is to examine the relationship between the phase and rainfall for the coming three or six month period. Figure 1 shows this relationship for Hyderabad, India and Quelimane, Mozambique. In each case, there is a higher chance of receiving any given amount of rainfall following a SOI Phase 2 than when following a SOI Phase 1; e.g., following a SOI Phase 1 there is 0% chance of exceeding 530 mm in the next three months in Hyderabad and 1000 mm in Quelimane. In SOI Phase 2 seasons, there is a 40% (Hyderabad) and 65% (Quelimane) chance of exceeding these amounts. In some locations, SOI Phase 3 and SOI Phase 4 often contrast in a similar manner to Phases 1 and 2. In other locations, Stone et al. (1996a) found that the relationship between phases and rainfall probability was reversed: Phase 1 related to higher rainfall and Phase 2 to lower rainfall. SOI Phase 5 was usually associated with rainfall probabilities that were distributed similar to those for all years combined; i.e., in such a year, knowledge of the SOI phase would not change the risk outlook for a decision-maker.

Stone et al. (1996a) applied this analysis to rainfall data collected worldwide (CDIAC, 1992). For each location, the probability of rainfall exceeding the median for the following three month season was calculated for each SOI phase (Figs. 2a and 2b). The data were spatially interpolated to produce 60 possible forecast maps of rainfall (one each for 5 phases x 12 months). Depending on the current SOI phase, the appropriate map can be examined to determine the seasonal outlook. In Figure 2a, a SOI phase of 1 (constantly negative) in May-June indicates relatively low probabilities of exceeding the median rainfall (potential drought) for July-September in much of western Africa, Pakistan, central India, Siberia and Mongolia, southern China, much of Southeast Asia, and most of Australia, New Zealand, Alaska, Central America and northeastern Brazil. In contrast, northern and central USA and much of southern South America could expect higher than median rainfall. Three months later (Aug.-Sep.) an SOI Phase 2 (constantly positive) indicates a low probability of receiving median rainfall in these latter areas (Fig. 2b), while eastern Australia, Indonesia and parts of northern South America would have a high probability of exceeding median rainfall.

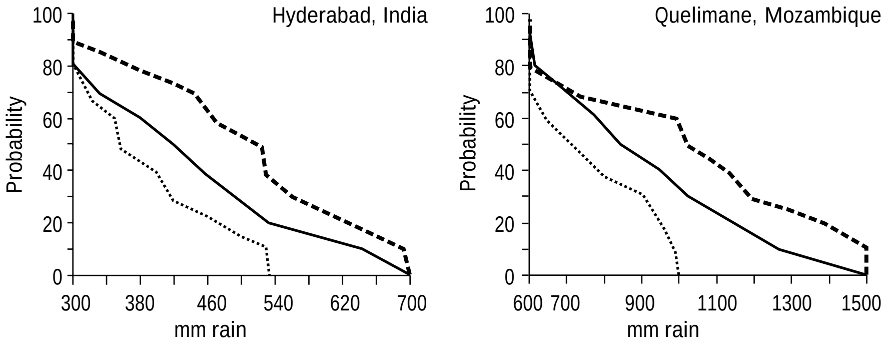

Figure 1. Cumulative probability of exceeding any rainfall amount during different SOI phases at Hyderabad, India, and Quelimane, Mozambique. In Hyderabad, the forecast is for the period June-Aug. Associated with the SOI phase in the preceding Apr.-May, while that in Quelimane is for the period Dec.-Feb. Associated with the SOI phase in the preceding Oct.-Nov. The dotted line is SOI phase 1 (consistently negative) while the dashed line is SOI phase 2 (consistently positive). Figure after Stone et al., 1996a. See text for explanation.

The use of SOI phases in decision-making in agriculture can occur over a range of scales (Hammer and Nicholls, 1996). In single locations, the SOI phase may be used to predict the likelihood that future seasonal rainfall will be above, equal to or below the median. At this level, the information can be used to improve on-farm decision-making, and software has been developed to assist this (Clewett et al., 1994). The system has also been extended to produce maps for Australia and recently for the world. Much of this information is maintained on-line on the Internet (QDPI, 1996), so that anyone with access can examine historic or current predictions of rainfall probabilities. Applications of these maps range from policy decisions about modifying cropping intensity to the marketing of commodities based on seasonal outlooks.

The SOI phase forecasting system can also be combined with more sophisticated descriptions of environments. For example, historical rainfall data can be used as input to a crop or pasture simulation model. Results from the model for each year may be grouped according to the SOI phase at the time of planting or prior to the flux of pasture growth. Using this approach for wheat, Hammer et al. (1996) showed how farmers can reduce risk by adjusting planting and management decisions based on the SOI phase at planting. If at planting time, the SOI phase indicates that the forthcoming seasonal rainfall is very likely to be lower than average, then the farmer may decide to not plant, to plant at a lower plant density, to use an earlier maturing variety or to apply only a small amount of

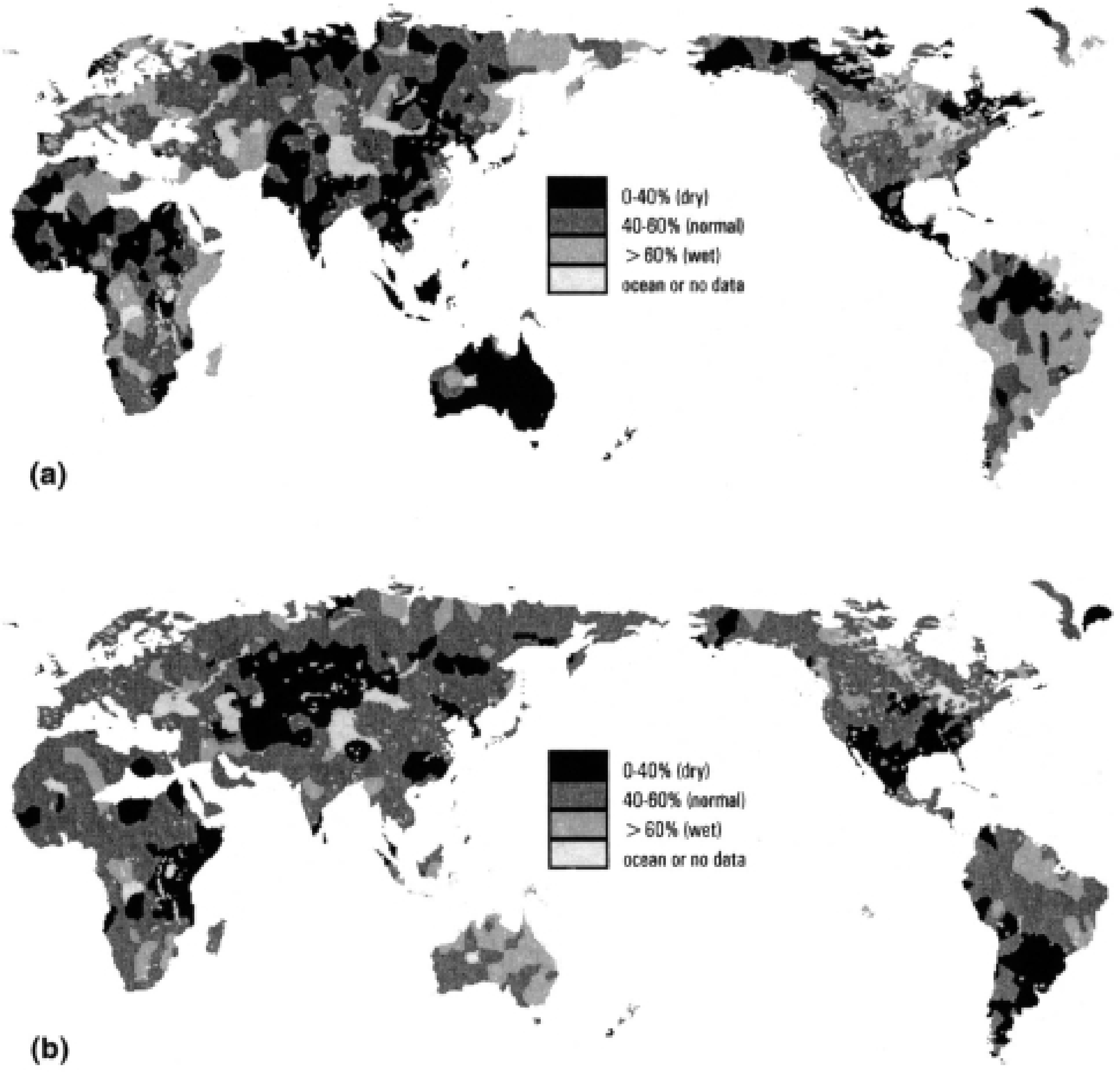

Figure 2. Worldwide forecast probability of exceeding median rainfall for (a) any Jul.-Aug. period based on an SOI Phase 1 (constantly negative) in May-June and (b) any Oct.-Dec. period based on an SOI Phase 2 (constantly positive) in Aug.-Sept. See text for explanation.

fertilizer. McCown et al. (1991) demonstrated that the same approach could be used by farmers in Kenya. Conversely, in seasons when the SOI phase indicates that rainfall is likely to be greater than average, the farmer may decide to use later-maturing varieties and apply management strategies that are suited to wetter seasons. Meinke et al. (1996) showed the utility of using SOI phases to influence planting and harvesting decisions for peanut in Australia. The spatial distribution of SOI phase effects has also been introduced to forecast crop yield (Goyne et al., 1996) and to produce drought alerts (Carter and Brook, 1996) over large pastoral regions in Australia.

Applications of the SOI phase forecasting system are developing quickly, and insights are being gained into how agriculture can use SOI phase / rainfall relationships. Two interesting questions arise from this research: are SOI phases equally valuable over locations and can insights into SOI phase / rainfall relationships be transferred between locations? In the rest of this paper, we further develop the work of a recent paper of Stone et al. (1996a) to determine similarities in the relationship between SOI phases and the probability of receiving median rainfall in locations around the world.

Analysis and Methodology

From Figures. 1 and 2, it is clear that different locations can have similar associations with the SOI phases. We explored this using cluster analysis. First we obtained the long-term median rainfall probabilities associated with each phase for each month for the approximate 3,500 locations in the dataset (each with >70 data years) used by Stone et al. (1996a). This is akin to drawing a vertical line through Figures 1a or b at the median rainfall value (50% probability) and obtaining the probabilities at the five points at which this line intersects with the five SOI phases. For each month, the probabilities in a matrix of locations by SOI phase were processed using PATN (CSIRO, Australia) to identify groups of locations that had similar patterns of probabilities across the five phases. Agglomerative hierarchal clustering was used with squared Euclidean distance as the difference measure. The data for similar locations was averaged at the five-group level.

Results and Discussion

Table 1 shows the probability of achieving median rainfall or greater in several locations around the world. In all sites except Quelimane, an SOI Phase 3 during May-June forecasts a low probability of reaching median rainfall in the next three months; i.e., the sites are likely to experience drought, relative to their median rainfall outlook. If the SOI is in Phase 4, then Dubbo would have a high chance of receiving above-median rainfall.

Table 1. Probabilities of receiving median rainfall or greater in the July-August period, based on different phases of the SOI in the previous May-June period.

	SOI Phase				
Location	1 (-ve)	2 (+ve)	3 (falling)	4 (rising)	5 (near zero)
Oxford, UK	61	62	33	40	46
Dubbo, Australia	38	57	32	75	33
Texcoco, Mexico	60	66	20	58	38
Quelimane, Mozambique	44	50	60	50	45
Hyderabad, India	40	52	16	54	64

The mean probability value for each SOI phase for each of five cluster groups was calculated for four periods in the year (Fig. 3): the Nov-Dec. SOI (predicting Jan-Mar rainfall), Feb-Mar SOI (predicting Apr-Jun rainfall), May-Jun SOI (predicting Jul-Sep rainfall) and Aug-Sep SOI (predicting Oct-Dec rainfall). Each figure represents a separate analysis, so the group numbers are not related from figure to figure. The degree to which a line differs from 50% for each phase indicates its usefulness in identifying variation in rainfall, compared to the median; that is, large deviations from 50% indicate that the phase is useful in discriminating among years.

As Stone et al. (1996a) observed (see above), phases can be related to an increase or decrease in the probability of receiving median rainfall or greater, and this can change with location and season. In Figure 3a, two location groups (1 and 5) had an increased probability of achieving median rainfall and two groups (3 and 4) had a decreased probability of achieving median rainfall, if the SOI was in Phase 1

(LHS of Fig. 3a). There was at least one group of locations in each graph for which probabilities of exceeding median rainfall were lower in Phase 1 than Phase 3, with Phase 2 usually intermediate (response type 1). These groups were 3, 1, 2 and 2 for Figures 3a, 3b, 3c and 3d, respectively. Conversely, there was a group of locations (response type 2) in which the probability associated with SOI Phase 1 was usually greater than that for Phase 3 (groups 5, 5, 5 and 4, respectively) in each month. For each time period, probabilities following SOI Phases 4 and 5 were fairly similar in all groups and had little affect on the grouping of locations. Further contrasts were usually related to an interaction of the Phase 1 and 3 pattern with that resulting from Phase 2 years.

While each group contained some members from regions spread all over the world, there were also some spatial relationships. Response type 1 (phase 1 associated with low probability of achieving median rainfall) was common in Australia, West Africa and Central America, while response type 2 (phase 1 = high probability) was common in North America and Europe. Knowledge of the spatial distribution of these response types might be exploited when trying to manage their agricultural systems. The membership patterns are a subject of further analysis not presented here.

The results in Figure 3 indicate that Phases 1, 2 and 3 seem to discriminate best among locations around the world, while phases 4 and 5 are not particularly useful. Experience in Australia is that phases 1 to 3 do tend to be the most important in separating different seasons (Hammer et al., 1996; Meinke et al., 1996). The utility of prior knowledge of a phase can be described as the difference between the probability obtained from all years (in this case it is always 50% for median rainfall) and the probability value obtained for a particular phase. On this basis, Phases 1 and 3 are especially useful, since they predict differences in probability from the median of up to 20% at most times of the year. However, Phase 1 would appear to be most useful in the Feb-Mar and Aug-Sep periods, while Phase 3 is equally useful in the same periods, albeit in different locations.

We have shown here examples of how the effects of ENSO on rainfall and agricultural production may be accommodated using the SOI Phase system. Some phases are related more consistently to median rainfall than others. However, there are also spatial linkages of these relationships, these are quite complex and may not be able to be simply explained by the phases alone. In particular, spatial linkages change with time of year so that areas that are likely to be in drought at one time of the year may not be so at a later stage.

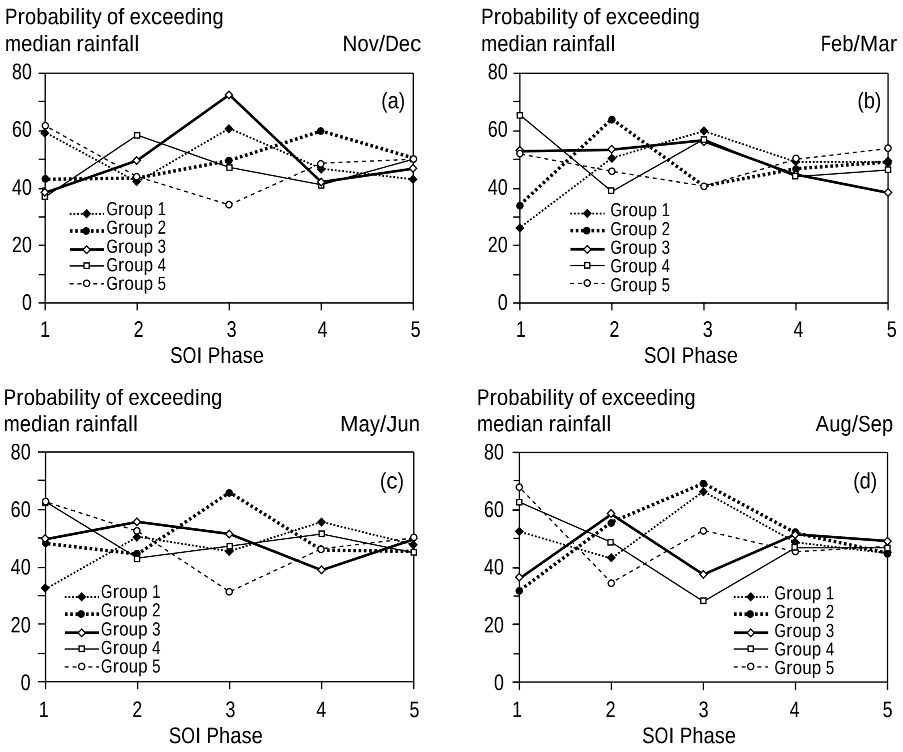

Figure 3. For each of four periods in the year (figures a to d), the relationship between SOI phase and probability of equaling or exceeding median rainfall in the following three months for five groups of locations derived by pattern analysis of > 3500 locations. Groups are not related from figure to figure.

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Drought and Low N Status Limiting Maize Production in Brazil

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Abstract

The Brazilian territory has an area of approximately 8.5 million km^2*, which is divided into five main regions with particular characteristics related to average climatic conditions and natural soil fertility. Climatic variations may be very accentuated within each particular region, but a common feature is the irregular distribution of rains, which causes droughts of variable intensities. Maize is an important crop in most Brazilian regions, occupying approximately 13 million ha and producing annually 28-30 million tons of grain. It has been estimated that drought problems, depending on year and intensity, reduce maize production by 14% to 28%. Another limiting factor for maize production in Brazil is the low natural fertility of the soils, especially in nutrients like phosphorus and nitrogen (N). It has been estimated that 80% of the soils in Brazil are deficient in N. Although fertilization is a common solution to this problem, its high costs make this option inaccessible to many farmers. The amount of supplemental N applied to maize in Brazil is low (36 kg N/ha), and of this only 50% to 60% is utilized by the crop. Considering that low N availability and drought are severe constraints to maize crops in Brazil, the National Maize and Sorghum Research Center (CNPMS/EMBRAPA) has initiated breeding programs aimed at the development of germplasm that performs more efficienctly under these two limiting conditions. Several genotypes have been developed on the basis of anthesis-silking interval selection for drought tolerance, and a variety is being developed for soils with low fertility where N is the most limiting nutrient.*

Tropical regions are usually affected by marked climatic variations, with frequent periods of no or irregularly distributed rainfall, causing serious crop losses. Drought effects are exacerbated by several effects, including low natural soil fertility, inefficient crop management practices, biotic stresses and lack of government programs to financially support farmers.

Brazil has an area of 8,547,407 km^2, which is divided into five distinct regions. Maize is cultivated and considered a socially and economically important crop in all of them. Table 1 shows the size of each region and portion of total maize production. The characteristics of each region are briefly summarized below.

Northern Region

The northern region covers seven states in the Amazon basin and is dominated by lowlands (0-200 masl), with abundant and well distributed rains (1300 to 3000 mm). Temperatures and relative humidity are commonly high throughout the year. Natural soil fertility is usually low and farmers use low levels of fertilizer and other inputs on their

Table 1. Brazil's geographical regions, their areas, and their respective contributions to national maize production.

Regions	Area (km^2)	% of total area	% national maize production[†]
Northern	3,869,638	45.27	2.35
Northeastern	1,561,178	18.26	5.32
Southeastern	927,286	10.86	28.43
Southern	577,224	6.76	46.86
Central Western	1,612,077	18.85	17.04
Total	8,547,403	—	—

[†] Estimate from 6 years (1987-1992).

crops. Maize is planted between October and December and drought is not a common problem for this crop.

Northeastern Region

The northeastern region covers the nine states which have the highest occurrence of drought in Brazil. Altitudes in the region vary between 0 and 1200 masl and the climate in general is hot and dry, including high temperatures at night. The only area within the region where rains are frequent and well distributed is along the coast, where a string of forests exists. In the interior, precipitation varies between 300 and 500 mm and its irregular spatial distribution greatly affects agricultural production. Rains are concentrated in a short 1-3 month period, and usually occur as heavy precipitation, with up to 50 to 80 mm per shower. Soils have low fertility and not much fertilizer is used. The start of the growing period for annual crops is highly variable (from November to May), depending on the beginning of the rainy season.

Southeastern Region

The southeastern region comprises four states that vary from 0 to 300 masl in altitude. Rain distribution is more uniform than in other regions, varying from 800 to 1500 mm annually. Nevertheless, short periods of dry weather (10-20 days) occur during flowering time. Normally the temperature is very high for nine months and then cold for the other three. Natural soil fertility is generally low or medium, but some areas have relatively high fertility. Soil fertilizer use is common and the sowing season is from October to November.

Southern Region

The southern region covers three states. Altitude varies from 0 to 1110 masl. Rain distribution is very uniform and intense throughout the year (800 to 1500 mm). During the summer, temperatures are very high during the day and very mild at night. During three to four months of the year, the weather is very cold and thermal inversions can occur at any time, resulting in rain storms. Natural soil fertility is from medium to high and most farmers use fertilizer. The level of technology used by farmers is usually high.

Central Western Region

The central western region includes three states and the Federal District, Brasilia. Rain distribution is very irregular, with annual variation from 800 to 1300 mm. Dry periods, commonly known as “veranico”, last from 10 to 20 days, and often coincide with flowering. The weather is predominantly hot, although temperatures are very mild during three months of the year. This region encompasses the majority of the Brazilian Cerrado. Natural fertility is from very low to medium, and the level of technology used by farmers has improved during the last few years. Crops are sown in October and November.

It is evident from these descriptions that rain distribution varies widely both between and within the regions. Furthermore, there are other factors constraining production, and they vary widely in importance across the regions. Specific data regarding drought-occasioned maize yield losses do not exist for Brazil. During the last two years, EMBRAPA has tried to organize a national database and develop simulation studies to assess the factors responsible for maize yield reductions. For the time being, reductions in maize area between planting and harvest and the fluctuations of maize yields between years may indicate the importance of drought, although other climatic factors and socioeconomic effects cannot be excluded (Table 2). For dryland conditions, cultivars that are drought tolerant or can escape drought during the more critical periods of plant development are much needed alternatives. Several public and private companies are trying to reduce the risk resulting from unstable rain distribution by developing very early-maturing cultivars that make the most efficient use of short rainy periods. Development of drought tolerant cultivars is one of the main goals of CNPMS. This effort was started in 1987 through the creation of a specific breeding program for tolerance to drought conditions. As a result, CNPMS has a population and several hybrids that they have begun to evaluate under water stress conditions. The population traces to nine S_4 lines, derived from synthetic elite NT. The methodology used to develop the lines was based on the selection of plants with short anthesis silking interval (ASI). The lines were crossed in a diallel and then recombined twice to form the population.

Three-way hybrids from parental lines selected for drought tolerance were evaluated in four locations in the year 1994/95, but drought stress only occurred in one location. Preliminary results shown in Table 3 include the 20 best hybrids for ASI and are from this drought stressed location. It is important to say that all the parental lines have zero or negative ASI values. Some hybrids had negative or very low ASI values; i.e., the stigmas were exposed before pollen release. In contrast, the controls had ASI values of 5 or 6 days. Although preliminary, these results clearly indicate that the short ASI observed in the parental lines was expressed in the F_1 generation. This was the case even when only 50% of the germplasm used to form a hybrid came from a short ASI parent. Plant and ear height of the high ASI hybrids was about average; these values were a little higher than for the controls. This may be explained by differences in the origin of the germplasm. High ASI hybrids tended to be more prolific than the controls.

Table 2. Maize production data, including planted and harvested area, reduction in area after planting, total production, and average grain yield for the five regions of Brazil, 1987-1992.

Regions	Area planted (ha)	Area harvested (ha)	Area reduction (ha)	Area reduction (%)	Production (t)	Yield (t/ha)
1987						
Northern	327,911	324,344	3,567	1.1	434,263	1.34
Northeastern	3,090,375	2,497,100	593,275	19.2	622,362	0.25
Southeastern	3,150,108	3,143,825	6,283	0.2	7,374,378	2.35
Southern	5,840,029	5,816,762	23,267	0.4	13,955,765	2.40
Central Western	1,730,381	1,721,397	8,984	0.5	4,415,641	2.57
Total	14,138,804	13,503,428	635,376	4.5	26,802,409	1.98
1988						
Northern	438,148	431,730	6,418	1.5	602,498	1.40
Northeastern	3,356,523	3,186,296	170,227	5.1	2,053,452	0.64
Southeastern	2,986,823	2,973,222	13,601	0.5	7,233,258	2.43
Southern	4,957,058	4,878,540	78,518	1.6	10,469,372	2.15
Central Western	1,713,011	1,695,215	17,796	1.0	4,389,456	2.59
Total	13,451,563	13,165,003	286,560	2.1	24,748,036	1.88
1989						
Northern	515,633	513,449	2,184	0.4	756,919	1.47
Northeastern	3,223,324	3,081,230	142,094	4.4	1,742,996	0.57
Southeastern	3,003,175	2,984,483	18,692	0.6	7,399,293	2.48
Southern	4,725,086	4,704,189	20,897	0.4	11,542,828	2.45
Central Western	1,661,274	1,648,433	12,841	0.8	5,130,556	3.11
Total	13,128,492	12,931,784	196,708	1.5	26,572,592	2.05
1990						
Northern	405,305	397,392	7,913	2.0	539,637	1.36
Northeastern	2,662,580	2,139,037	523,543	19.7	648,582	0.30
Southeastern	2,743,160	2,704,098	39,062	1.4	5,258,540	1.94
Southern	4,751,136	4,737,300	13,836	0.3	11,792,614	2.49
Central Western	1,461,590	1,416,480	45,110	3.1	3,108,401	2.19
Total	12,023,771	11,394,307	629,464	5.2	21,347,774	1.87
1991						
Northern	449,199	425,070	24,129	5.4	610,000	1.44
Northeastern	3,088,884	2,865,033	223,851	7.2	1,844,914	0.64
Southeastern	3,157,396	3,152,181	5,215	0.2	8,154,077	2.59
Southern	5,357,540	5,116,891	240,649	4.5	8,397,305	1.64
Central Western	1,527,628	1,504,526	23,102	1.5	4,578,044	3.04
Total	13,580,647	13,063,701	516,946	3.8	23,584,340	1.81
1992						
Northern	456,546	448,656	7,890	1.7	645,444	1.44
Northeastern	3,001,298	2,569,283	432,015	14.4	1,140,425	0.44
Southeastern	3,267,412	3,243,697	23,715	0.7	8,162,727	2.52
Southern	5,657,386	5,646,282	11,104	0.2	16,074,118	2.85
Central Western	1,505,442	1,455,691	49,751	3.3	4,483,413	3.08
Total	13,888,084	13,363,609	524,475	3.8	30,506,127	2.28
6 year average	13,368,560	12,903,639	464,922	3.5	25,593,546	1.98

Source: Brazilian Statistics Yearbook, years 1994, 1993, 1992, 1991, 1990, 1989.

Some interesting comparisons can be made between the hybrids and controls. The three-way hybrids used as controls are excellent when planted in environments with no water stress (data not shown), but under stress they show very low yield and a low shelling percentage (Table 3). By comparison, the 20 best hybrids for ASI showed higher productivity (7.0 to 8.9 t/ha) and a higher shelling percentage. If we take 8 tons of grain/ha as a reference for the five best ASI hybrids and compare it with the average of the controls, 5.5 t/ha, a yield difference of 30% is observed.

These preliminary results clearly indicate that the selection for short ASI can be an efficient method for developing drought tolerant cultivars and that water stress during flowering is a constraint on maize production. The use of drought tolerant cultivars, however, is not a guarantee that yield potential is fully expressed by a variety or hybrid. Other factors — low soil fertility, for example — can greatly influence yield as well.

Nitrogen is deficient in about 80% of the Brazilian soils. These tropical soils typically have enough N to produce a 2 to 3 t / ha grain yield, given that all the other factors are ideal. According to the National Association for Fertilizer Diffusion (ANDA) and the Brazilian Association of Potassium Research (POTAFOS), use of fertilizers for maize increased 23.9% from 1990 to 1993 (Table 4), and market analysis research suggests that increased fertilizer use will continue in the years ahead. In 1993, 145 kg of fertilizer was applied to maize on average. Assuming that this fertilizer was mainly applied using the formulation 10-15-15 (NPK, POTAFOS), applied N was around 14.5 kg / ha. If only 50% of this ultimately found its way into the plant (50% fertilizer efficiency), then only 7.25 kg / ha of N were available for the maize crop. This amount represents 50% of the requirement for a 5 to 6 t / ha yield for farmers using a low or medium level of technology. Clearly, the low N level of the Brazilian soils combined with the small amount that is applied every year is limiting maize production in Brazil. On the other hand, it is known that maize is highly responsive to N and that the largest responses are obtained from application rates between 30 and 50 kg / ha. Experimental data from 459 trials indicates that rates varying from 45 to 160 kg / ha generated yield increases from 6 to 197%. However, farmers are hesitant to use N fertilizer due to the high price of fertilizers and the risk of drought. One alternative to diminish risks in vulnerable rainfed agricultural systems is to develop cultivars with a high capacity for nutrient utilization and an almost linear response to nutrient levels. CNPMS is working to develop maize varieties for low fertility soil conditions. Preliminary results indicate that progenies can be developed which lose little yield when moved from an N+ to an N- environment (Santos et al., 1997).

We believe that exploring genetic variability will be the best strategy to minimize factors limiting maize production in tropical environments. While doing this it will be important to maintain close interactions with scientists from other research areas and with other research institutions, and to develop methodologies that result in consistent progress from efficient selection for desired traits.

Table 3. Mean values in maize under drought during flowering for male flowering (MF), female flowering (FF), anthesis-silking interval (ASI), plant height (PH), ear height (EH), ear index (EI), ear weight (EW), grain weight (GW), and shelling percentage (S). Sete Lagoas - MG, Brazil.

Treatments	MF (days)	FF (days)	ASI (days)	PH (m)	EH (m)	EI	EW (t/ha)	GW (t/ha)	S (%)
HT 17	58.0	58.5	+0.5	2.17	1.25	1.04	11.33	8.99	79.4
HT 38	56.0	55.5	-0.5	2.12	1.37	1.02	11.12	8.49	76.4
HT 15	57.0	57.5	+0.5	2.10	1.32	1.04	11.03	8.36	75.8
HT 29	57.0	58.5	+1.5	2.22	1.40	1.02	10.71	8.36	78.1
HT 10	57.0	56.0	-1.0	2.15	1.35	1.02	10.28	7.52	73.2
HT 25	56.0	55.5	-0.5	2.20	1.27	1.00	10.24	8.11	79.2
HT 19	58.5	58.5	0.0	2.32	1.37	1.00	9.59	7.38	77.0
HT 26	58.0	59.5	+1.5	2.37	1.65	1.08	9.30	6.88	74.0
HT 37	56.5	57.0	-0.5	2.07	1.32	0.99	9.24	7.60	82.3
HT 24	57.0	57.5	+0.5	2.25	1.35	0.99	9.16	6.61	72.2
HT 13	57.5	58.0	+0.5	2.17	1.37	1.02	9.14	7.02	77.0
HT 11	58.5	58.5	0.0	2.05	1.27	1.02	9.11	7.14	78.4
HT 27	58.5	58.5	0.0	2.07	1.40	0.91	8.90	6.99	78.7
HT 06	59.5	61.0	+1.5	1.95	1.27	0.87	8.66	6.56	76.8
HT 40	57.5	58.0	+0.5	2.00	1.37	1.02	8.25	5.88	72.3
HT 22	59.5	60.0	+0.5	2.00	1.27	0.86	8.24	6.23	75.6
HT 32	57.5	58.5	+1.0	2.12	1.22	0.86	8.22	6.37	77.5
HT 45	57.0	57.0	0.0	2.15	1.35	1.00	8.02	6.19	77.2
HT 42	57.0	56.5	-0.5	2.10	1.27	0.98	7.99	6.02	75.4
HT 28	56.0	57.0	+1.0	2.05	1.25	0.85	7.78	5.64	73.0
P 3041 (check)	61.5	66.5	+5.0	1.95	1.22	0.98	7.88	5.52	70.1
ICI 8501 (check)	62.0	68.0	+6.0	2.00	1.22	0.64	6.32	4.74	75.0
XL 370 (check)	63.0	69.0	+6.0	1.95	1.22	0.91	4.85	3.43	70.8
CV%							13.2	15.1	

Table 4. Grain yield, fertilizer applied (kg/ha), and total fertilizer utilized on maize in Brazil during 1987, 1990 and 1993.

Years	Yield (t/ha)	Fertilizer (kg/ha)	Total fertilizer ('000 t)
1987	1.99	99	1,340
1990	1.87	117	1,350
1993	2.44	145	1,910

Efecto del Estrés Hídrico en el Rendimiento de Maíz en Argentina

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Abstract

There is a diminishing pattern of average rainfall from east (1000 mm) to west (600 mm) in the maize areas of Argentina. The crop is exposed to water deficits during flowering which cause yield reductions and variability across years. Even in the 6th Region, where the highest production and yields per hectare are obtained, there is a 50% probability of at least a 50 mm water deficit during the critical period of flowering. Severe rainstorms are common in most of the year, causing runoff and erosion. This and the intense use of soils hamper the infiltration and retention of water, making high yields extremely dependent on timely rains and farmers averse to risking investment in nitrogen fertilization. This study assesses maize yield losses in Argentina due to drought and their economic importance. Different crop strategies, including irrigation and fertilization, were simulated by the CERES-Maize model using the climatic data for 20 years and edaphic information for the main regions. It was concluded that the average annual yield loss caused by drought in Argentina was 1.2 million tons of maize, with an economic value of 150 million U.S. dollars.

La región cultivada con maíz en Argentina comprende nueve subregiones con condiciones ecológicas, producción total y productividad por hectárea diferentes (Cuadro 1). Se encuentra entre los paralelos 31º y 40º de latitud S y los meridianos 57º y 65º de longitud O y los límites climáticos corresponden a las isotermas de 17ºC al N y 15ºC al S, las isohietas de 1000 mm al NE y 600 mm al O. El gradiente latitudinal de la temperatura media anual es de 0.7ºC por grado de latitud. El mes más cálido es enero (temperatura media de 23ºC) y el más frío julio (9-10ºC). La amplitud térmica aumenta de E a O de 12 a 15ºC. El período libre de heladas varía entre 180 y 260 días, aunque la fecha de la primera y última helada es bastante variable entre los año. El riesgo de heladas tardías a fin de septiembre en el norte de las subregiones VI y IV y a mediados de octubre al sur de las mismas es de dos años de cada diez.

Aproximadamente, 75% del área sembrada corresponde a las subregiones IV, VI y VII. La subregión VI es la más importante por su producción y contribuye con aproximadamente 35% de la producción total nacional. Le siguen en importancia productiva las subregiones IV (22%), VII (15%), VIII (9%), IX (7%), y I (5%). Las subregiones II, III y V son las menos relevantes ya que en conjunto apenas representan 5% de la producción y del área sembrada a nivel nacional.

Cuadro 1. Medias de producción, área sembrada y rendimiento en Argentina para los períodos agrícolas 1990/91 a 1994/95.

Subregión	Producción (t x 1000)	Area sembrada (ha x 1000)	Area cosechada (%)	Rendimiento medio (t/ha)
I	647	218	97	3.09
II	49	18	93	2.88
III	4	21	11	1.56
IV	2353	644	93	3.92
V	457	106	95	4.50
VI	3438	644	97	5.50
VII	1414	589	65	3.71
VIII	926	210	92	4.77
IX	721	218	86	3.85
Total	10009	2668		4.29

Las subregiones más importantes por su producción se localizan en el interior de la denominada pampa húmeda-subhúmeda. Según la clasificación climática de Koeppen, la región pampeana corresponde al clima subtropical húmedo, caracterizado por un verano cálido y sin estación seca.

Para Pergamino, localidad representativa de la subregión más importante (VI), el promedio de lluvia anual es de 944 mm, pero con una fuerte variabilidad interanual. Entre los meses de octubre y abril se recibe 76% del total de las lluvias anuales. Las probabilidades de deficiencias hídricas son mayores en diciembre y enero, período que corresponde a los estados fenológicos de aparición de la última hoja hasta comienzo del llenado efectivo del grano. Según Totis y Rebella (1980) citados por Zeljkovich et al. (1984), la probabilidad de deficiencias hídricas superiores a 50mm es 50%. En la subregión VI se cultiva maíz sobre suelos argiudoles, que corresponden a diferentes series que pueden definirse por el grado de desarrollo del horizonte B. La textura de este horizonte aumenta desde el O hacia el E. La capacidad de reserva de agua útil en el perfil hasta 150 cm de profundidad es de 227 mm, de los cuales 115 mm se almacenan en los primeros 90 cm (Guevara, 1991). La ocurrencia de lluvias intensas, mayores de 30mm en 30' en primavera-verano-otoño, tiene consecuencias erosivas. En tales circunstancias, en promedio 65% del total de lluvia recibida se pierde por las escorrentías en los sistemas de labranza con arado de rejas y 37% en siembra directa y combinada (Berón y Blotta, 1995).

En las subregiones IV y VII la deficiencia de agua durante el verano es más severa debido a la disminución de las lluvias y al aumento de la evapotranspiración potencial (ETP) por las mayores temperaturas. Los suelos predominantes en las subregiones IV y VII son del tipo haplustol, con una baja capacidad de almacenamiento del agua.

La media nacional de rendimiento por hectárea para los períodos agrícolas 1990/91 a 1994/95 fue de 42.9 q/ha y 47.2 q /ha, respectivamente. Macagno et al.(1992) señalaron que, a pesar de una tendencia general a la reducción del área de siembra durante el período comprendido entre 1970-1992, la producción nacional se mantuvo relativamente estable debido a una tasa de aumento anual de la productividad de 2.3%. De ese aumento, 50% fue debido a mejoramiento genético. Esa evaluación concuerda con la de Eyhérabide et al. (1994), quienes calcularon para el período 1978 - 1993 una tasa de ganancia genética en productividad cercana a 1% anual, tanto en ambientes favorables como desfavorables.

El análisis de regresión de los rendimientos medios de cada subregión durante la última década indica que los aumentos de productividad ocurrieron en todas ellas, con excepción de la IV y IX (Cuadro 2). Sin embargo, los coeficientes de determinación más elevados resultaron aproximadamente de 50%, revelando la importancia de las variaciones interanuales de productividad no atribuibles a mejoras tecnológicas.

El objetivo de este trabajo fue evaluar las pérdidas del rendimiento de maíz causado por deficiencias hídricas y cuantificar su valor económico en la región maicera total.

Materiales y Métodos

A partir de una serie histórica de veinte años de datos climáticos y con la información de características edáficas de Manfredi, Pergamino y Anguil, localidades representativas de las tres principales subregiones maiceras (IV, VI y VII, respectivamente) se simularon mediante el modelo Ceres-Maize DSSAT v3.0, diferentes estrategias productivas. Estas estrategias incluyeron en todos los casos siembras en fechas consideradas

Cuadro 2. Rendimiento medio en el período 1985/86 a 1994/95 en las principales subregiones maiceras de Argentina.

	Rendimiento				
	Media		b		CV
Subregión	(t/ha)	D.E.	(q/ha/año)	R_2	(%)
I	2.69	0.39	1.2*	0.49	14.5
IV	3.30	0.82	1.3ns	0.20	24.9
V	3.61	0.88	2.6*	0.48	24.2
VI	4.74	0.66	2.1**	0.52	13.9
VII	3.33	0.46	1.2*	0.41	13.9
VIII	4.36	0.49	1.1*	0.35	11.2
IX	3.96	0.54	-0.4ns	0.06	13.6

b: coeficiente de regresión;
D.E.: desviación estandar;
R_2: coeficiente de determinación;
* y **: significativo al 5% y 1% respectivamente, de probabilidad; ns: significativo.

óptimas, con y sin aplicación de N, en condiciones de secano y de riego complementario. En las simulaciones se consideró una dosis reducida de 30 kg de N por ha, aplicados en el momento del escardillado. Los coeficientes genéticos utilizados correspondieron al cultivar híbrido de tres líneas y ciclo completo Dekalb 3S41.

Para cuantificar el perjuicio en cada subregión se consideraron los niveles de producción promedio para el último decenio, la probabilidad de ocurrencia de deficiencias hídricas, y las diferencias de rendimiento entre las simulaciones con y sin riego complementario, tanto en condiciones de fertilidad natural, como con aplicación de fertilizantes. Esas diferencias referidas al nivel promedio de rendimiento bajo riego complementario fueron denominadas «incidencia». Para las subregiones no contempladas en las simulaciones, la incidencia se estimó a partir de la información provista por informantes calificados.

Las pérdidas de rendimiento a nivel de toda la región maicera argentina se calcularon mediante la suma de los perjuicios de cada subregión, resultantes cada uno del producto de la probabilidad de ocurrencia de deficiencias hídricas, incidencia y producción promedio. El perjuicio económico se estimó tomando una cotización de referencia de 120 dólares estadounidenses por tonelada (precio en el puerto de Buenos Aires para junio de 1995).

Resultados y Discusión

Se observó que en Pergamino y Manfredi las estrategias de manejo con aplicación de N aumentaron el promedio de rendimiento aproximadamente 60% en condiciones de secano y 90% con riego complementario respecto a los promedios de estrategias sin aplicación de fertilizantes. La aplicación de riego complementario mejoró el rendimiento aproximadamente 16% en ambas condiciones de fertilidad. La supresión de deficiencias hídricas mediante el riego complementario permitió reducir notablemente la variabilidad interanual de los rendimientos (comparar las desviaciones estándar para ambas situaciones). Los rendimientos obtenibles y la desviación estándar en situaciones de secano con aplicación de N fueron superiores a los correspondientes a las situaciones de secano sin aplicación de N (Cuadros 3 y 4). La mayor variabilidad interanual debe atribuirse, a la igualdad de otras condiciones, a la menor eficiencia de la fertilización que ocurre en años con deficiencias hídricas en los momentos críticos. En Anguil (Subregión VII), la probabilidad de deficiencias hídricas es mayor que en las otras dos subregiones, lo que queda evidenciado por el incremento en el rendimiento (47%) como resultado del riego complementario (Cuadro 3).

Cuadro 3. Rendimiento máximo, mínimo, medio y su desviación estándar para diferentes estrategias de cultivo simuladas por el modelo Ceres-Maize (D=secano, I=irrigado, 0=sin fertilización, 30=fertilizado con 30 kg de N) en las tres principales regiones de cultivo de maíz de Argentina.

		Condición		Rendimiento (t/ha)				Dif. de
Localidad	Subregión	H_2O	N	Medio	Máximo	Mínimo	D.E.	Rend. %
Pergamino	VI	D	0	4.69	6.21	1.90	1.29	100
		I	0	5.49	6.46	3.30	0.72	117
		D	30	7.56	10.18	3.39	1.99	100
		I	30	8.75	10.37	6.21	1.04	116
Manfredi	IV	D	0	3.86	5.14	1.53	1.04	100
		I	0	4.46	5.03	3.64	0.37	116
		D	30	6.46	9.08	2.26	1.97	100
		I	30	7.51	8.93	6.51	0.57	116
Anguil	VII	D	0	3.51	6.00	0.68	1.68	100
		I	0	5.16	5.95	4.05	0.48	147

Cuadro 4. Diferencias de rendimiento máximas, mínimas, y medias entre distintas simulaciones de estrategias de cultivo.

		Diferencia de rendimiento			
		Media			
Comparación entre estrategias de cultivo	Localidad	(t/ha)	(%)	Máxima	Mínima
Irrigación vs.	Pergamino (VI)	0.80	117	3.13	0.00
Secano, sin fertilización	Manfredi (IV)	0.60	116	2.33	0.00
	Anguil (VII)	1.74	147	5.15	0.00
Irrigación vs.	Pergamino (IV)	1.19	116	4.84	0.00
Secano, con fertilización	Manfredi (IV)	1.05	116	4.54	0.00
Irrigación y fertilización	Pergamino (VI)	4.06	186	6.90	3.10
vs. Secano no fertilizado	Manfredi (IV)	3.65	194	5.27	2.23

Las disminución de rendimiento atribuible a deficiencias hídricas calculadas mediante la simulación fueron semejantes a las obtenidas en estudios previos; así, las deficiencias hídricas pueden inducir disminuciones de más de 50%, dependiendo de la duración, intensidad y del momento en que ocurra el fenómeno. La probabilidad de disminución del rendimiento se incrementa notablemente a partir de la diferenciación de la panoja en el ápice de crecimiento, con un máximo alrededor de la floración (Robelin, 1962).

El análisis de regresión de los datos de tres períodos agrícolas que contrastan entre sí, en la localidad de Pergamino con efecto de déficit hídrico (Guevara, 1991; Oyarzábal et al., 1980) mostró que 34% de la variabilidad interanual de los rendimientos se explica por la variación de las precipitaciones en los meses de diciembre y enero (pre y postfloración). Una respuesta semejante se observó previamente para la subregión IX (Delpech y Darwich, 1981) . Otras experimentaciones que contemplaban diferentes niveles de disponibilidad hídrica (secano e irrigación) durante tres campañas agrícolas y para diferentes híbridos de maíz mostraron 40% de disminución del rendimiento (Zeljkovich, 1984) .

Las pérdidas promedio calculadas alcanzarían aproximadamente 1.2 millones de t, lo que significa un perjuicio económico cercano a los 150 millones de dólares estadounidenses (Cuadro 6). Si se tiene en cuenta que el riesgo de ocurrencia de deficiencias hídricas en los momentos críticos de desarrollo del cultivo es un factor que ha afectado la adopción generalizada de la fertilización nitrogenada, ya que disminuye su eficiencia, la cuantificación antes indicada deberá considerarse conservadora.

Debido a la importancia de la sequía como factor que limita el rendimiento de maíz, el INTA ha definido una estrategia de intervención a fin de reducir los efectos de la misma. Desde el punto de vista de la transferencia tecnológica, se debe dar énfasis a la recomendación de prácticas culturales que favorezcan la captación de agua de lluvias por disminución de las pérdidas por escorrentías y evaporación del suelo. Experimentos con distintos sistemas de labranza en la subregión VI (Zeljkovich, 1995) permitieron concluir que si bien no fue suficiente para evitar la reducción del rendimiento por sequías, el sistema de siembra sin labranza es, en suelos que no están físicamente degradados, la mejor alternativa para mejorar los rendimientos de maíz y disminuir su variabilidad interanual. Este sistema de siembra representaría una forma potencial de proveer mayor cantidad de agua para los cultivos, reduciendo las escorrentías y la evaporación e incrementar el almacenaje de agua en el suelo. Por otro lado, se propicia la difusión del riego complementario, y para ello el INTA provee de información sobre balance hídrico de cada cultivo, además de haber desarrollado un programa (software) apropiado para el cálculo de necesidades de riego. Es importante

Cuadro 5. Deficiencias hídricas decádicas (30 días anteriores y posteriores a la floración) y rendimiento promedio de maíz en tres períodos agrícolas en la región de Pergamino.

Estación de cultivo	Deficiencias hídricas decadicas (mm) 1	2	3	4	5	6	Rendimiento (t/ha)
1980/81	47	47	69	52	13	6	7.69
1982/83	59	43	106	64	67	71	2.38
1986/87	60	70	97	59	74	41	4.51

1 = primera década de diciembre
6 = tercera década de enero

Cuadro 6. Producción promedio (período 1990/91 A 1994/95), probabilidad de ocurrencia de deficiencias hídricas (PDH), incidencias de las deficiencias hídricas (IDH) y estimaciones de pérdidas de producción promedio para las principales subregiones maiceras.

Subregión	Producción (t x 1000)	PDH	IDH	Pérdidas de producción (t x 1000)
I	647	0.50	0.20	65
IV	2353	0.50	0.16	188
V	457	0.50	0.17	39
VI	3438	0.50	0.17	292
VII	1414	0.70	0.47	465
VIII	926	0.50	0.20	93
IX	721	0.40	0.17	49
Total	10009			1191

destacar que para gran parte de la subregión VI, es factible el riego complementario. De la experiencia disponible (Génova, 1992) se concluye que los niveles salinos y de sodio de suelos representativos de gran parte de la subregión VI no fueron afectados por varios años de riego complementario, cuando estuvieran bien drenados y no tuvier an capa friática cercana. Ello sería posible gracias a que se trata de riegos ocasionales (en promedio 180 mm por ciclo de cultivo), al régimen pluviométrico de la subregión, y a las buenas características de drenaje y elevados niveles de calcio intercambiable en los horizontes A y B. Finalmente, el INTA y la Universidad de Buenos Aires poseen un proyecto conjunto cuyo objetivo es identificar caracteres morfofisiológicos asociados con la tolerancia al estrés hídrico en materiales adaptados a la región pampeana, que permitan ser utilizados como criterio de selección en el programa de mejoramiento genético.

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The Impact of Drought and Low Soil Nitrogen on Maize Production in the SADC Region

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Abstract

Maize is the staple food of the people of the Southern African Development Community (SADC) countries: Angola, Botswana, Lesotho, Malawi, Mauritius, Mozambique, Namibia, South Africa, Swaziland, Tanzania, Zambia and Zimbabwe. It contributes, on average, 40% of the calories consumed in peoples' diets. Drought and low soil fertility are two major constraints to maize production in the region. The SADC region has been experiencing a series of droughts over the past five years, with the 1991/92 drought being the worst of the century. Food production was drastically reduced, leading to governments seeking food aid from the international community. The region's cereal harvest for 1994/95 was only 15.7 million tons, whereas direct consumption needs were 23.3 million tons. Of the 7.1 million ton deficit, 4.9 million tons were maize. Declining soil fertility, particularly nitrogen, is probably second in importance to drought as far as low maize yields are concerned in SADC countries. This is reflected in the wide gaps between researchers' and smallholder farmers' maize yields. In most countries farmers' yields average less than 1 t/ha, whereas researchers often obtain 10 t/ha or more. The potential of improved germplasm cannot be achieved by smallholder farmers mainly due to low and declining soil fertility.

Drought, low soil fertility, and stalkborers were highlighted as major constraints to maize production by maize breeders from southern and eastern Africa at a three-day meeting held at the CIMMYT Midaltitude Research Station in Harare, Zimbabwe, in March 1995. Drought causes a 10-50% annual yield loss on 80% of the area planted to maize in southern Africa (Short and Edmeades, 1991). The lack of early maturing varieties was also listed among the four most important constraints, with a broad range of justifications cited, including drought escape. The southern African region has been facing severe droughts over the past 5 years (1991-1995), the worst of which was during 1991-92. Total annual rainfall and distribution have been very poor (Figs. 1 and 2). A Regional Early Warning System (REWS) was set up in Harare,

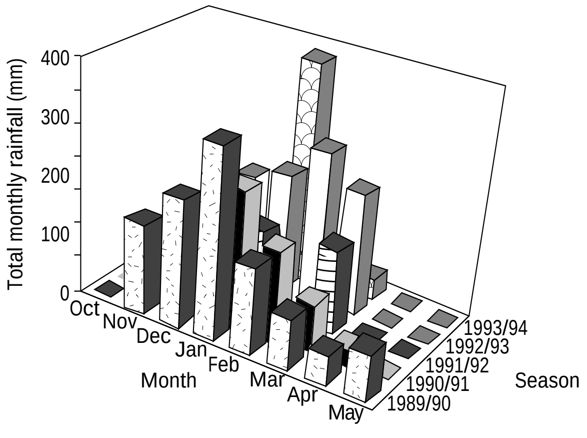

Figure 1. Rainfall distribution Chitedze, Malawi (lat. 13 59"S, long. 33 38"E, alt. 1000 m), 1989-90 to 1993-94.

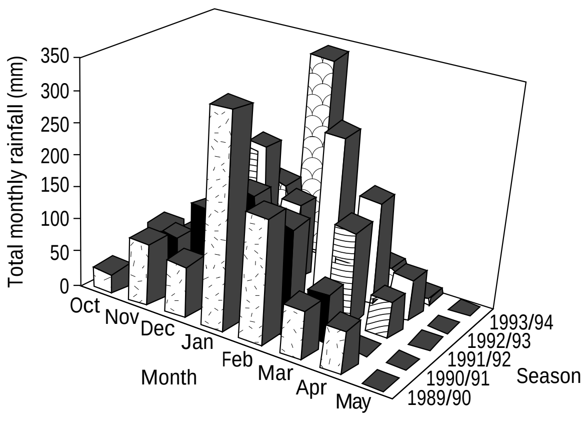

Figure 2. Rainfall distribution, Harare (DR & SS), Zimbabwe, (lat. 17 48", long. 31 03", alt. 1506 m), 1989-90 to 1993-94.

Zimbabwe, by the Southern African Development Community (SADC), to forecast and monitor food production. It acts as a coordinating unit for making contacts with the international donor community on food aid matters, particularly during times of natural disasters, such as drought.

Maize is the most important food crop in the region, accounting for over 40% of the total calories in diets. The population of the original nine SADC member states was just over 81 million in 1991, and has a high average growth rate of 3% (Table 1). Thus, the need for increased food production cannot be overemphasized. This paper highlights the impact of the recent drought and low soil fertility on maize production in the SADC region, and review what governments are doing to alleviate the situation.

Maize Production

The trend of annual maize production during the last 20 years for eight SADC member states (Angola, Lesotho, Malawi, Mozambique, Swaziland, Tanzania, Zambia, and Zimbabwe) shows a gradual increase from 7 million tons in 1976 to a peak of 9 million tons in the 1988-89 season (Fig. 3). Production fell drastically to a low of 4 million tons in the 1991-92 drought. In general, before the drought, the region was self-sufficient for maize production. Some countries, such as Malawi, South Africa and Zimbabwe, produced enough grain for local consumption and a surplus for export. The period 1991-92 to 1994-95 was very unfavorable for maize production, as reflected in the maize balance sheet (Table 2), and the region had to rely heavily on imported grain. For example, the 1991-92 grain deficit was more than 5 million tons and the region imported 4 million tons of grain to meet demand. Grain deficits for the following two years were smaller mainly because Malawi, Zambia and Zimbabwe enjoyed slightly improved rainfall, resulting in positive domestic balances for these three countries

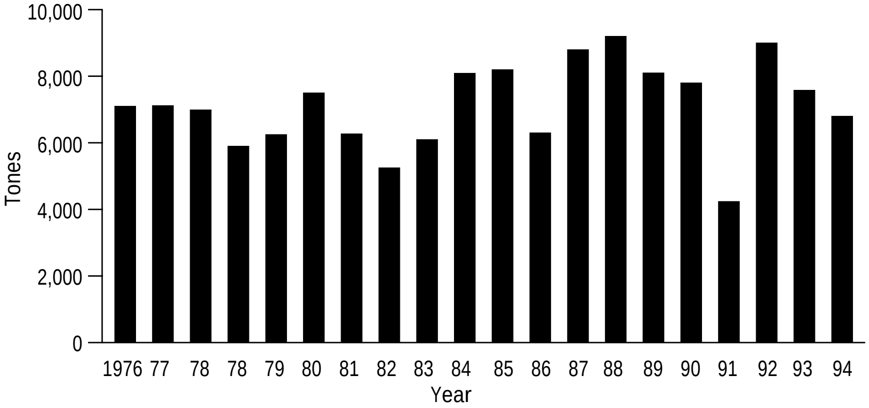

Figure 3. Maize production in the SADC Region during 1976-1995 ('000 t).

Table 1. Importance of maize in the SADC region, 1990-91.

	Population ('000)	Average annual population growth rate (%)	Maize share in total calories (%)
Angola	10002	2.7	19
Botswana	1297	3.3	31
Lesotho	1623	2.6	44
Malawi	8522	3.7	63
Mozambique	16364	3.0	40
Swaziland	774	3.2	46
Tanzania	24656	2.6	24
Zambia	8140	3.4	60
Zimbabwe	10013	2.9	45
SADC Region	81391	3.0	41.3

Adapted from: SADC Regional Early Warning System Quarterly Bulletins, 1992.

Table 2. Maize production balance sheet ('000 tons) for SADC countries, 1991-92 to 1994-95.

Year	Lesotho	Malawi	Mozambique	Swaziland	Tanzania	Zambia	Zimbabwe	All SADC
1992								
Domestic availability	53	931	169	56	2281	565	419	4890
Total requirements	269	1896	1168	176	2432	1600	2137	10671
Domestic balance	-216	-965	-999	-120	-151	-1035	-1718	-5781
Current import	178	252	681	91	51	682	1446	4062
1993								
Domestic availability	108	2078	611	102	2396	1740	2776	10160
Total requirements	265	1864	1148	162	2530	1708	2587	11306
Domestic balance	-157	215	-537	-60	-134	32	189	-1146
Current import	186	88	464	28	14	0	421	1371
1994								
Domestic availability	69	1724	765	71	2614	823	2029	15496
Total requirements	280	1931	1040	122	2663	1313	2271	17917
Domestic balance	-211	-207	-275	-51	-49	-490	-242	-2421
Current import	155	200	152	38	0	444	500	1805

Adapted from: SADC Regional Eraly Warning System Quarterly Bulletins, 1992-1995.

(Table 2). In 1993-94 and 1994-95, all food balances were negative due to prolonged drought and the depletion of grain reserves.

Food aid

Governments of the region have been appealing through the SADC Regional Early Warning System for food aid from the international community since 1991. A major component of the appeal for 1994-95 was for food aid for Lesotho, Malawi, Swaziland, Zambia and Zimbabwe, for whom 0.52 million tons was sought, at an estimated cost of US$90.7 million. Assistance to ensure minimal nutrition levels for vulnerable groups required a further US$45.3 million. Overall, the total cost of the appeal was US$270 million. This did not include the significant costs to the region itself for depleted grain reserves, distributing rations, implementing rehabilitation schemes for water and pastures, special welfare programs, or ensuring market supplies of maize grain (SADC REWS Quarterly Bulletins, 1995).

Germplasm for Drought and Low Nitrogen Conditions

Of yield losses caused by drought, the most serious are due to moisture stress occurring during flowering (Edmeades et al., 1993) when farmers can no longer replant. CIMMYT has focused on developing techniques for improving maize tolerance to drought during flowering. Improvement for drought tolerance in Tuxpeño Sequía resulted also in improved performance under low soil nitrogen conditions (low N). Gains in yield under low N due to selection for drought tolerance over several populations averaged 135 kg/ha/cycle (Lafitte et al., 1997). Advanced cycles of Tuxpeño Sequía and Pool 26 Sequía outyielded their respective initial, unimproved versions under low N by 28 and 49%, respectively. These findings are encouraging.

In the CIMMYT-Zimbabwe Maize Program, Population ZM 601 is undergoing improvement for drought tolerance. In addition, Tuxpeño Sequía has undergone two cycles of selection, adapting it to Zimbabwe conditions (Magorokosho and Pixley, 1997). Several materials being screened for drought tolerance under rainfed conditions at the drought-prone sites Makoholi and Matopos, Zimbabwe. Two populations, Drought A and Drought B, were developed at CIMMYT-Zimbabwe, with emphasis on drought tolerance. The materials that went into the two populations were mostly selected based on pedigrees known to possess drought tolerance. These included K64R, and some versions of N3 and SC that were found to be heat tolerant (Pixley, personal communication). CIMMYT is currently in the process of setting up a project for breeding drought and low N tolerant maize in the SADC region. The project will be based at CIMMYT's midaltitude research station in Zimbabwe. This project is coming at an opportune time. Countries in the region have limited resources (human, financial and material) to effectively tackle this problem.

Most commercial seed companies in Zimbabwe devote some research to the development of maize hybrids suited to drought-prone areas. For example, the Seed Cooperative of Zimbabwe, a major producer of hybrid maize seed in Zimbabwe, devotes 50% of their resources to developing short season hybrids as a mechanism for drought escape (Caulfield, personal communication). Hybrids SC401, SC501 and SC509, are said to have good heat and drought tolerance. Most, if not all, of the seed companies in Zimbabwe follow a strategy of breeding maize under favorable conditions and later extensively testing the most promising materials in a broad range of environments, including drought-prone sites. By contrast, methods developed at CIMMYT suggest drought-tolerant maize can best be developed by breeding under carefully managed drought stressed conditions (Edmeades et al., 1997; Short and Edmeades, 1991).

Impact of Low Soil Fertility on Maize Production

It would appear that little has been done to assess the impact of low soil fertility on maize production in the SADC region, except for studies on response of maize to various nutrients, mainly nitrogen, phosphorus and potassium. Hence, this paper will present information on fertilizer use by smallholder farmers and the yield gap, for countries where such information is available (Malawi and Zimbabwe).

The “yield gap” may be defined as the difference between average yields obtained by farmers and the yields possible with improved cultural practices (FAO, 1984). These will vary from country to country and from one system (smallholders) to another (estate farmers). In Malawi, Coffmann (1992) calculated a yield gap of 90% between practical yields with currently available maize varieties and the estimated national average yield; i.e., yields in farmers’ fields were only 10% of those on the station. This is one of the widest reported anywhere. Coffmann, however, combined the average yields of hybrids, composites and local maize cultivars. When the practical average yield is separated by cultivar ‘type’ and compared with yield results obtained under high management on research stations and farmers’ fields, the yield gap for hybrids ranged from 53 to 61% (Zambezi et al., 1993). This gap is likely due to differing combinations of crop management practices, water supply and soil fertility.

Heisey and Smale (1995) found a difference in maize yields between local maize (1 t/ha) and hybrid maize (2.9 t/ha), under smallholder farming conditions in a survey conducted in some Agricultural Development Divisions of Malawi. In Zimbabwe, Mashingaidze (1994) observed that the average maize yield in communal lands (smallholders) was about 1.0 to 1.5 t/ha, as compared to about 5 t/ha in the commercial farming sector. Major factors limiting maize yields in the communal lands were reported to be drought, poor soil and fertilizer management, low plant populations, late planting, poor weed control and labor shortage (Mataruka, 1985). The task of reducing the yield gap is formidable, especially considering the high cost of fertilizers and the frequent occurrence of drought.

Fertilizer Management by Smallholder Farmers

In a survey conducted in Malawi in 1990-91 (Zambezi and Jones, 1991), widespread fertilizer use by smallholder farmers was observed. The credit system played a major role in facilitating fertilizer use by smallholder farmers, because fertilizer was part of a technology package which also included hybrid maize seed. In general, farmers purchasing fertilizer tended to apply it once at low rates at any time in maize crop development from knee height to tasselling. Smale et al. (1991) observed that most smallholders in Malawi applied basal fertilizer after emergence, rather than at planting, as is currently recommended for commercial farmers on the basis of station research results. Reasons given by farmers for delayed applications included shortage of labor at planting time, risk of wasting fertilizer if the plant does not emerge, and fertilizer ‘burn’ or salt damage inhibiting germination. Jones and Wendt (1995) showed that a farmer could expect to get 16 kg of maize/kg of nutrient, when growing local maize. The return from hybrid maize was 18 kg with the same nutrient package.

Data on fertilizer use by smallholder farmers in Zimbabwe (Rohrbach, 1989) and Malawi (Guide to Agricultural Production in Malawi, 1993-94) show that Zimbabwe farmers apply more fertilizer (80 kg nutrients/ha) than their Malawian counterparts (14 kg nutrients/ha) (Table 3). Considering the nutritional

Table 3. Fertilizer distribution to small-scale farmers in Malawi and Zimbabwe.

	Year	Maize area (ha)	Quant. fert. distributed (tons)	Fertilizer (kg nutrients/ha)
Malawi				
	1988/89	1270822	78429	16.2
	1989-90	1343784	101261	8.8
	1990-91	1391878	115270	9.4
	1991-92	1368093	131766	10.1
	1992-93	1326978	150000	13.2
Mean				14.8
Zimbabwe				
	1978	700000	25000	35.7
	1979	600000	25000	41.6
	1980	900000	27000	30.0
	1981	1000000	90000	90.0
	1982	1100000	69000	87.3
	1983	1050000	98000	93.3
	1984	1136000	106000	93.3
	1985	1018000	127664	125.4
	1986	1000000	130000	130.0
Mean				80.7

Adapted from: D.D. Rohrbach (1989) Guide to agricultural production in Malawi, 1993-94.

needs of the maize plant, both rates are far too low. A large proportion of the maize area does not get any fertilizer at all. Nutrients are being removed with every harvest, without replenishment. The soil fertility problem is further worsened by the widespread removal of crop residues for use as animal feed or other purposes. These figures indicate that there is a lot of room to increase maize production by increased fertilizer application, while using appropriate available germplasm.

SADC's Response to Drought

Every SADC member state has taken action in its own right to mitigate the effects of drought. Strategic grain reserves have been drawn down to meet the needs of vulnerable groups and to maintain supplies in the marketing system. Registration of the people in need was undertaken in many countries, together with arrangements, where possible, to meet their food needs (SADC REWS Quarterly Bulletins, 1991-1995). National drought task forces have been set up in many countries, and these have been instrumental in coordinating relief supplies. In all member states, resources have been mobilized to meet the increased import requirements. As there is no grain available for export in the region, all imports have to be sourced from overseas. At a recent meeting in Malawi, the SADC Council of Ministers agreed to set up 10 projects valued at US$63.17 million for establishing regional food reserves as a cushion against shortfalls during drought and natural disaster (*Zimbabwe Herald*, April 17, 1995). Action has also been taken to conserve water, especially at rural schools and clinics. Two irrigation projects are under way in Zimbabwe in dry areas Chiweshe (near Mazowe) and Nyamemba (Wedza District), estimated to cost Z$31 million (US$3.4 million) and Z$1 million (US$111,000), respectively. The first will supply the needs of 300 households, the second an additional 35 households (*Zimbabwe Sunday Mail*, June 11, 1995). Malawi is about to set up an irrigation project in the semi-arid Shire Valley area, with funding from France (Radio Malawi).

In general, governments have encouraged their farmers to grow drought tolerant crops such as sorghum and millet. However, these are by no means the only interventions that SADC member states have put in place to mitigate the effects of drought.

Smallholder Credit Systems

Some governments have tried to encourage use of fertilizer on maize by smallholder farmers by establishing smallholder loan schemes. The problem with this system is that removal of government subsidies has pushed up fertilizer prices to such an extent that farmers would find it difficult to repay loans, even in a good season. Conroy (1992) reported that the share of hybrids in the maize area in Malawi declined for the first time in 8 years, and fertilizer use decreased to less than 70,000 tons, compared with 180,000 tons in 1992-93. This severe reduction in inputs was caused by the collapse of the smallholder credit system in 1992 and 1993. The reduced use of fertilizer and hybrid seed may lead to a sharp decline in maize production, and thereby exacerbate food security problems for most of the rural population. Conroy further observed that less than 35% of smallholder farmers used fertilizer, and these were typically farmers with above-average farm sizes and access to seasonal agricultural credit. Removal of subsidies on fertilizer in Malawi over the past two years, has resulted in a three-fold increase in fertilizer prices. Fertilizer price subsidies were also removed in Zimbabwe in 1995, and prices there have risen three times in less than a year.

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Characterization of Drought Stress in the Major Maize Production Zones of Kenya

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Abstract

Maize, the most important cereal crop in Kenya, is grown from sea level to more than 2300 m elevation. With the use of geographic information system (GIS) techniques, six distinct maize agro-climatic zones have been defined for the main rainy season in Kenya. The objective of this study was to characterize each of these zones for the degree and timing of drought stress. For each of the six maize zones, two representative sites with extensive weather records were used. Long-term means for rainfall for 10 d periods were compared to the potential evapotranspiration of the same period at each site. Maize phenological development was superimposed on these data. In the highland and moist transitional zones, which comprise 75% of the maize area, drought occurrences were limited. The moist midaltitude zone had the greatest variability in moisture stress between sites, and late season drought is consistently a problem. The dry midaltitude and dry transitional zones experience the most severe drought, especially during grain filling and early in the season. In the lowland tropics, significant moisture stress occurs during the first 20 d of the season and during the last 40 d of growth. These data suggest that drought tolerance is needed for germplasm being developed for four of the six zones.

Maize is the most important cereal crop in eastern Africa. In Kenya, it is cultivated on more than 1.4 million ha, over a wide range of agro-climatic zones stretching from sea level to well over 2300 m in elevation. Various methods have been used to classify the major maize production zones. Most recently Hassan et al. (1996a) employed geographic information system (GIS) techniques to develop a modern categorization format for the main rainy season (March to August). Six agro-climatic zones were identified. Drought is widely understood to be the major constraint in two of these zones, namely the midaltitude dry and dry transitional zones. Drought also occurs to a lesser degree in the other maize-growing zones.

Drought can be defined as any duration without rainfall which is long enough to reduce plant growth. In practical terms it occurs when available soil water fails to meet the plant's transpiration demand for a reasonable period during growth. Thus rainfall, soil water storage capacity, potential evapotranspiration and crop phenology and crop development stage must all be considered when assessing the impact of drought on production.

Drought effects have not been well quantified. Several studies have focused largely on the total rainfall received within the growing season (Dowker 1963; Stewart and Faught, 1983; Wafula, 1995). However, distribution of rainfall within the season is often more critical than total amount. Little effort has been directed towards describing how the level of water stress during crop development might affect grain yields of maize. Detailed physiological studies on maize varieties in the cool and wet highlands of western Kenya have been conducted (Cooper and Law, 1977), but they did not evaluate the occurrence of water-deficit periods during critical stages of crop growth. Such an evaluation is needed for each of Kenya's maize production environments to better target research efforts. The objectives of this study were to quantify the occurrence and timing of drought for each of the six maize agro-ecologies in Kenya.

Materials and Methods

The long-term seasonal rainfall patterns for March to August were assessed for twelve sites, two for each of the six agro-ecological zones (Table 1), using 14-54 years of records already gathered for the Maize Data Base Project (MDB), the Fertilizer Use Recommendation Project (FURP, 1987) and by research scientists at KARI's Katumani Research Center. The six zones varied in altitude, length of growing season, and seasonal rainfall (Table 1). Several maize cultivars have been developed to meet the varied requirements of these diverse maize growing zones in Kenya. The zones are considered distinct from each other, based on climatic criteria, though some cultivars are broadly adapted and grown in more than one zone.

Using 10 d intervals within a typical cropping season, rainfall and potential evapotranspiration were computed for each site. The water requirement of the maize crop was estimated for each 10 d period using the CERES-Maize model (Jones and Kiniry, 1986) and genetic parameters for varieties relevant to each production zone. The coefficients for converting potential evapotranspiration to plant water use at different growth stages were obtained from FURP manuals published for each site (FURP, 1987). Information on the phenological development of maize varieties recommended for production in each maize agro-ecology was adapted from FURP, after consultation with KARI maize breeders. A period of 10 d was arbitrarily considered to be the duration of a dry spell needed to start reducing the growth of the maize crop because of the effects of water deficits. Deficits in the water balance for each 10 d could, therefore, be used by breeders to characterize the type of water stress found in a given production zone.

There was some variability in rainfall amount and distribution between the two sites selected to represent each maize zone. Nevertheless, data were averaged for the two sites to develop an 'average' water budget for each zone. Where differences between the two sites were large enough to significantly affect the results, these were noted.

Table 1. Characteristics of study sites and the genotypes which are adapted to each of the six agro-climatic zones in Kenya.

Zone	Site	Elevation (masl)	Recommended variety	Days to maturity (d)	Years of data	Seasonal rainfall (mm)
Highlands	Turbo	1850	H625	180	18	750
	Baraton	1960	H625	190	22	670
Moist Transitional	Kitale	1800	H625	160	23	612
	Kakamega	1530	H625	150	23	780
Moist Midaltitude	Alupe	1170	H622	160	27	840
	Bukiri-Buburi	1220	H512	150	27	580
Dry Transitional	Katumani	1550	Katumani	100	27	230
	Weruga	1460	Katumani	110	54	550
Dry Midaltitude	Kitui	1140	Makueni	100	27	260
	Makueni	1170	Makueni	80	27	175
Lowland	Kichwa Simba	140	Pwani	110	23	750
	Msabaha	30	Pwani	110	23	600

Results

The highland zone had a positive water balance throughout the growing season, with the exception of the first 20 d (Fig. 1). This apparent early-season water deficit probably results from variation in the actual start of the growing season. A fixed planting date was used when summarizing rainfall data. In practice, farmers probably avoid this stress by planting when rainfall has become reliable.

In the moist transitional zone, there was some stress early in the season, extending up until 10 d before flowering (Fig. 1). Thereafter there was a positive water balance, with the exception of some stress during late grain filling. In the moist midaltitude zone, there was considerable variability between sites in rainfall pattern (Table 1). Except during 30 of the last 40 d of grain filling, water requirements were met by precipitation (Fig. 1).

Within the dry midaltitude zone, Kitui had a one-week shorter growing season than Weruga, though the timing of drought stress was similar (Table 1). Within this zone, drought stress begins soon after flowering and increases in intensity throughout the reproductive and grain filling stages (Fig. 2). The pattern of water stress in the dry midaltitude zone was similar to that of the dry transitional, although the stress was more intense and it commenced earlier in the growing season (Fig. 2). This was the only zone with a negative water balance throughout the growing season.

The lowland zone was characterized by a negative water balance during the first 20 d, and 30 of the last 40 d of plant growth (Fig. 2). Late season stress is quite intense in this zone.

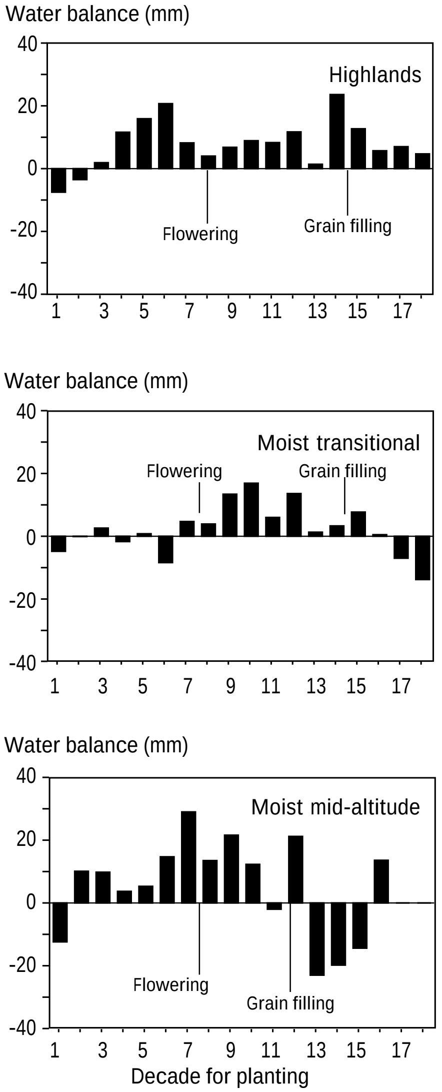

Figure 1. The seasonal water balance and major maize growth stages for the highland, moist transitional, and moist midaltitude maize zones in Kenya.

Discussion

Results presented show that among all maize agro-climatic zones in Kenya, the highland zone is the least prone to water stress (Fig. 1), and there is little need for incorporation of drought tolerance into germplasm being developed for this area. However, the erratic nature of the beginning of the rains is noted in our analysis, and this was also identified by farmers as a priority problem in a recent survey (Hassan and Njoroge, 1996).

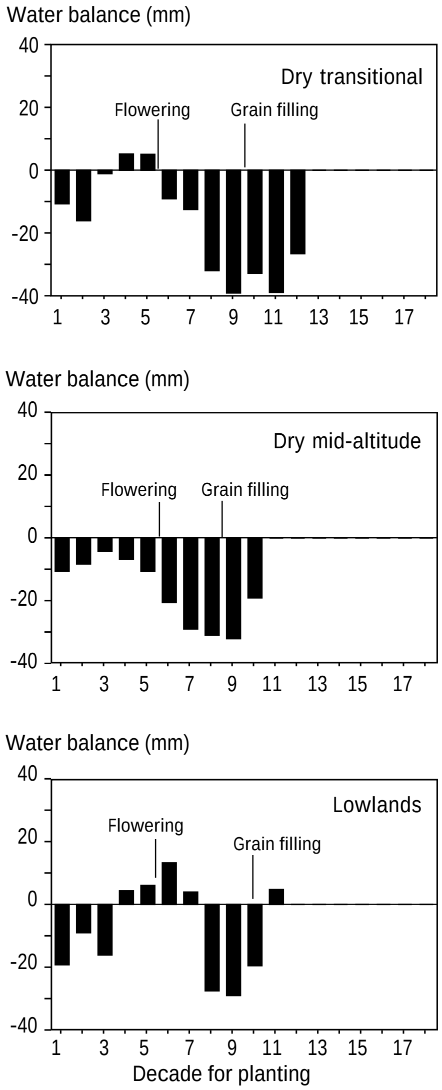

Figure 2. The seasonal water balance and major maize growth stages for the dry transitional, dry midaltitude, and lowland maize zones in Kenya.

The moist transitional zone is particularly important for maize production in Kenya. This agro-climatic zone covers some 420,000 ha, or about 40% of the entire area sown to maize in Kenya. After the highlands, the moist transitional zone is the least affected by drought. Results indicate that drought is probably not a major constraint for the sites included in the analysis from this zone. The average water balance at the beginning of the season is near zero, indicating that stress may occur in some seasons and at some sites during the season. Given the size and importance of this zone, a more thorough analysis of spatial variability for seasonal rainfall within the zone is justified. Additional support for this is provided by farmers within this zone, indicating that variable rainfall is an important constraint to maize production (Hassan et al., 1996b).

The moist midaltitude zone displayed the greatest spatial variability in moisture stress in our analysis. Data indicate that water stress can be quite significant during the grain filling stage in this zone, which includes about 10% of the area sown to maize in Kenya and receives the least emphasis by the National Maize Research Program. A critical look at developing varieties that can tolerate drought in the latter half of the grain filling period is merited for this zone.

For the dry transitional and dry midaltitude zones, our study confirms the findings of Stewart and Faught (1983) that maize production is seriously reduced by drought in at least six out of ten years. It is not surprising that previous studies on climatic risk (e.g., Dowker, 1963; Wafula, 1995; Keating et al., 1993) have been focused on these short season, semi-arid areas. The crop cycle length and seasonal rainfall variability have been used by breeders as major guiding factors in variety development for these zones (Dowker, 1963; Njoroge and Ngure, 1987). The variety traditionally grown in these areas is the early-maturing 'Katumani Composite', which was bred to escape severe late-season stress. Our analysis suggests that earliness should continue to be a major breeding objective for these zones, but that additional emphasis should be given to incorporating stress tolerance for all stages of plant development, and particularly the sensitive flowering stage.

The lowland tropics are the least important zone for maize production. Moisture stress is an important production constraint during the first 20 d of plant growth, and during the last 40 d of grain filling. Thus, both early-season and late-season drought tolerance is important for varieties for the lowlands.

Conclusion

This analysis suggests that drought tolerance of one sort or another is needed for germplasm being developed for four of the six agro-climatic zones. In the past, significant research resources have only been directed towards alleviating this problem in the two semi-arid zones. There is therefore a need to expose breeding materials and segregating progenies designated for the moist midaltitude zone and the lowland tropics to drought stress in a systematic manner. This should involve the use of water deficits timed to coincide with those periods of crop development when drought is most likely to affect grain production under farmers' conditions.

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Impact of Drought and Low Nitrogen on Maize Production in Asia

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Abstract

Drought and low levels of available nitrogen (low N) are two of the major limiting factors in maize production in Asia. The regular occurrence of drought, particularly that related to the El Niño phenomenon, has brought severe yield losses to the affected countries in the region. Low N, on the other hand, has been exacerbated by inappropriate farming systems practiced by farmers. Continuous monocropping of maize on large tracts of land with little, if any, provision for soil fertility maintenance, has contributed to the rapid depletion of soil nitrogen. Soil erosion, largely caused by massive deforestation and cultivation of steep slopes, has also been a major factor in rapid loss of soil fertility. A survey was conducted during the Sixth Asian Regional Maize Workshop in India, November 1995, to determine the effect of drought and low N on Asian maize yields. It revealed that each stress affects about half of the total maize growing area in Asia. Yield losses due to drought and low N were estimated to range from 10-75% and 10-50%, respectively. Considering the importance of maize as a feed and staple food in the region, these staggering yield losses could threaten the food security of Asia. Development of stress tolerant maize germplasm should be vigorously pursued as part of a long-term solution. The status of maize breeding programs, including innovative screening techniques, new cultivars developed, and collaboration among public and private research institutions in selected Asian countries, are discussed.

Maize is considered an economically and politically important cereal crop in Asia, and is a major ingredient for food and feed products. It assumes a role second to rice in the farming sector and macroeconomy of the region. About 40 million hectares are planted annually to maize in Asia, producing 130 million metric tons, or around 30% of the total world maize production. At present, practically all of the Asian countries are importing maize because of relatively low production coupled with increasing demand due to the rapid expansion of the poultry and livestock sector. In 1990-92 for example, a total of 5.7 million metric tons were imported by Asian and Pacific countries (CIMMYT, 1994). In the light of rapid population growth also occurring in the region, there is an urgent need to dramatically increase maize production in order to avert severe food shortages and consequent political instability.

Among the major constraints to increased production are abiotic factors such as drought and low levels of soil nitrogen (low N). The regular occurrence of drought, particularly those resulting from the *El Niño* phenomenon, have brought severe yield losses in the affected countries. *El Niño* is described as a large scale shift in water currents and winds of the equatorial and tropical Pacific, resulting in extreme climatic changes characterized by excessive rains and strong winds in some areas and drought in others (Tibig, 1995). In 1982-83, *El Niño* brought extreme drought to Indonesia, Philippines, and Southern India (Glantz, 1984).

Low N has been exacerbated by inappropriate farming systems practiced by farmers in Asian countries. Continuous cultivation of maize as a monocrop on large tracts of land, with little if any provision for soil fertility maintenance, has contributed to the rapid depletion of soil nitrogen. Soil erosion, largely caused by massive deforestation and cultivation of steep slopes, has also been a major factor in rapid loss of soil fertility.

This paper is intended to be a 'situation' report on the effect of drought and low N in the Asian region in terms of area affected and the estimated yield loss. It also provides a brief review of the status of breeding for drought and low N tolerance in selected Asian countries.

Materials and Methods

A survey was conducted during the Sixth Asian Regional Maize Workshop held in India from October 30 to November 4, 1995. The workshop was attended by maize breeders, researchers and policy makers, including both public and private sector personal from 11 Asian countries. A survey form was distributed to representatives of each country. Data requested were as follows:

1. Total maize growing area.
2. Drought affected maize growing area.
3. Percent yield loss due to drought.
4. Low N affected maize growing area.
5. Percent yield loss due to low N.

Estimates of lost grain production for each country due to drought or low N were calculated using the formula:

$$Y_{red} = [\text{Area affected x \{Average yield/(100 - \% yield loss)\} x \% yield loss}]$$

where:

Y_{red} = reduced grain production (tons) due to drought or low N
Area affected = number of hectares thought to be affected by drought or low N.
Average yield data (t ha^{-1}) were obtained for each country from CIMMYT (1994)
% yield loss = percent yield reduction due to drought or low N.

Average yield per unit area was adjusted by dividing it by the difference between 100% and the % yield loss. This was necessary because the recorded total production and the consequent yield per unit area is already a result of the cumulative effects of biotic and abiotic stresses. Where respondents gave a range, for example, 20 to 30% yield loss, the midpoint of this range was used in the various calculations. Other factors such as cultivars and their interaction with environmental factors could not be determined from the data, and potentially could bias the result. Notwithstanding its weaknesses, this formula should provide a rough estimate of lost grain production due to the two environmental stresses.

Results

The countries represented in the survey account for about 90% of the maize growing area in southern Asia (Table 1). Drought affected area in these countries ranged from 23% of Vietnam to 85% of Laos, with a mean response of 49%, and suggesting that 7.8 million hectares of the region are affected. India registered the highest absolute area affected, 2.5 million hectares, followed by Indonesia and S. China with 2.2 and 1.15 million hectares, respectively. Yield losses due to drought ranged from a low estimate of 10% in China to as high as 75% in Nepal, with the mean of estimates being 37%. This translates into reduced grain production ranging from 0.04 million tons (Vietnam) to 1.60 million tons (Philippines) and a total of 6.40 million tons for the nine Asian countries represented in Table 2 (Taiwan was excluded because of a lack of production data). In absolute terms, the Philippines and S. China have the highest grain production losses due to drought.

Maize area affected by low N ranged from 19% of Taiwan to 80% of Laos and Nepal, with a mean response of 51% (Table 1). The 8.4 million hectares affected across the region represents 49% of the total maize area. Again, India had the largest affected area with a total of 3 million hectares, or half its maize growing area. The Philippines, S. China and Indonesia also have extensive areas affected, with 1.8, 1.2, and 1.0 million hectares, respectively. Percent yield loss was highest in India (50%), while S. China and Thailand were the least affected with only 10 to 20% yield losses. Low N caused an estimated loss in grain production of 4.5 million tons in India (Table 2), which is over half of the 8.6 million tons of grain production lost to low N in the region. India (4.50 million tons), the Philippines (1.23 million tons), S. China (1.50 million tons) and Indonesia (0.94 million tons) account for 95% of the grain production losses due to low N.

Discussion

It is clear from the survey results that substantial grain production losses are caused by drought and low N in the Asian region (Tables 1 and 2). Both stresses affect about a half of the maize production area. In fact, they may easily be the leading factors limiting maize production. The production loss estimates (6.35 and 8.60 million tons) due to drought and low N individually account for losses of potential production of about 16 and 22%, respectively, or 38% of production if taken together. Of course, the effects of these two factors can not be considered independently. For example, the effect of low N on general plant vigor, rooting depth and biomass formation renders the plant more susceptible to drought. Hence, the cumulative negative effect on grain yield might be greater than the additive effects of each stress. The impact of these stresses on maize production in Asia cannot be overemphasized.

Table 1. Summary of responses to the questionnaire regarding the effect of drought and low soil nitrogen fertility on maize production in Asia.

	Maize growing area (‘000,000 ha)	Drought affected area (‘000,000 ha)	Yield loss due to drought (%)	Low N affected area (‘000,000 ha)	Yield loss due low N (%)
India	6.00	2.50	20-30	3.00	50
Indonesia	3.20	2.20	15	1.00	30
Laos	0.04	0.03	65	0.03	35
Nepal	0.75	0.34	40-75	0.60	20-30
Philippines	3.00	1.00	50	1.80	30
S. China	2.20	1.15	10-30	1.20	10-20
Sri Lanka	0.05	0.03	30	0.03	25
Taiwan	0.07	0.02	25-35	0.01	20-30
Thailand	1.40	0.43	23	0.51	20
Vietnam	0.50	0.12	15-20	0.21	35-40
Total	17.20	7.82	8.39		
Mean	1.72	0.79	37	0.84	29

Table 2. Estimated reduction in grain production in nine Asian countries due to drought and low available soil nitrogen (low N).

	Average grain yield† (t ha^{-1})	Total grain production (‘000,000 tons)	Area affected by drought (%)	Production loss due to drought (‘000,000 tons)	Area affected by low N (%)	Production loss due to low N (‘000,000 tons)
India	1.50	9.00	42	1.25	50	4.50
Indonesia	2.20	7.04	69	0.85	31	0.94
Laos	2.06	0.08	85	0.12	80	0.03
Nepal	1.60	1.20	45	0.71	80	0.32
Philippines	1.60	4.80	50	1.60	60	1.23
S. China	5.00	11.00	52	1.43	55	1.05
Sri Lanka	1.07	0.05	60	0.01	60	0.01
Thailand	2.60	3.64	31	0.34	37	0.33
Vietnam	1.50	2.25	22	0.04	42	0.19
Total	39.06	6.35	8.60			
Mean	2.13	3.91	49	0.64	51	0.86

† Source: CIMMYT (1994).

The regular occurrence of longer and more devastating drought in tropical Asia is an alarming problem. Drought (and flooding) ascribed to the *El Niño* effect has been increasing in frequency in recent years. Additionally, these anomalous weather conditions should be viewed against a backdrop of other modulating (sometimes overwhelming) influences in the environment (Glantz, 1984). The unabated cutting of trees and the increased carbon dioxide load in the atmosphere may contribute significantly to the greenhouse effect and fluctuations in weather patterns (see Chapman et al., 1997) which are thought to result in more frequent drought.

Low N will continue to be a major constraint to maize production, especially in light of continuous and intensive monocropping and unsustainable farming practices. It has been estimated that the potential for loss of fertilizer N is substantial, particularly in tropical soils. For example, Poss and Saragoni (1992) found that 36-153 kg N ha^{-1} had leached below the root zone (150 cm) during the growing season. Myers (1988) reported that maize takes up only 20 to 40% of available N during the main 3 to 5 months of the growing season. The problem facing Asian farmers is that the capacity of soil to supply N declines rapidly once agricultural activities commence, and the N derived from the breakdown of organic matter must therefore be supplemented. For productivity to be sustained at the current levels, let alone increased in the future, N removed as agricultural produce or lost from the system must be replenished (Peoples et al., 1995). Rapid population growth in Asia, coupled with rising costs of inorganic N, make it increasingly difficult to maintain soil fertility.

A major issue is how to increase maize production in Asia, given these environmental stresses. In the case of drought, governments are continuing to invest in costly irrigation systems, but will these systems be sustainable in the long run? Related to this is the probability that the rapid deforestation in the region will create a long-term water availability problem because of damage to natural catchments. For low N soils, the addition of inorganic N hinges on the buying power of small farmers. More often than not, the cost of fertilizer and the establishment of irrigation facilities are beyond their means. Environmental concerns related to the continuous use of inorganic fertilizer may also make this practice unsustainable in the long run. The use of organic fertilizer, compost, green manure, or biological N fixation are generally seen as better alternatives (Peoples et al., 1995), but their ability to supply enough N to produce needed food for an increasing population is still hotly debated.

Technologies developed to combat the effects of stress conditions such as drought and low N should be economically viable, ecologically sound and socially acceptable. The best approaches may be the development of improved varieties. Improved varieties are often recognized as having contributed a very large portion of modern agriculture's increased productivity. As drought or low N tolerant maize varieties become available, their adoption should be reasonably rapid because their use involves no additional cost (apart from the initial seed cost), and existing cropping systems and soil and water management practices are not affected.

In Asian countries, breeding for drought tolerance was started by farmers practicing mass selection – they selected individual ears to use as seed for the next season. In the Philippines, for example, an indigenous early-maturing variety called 'Tiniguib' has been found to tolerate drought, highly weathered soil, and common pests such as downy mildew and corn borer. Although its yield potential is relatively low compared to improved open-pollinated varieties (OPVs), this variety is preferred by farmers that grow maize for their household needs. These farmers (who are mostly in marginal environments) prefer Tiniguib for its ability to survive and produce harvestable yield in less fertile soil and during periods of water deficit.

Most formal maize breeding work in Asia is still done by public research institutions. Collaboration of national maize breeding programs with CIMMYT, in particular, have facilitated the exchange of improved germplasm and have led to the development of improved varieties. The establishment of CIMMYT's Asian Regional Maize Program has effectively channeled useful tropical and subtropical germplasm into national programs. Germplasm improvement by private seed companies has also been an essential step in the provision of superior cultivars, particularly hybrids.

Research on drought tolerance in maize has generally resulted in the development of better screening techniques and consequently better varieties. Using a drought index in conjunction with controlled field conditions has been effective in identifying tolerant germplasm (Prasatsrisupab et al., 1990). For seedling evaluations, a high temperature treatment ordered entries similarly to induced drought (Del Rosario et al., 1991), using a simple, rapid and reproducible technique which is less affected by day-to-day variation in environmental conditions. Anthesis-silking interval (ASI), leaf rolling, and other morpho-physiological parameters have also been utilized effectively to screen for drought tolerance in maize.

Early-maturing cultivars have been employed by breeders as a method of drought avoidance. The Institute of Plant Breeding (UPLB), Los Banos, Philippines, for example, developed two early-maturing varieties (IPB Var 7 and IPB 949) which perform very well during the dry season in the Philippines. Other countries in the region, such as India, Indonesia, and Thailand, have also used this strategy.

Variety x fertilizer trials are a common means of identifying cultivars that thrive in less fertile soil. Lantin and Octavio (1985) observed that hybrids can outperform OPVs under both low and high N regimes. Additionally, better performing varieties in high N soil were usually the better ones in low N soil. This indirect selection has proven to be cheaper than directly selecting under stress (low N) conditions.

The twin problems of drought and low N have serious implications for food security, not only in Asia, but for the whole world. Development of tolerant varieties is seen as a long-term solution to these problems, but will require additional research resources. Other prospects include the utilization of non-conventional hybrids in stress-prone environments, farmers' active involvement in the selection process, and the use of biotechnology, which could provide powerful tools to complement conventional approaches to maize improvement. Lastly, collaboration among national programs and with international centers like CIMMYT should be strengthened. These collaborative activities should involve germplasm exchange, staff training and information dissemination.

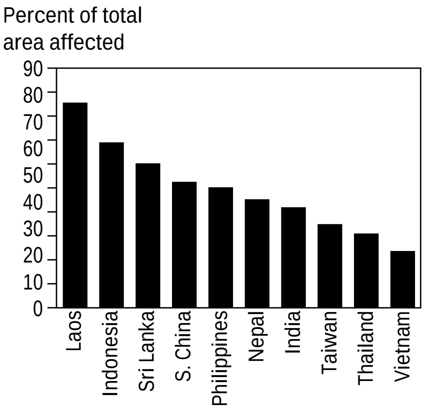

Figure 1. Percent of total maize area affected by drought.

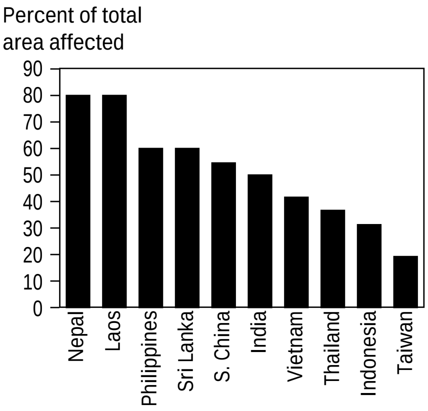

Figure 3. Percent of total maize area affected by low N.

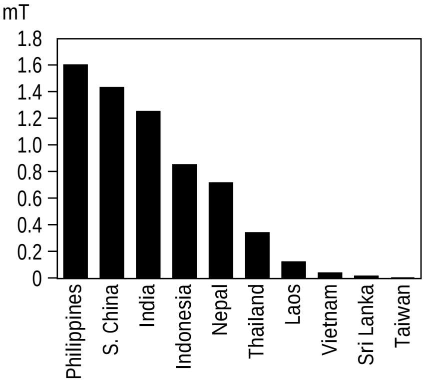

Figure 2. Estimated grain yield reduction due to drought. (in millions of tons)

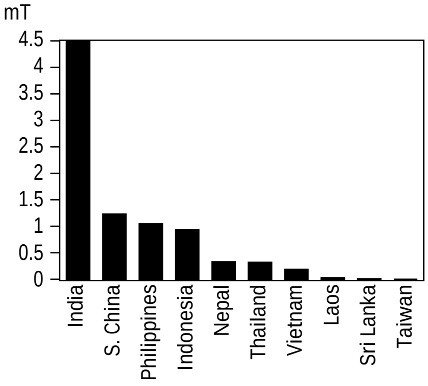

Figure 4. Estimated grain yield reduction due to low N. (in millions of tons)

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Meeting the Nitrogen Requirements of Maize Grown by Resource-Poor Farmers in Southern Africa by Integrating Varieties, Fertilizer Use, Crop Management and Policies

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Abstract

Nitrogen (N) deficiency, and associated poor soil fertility, are common features of smallholder fields cropped to maize in southern Africa. Use of maize genotypes with improved N-use efficiency (NUE) implies an important yield benefit at modest additional recurrent cost to the farmer, making them relatively attractive for adoption by resource-poor African smallholder farmers. However, current estimates of genetic gain for NUE in maize would limit grain yield improvements to around 25 to 40% (0.3 to 0.5 t ha^{-1}) of current smallholder farm yields. This is far short of the doubling or tripling of average maize grain yields required to feed southern Africa into the initial decades of the 21st century. In well-watered maize areas, larger amounts and improved types of inorganic and organic N fertilizer inputs and their better management are likely to continue to provide most productivity gains. This paper presents a strategy of modest inorganic fertilizer inputs combined with biological N fixation and organic matter from additional legumes. Several promising technological interventions — better targeted inorganics involving micronutrient supplementation, practical legume systems, combined high quality organic matter with inorganics, and interaction with moisture and with other management interventions — are discussed and their technological and economic feasibility is assessed. We also consider research costs and time lags, probability distributions of research outcomes, necessary institutional and policy support for widespread adoption, management complexity, and effective ways of deploying soil fertility technologies on smallholder farms through the integration of research and extension and the institutions involved.

It is now widely recognized that poor soil fertility (particularly nitrogen deficit), is the most severe and widespread constraint to smallholder maize productivity and to long-term food security in southern Africa (see Blackie, 1994, 1995; Kumwenda et al., 1995; and for sub-Saharan Africa in general see Blake, 1995). Rosegrant et al. (1996) calculate that the demand for maize grain in sub-Saharan Africa will rise from 21.3 million tons per year in 1990 to over 52 million tons in 2020. Kumwenda et al. (1995 and 1996) reviewed the causes and extent of soil fertility decline in the maize-based cropping systems of southern Africa and concluded that the challenge is so large that farmers will need to combine gains from improved germplasm with improvements in their management of soil fertility. Combinations of several organic and inorganic fertilizer sources at practical rates are central to better management.

To address the soil fertility constraint we examine the size of productivity gains likely to result from the deployment of N-use efficient (NUE) maize on smallholder farms in southern Africa. We conclude that this can provide only a modest part of the required gains. We propose and outline the components of a strategy that integrates NUE maize with modest inorganic and organic fertilizer inputs, timely crop management, and the policies to support implementation by resource-poor farmers.

N-Use Efficient Maize and Its Role

Tropical maize genotypes with improved NUE are being developed. At CIMMYT in Mexico, three cycles of full-sib recurrent selection for grain yield under low soil N (zero N added), while maintaining grain yield under high soil N (200 kg N ha^{-}

^{1} applied per cycle), were conducted in a lowland tropical population, Across 8328 (Lafitte and Edmeades, 1994a,b). This resulted in a per cycle increase in grain yield under low N of 75 kg ha^{-1} (2.8%), and 137 kg ha^{-1} (2.3%) with high rates of N fertilizer (Lafitte and Edmeades, 1994b). Lafitte et al. (1997) now report that genetic gains in grain yield per cycle in this population with small and large amounts of available N have been maintained through Cycle 5.

NUE has also attracted attention from maize breeders in Africa. Zambezi et al. (1995) identified three hybrids that yielded well at both low and high N in Malawi. Work at CIMMYT-Zimbabwe in the population ZM609, which is adapted to mid-altitude areas of southern and eastern Africa, led to large initial gains in NUE (Short and Edmeades, 1991), but recent progress has been inconclusive (see Pixley et al., 1995). The use of NUE maize implies an important yield benefit at modest additional recurrent costs to the farmer, making it relatively easy for resource-poor African smallholder farmers to adopt. Several updates on progress are found in these proceedings (see, for example, papers by Lafitte et al., 1997; Sibale and Smith, 1997; Kling et al., 1997).

While the development of NUE maize is an important contribution, it is, unfortunately, only likely to provide a minor part of the large productivity gains that are required in many parts of the world, including southern Africa. It is also important to remember that these gains have yet to be incorporated into germplasm adapted to African soil conditions. There will be time lags of several years and inefficiencies before this occurs and for the resulting varieties and hybrids are actually adopted by farmers.

In southern Africa at present, aggregate maize yields are currently about 1.1 t ha^{-1} (excluding South Africa; calculated from FAO Agrostat PC files). Improved maize covers about 55% of the total maize area (CIMMYT, 1994). We first calculated the expected impact on aggregate yield resulting from feasible expansion of improved maize to cover about 80% of total maize area, with no other management changes. In all countries where improved maize currently covers less than 75% of the national maize area, we assumed improved maize would expand to 75%, except in countries where this would involve expansion into particularly dry production zones as indicated by the CIMMYT Maize Program (1988). For this additional area the yield gains from switching from unfertilized farmers' varieties to unfertilized improved varieties or hybrids were assumed to vary from 30 to 50%, depending on ecology. The upper figure of 50% was only used in cases where some trial data are available to support this estimate (Byerlee et al., 1994). Additional production from this scenario would only raise regional aggregate yields to 1.2 t ha^{-1}. Most of the additional production in this scenario would come from Malawi, and to a lesser extent Angola, where area planted to improved maize is small compared to what it might be.

Achievable grain yield gains per ha can be calculated for NUE germplasm adapted to African conditions when grown by smallholder farmers in southern Africa, taking gains in NUE for tropical maize reported by CIMMYT, Mexico, (see above) as the starting point. We compared these gains to those necessary to feed southern Africa into the early decades of the 21st century. We assume 80% adoption (i.e., on all the area feasibly planted to improved maize in the near future) of NUE maize within 10 years, with an achieved yield gain of 100 kg grain ha^{-1} for each of 5 cycles with current modest inputs of N by farmers (using average yield gains from Lafitte and Edmeades, 1994b), no change in other inputs or soil fertility, and an optimistic 75% reproduction of those gains on smallholder farms. With these conditions, maize grain yields could rise from 1.2 t ha^{-1} in southern Africa to about 1.5 t ha^{-1} (an increase of around 25%) (Fig. 1). With an optimistic scenario of the same rate of gain in grain yield per cycle for 8 cycles, this would imply that average smallholder grain yields would be still under 1.7 t ha^{-1} (an increase of around 40%). This is far short of the doubling and tripling of average grain yields required to feed southern Africa into the initial decades of the 21st century (Blackie, 1995).

Southern Africa is moving into an increasingly recurrent structural food deficit (Zambezi and Mwambula,1997; Jayne et al., in prep.). While much of this deficit is attributable to dry and variable production conditions, some relatively well-watered countries such as Malawi are now unable to feed themselves. Kumwenda et al. (1995) describe the current scenario in

Malawi where, because of the rising human population, shortage of land and declining crop productivity, national maize production is already in a small but widening deficit. More optimistically those authors showed that, with concurrent adoption of both improved germplasm and better management practices, sufficiently large productivity gains can be obtained over the long term. Hybrid maize, when combined with efficiency gains from already proven better fertilizer inputs and management on-farm, was calculated to have the potential to move the country into surplus but only until 2015.

Figure 1 depicts many of the options for raising maize yields to the desired levels. These involve contributions from inorganic, organic and management sources. Interactions among these sources can be large and important, and are the subject of much current research and present many opportunities for the farmer. We now turn more specifically to address the nature and scale of the additional soil fertility contributions to maize growth and yield required to achieve and sustain the needed maize productivity gains.

Inorganic Fertilizer Inputs and Management

In well-watered maize areas, larger amounts, improved types and better management of inorganic and organic N fertilizer inputs are likely to continue to provide most productivity gains. We envisage a strategy of modest inorganic fertilizer inputs combined with biological N fixation and organic matter from additional legumes, and from crop residues and manure. We outline here the most promising technologies for southern Africa — better targeted inorganics, practicable legume systems, high quality organic matter combined with inorganics, and interaction with other management interventions — and assess their technological and economic feasibility. We draw heavily from Kumwenda et al. (1995 and 1996), where a more comprehensive recent treatment of the role of various options can be found .

Some limiting factors to fertilizer use in Africa

Since the 1960s, fertilizer use has been growing in sub-Saharan Africa at around 6.7% annually, but growth in application rates per ha has slowed since about 1980. Current use is just 10 kg of fertilizer nutrients per ha of arable land per year. Though application rates in southern Africa are somewhat higher and maize is the most important crop in terms of total nutrient consumption, many farmers do not use inorganic fertilizers. A little over one-third of the maize in the region receives some inorganic fertilizer (Heisey and Mwangi, 1996).

Relatively high nutrient-grain price ratios and higher levels of production risk are two of the underlying reasons behind low use of fertilizer in Africa (McCown et al., 1992; Heisey and Mwangi, 1996). Fertilizer is more expensive in southern Africa, for example, than in most other parts of the developing world (Table 1) and it will remain a high cost item for African farmers for the foreseeable future. Regarding risks, Figures 2a and 2b plot national aggregate maize yields against the trend-adjusted coefficients of variation in those yields over time for countries in Africa, Asia, and Latin America where maize production is 400,000 tons or more annually, excluding China, Brazil, and Argentina. For countries with approximately the same yield levels, yield variability is

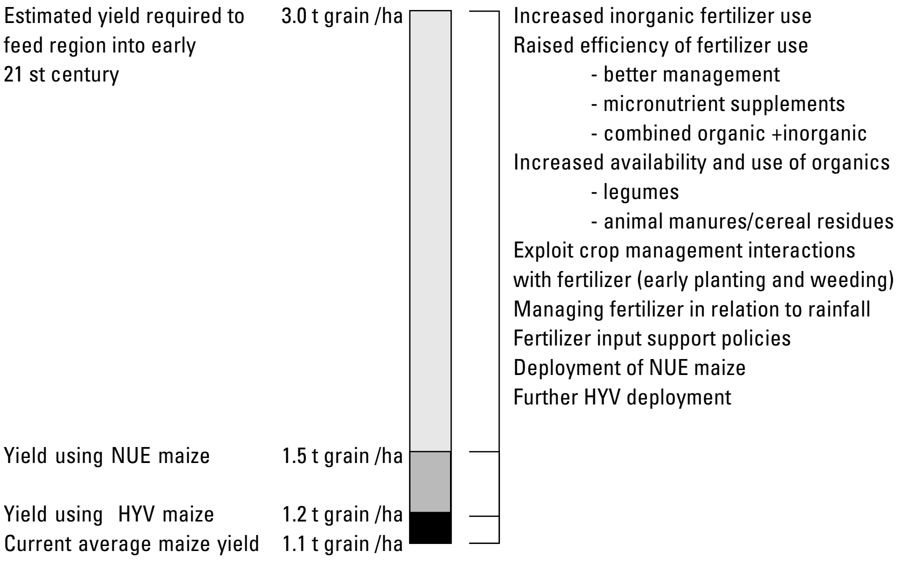

Figure 1. Possible contributions from N-use efficient maize and soil fertility factors to raising maize productivity in southern Africa.

nearly always higher in Africa. Part of this could result from the smaller size of African countries compared with large countries such as India, Indonesia, or Mexico — in small countries variations in climate affect a larger proportion of crop production simultaneously. Variability in yields could also be related to greater variability in policy, prices, and input use in Africa. Nonetheless, greater climatic variability seems increase risks for farmers and reduce incentives to use costly inputs such as fertilizer.

As a result of these cost and risk factors, expanded use will depend on generating better returns from fertilizer through greater efficiencies in its use, and, particularly in drier areas, adjusting fertilizer use in response to rainfall events (see below).

Increasing inorganic fertilizer use through improved use efficiency

Much work has been done in the region to tailor inorganic fertilizer types, amounts, timing and placement to the conditions under which smallholders produce maize, and further improvements in efficiency are likely once these have been translated into helpful recommendations and used by farmers (see Kumwenda et al., 1995). For example, in Malawi supplementation of basal NP fertilizer with S and Zn, reduction in P application rates, banding application of basal and topdress fertilizer (compared to the current dollop method), and earlier application of basal fertilizer and topdress N fertilizer are all ways to improve productivity and reduce

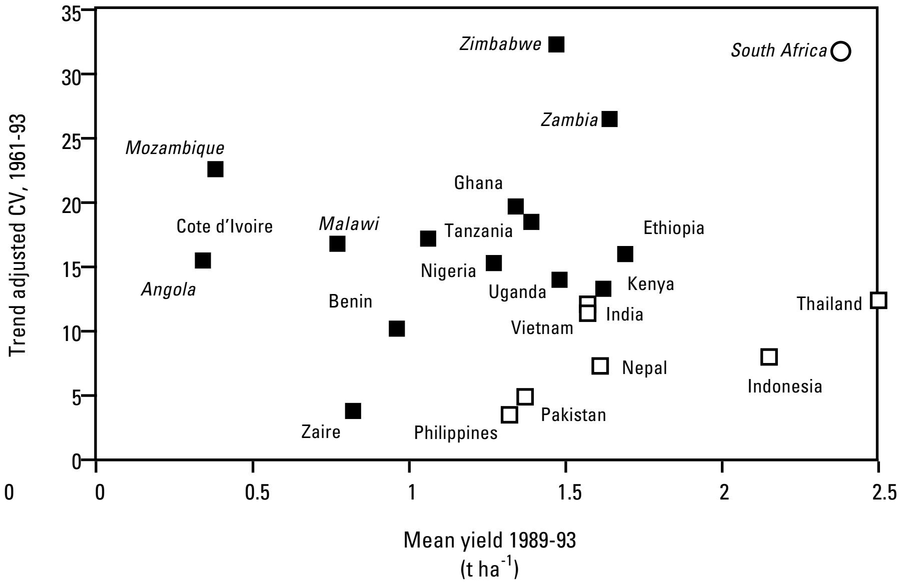

Figure 2a. Yield and yield variability in Africa and Asia.

Table 1. Nitrogen-maize price ratios (price per kg N/price per kg grain) in southern Africa and other developing countries.

Country or region	Nitrogen-maize time period	Price ratio
		(median)
Malawi	1977-1987	10.7
Malawi	1988-1994	7.7
Malawi	1995 on	?
Zimbabwe	1980-1994	6.4
Mozambique	1992	4.3
Zambia	1971-1989	3.3
Zambia	1990-1994	5.4
Lesotho	1992	4.8
Swaziland	1988	4.9
Asia	1980-1992	2.7
Latin America	1980-1992	3.8

Sources: CIMMYT World Maize Facts and Trends, various issues; J. Howard, personal communication; S. Waddington, personal communication; Heisey and Smale (1995).

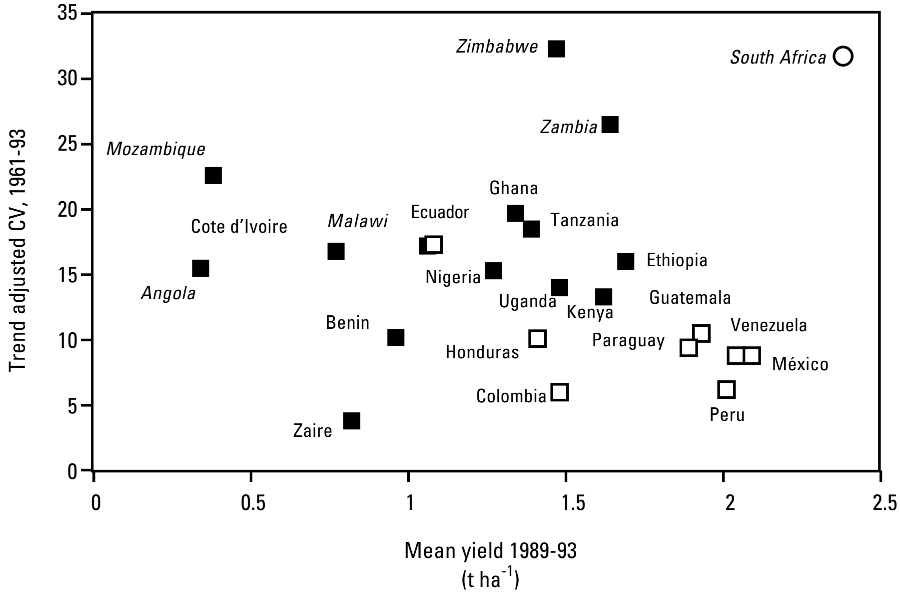

Figure 2b. Yield and yield variability in Africa and Latin America.

labor (Wendt et al., 1994; Jones and Wendt, 1995). Micronutrient supplementation, when targeted to deficient soils in Malawi, provides a striking example of how N fertilizer efficiency for maize can be raised. The addition of S and Zn, when targeted to deficient fields, increased maize yields by 40% over the standard NP recommendation alone (Wendt et al., 1994; Kumwenda, et al., 1995), with little extra cash cost. A major verification and extension effort is now under way in Malawi to inform farmers about these findings (see Kumwenda, 1996).

Combined inorganic + organic inputs

Another important way of raising fertilizer use efficiency in tropical soils is to combine small amounts of high quality organic material with inorganic N (Ladd and Amato, 1985; Snapp, 1995). Soil organic matter (SOM) from organic inputs helps retain mineral nutrients in the soil and make them available to plants in small amounts over many years as the SOM is mineralized (Woomer et al., 1994). Organic + inorganic combinations are promising, since they appear to improve maize yield over the long term by more than the additive effect of the contributions from N and other nutrients (see Kumwenda et al., 1995), partly through nutrient release in better synchrony with plant demand (Myers et al., 1994). Research is now generating examples of yield gains available in southern Africa through inorganic + organic combinations (for preliminary examples, see Table 2). There is still uncertainty about the magnitude of gains on farmers' fields where inherent soil fertility is poor and water deficits and management compromises likely. Many farmers already recognize these effects and combine, where possible, small amounts of high-quality organic inputs with inorganic nutrients. The use of combined nutrients can help overcome the challenge posed by the cost of inorganic N, because smaller amounts of inorganic fertilizers are required and they are used more efficiently. Difficulties occur, however, in producing enough plant biomass on farm. This means that the management of inorganic N with organic N from several sources becomes complex.

Increasing the Availability and Use of Organic Sources of Fertility

Current organic inputs on most smallholder farms in the tropics cannot maintain SOM. Ways need to be found to encourage the adoption and production of more organic materials. Kumwenda et al. (1995) listed grain legumes, rotations, green manure, intercropping, agroforestry and animal manure as the main options.

Table 2. Gains in maize yield[†] through inorganic + organic fertilizer combinations at rates practical on-farm in Malawi and Zimbabwe.

			Maize grain yield (t ha^{-1})				
Organic fertilizer	Inorganic fertilizer	Location and season	No fertilizer	Organic alone	Inorganic alone	Organic + inorganic combination	Yield of combination as a percent of alone treatments
Leucaena leucocephala alley cropped with maize. 1.5 - 2.5 t ha^{-1} *Leucaena* leaf prunings applied to maize	30 kg N ha^{-1} applied to maize crop	Chitedze Research Station, Malawi 1988-1990	2.24	3.32	2.72	3.60	119
Pigeonpea intercropped with maize previous season. Pigeonpea residues	48 kg N ha^{-1} applied to maize crop	Lunyangwa Research Station, Malawi 1993-1995	0.87	1.70	1.98	2.31	126
incorporated into soil Cattle manure 13-25 t ha^{-1} broadcast and ploughed in before planting	112, 17 and 16 kg ha^{-1} of N P K as a split basal and topdress	6 communal farms Wedza and Chinyika, Zimbabwe in 1994/95, a drought year	0.79	1.11	1.30	1.93	160

[†] Reported gains are from the first cropping season after fertilizer application. Additional gains can be expected in following seasons.

Source: Kumwenda et al., 1995.

The role of legumes

Legumes are central to biological N input and they dominate choices for raising soil fertility in smallholder maize-based cropping systems. Giller et al. (1994) conclude that biological N fixation from legumes can sustain tropical agriculture at moderate levels of output, often double those currently achieved. Under favorable conditions green manure crops generate large amounts of organic matter and can accumulate 100-200 kg N ha^{-1} in 100-150 days in the tropics.

Legumes remain marginal in many of the maize-based systems of the region. Because much of the work underlying legume-based technologies has been done on research stations, insufficient account has been taken of the need to tailor these technologies to farming circumstances where labor is short or where markets for grain legumes are easily depressed by oversupply. Additional P is often required to obtain satisfactory growth of legumes on many farmers' fields (Kumwenda et al., 1995) — a necessary fertilizer "kick start" that may be too costly or unavailable. Legume seed may be hard to obtain (Giller et al., 1994). Legume establishment is challenging due to poor soil quality (poor nutrient status and tilth of degraded soils) and lack of farmer experience with legume agronomy. Finally, the family may not be able to release land from staple food crops.

For many farmers there is often a conflict between the short-term requirement to meet today's food supply and building up the long-term soil fertility for tomorrow's food needs. Farmers discount the value of a benefit that will only be achieved in several years time from investments made today. Those legume systems that are best as soil improvers (hedgerow intercrops, green manure and improved fallow) tend to have few other uses and occupy land. Consequently, they are less likely to be adopted (Fig. 3). Broadly speaking, the larger the likely soil fertility benefit from a legume technology, the larger the initial investment required in labor and land, and the fewer short-term food benefits. Opportunities to use legumes in ways that also help to reduce other production problems — such as the associated control of *Striga* and other weeds from a cowpea (*Vigna unguiculata*) intercrop with maize — need to be exploited to improve adoption prospects.

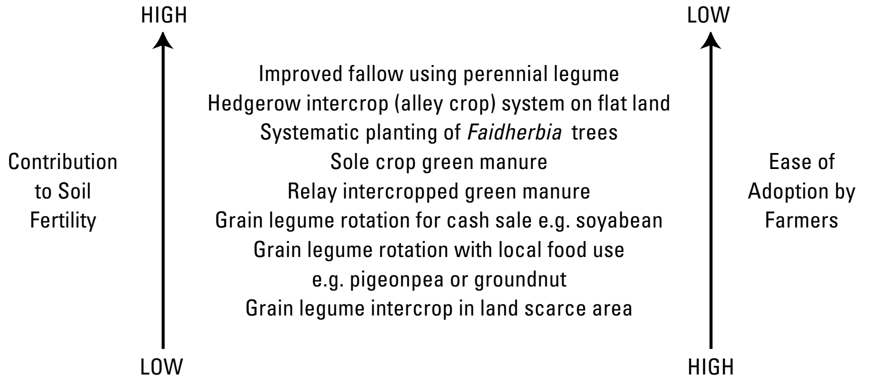

Figure 3. A central dilemma with legume technologies in smallholder maize-based systems: Approximate contribution to soil fertility vs. ease of adoption.

Grain legumes offer a good compromise of promoting farmer adoption (by providing some grain and sometimes leaf for food) and improving soil fertility (fixing some N and having reasonable shoot and root biomass) (see Kumwenda et al., 1995). Self-nodulating promiscuous types of soybean (*Glycine max*) with small N and C harvest indices (Giller and Mpepereki, 1996), and pigeonpea (*Cajanus cajan)*, groundnut (*Arachis hypogaea*), dolichos bean (*Dolichos lablab*) and cowpea are among the most promising in Malawi, Zimbabwe and Zambia. Late maturing pigeonpea is especially promising as an intercrop with maize in densely populated areas where land is scarce and animals are few, such as southern Malawi (Kumwenda et al., 1995).

Legume rotations are an important practice for maintaining soil fertility for farmers with sufficient land holdings. The yield response of a cereal crop following a legume can range from nil to substantial. As an example of what can be achieved in Malawi, MacColl (1989) showed that the grain yield of the first crop of maize following pigeonpea averaged 2.8 t ha^{-1} higher than that of continuous maize that received 35 kg N ha^{-1} each year. In Zimbabwe, Mukurumbira (1985) showed large increases in maize yields following groundnuts and bambara nuts (*Voandzeia subterranea*), without supplemental inorganic N. The amount of N returned from legume rotations depends on whether the legume is harvested for seed or forage or incorporated as green manure. Under smallholder conditions, when legume stover is removed there may be little or no net N contribution to the soil (Giller et al., 1994), and N recoveries by a cereal crop planted the following season are often small, usually between 20 and 50% (see Giller and Mpepereki, 1996).

Improved fallow using *Sesbania sesban* is a way of adding significant amounts of N and organic matter to soil, where land is not limiting and short duration (2-3 year) fallows are common, such as in Zambia. On station in Eastern Province, Zambia, maize yielded between 3 and 6 t ha^{-1} of grain for each of four years following a two-year improved fallow, compared to 1-2 t ha^{-1} in the unfertilized control (Kwesiga and Coe, 1994).

Alley cropping (or hedgerow intercropping) has been shown in the region to raise maize grain yield and increase soil fertility, but the technology is labor intensive and management sensitive (see Kumwenda et al., 1995). In Malawi *Gliricidia sepium* and *Senna spectabilis* have both shown potential to produce more biomass in a wider range of ecologies than the most widely researched hedgerow intercrop species, *Leucaena leucocephala* (Bunderson, 1994). *Faidherbia albida* is a vigorous leguminous tree that has the unique characteristic among African savanna tree species of retaining its leaves in the dry season and shedding them at the onset of the rains, enriching the topsoil in plant nutrients and organic matter. Saka et al. (1994) have described how natural stands of the tree have been used to raise smallholder maize yields in Malawi. Although the value of *F. albida* is well recognized by farmers, the tree is just starting to be integrated systematically into suitable maize growing areas by agricultural development projects.

Cereal residues and animal manure

Maize stover contains relatively small amounts of nutrients, but it can contribute to the productivity of the soil. Careful management of such residues is required, since N can be immobilized at the time of peak maize N requirements, which can result in poor crop growth (Nandwa et al., 1995).

In unimodal rainfall areas, maize stover is often fed to livestock. This practice is especially common in areas with sandy soils, where the soil contains little N and stover breakdown in the soil tends to be slow. This is an important way of cycling the nutrients from residues in a way that makes them more beneficial to the crop. Where, as in Zimbabwe, cattle are common in smallholder areas, farmers often apply cattle manure to fields that will be planted to maize. Research shows that the most efficient use of manure is to combine it with some inorganic fertilizer (Murwira, 1994), a common practice. Station-placement or dribbling of cattle manure into the planting furrow each year, rather than broadcast application at high rates every few years, are promising ways of increasing the recurrent crop yield benefits (Munguri et al., 1995).

N Use and Water: Exploiting the Link

In semi-arid areas the high risk of little response to fertilizer in most years is a major reason why farmers use little or no fertilizer (see Kumwenda et al., 1995; Waddington et al., 1995). However, the efficiency (measured through grain production per resource input) of both water use and N use is raised when both are in adequate supply. There are three main aspects to exploiting this link.

First, similarity in physiological mechanisms for NUE and drought tolerance in maize mean that genotypes developed with greater tolerance to water deficits may have improved NUE (Lafitte and Bänziger, 1995; Lafitte et al.,1997). The magnitude and durability of these gains have yet to be demonstrated on farm in southern and eastern Africa. Dual-stress tolerant maize has the potential to reduce significantly the risk of cropping maize in low rainfall areas and promote the use of fertilizers and improved management there.

Secondly, for existing maize genotypes in semi-arid areas of southern Africa, the more routine management of N fertilizer based on rainfall events (“response farming” techniques, Stewart and Kashasha, 1984; Stewart, 1991) will also lead to gains in fertilizer efficiency and help farmers to take full advantage of wetter years in those dry zones by committing more N fertilizer. These gains can be large; 25-42% more grain yield and 21-41% more profit than from existing recommendations on smallholder farms over 5 years in

Zimbabwe (Piha, 1993). Preliminary results from a wider verification of the approach with smallholders shows promise. This work is linked to loans for seed and fertilizer inputs (Piha, 1996).

Finally, water harvesting and water retention techniques may interact positively with both fertilizer and varieties in drier areas (Vogel et al., 1995; see also Sanders et al., 1996, for the Sahel). Soil type is a significant technical factor (with highly variable yield benefits on sandy soils), and high labor costs an important economic issue, in optimizing water availability through tied ridging and pot-holing.

All of these approaches can be refined through the use of crop simulation models to predict outcomes under variable water and N conditions. When coupled to a geographic information system (GIS), outputs can be used to delineate target agro-ecological areas or groups of farmers for which a particular input level is appropriate Dent and Thornton, 1988; Keating et al., 1992).

Taking Advantage of Management Interactions

In much of southern Africa, the rainy season is unimodal and lasts 4-5 months. Positive interactions between crop management factors (early planting and timely weeding) and N fertilizers can be large and need to be exploited to provide further gains in NUE. In the region there is a clear relationship between the early planting of maize, just after the onset of the rains, and high grain yield Shumba et al., 1989; MacColl, 1990). In Zimbabwe, farmers commit more top-dress N fertilizer to earlier planted maize than to later plantings (Shumba et al., 1989; Waddington et al., 1991).

Timely weeding can also raise fertilizer use efficiency. Kabambe and Kumwenda (1995) in Malawi showed that farmers who weed twice at the critical periods for maize can achieve a higher yield, with half the fertilizer, than farmers who weed only once. Soil fertility decline may cause the build-up of the parasitic weed *Striga* spp., and thereby reduce maize production. Data from long-term trials in Kenya show that incorporated crop organic matter and NP inorganic fertilizer help reduce *Striga* parasitism (Odhiambo and Ransom, 1995).

The Economics of Meeting Maize Nitrogen Requirements

Many economic considerations for weighing alternative technological options have been implicit in our discussion to this point. In this section, we briefly describe tools for analyzing the effects of different means of meeting nitrogen requirements. The simpler cases involve analyzing effects of different nitrogen sources or management options on the nutrient requirements of a single crop of maize. More complicated analysis is required when looking at longer-run soil management strategies, in which the pattern of maize yields over time, the relative values of maize yield now vs. maize yield at various points in the future, and the value of inter- or rotation crops all enter into the valuation of alternative strategies. Analysis is also complicated when variations in response caused by variations in climatic factors are considered.

Farm-level nitrogen response and economic incentives

Farm-level economics of different strategies for supplying nitrogen to maize range from relatively simple to more complex, depending on the type of intervention analyzed. Three types of intervention — nitrogen-use efficient maize, increasing fertilizer-use efficiency, and exploiting interactions with other management factors such as date of planting or weeding — can all be examined in a fairly straightforward fashion by considering the simple yield response curve for maize to applied nitrogen. On such a response curve, the economic optimum for the farmer is determined by the point at which the gradient of the curve is given by the ratio of the nitrogen price to the maize price. For the analysis to be realistic, both input and output prices must be the actual prices faced by farmers, and the ratio should be adjusted to take into account the minimum marginal rate of return the farmer requires on his resource investment (Jauregui and Sain, 1992). If a cash constraint reduces nitrogen application below this point, the constraint can be simply represented by a vertical line at the point of actual use.

Nitrogen-use efficient maize, increasing fertilizer use efficiency, and interactions with other management factors should either change the intercept of the response function, its slope, or both. For example, selection for NUE maize that focuses only on low N treatments may raise the intercept but reduce the slope, so that at high N levels yields are approximately the same. Selection that exploits both low and high N treatments may raise the intercept and leave the slope approximately unchanged, so that yield gains are obtained at high N as well (Lafitte and Edmeades, 1994b).

When response curve slopes and intercepts shift, the new cost structure for the farmer may not be determined simply by the old price ratio. If the new technology requires more labor, more complex management, or other purchased inputs such as a micronutrient, this in effect could raise the "shadow price" of nitrogen. Nonetheless, even if the shadow price of nitrogen rises, the new technology will be superior for the farmer if it reduces costs per unit of maize output even after the costs of additional labor, etc., have been accounted for. An "adjusted shadow price" of nitrogen can also be calculated by observing the point on the old response curve that would have been necessary to obtain the same yield that can now be economically attained with the new technology. In many instances the *adjusted* shadow price may be below the old price of nitrogen, even if the shadow price rises.

The economics of obtaining nitrogen from organic sources or of adjusting applied nitrogen according to rainfall can be considerably more complicated. In the former case, if it were simply a matter of choosing the source of nitrogen, the framework outlined above would still serve. In the simplest case, the farmer would use only the cheapest source of nitrogen. If the farmer uses both inorganic and organic sources of nitrogen because of limitations on the supply of nitrogen from one or the other source, this could still be accommodated within simple response function analysis. Differences in labor and management costs between organic and inorganic sources, or differences in problems with pests, could also be handled by modifying shadow prices. There are two aspects of organic nutrient sources, however, that require considerable extension of the basic economic analysis framework. First, control of timing and amounts of nitrogen released from organic sources can be much less precise than with inorganic sources (see Myers et al., 1994; Palm, 1995). This means that a complete economic analysis may require a probabilistic approach (see below for the related case of response farming). Second, as we have noted, organic sources of nitrogen can also contribute to soil organic matter status. Of course, use of inorganic fertilizer can also have positive effects on soil organic matter, but as Figure 3 suggests, in general sources that contribute the most to soil organic matter contribute relatively little to immediate grain output, and vice versa (Janssen, 1993). For the purposes of economic analysis, the essential problem is that integrating two criterion variables — yield and soil organic matter — into a single decision framework will probably require intertemporal analysis involving flows of costs and benefits over time. Explicit tradeoffs between grain yields now and grain yields in the future must be made.

Economic analysis of response farming, too, is complicated by the need to incorporate probabilities explicitly into the analysis. In other words, depending on rainfall patterns, the response of maize to nitrogen may vary, and the probabilities of different kind of responses must be explicitly assessed. The way farmers define risks, and their risk preferences, may also need to be elicited (McCown et al., 1992).

Policy

Any technology development and diffusion strategy will be affected by policies. This refers not only to general agricultural sector policy or price policy, but also to longer-term policies, including those determining the amount and direction of agricultural research, the quality and coverage of agricultural extension, and the financial services available to farmers. Each technology alternative we have considered has a different complex of supporting policy questions. Deployment of NUE maize will require particular attention to seed industry policies (Morris, forthcoming) as well as some research cost. Policies surrounding inorganic fertilizer use have been reviewed by Ndayisenga and Schuh (1995) and Heisey and

Mwangi (1996). "Knowledge-intensive" technologies managing certain organic nutrient sources or response farming) will, in general, have relatively higher agricultural research and extension costs, and will in the longer term be more likely to succeed in somewhat better educated populations.

The point to be made here is that all technical alternatives bear not only private costs to the farmer, but social costs in terms of policy formulation and implementation as well. These costs from a social point of view will be determined not only by costs at a particular point in time, but by the likelihood of success of each research strategy, the time lag in technology development and diffusion, and the number of farmers eventually likely to adopt a given technology (Alston et al., 1995). It is very easy to note that the "correct" aggregate allocation of nitrogen from various sources is determined by the situation in which the last unit of nitrogen obtained from all sources has the same *social* cost. It is very difficult in practice to determine this allocation. Nonetheless, in the last section, we turn to some aspects of optimizing nitrogen availability from different sources from the research-extension-farmer participation perspective.

Integrating the Components: Resource Requirements and Adoption Integration and Decision Support

Effective ways of deploying sources of soil fertility on smallholder farms have attracted much attention recently. There is broad agreement that an array of integrated research and extension tools ranging from basic process research through widespread on-farm targeting and verification are required. All need to be organized in a more interactive institutional mode with the effective participation of the main client, the farmer Swift et al., 1994; Palm et al., 1996; Kumwenda et al., 1995). When interactions between the type of work and key players are included, this can quickly become complex (Fig. 4) and difficult to maintain. Basic-process-oriented research is required to understand the nutrient flows in tropical soils and crops, opportunities to synchronize nutrient availability with crop demand, and root behavior (Myers et al., 1994; Palm, 1995; Giller et al., 1996; Kumwenda et al., 1995). Farmer participation is essential as well. Development of problem-solving soil fertility research and extension initiatives driven by farmer demands is the key to reaching the resource-poorest farmers (Swift et al., 1994; Minae, 1996).

Palm et al. (1996) have attempted to integrate process understanding and farmer appropriate recommendations in a decision support system involving computer databases and models. This system selects organic inputs and their management for a given cropping system, soil type, and environment. It involves socioeconomic as well as biophysical characterization, and field testing of technology options as inputs into the model.

Farm management

For both organic and inorganic sources of soil fertility, important practical questions for smallholders remain to be answered for many situations. Information is largely incomplete on the optimum use of small amounts of inorganic fertilizers, on the best combinations of organic and inorganic fertilizers for particular farm circumstances, on how to produce sufficient amounts of organic manure under poor fertility conditions, on the best management compromises in the use of labor between critical seasonal tasks, and on adjusting fertility management according to the seasonal rainfall and other external factors. Farmers are looking for ways to combine inputs and employ them in ways that minimize additional cash, labor and land requirements.

Flexible, conditional soil fertility recommendations that better address actual nutrient deficiencies, take advantage of cropping system opportunities, are efficient in the highly variable rainfall regime faced by most smallholders, and are compatible with farmer socio-economic circumstances take us part of the way. Flexible approaches to recommendations (using "decision trees"), not just area specific messages, are becoming available in Malawi (Snapp and Benson, 1995).

Nevertheless we need to move beyond just 'recommendations' and 'messages'. However flexible and targeted they are, they provide only part of the information that farmers require. High quality farm management through continuous collegiate links between farmers, farmer groups, and farm management advisors (provided by input suppliers, government extension services and NGOs) is required (see Blackie and Herdt, 1996; Kumwenda et al., 1995). The challenge is out to the contributors in Figure 4 to do this in the most effective and efficient way, tailored for each situation.

Conclusion

We have pointed out that the problems of reconciling increased maize productivity with the slowing or reversing of natural resource degradation, especially soil fertility, means that smallholder farmers will have to integrate gains from use of improved, NUE maize with improved soil fertility management through use of several fertilizer sources. This is a great challenge to resource-poor farmers and the research, extension, input supply and policy sectors that support them. Future research should address effective and practicable options for combining the components of more efficient varieties, inorganic nutrients, N from organic sources, and alternative management strategies on-farm to derive maximal N benefits for minimal additional cash, labor and land.

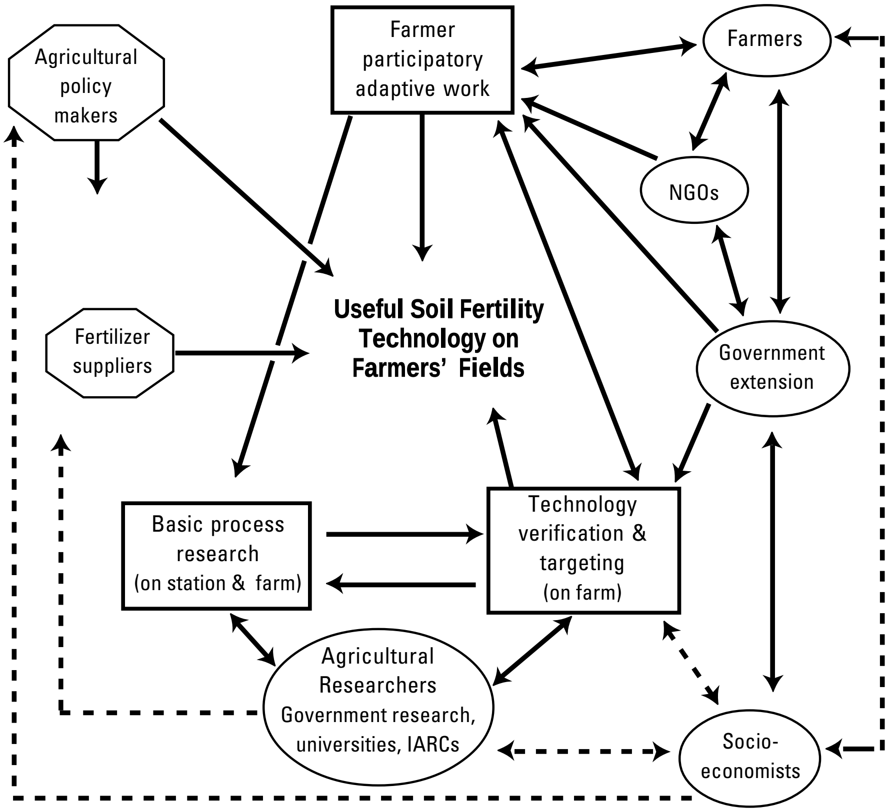

Figure 4. Contributors to the integrated deployment of soil fertility technologies for smallholder farmers.

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Restricción en la Producción de Maíz a Causa de la Sequía en Venezuela: Potencial Genético para su Solución

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Abstract

Maize is the most important cereal crop in Venezuela, both as the principal source of dietary energy for the population and for its contribution to the national economy. Approximately 450,000 ha are harvested annualy, of which 75% are in the Western and Central Plains and the Yaracuy River Valley. These three regions have notably different edaphoclimatic conditions: the landscape in the Central Plains is eroded hills, in the Yaracuy River Valley foothills, and alluvial plains in the Western Plains. These are subject to erosion and have marked variations in the quantity and distribution of rainfall from one year to the next. The principal objective of genetic improvement work has been yield and certain biometic traits, rarely taking into account selection of materials with tolerance to factors that limit production: water stress, low soil fertility, oxygen deficit, acidic soils, etc. With a sustainable agriculture focus in maize production, work is under way on conservation tillage – but genetic materials are for low-input agriculture, although some have been developed that possess tolerance to oxygen deficit and to the fall armyworm. Several criteria are suggested which highlight the importance of formulating a program of research and genetic improvement to produce materials with drought tolerance in a maize-rotation crop production system in the regions noted.

El maíz es el cereal más importante en Venezuela, por la extensión del área cultivada y por sus aportaciones, especialmente energía, en la nutrición de gran parte de la población. Su aporte a la economía del país (2,817,498 bolívares) en 1994 representó 19% del valor de la producción del sector agrícola vegetal.

El rendimiento promedio actual es de 2133 kg/ha, el cual es notablemente diferente a los logrados a nivel experimental y en las mejores fincas. Aunque, se cuenta con diversas tecnologías tendientes a mejorar la productividad del maíz, también existen numerosas restricciones en los sistemas de producción, las cuales imposibilitan que los cultivares expresen su máximo potencial de rendimiento, entre ellas están las restricciones bióticas y abióticas: cultivares no adaptados a ciertas condiciones edafoclimáticas, plagas, enfermedades, disponibilidad de agua y fertilidad del suelo; y las restricciones socioeconómicas: altos costos y baja rentabilidad, tradición, aptitudes, conocimientos de la tecnología disponibles, disponibilidad de insumos, duración del período de recolección y los problemas relacionados con la recepción del producto a nivel de planta.

Hasta el presente el mejoramiento genético ha sido orientado a la obtención de híbridos de alta capacidad de producción con una tecnología de altos insumos y desarrollados en muy pocas localidades del país. Los nuevos enfoques deben orientarse a la obtención de plantas que toleren altas densidades de población, estrés hídrico (sequía), suelos ácidos y bajos contenidos de nitrógeno, para contribuir significativamente en la solución de algunas de estas restricciones que están limitando a los sistemas de producción de maíz. Los objetivos del presente trabajo son presentar los factores que limitan la producción de maíz en las principales zonas productoras de Venezuela, proponer algunos lineamientos que permitan la formulación de programas de investigación en mejoramiento genético, fundamentalmente hacia la obtención de materiales de alta plasticidad, con tolerancia a estrés hídrico y a condiciones de bajo nitrógeno, enmarcados dentro del concepto de una agricultura sustentable y señalar la conveniencia de que estos programas tengan un enfoque interinstitucional e interdisciplinario, para optimar los escasos recursos humanos existentes y minimizar los costos operativos de los mismos.

Síntesis de los Factores que Limitan en las Zonas Productoras

El conocimiento de los factores que afectan a los sistemas de producción de maíz en Venezuela, ha permitido conocer las causas que limitan el mejoramiento de la productividad y la expansión de las áreas agrícolas para este cereal, algunas de las cuales se comentan a continuación.

Las tres regiones en las que se cultiva el 75% del maíz en Venezuela son los Llanos occidentales, los Llanos Centrales y el Valle Medio del Río Yaracuy. La mayoría de las zonas productoras se ubican por debajo de los 300 msnm, donde es frecuente que durante el ciclo de los cultivos se presenten temperaturas máximas superiores a 32 ºC, lo que provoca el cierre estomático diurno, disminuyendo así la fotosíntesis neta y la síntesis de carbohidratos. También es frecuente que las temperaturas mínimas superen los 23 ºC, favoreciendo las respiración nocturna.

Aunque, las áreas con mayor potencialidad para el cultivo tienen una precipitación superior a los 800 mm, su distribución irregular puede dar origen a déficits hídrico o excesos de humedad en ciertos periodos; esto, reducen significativamente la producción. Los problemas de déficits son más frecuentes hacia las zonas de colina en el Estado Guárico y en el piedemonte del Valle del Río Yaracuy, por el buen drenaje superficial de los suelos. Por el contrario, en los Llanos Occidentales la causa principal de la merma de los rendimientos son los problemas de drenaje (falta de oxígeno), tanto superficial como interno, ocasionado por la topografía muy plana de los terrenos y el predominio de texturas finas, aunque también es frecuente el déficit hídrico en las áreas de bancos con textura gruesas.

Los problemas de déficits hídricos y de falta de oxígeno, son favorecidos en las zonas de los Llanos Occidentales y en el Estado Guárico, por el uso indiscriminado de la rastra, que ha conllevado a la formación de capas endurecidas a poca profundidad (10-15 cm). Este factor es menos limitativo en la zona del Yaracuy Medio, donde los productores han utilizado arado o el big-rome antes de la rastra.

Las tres zonas productoras se caracterizan por una gran variabilidad de sus suelos, desde texturas arcillosas a franco arenosas, pH ácidos a alcalinos y sometidos a procesos de erosión geológica y antrópica, especialmente en las áreas con pendientes pronunciadas. En la región de los Llanos Occidentales, en general los suelos tienen altos contenidos de limo y arena muy fina, que inducen la compactación natural de los suelos, favoreciendo el déficit de oxígeno durante la época de lluvias.

En las tres zonas predominan suelos con moderados a bajos contenidos de fósforo y potasio, por lo que es frecuente el uso de altas cantidades de fertilizantes de fórmula completa, que contribuyen al incremento en los costos de producción y a problemas de contaminación de acuíferos y cursos de agua. En las zonas productoras de Portuguesa y del Yaracuy Medio, predominan los productores que utilizan una agricultura mecanizada, con sistemas de labranza convencional y de altos insumos. En Guárico predominan los productores con menor tecnología, con siembras al voleo y cosecha a mano.

El acame de las plantas, ocasionado por los vientos, es uno de los factores que más contribuye a la reducción del rendimiento y de la calidad del grano, incluyendo la presencia de aflatoxinas por infección con hongos. Solo recientemente ha aparecido en el mercado un cultivar de maíz con características muy favorables para minimizar este efecto del viento. El acame es muy importante en las áreas productoras del Estado Guárico, donde es muy frecuente un retraso considerable en el período de recolección, por escasez de equipos de cosecha y por el sistema de siembra al voleo. La Fundación DANAC ha iniciado en su programa de mejoramiento genético la selección de materiales resistencia al acame con resultados halagadores.

Existen diferencias importantes en los sistemas de producción de maíz utilizados en las tres zonas. En el Estado Guárico predominan los sistemas cerealeros (maíz, sorgo) con ganadería, donde al finalizar la cosecha del maíz, los restos vegetales son pastoreados por el ganado, dejando la superficie del terreno desnuda y compactada. En el Valle Medio del Río Yaracuy, donde predominan pequeños productores, los terrenos son preparados muy temprano, quedando también las superficies expuestas y solo un reducido número de agricultores siembran después del maíz algunas leguminosas comestibles. En los Llanos Occidentales, especialmente en algunas áreas de el Estado Portuguesa, la presencia de un nivel friático a poca profundidad, permite obtener otras cosechas de ciclo corto (ajonjolí, sorgo, girasol, leguminosas comestibles), es decir se preparan los terrenos dos veces al año y con un excesivo número de pases de rastra, con el consecuente deterioro del suelo, debido al reducido tiempo para preparar los terrenos, impuesto por el régimen de lluvias y por la retención de humedad de los suelos. La agricultura altamente mecanizada, en la que la tierra se deja al descubierto y se utilizan grandes cantidades de agroquímicos, está contribuyendo al rápido deterioro del recurso suelo, a la contaminación de los cursos de agua y de los reservorios construidos por el Estado Venezolano para suplir las necesidades de agua de las comunidades rurales.

La producción de maíz actualmente se fundamenta en el uso de híbridos convencionales (95% del área sembrada) y muy poco en materiales de alta plasticidad, sin tomar en cuenta la gran diversidad de zonas edafoclimáticas y tipología de productores, por lo que la alta capacidad genética de los cultivares utilizados se ve minimizada.

Lineamientos para un Programa de Mejoramiento Genético en una Agricultura Sustentable

En los últimos años se viene discutiendo entre los técnicos del agro Venezolano, la necesidad de utilizar el enfoque de sistemas como herramienta indispensable en una estrategia de sustentabilidad de la agricultura. Sánchez (1995) sostiene que los criterios de sustentabilidad se apoyan en:

1. El uso de especies vegetales y animales cuya producción no sea críticamente afectadas por las condiciones ambientales (distribución de las lluvias y humedad ambiental, alta temperatura y acidez del suelo).
2. Optimación del aprovechamiento del agua y de los nutrimentos, utilizando apropiadamente el período de lluvias mediante la combinación y frecuencia de cultivos de diferentes ciclos.
3. Manejo apropiado de la superficie, evitando exposición continua del suelo a los efectos del clima, que puedan desencadenar procesos erosivos o de degradación biológica.
4. Mantenimiento de las actividades productivas diversificadas y continuas para mejorar la rentabilidad de los sistemas de producción y el aprovechamiento integral del medio.

Estos conceptos han estado presentes en las investigaciones venezolanas desde hace muchos años. En 1970, se iniciaron los primeros intentos para introducir la siembra directa en los sistemas de producción con maíz en Venezuela (FUSAGRI, 1976) como una vía para reducir las pérdidas de suelo y minimizar el efecto del déficit hídricos en los rendimientos. A nivel experimental se ha comprobado que es una excelente alternativa para aquellas zonas con suelos en colinas, con buen drenaje externo, o para zonas planas, con suelos de buen drenaje interno; y sólo hasta 1994, se inició un desarrollo de cierta importancia en el Estado Guárico, donde en 1995 se establecieron unas 10,000 ha con siembra directa.

El criterio de sustentabilidad basado en la variabilidad del germoplasma, ha estado también presente en los programas de mejoramiento genético emprendidos en Venezuela, particularmente, en las décadas de los años 40 y 50, cuando se lograron las primeras variedades. Desde 1950 ya recomendaban en el mejoramiento varietal tomar en cuenta principalmente factores como: productividad, resistencia a plagas y resistencia a sequía. A partir de esa época se dio mayor énfasis a la formación de híbridos convencionales, los cuales son utilizados indiscriminadamente en todas las condiciones de clima y suelos del país. Afortunadamente el FONAIAP y otras instituciones privadas (DANAC, PROSECA, FUNIAPROT, etc.) han mantenido actividades que aunque modestas, han conducido a la generación de un grupo de cultivares e híbridos no convencionales, que han mostrado buena adaptabilidad a diferentes condiciones edafoclimáticas y que están disponibles para su utilización a mayor escala comercial. Especial mención merecen los trabajos realizados en la estación experimental Portuguesa del FONAIAP en Araure, donde se seleccionó un cultivar tolerante al déficit de oxígeno en el suelo, y el Centro Nacional de Investigaciones Agropecuarias del FONAIAP en Maracay, donde se seleccionó un cultivar tolerante al gusano cogollero. Además, recientemente en la Fundación DANAC, en San Javier, Estado Yaracuy, se han iniciado estudios para seleccionar materiales tolerantes a déficits moderado de agua, que les permitirá tener germoplasma para su programa de mejoramiento genético bajo el concepto de agricultura sustentable.

La eliminación de los subsidios, las elevadas tasas de interés, el endeudamiento de los productores, la inflación de los insumos, etc., se ha traducido en un crecimiento casi nulo del sector agrícola (Fig. 1). Por otra parte, los resultados obtenidos en 1994 respecto a la tasa promedio de crecimiento en los últimos tres años, mostraron una agudización del deterioro de la agricultura (Agroplan, 1994, citado por Castillo, 1994).

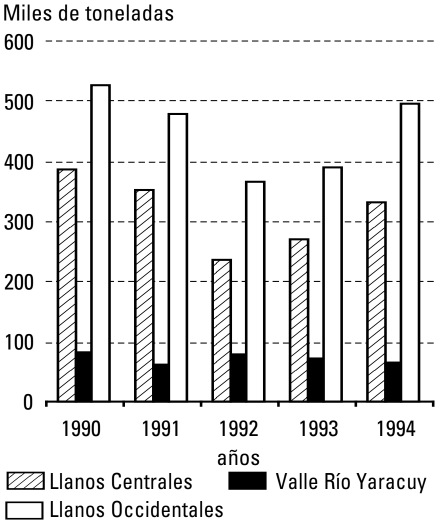

Figura 1. Producción de maíz en miles de toneladas. Peíodo 1990-94

A continuación se señalan algunos criterios que destacan la importancia de la formulación de un programa de investigación en mejoramiento genético para la producción de materiales de maíz tolerantes al estrés de humedad que formen parte de los sistemas de producción de las principales regiones productoras de maíz:

1. Debido a que el número de factores limitativos es muy elevado, convendría dar prioridad a los más importantes, según su mayor incidencia y efecto en el rendimiento. En este sentido, el déficits hídrico tienen un papel relevante.
2. En el país existe un grupo de investigadores con alto nivel académico, quienes realizan investigación en maíz, adscritos a diferentes instituciones (Universidades, centros de investigación, fundaciones privadas, entes gubernamentales, asociaciones de productores), donde todos, de una manera u otra, tienen limitaciones económicas, que reducen notablemente su campo de acción. También debe destacarse, que muchas de estas instituciones cuentan con una gran cantidad de equipo subutilizados.
3. Una vía para impulsar el mejoramiento genético, como plataforma de una agricultura con criterios de sustentabilidad, es aprovechar esos recursos físicos y humanos, mediante acciones en conjunto, donde las actividades sean complementarias. Para ello, es necesario la realización de un plan mancomunado, donde cada institución se integre en las actividades donde mejor puedan aprovecharse los recursos humanos y técnicos disponibles. De esta forma se logrará la integración de los mejoradores con otras áreas de especialización.
4. La disponibilidad de personal calificado de alto nivel, constituye el componente fundamental para garantizar el éxito de los programas de investigación y producción de maíz. Por lo que se justifica mejorar y formar los técnicos necesarios para organizar equipos interdisciplinarios que trabajen en el mejoramiento del cultivo de maíz a nivel local y nacional.
5. Una de las instituciones constituyentes del plan debe asumir las funciones de coordinación del proyecto, para garantizar la continuidad del mismo, asegurar la planificación y uso de los recursos y establecer las prioridades según las directrices.
6. Los programas de mejoramiento genético deben contar con directrices y marcos de referencia bien definidos, los cuales deben estar basados en los estudios de sistemas de producción realizados por diferentes instituciones del país.
7. Desarrollar materiales adaptados a los sistemas de producción que sean sostenibles, mediante diversificación agrícola, la rotación/asociación de cultivos y el manejo integrado de plagas y enfermedades.
8. Las tecnologías a desarrollar deben permitir el uso racional de los recursos naturales y posibilitar el equilibrio ecológico y la sostenibilidad de los agrosistemas.

9. El enfoque del programa debe orientarse hacia un proceso eficaz de generación, transferencia y adopción de tecnologías que sean apropiadas a las circunstancias agroecológicas y socioeconómicas de la realidad regional.
10. Concretar el programa de mejoramiento en las regiones de importancia dentro de un enfoque de sistemas de producción.

Conclusiones

1. Los sistemas de producción de maíz en Venezuela se ubican en zonas que presentan una gran diversidad de suelos, sometidos a procesos de erosión geológica y especialmente antrópica. En estas zonas también existe gran variabilidad del clima, particularmente en la distribución y cantidad de las lluvias. Estos factores determinan fluctuaciones en los rendimientos de maíz de un año a otro.
2. Las diferentes zonas productoras tienen en común que muchos de sus suelos poseen contenidos bajos de nitrógeno, fósforo y potasio.
3. Existe una gran variabilidad en el nivel tecnológico de los productores. En los llanos Occidentales y en el Valle Medio del Río Yaracuy predominan agricultores con una alta tecnología; en la primera zona además de maíz se cultivan otras especies, pero en la segunda la poca disponibilidad de agua limita la siembra de un segundo cultivo. Por el contrario, en al región de los Llanos Centrales predomina el sistema cereales-ganadería, caracterizado por su alto poder extractivo.
4. La gran variabilidad de los sistemas de producción con maíz ha sido escasamente tomada en cuenta en los programas de mejoramiento genético, los que predominantemente han sido orientados hacia la generación de híbridos convencionales.
5. Los graves problemas de conservación de suelos y de contaminación ambiental de nuestras zonas productoras de maíz, ameritan que se inicien esfuerzos importantes hacia el desarrollo de una agricultura con criterios de sustentabilidad. Es ahí hacia donde el enfoque del mejoramiento genético tiene que volcarse, tomando en cuenta las grandes diferencias existentes en los sistemas de producción (tipología de los productores, limitativas edafoclimáticas, etc.), los requerimientos de la agroindustria y sobre todo, inducir la reducción de los costos de producción y contribuir a la implantación de los sistemas de labranza conservacionista.

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Incidencia de la Sequía en el Perú:
Estrategias para Superar esta Limitante

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Abstract

There are three main geographical regions in Peru: the coast, the mountain zone, and the jungle. Yellow flint maize is sown in both the coastal zone and the jungle, whereas only floury maize is grown in the mountains. In the coastal zone, maize is being replaced by more profitable crops. Consequently, yellow maize cropping is gradually shifting towards the jungle, and its use is reaching similar proportions in both the coastal plains and the jungle. In the jungle and mountain zones, agriculture is mainly rainfed with alternating periods of rainfall and drought, making agriculture a high-risk, low-return activity. Drought is estimated to affect up to approximately 30% of the cultivated area. Dry spells of one to five weeks may occur during any stage of crop development. Losses in grain production from 25-30% are the result; under severe drought stress, losses may be as high as 50%. To lay the foundation for large-scale production in these two regions of Peru, a genetic improvement program is proposed to develop cultivars with traits adapted to the regions' agroecological conditions, principally drought tolerance. This is to be achieved through varietal introduction, selection and hybridization, using both conventional breeding methods and biotechnology. This effort is certain to help reduce maize imports, which currently exceed a half a million tons per year.

El Perú tiene tres regiones naturales bien delimitadas donde se produce maíz: costa, sierra y selva, los dos tipos de maíz que se siembran en el país son: *amarillo duro* en la costa y la selva a altitudes menores de 2,000 m y *amiláceo* (incluido morocho) a altitudes mayores a los 2,000 m. Este cereal es considerado uno de los cultivos más importantes en el país (Cuadro 1), pues se siembran aproximadamente 370,000 ha (1964-91) con un rendimiento promedio nacional de 2.10 t/ha. El 49% del área corresponde a maíz amarillo duro distribuido en la costa y la selva y 51% a maíz amiláceo distribuido en la sierra (Fig. 1).

La demanda anual de maíz es aproximadamente de 1,100,000 t, sin embargo la producción estimada es de 560,000 t con un rendimiento promedio de 3.64 t/ha en costa, 1.80 t/ha en selva y 1.05 t/ha en sierra. Existe un déficit de producción que determina la importación anual de más de medio millar de t.

Cuadro 1. Producción nacional de los principales cultivos en el Perú, periodo 1990-1993 (miles de t).

Cultivos	Costa norte	Sierra	Selva	Total pais
Consumo humano				
Arroz	506.7	293.8	509.3	1309.8
Maíz amiláceo	55.7	186.3		
Papa	195.9	128.6	1491.9	
Trigo	31.1	392.6	49.0	
Frijol grano	18.1	43.9	7.6	700.2
Plátano	200.9	21.2	264.4	438.5
Yuca	82.1	113.2	151.7	
Naranja	5.7	9.9	17.1	192.1
Limón	175.5	3.3		
Consumo industrial				
Maíz amarillo	305.8	91.6	194.4	591.8
Café	26.8	76.0	13.9	116.7
Algodón	33.5	3.4	36.4	
Caña de azúcar	3437.1	4342.7		
Sorgo	15.9	16.9		

Debido a la heterogeneidad climática del país en la costa, debido a la ausencia de lluvias, la agricultura que se practica es casi en su totalidad de riego y durante todo el año (Fig. 2). Sucede lo contrario en la selva y la sierra donde las condiciones climáticas determinan una agricultura predominantemente de secano y el inicio de las siembras coincide con el inicio del período de lluvias; frecuentemente, la

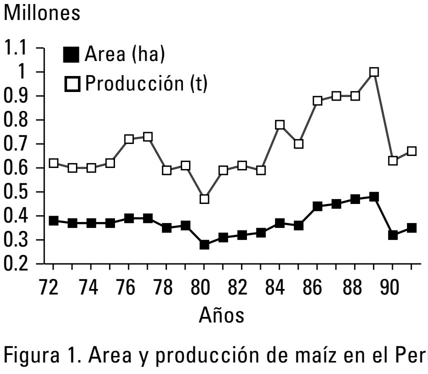

Figura 1. Area y producción de maíz en el Perú.

precipitación es errática y/o insuficiente, esto ocasiona situaciones de alto riesgo para el cultivo (Figs. 3 y 4).

Por lo impredecible del régimen de precipitaciones y la alta probabilidad de sequía durante los meses de cultivo, así como la escasa disponibilidad de agua para riego en la selva y la sierra es casi imposible utilizar mecanismo de escape como: siembras tempranas o uso de variedades precoces, por lo que la alternativa para superar esta limitación será contar con variedades tolerantes a la sequía asociado con un buen potencial de rendimiento.

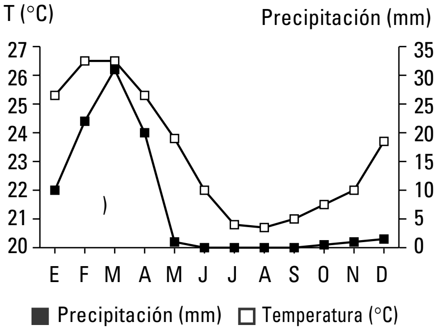

Figura 2. Condiciones climatológicas de la costa norte del Perú (Promedio de 30 anos).

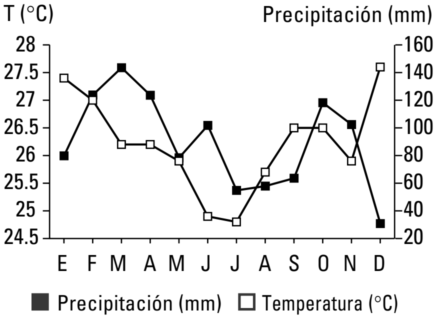

Figura 3. Condiciones climatológicas de la selva Peruana (Promedio de ocho anos).

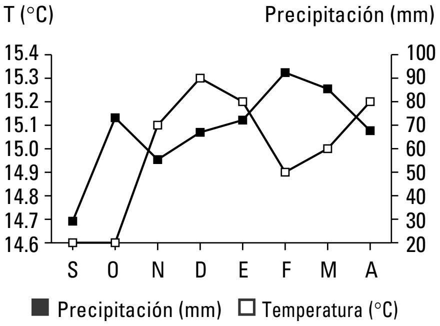

Figura 4. Condiciones climatológicas de la sierra norte del Perú (Promedio de 13 anos).

Importancia del Cultivo

El maíz es uno de los cultivos más importantes en el país por la superficie sembrada y por el porcentaje de tierras que ocupa anualmente respecto a la superficie nacional (35%).

El maíz amarillo duro es un producto de gran demanda en el mercado nacional, es usado principalmente para el consumo directo y/o a través de alimentos balanceados para la producción avícola. La producción de maíz amarillo duro es variable y no logra satisfacer la demanda interna, esto genera salida de divisas como resultado de las importaciones. Su cultivo se ubica en siete departamentos en las regiones de la costa y la selva con un área cultivada de 142,530 ha durante 1992.

El cultivo de maíz amarillo duro en la costa se practica bajo condiciones de preparación mecanizada del suelo. La siembra generalmente es manual y aunque la densidad de siembra (semilla/ha) es la recomendada, el número de plantas establecidas es menor debido principalmente al daño por gusanos de tierra. Se usa generalmente fertilizante nitrogenado y la cosecha es manual.

En la selva predomina el sistema de desmonte manual (rosa, tumba, picacheo y quema) utilizándose suelos marginales con mucha pendiente. El sistema de siembra es manual usando un trozo de madera o «tacarpo» para hacer un hoyo y depositar la semilla. Generalmente no se usa fertilizante y la cosecha se realiza en forma manual.

El maíz amiláceo y morocho es uno de los cultivos más importantes en el Ande peruano, tanto por el área que ocupa, por su participación en la dieta alimenticia así como en la generación de ingresos para la economía del agricultor. Ecológicamente se desarrolla desde los 1,500 hasta los 3,500 metros de altitud, característica que determina una amplia gama de variedades adaptadas a cada piso ecológico. Las características generales de los principales indicadores productivos señalan que en promedio el área cultivada durante 1992 fue de 194,963 ha, destacando la sierra norte y sur como las principales zonas de producción. El sistema de siembra que predomina es el de «cola de buey» y la densidad de siembra es variable dependiendo del sistema de producción y del uso que se dará a la cosecha la cual se hace manualmente.

Factores climáticos adversos como la sequía en la selva y sequías, heladas y granizo en la sierra, se presentan con cierta frecuencia. Estos factores de riesgo limitan el uso de tecnologías que permitirían incrementar la productividad del maíz en estas dos regiones.

Factores Limitativos en la Producción de Maíz

Los factores más limitativos en la producción del cultivo se dan en las regiones de la sierra y la selva estos pueden ser agrupados en :

- Climáticos, debido a que el maíz se siembra desde el nivel del mar hasta los 3,500 metros de altitud, la sequía y las heladas constituyen un factor fuertemente limitador.
- Edáficos, las siembras se realizan en suelos marginales superficiales, pedregosos y de baja fertilidad, con topografía accidentada, que implica la siembra en pendientes y laderas, con la consecuente pérdida del suelo.
- Fitosanitarios, fuerte incidencia de plagas y enfermedades, constituyendo estas últimas el factor biótico más importante en la sierra.
- Falta de infraestructura hidráulica y escasa disponibilidad de agua para riego.

Para superar los factores antes señalados se plantean los siguientes objetivos:

- Participar en un Proyecto Colaborativo de Mejoramiento Genético con la finalidad de aprovechar el Germoplasma y la Tecnología generada por CIMMYT para desarrollar y liberar cultivares mejorados tolerantes a sequía, adaptados a las condiciones ecológicas de país.
- Participar en la ejecución de trabajos conjuntos con otros Programas Nacionales propiciando el intercambio de germoplasma

Para cumplir estos objetivos se seguirán las siguientes estrategias:

- Aprovechar la capacidad instalada y los recursos humanos de nuestro Programa para la ejecución de actividades.
- Introducir y evaluar material con características de tolerancia a sequía y buen potencial de rendimiento a fin de identificar y seleccionar los que se adapten a nuestras condiciones ecológicas.

Conclusiones

La consecución de los objetivos planteados permitirá:

- Establecer las bases que permitan una producción masiva y extensiva del cultivo en las regiones de la sierra y la selva y coadyuvar a atenuar los niveles de importación de maíz.
- Estabilizar la productividad del cultivo bajo condiciones de humedad del suelo limitada, reduciendo el riesgo en la producción maicera.
- Desarrollar un Programa de Mejoramiento Genético para la obtención de variedades mejoradas tolerantes a sequía.

Mejoramiento de Maíz y Estrategias de Producción para Temporal de la Región Semiarida y Árida del Centro-Norte de México

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Abstract

The highland region in the North-Central part of Mexico is located in the states of Zacatecas, Durango, San Luis Potosí, Aguascalientes and Guanajuato. In this region, 760,000 ha are sown to maize under rainfed conditions, particularly in microregions where the crop can take advantage of runoff waters or residual moisture. Approximately 400,000 ha in this region have 200 to 400 mm of rainfall over a period of 70 to 90 days, with average temperatures from 15 to 20° C. In the remaining area, average termperatures are the same but rainfall is between 350 to 500 mm over a period of 80 to 100 days. Sixty percent of these highlands soils have a depth of 50 cm or less with an organic matter content lower than 1%; therefore, moisture retention capacity is very low. Maize breeding efforts have produced open pollinated varieties of a range of maturity types (from 95 to 120 days), developed from landrace populations adapted to the area's typical late-season drought. Maize fertilization rate is from 20-30-00 to 60-40-00. Water harvesting practices are recomended. Maize stubble is used as cattle feed.

De acuerdo con Stretta y Mosiño (1963) y Contreras (1990), las zonas semiáridas y áridas del centro-norte de México (C-N) comprenden gran parte de los estados de Zacatecas, Durango, San Luis Potosí, Guanajuato y Aguascalientes y una pequeña parte de Jalisco.

Las estadísticas de la SAGAR indican que desde siempre el cultivo de maíz ha ocupado el segundo lugar en importancia agrícola en ésta zona; entre 1991 y 1994 cubrió 30 y 35% del área cultivada, con 870 mil ha. De ésa superficie la mayor parte (87%) es de temporal y de esa una muy pequeña se cultiva bajo los sistemas de producción de bajío, abanicos aluviales o "de húmedo" (Charcas et al., 1980; Osuna y Luna, 1989).

De la superficie total de temporal sembrada con maíz en la región C-N, en promedio 27% no produce grano, principalmente por efecto de la sequía (Luna, 1993) (Fig. 1) y los rendimientos oscilan entre 0.30 y 0.45 t/ha en Aguascalientes, San Luis Potosí, Guanajuato y Jalisco y entre 0.67 y 0.77 t/ha en Zacatecas y Durango.

Aún con los bajos rendimientos, el cultivo de maíz de temporal es muy importante en la región C-N, pues representa un cultivo de subsistencia para más de 320 mil familias que obtienen forraje para sus animales o para vender y lo más importante, tienen la esperanza de cosechar algo de grano (Montañez y Warman, 1985; Luna y Zárate, 1994).

Descripción de la Región Centro-Norte de México

La región semiárida-árida se localiza entre los 21 ° y 26 ° de latitud N, 99 ° y 106 ° de longitud O y 1700 a 2200 msnm. Predominan los climas BS$_1$kw(w)(e) y BS$_1$hw(w)(e) en el área de regular productividad y los BS$_0$ en la de baja productividad (Luna y

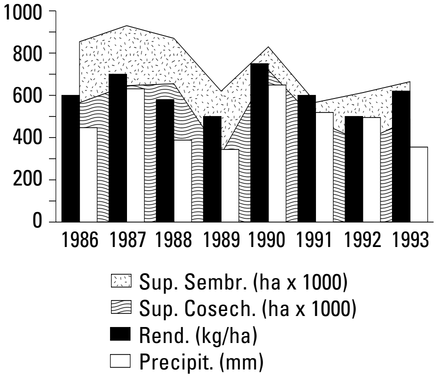

Fig. 1. Superficie sembrada y cosechada de maíz de temporal, rendimiento y precipitación media estimada (junio-octubre) en, Zacatecas, Durango y Aguascalientes

Zapata, 1988; Luna, 1993). En aquella área la precipitación fluctúa entre 400 y 500 mm, en un ciclo de cultivo de 110 a 120 días y la temperatura media está entre 15 ° y 21 °C; en la otra los valores correspondientes son 250 y 400 mm, 80 a 100 días por ciclo y 15 ° a 20 °C. En casi toda la región 65% de la lluvia se registra antes de la antésis.

Aproximadamente, 51% de los suelos tienen menos de 50 cm de profundidad, 46% entre 50 y 100 cm y su contenido de materia orgánica es inferior a 1%; por esto, su capacidad de retención de humedad es muy baja, no obstante que predominan las texturas cercanas a la franca.

Problemas Tecnológicos de Producción

Los bajos rendimientos del maíz de temporal en la zona C-N son resultado de la poca agua disponible para el cultivo, sobre todo durante la floración y el llenado del grano; pueden agregarse la temperatura relativamente baja, aunque existen genotipos adaptados a esta condición (Luna, 1993), el uso de fertilizantes en solamente 40% del área sembrada, la deficiente fertilización por cantidad y oportunidad, el uso de genotipos de baja productividad, etc. (Luna y Zapata, 1988; Luna, 1993). Además, las causas principales por las que en algunas ocasiones no se cosecha grano son: el corto período con lluvia, el inicio tardío del temporal, el inicio temprano de heladas y la siembra de genotipos de ciclo más largo del requerido (Luna, 1993).

Mejoramiento Genético y Prueba de Cultivares

El objetivo general del mejoramiento genético de maíz en la región C-N, ha sido disponer de genotipos de ciclo vegetativo adaptado a las condiciones regionales, tolerantes a la sequía y resistentes a enfermedades y al acame; con ello, se pueden disminuir los riesgos de pérdida por sequía y heladas.

En la primera etapa, iniciada en 1966 (Luna, 1993), se probaron variedades de polinización libre (PL) e híbridos formados en valles altos, el bajío y la región templada semiárida y árida (TSA); sobresalieron los cultivares Cafime y VS-201 (Cuadro 1). El cv. Cafime se liberó en 1958 y producto de la mezcla de cruzas AxB de la raza Bolita (M.S. Edmundo Taboada R., comunicación personal, 1981) y el VS-201 que es la mezcla de semilla de mestizos de la líneas S_1 derivadas de Cafime, y el mismo como probador (Dr. A. Muñoz O., comunicación personal, 1976).

Después se probaron cientos de cultivares PL e híbridos generados en el Campo Experimental Pabellón. Sus principales formadores fueron los doctores Esteban Betanzos M. y Odón Miranda J. Usaron como fuente genética principal las razas Cónico Norteño, Bolita y el Compuesto Mich. 21, tolerante a sequía. Esta etapa se concluyó con la liberación de los cultivares e híbridos indicados en el Cuadro 2 y VS-203 y H-222.

Entre 1974 y 1976, se evaluaron bajo temporal 1353 colectas de maíz de la región C-N y de Valles Altos (Zapata y Luna, 1989; Ortega et al., 1991); de ahí se derivaron compuestos con colectas sobresalientes, como el compuesto de colecciones blancas (CCB), formado con 81 colectas; el Con-Bol formado con colectas de las razas Cónico Norteño y Bolita, seleccionadas por aptitud combinatoria general (Martín del Campo, 1980). Se llevaron a cabo programas de mejoramiento genético en los compuestos y en colectas individuales: Zac 57, Zac 218, Zac 227, VS-201, en un compuesto formado por 442 familias de medios hermanos, provenientes del CIMMYT (CABG) y en otro formado con 50 mazorquitas cosechadas como único producto de un lote de 400 colectas de Zacatecas, Chihuahua, Durango y Aguascalientes, sembrado bajo temporal en 1974 en Calera, Zacatecas (Cal 74).

Los programas de mejoramiento comenzaron entre 1975 y 1977 en Zacatecas, Durango y Aguascalientes (Zapata y Luna, 1989) y se cubrieron las siguientes etapas:

Cuadro 1. Rendimiento de grano y días a floración de algunos cultivares de maíz probados bajo temporal entre 1967 y 1969 en Durango, Méx.

Cultivar	Rendimiento medio (t/ha)	Días a floración
VS-201	1.29	66
Cafime	1.09	66
Criollo Local	0.92	66

Fuente: Luna et al. (1971)

Cuadro 2. Rendimiento de grano y días a floración de algunos maíces probados bajo temporal en la región norte-centro de México.

Cultivar	Rendimiento (t/ha)	Días a floración	Ambientes de prueba
VS-202	1.8	61	65
H-204	2.2	62	54
Cafime	1.9	65	100
VS-201	2.2	67	101
H-221	2.1	71	59

Fuente: Luna et al., citados por Zapata y Luna (1989).

1. Selección familiar de medios hermanos bajo riego-sequía en VS-201, Zac. 58 y Cal 74, con 20% de presión de selección entre familias y 33% dentro de ellas.
2. Selección familiar de medios hermanos bajo temporal en el CCB y CABG, con 20% de presión de selección entre familias y 25% dentro de ellas.
3. Selección familiar de progenies autofecundadas en Zac. 218 (no se concluyó).
4. Selección masal bajo riego y bajo sequía de VS-201, Zac. 58 y Cal 74, con 5% de presión de selección.
5. Selección masal bajo temporal y masal visual estratificada en Zac. 217 (no hubo avance genético).
6. Selección masal convergente-divergente en Zac. 218 (no se concluyó).
7. Selección masal bajo condiciones limitadas y favorables en Zac. 218.
8. Retrocruzamientos con fuentes de Opaco 2 y Harinoso 2 (no se concluyó).
9. Observación de generaciones avanzadas de híbridos de temporal.
10. Evaluaciones morfológicas y fisiológicas.

Algunos programas de mejoramiento tuvieron más éxito que otros y sólo de algunos se derivaron cultivares mejorados. No se ha intentado la formación de híbridos debido la baja producción de semilla y lo costoso de su producción.

En todas las etapas de mejoramiento se incluyeron entre 35 mil y 40 mil plantas por ha y con excepción de la etapa 7 la fertilización aplicada fue 40-40-00, de acuerdo con la recomendación regional.

Los resultados de las etapas antes enumeradas se localizan en diversas fuentes (Zapata y Luna, 1989) y a continuación se indican algunos.

Selección Familiar de Medios Hermanos Bajo Riego-Sequía en Cal 74

Se completaron siete ciclos, pero únicamente hasta el cuarto hubo avance genético. Se obtuvo el cultivar V-209, con periodo de 100 días a madurez fisiológica, liberado para áreas con condiciones deficientes de la región C-N, además es más uniforme y tolerante a la sequía que Cal 74 (Cuadro 3).

En siete experimentos realizados entre 1987 y 1988 en Aguascalientes y San Luis Potosí, uno en el S de Nuevo León y otro al N de Guanajuato, V-209 rindió en promedio 0.8 t/ha, con límites entre 0.34 y 1.10 t/ha, lo anterior contrasta con el rendimiento de los criollos locales que en promedio fue 0.54 t/ha, con límites entre 0 y 0.75 t/ha (Gutiérrez et al., 1990).

Selección Familiar de Medios Hermanos Bajo Temporal en el CCB

Se realizaron cinco ciclos de selección; aquí se muestran algunos resultados de los tres primeros (Cuadro 4). Por falta de recursos este programa se suspendió, como otros; se esperaba derivar alguna variedad PL para el área de temporal favorable.

Cuadro 3. Rendimiento de grano y días a floración de maíces probados bajo temporal en 15 experimentos en el estado de Zacatecas.

Cultivar	Rendimiento (t/ha) B	Rendimiento (t/ha) BA	Días a antesis
V-209	1.4 - 2.3	0.51 - 0.71	60
Cal 74	1.1 - 2.2	0.48 - 0.70	60
Criollo regional	1.0 - 1.8	0.00 - 0.65	62

B: ambientes con 300 a 400 mm de lluvia en el ciclo, BA: ambientes con 200 a 280 mm de lluvia en el ciclo. Fuente: Gutiérrez et al. (1990).

Selección Masal en VS-201

Se realizaron siete ciclos con diversas modalidades y presiones de selección; aquí, solamente se presentan los resultados de las entidades de prueba, con 5% de presión de selección en las que se obtuvieron mejores respuestas. El VS-201 se adapta mejor a condiciones de temporal favorable de la región C-N (Cuadro 5). En Aguascalientes, donde se registran las lluvias más irregularmente, se obtuvieron los menores rendimientos; en contraste en Durango, donde se realizó la selección y hay mejores condiciones hubo mayores rendimientos. En la selección bajo riego se incrementó el período para el inicio de la antesis.

Selección Masal Bajo Temporal en Cal 74

El cv. Cal 74 es un maíz para condiciones poco favorables de la región C-N, por esta razón la mejor respuesta se obtuvo en el área de temporal deficiente de Zacatecas, donde se realizó la selección (Cuadro 6).

Cuadro 4. Rendimiento de grano y días a antesis del compuesto de colecciones blancas (CCB) y sus derivados mediante selección.

Cultivar	Rendimiento (t/ha) B	Rendimiento (t/ha) BA	Días a antesis
CCB	2.6	1.4	67
I CSF	2.6	1.7	67
II CSF	2.7	1.9	65
III CSF	2.7	2.0	65
VS-201	1.8	1.3	68

B: ambientes con lluvia arriba de la media, BA: ambientes con lluvia abajo de la media, CSF: ciclo de selección familiar. Fuente: Castro et al., citados por Zapata y Luna (1989).

Selección Masal Bajo Condiciones Favorables (SMCF) y Bajo Condiciones Críticas (SMCC) en Zac. 218

El Zac. 218 es una colecta de Sombrerete, Zacatecas, lugar de condiciones favorables de la región C-N, el ciclo vegetativo de esta colecta es similar al del cv. VS-201 y es de alta aptitud combinatoria general (Martín del Campo, 1980). El programa de selección se realizó en Aguascalientes, Zacatecas y Durango; en el primer sitio se tuvo avance genético en el rendimiento cuando la selección se realizó en condiciones favorables y críticas, y en los otros dos solamente cuando se realizó en condiciones deficientes. Del ciclo III de selección masal bajo condiciones críticas, se derivó el cv. V-210, ya liberado, para el que las condiciones favorables y críticas son: densidad de 40 mil y 50 mil plantas por ha y fertilización de 40-40-00 y 20-20-00, respectivamente.

Generaciones Avanzadas de Híbridos para Temporal de la Región C-N

Entre 1983 y 1985 se hicieron seis pruebas en Durango y tres en Zacatecas, bajo temporal. Se observó mínima reducción del rendimiento, pero mayor variabilidad en las generaciones avanzadas. Lo primero puede deberse al hecho de que los híbridos se formaron con líneas S_1; además, que las líneas del H-204 tienen origen común (raza Cónico Norteño). Estos híbridos se usaron muy poco, pues hubo desinterés en la multiplicación de la semilla, no obstante su superioridad respecto a los cultivares recomendados previamente.

La variabilidad genética del material utilizado como fuente de mejoramiento influyó en la respuesta a la selección; también, influyeron las condiciones específicas bajo las que se desarrollaron los programas de mejoramiento. Existió la tendencia de que las pruebas bajo condiciones críticas respondieron mejor respecto a las realizadas bajo condiciones favorables.

Evaluaciones Morfológicas y Fisiológicas

Peña (1981) observó que el peso y volumen de la raíz de las plántulas de VS-201, fueron menores que los de sus derivados por selección masal o familiar. El área foliar y diámetro del tallo de las plantas maduras se correlacionaron positivamente con el rendimiento del grano y negativamente con los días a antesis. En relación con los mismos genotipos, Gutiérrez (1986) observó que algunos de los compuestos derivados por selección masal o familiar, mostraron mayor tasa de transpiración que el VS-201 original, resistieron más tiempo la condición de marchitez permanente, formaron mayor área foliar y las semillas germinaron en mayor porcentaje a 15 atmósferas de presión osmótica.

Luna y Gutiérrez (1993) anotan que los maíces precoces de la región C-N, criollos o mejorados, muestran un intervalo corto entre la antesis y el jiloteo, tanto en condiciones favorables como desfavorables de cultivo. El Cal 74 al pasar de la prueba de riego a la de sequía, se redujo 69% el rendimiento de grano de la variedad original y del compuesto derivado por el índice riego-sequía, mientras que el de los compuestos derivados por selección bajo riego o bajo sequía, En promedio, el número de granos por mazorca se redujo 53%, el peso del grano 16%, la longitud de la mazorca 22% y su diámetro 13%. El número de granos por mazorca y el peso de grano se correlacionaron positiva y negativamente con el rendimiento del grano, respectivamente.

Cuadro 5. Rendimiento de grano (t/ha) del maíz cv. VS-201 y los ciclos de selección masal que tuvieron mayor rendimiento bajo temporal en tres entidades de la región Centro Norte.

Modalidad	Aguascalientes		Durango		Zacatecas	
de selección	B	BA	B	BA	B	BA
Masal sequía	2.9	0.8	-	-	-	-
Masal prolificidad sequía	-	-	4.1	3.3	-	-
Masal riego	-	-	-	-	2.7	1.5
VS-201	2.3	1.0	2.4	1.4	3.5	1.9

B: ambientes con lluvia arriba de la media, BA: ambientes con lluvia abajo de la media, Fuente: Castro et al., citados por Zapata y Luna (1989).

Cuadro 6. Rendimiento de grano (t/ha) del compuesto de selección masal obtenido bajo temporal del Cal 74.

	Aguascalientes		Durango		Zacatecas	
Compuesto	B	BA	B	BA	B	BA
SMT	1.3	0.9	3.3	1.7	3.0	1.9
Cal 74	2.1	1.1	3.1	1.7	2.4	1.3

B: ambientes con lluvia arriba de la media, BA: ambientes con lluvia abajo de la media, SMT: compuesto de selección masal obtenido en temporal. Fuente: Castro et al., citados por Zapata y Luna (1989).

Gutiérrez y Luna (1990) observaron que la frecuencia estomática de los compuestos formados por selección familiar bajo riego-sequía o bajo sequía fue de 34/mm^2 y en el original y en el compuesto por selección bajo riego fue 43/mm^2; aunque la tasa de transpiración no se modificó notablemente, 15.8 g/dm^2/día y 16.1 g/dm^2 /día, respectivamente.

Prácticas Culturales

Los objetivos principales de la investigación sobre prácticas culturales para maíz de temporal en la región C-N han sido: integrar los paquetes tecnológicos de acuerdo con las condiciones ecológicas de cada área de producción (orientación para el más efectivo del agua de lluvia y del suelo) y disminuir los costos y riesgos de producción.

Así, con base en los resultados de diversas investigaciones se han reconocido las dosis de fertilizante, densidades de siembra, fechas de siembra, formas de control de arvenses y plagas, etc., más adecuadas para cada región. También se han realizado investigaciones sobre balance hídrico, captación y conservación del agua de lluvia y su efecto en la labranza, disminución de uso de maquinaria, etc.

En un estudio sobre balance hídrico en maíz de temporal en Aguascalientes (Martínez G. citado por Zapata y Luna, 1989) se detectó un déficit fuerte de humedad para el cultivo, en las etapas de floración y llenado de grano (Cuadro 9).

El mismo investigador (Martínez G., citado por Zapata y Luna, 1989) observó que en las siembras de maíz de temporal en Aguascalientes, donde la precipitación fue de 239 mm entre la siembra y la floración, y solamente 20 mm después, el sistema de microcuencas aportó 74 mm más de agua al cultivo, respecto de las siembras en surcos y en plano. Los rendimientos de rastrojo en microcuencas, surcos y en plano fueron: 2.6, 2.2 y 1.7 t/ha, respectivamente. Resultados semejantes presenta Martínez B. en el mismo documento.

También Martínez G. (citado por Zapata y Luna, 1989) observó amplia ventaja al cubrir el suelo con plástico negro, respecto de la siembra tradicional (Cuadro 10).

Osuna C. y Muñoz R. (citados por Zapata y Luna, 1989) anotan que se obtuvieron un rendimiento de 1.7 t/ha en temporal en Durango cuando se barbechó y se dieron dos rastreos, 1.9 con dos rastreos y un barbecho cada tres años, 2.2 con cinceleo más un rastreo, 1.7 con un barbecho y un rastreo y 1.9 con solamente un rastreo; también observaron que a menor preparación del suelo correspondió mayor densidad de arvenses. Resultados semejantes obtuvieron Escobedo (1984) y Verástegui (1991) en Zacatecas y Martínez M. (citado por Zapata y Luna, 1989) en Aguascalientes.

Cuadro 7. Rendimiento de grano (t/ha) de los compuestos de selección masal derivados del Zac. 218.

Compuesto	Aguascalientes		Durango		Zacatecas	
	B	BA	B	BA	B	BA
I CSMCF	3.4	1.8	2.6	1.8	2.7	1.5
II CSMCF	3.5	1.7	2.8	2.2	2.7	2.3
III CSMCF	1.5	1.5	2.3	2.0	2.9	2.9
I CSMCC	3.4	1.3	2.6	2.0	3.3	1.5
II CSMCC	3.4	1.2	2.7	2.2	2.6	1.8
III CSMCC	1.9	1.9	2.2	2.2	2.6	2.6
Original	2.1	0.9	3.1	1.9	2.6	1.8
VS-201	1.9	1.1	3.3	1.9	2.4	1.6

B: ambientes con lluvia arriba de la media, BA: ambientes con lluvia abajo de la media, CSMCF: ciclo de selección masal bajo condiciones favorables, CSMCC: ciclo de selección masal bajo condiciones críticas, Fuente: Ramírez et al., citados por Zapata y Luna (1989).

Cuadro 8. Resultados de la evaluación de generaciones avanzadas de híbridos de maíz de la región C-N.

Genotipo	(t/ha)	Rendimiento (%)	Desviación estándar (kg/ha)	Días a antesis
H-204	2.4	100	371	62
H-204 F4	2.2	92	430	64
H-221	2.0	100	407	73
H-221 F4	2.1	104	497	71
H-222	2.2	100	487	70
H-222 F4	2.1	97	604	70

Fuente: Castro y Zapata, citados por Zapata y Luna (1989).

Cuadro 9. Déficits de humedad y escorrentías en maíz de temporal en Aguascalientes.

Etapa de crecimiento	Lluvia (mm)	Déficit (mm)	Escorrentía
0-45 días	160	+38	29
46 a floración	56	+28	16
Floración	2	-35	0
Llenado grano	18	-47	0

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Cuadro 10. Respuesta del maíz de temporal con y sin acolchado con plástico sembrado en dos localidades de Aguascalientes.

	Sandovales		El Retoño	
Variable	Plástico	Tradicional	Plástico	Tradicional
IAF	2.04	1.26	1.59	1.10
Materia seca (g/planta)	146	66	83	55
Rendimiento de grano (t/ha)	2.10	0.20	1.00	0.00

La Sequía y sus Consecuencias
para el Maíz en las Islas de Cabo Verde

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Abstract

A brief description is presented of the characteristics of agriculture on the archipelago of Cabo Verde, with emphasis on rainfed agriculture (maize-bean association), traditional and subsistence agriculture, which is carried out under unfavorable conditions from planting through harvest time. Cabo Verde has an area of 4,033 km2 and rainfed agriculture is practiced on 97% of the cultivated land, with very low productive potential due to scarce rainfall. As a result, it is necessary to introduce new cultivation techniques and drought-tolerant maize cultivars. The climatic conditions and the morpho-pedological characteristics of the islands are not very favorable for agricultural exploitation. Thus we recommend the reconstitution and preservation of the natural vegetation, and an increase in reforestation, as an alternative to enhance the fragile ecosystem.

El archipiélago de Cabo Verde, con una superficie de 4 033km^2, está situado en el Océano Atlántico, entre el Trópico de Cáncer y el Ecuador, cerca de 1 400 km al SSO de las Islas Canarias. Está constituido por 9 islas y 8 islotes, su población es aproximadamente de 353 000 habitantes. La Isla Santiago con 991 km^2 es la más importante, pues 52% de su área es cultivable y ahí reside 50% del total de la población del país. Las islas con relieves más pronunciados son Fogo, Santo Antão y Santiago, con altitudes máximas de 2 829 m, 1 979 m y 1 373, respectivamente.

La explotación de las tierras se realiza principalmente en pequeñas parcelas de temporal, de subsistencia y con agricultura tradicional en condiciones naturales muy difíciles. La agricultura de secano constituida por los cultivos asociados de maíz y frijol, son la base de la alimentación de la población. La agricultura con riego, en el fondo de las riberas, se practica sólo en pequeñas áreas, y para esto se utilizan aguas subterráneas.

El Cultivo de Maíz en las Islas de Cabo Verde

El cultivo de maíz fue introducido a Cabo Verde, aproximadamente, en el siglo XVI, desde América del Sur, con cultivares provenientes de Brasil y Argentina por navegantes portugueses.

Desde su implantación hasta la actualidad, el cultivo del maíz se ha desarrollado en condiciones poco favorables; así, se ha inducido una selección del maíz caboverdiano que se manifiesta en resistencia a prolongados períodos de déficit hídrico, parásitos comúnmente encontrados en Africa tropical, gran crecimiento vegetativo en condiciones edáficas y climatológicas favorables y su gran capacidad para adaptarse al sistema tradicional de cultivo en asociación con el frijol.

El maíz se cultiva en 30 000-35 000 ha y poco más de 80% se desarrolla en condiciones edafoclimáticas desfavorables, hasta el periodo vegetativo (Cuadro 1). La siembra se realiza en secano, a mediados de julio, por hábito y por disponibilidad de mano de obra, pues con el terreno húmedo, la siembra tendría que realizarse en menos tiempo. Se colocan entre 3 y 4 granos de maíz con 2 a 4 granos de diferentes cultivares de frijol, a una profundidad aproximadamente de 5 a 7 cm, en huecos cuya distancia entre sí generalmente es de 80 cm a 120 cm y la densidad de la población puede fluctuar entre 28 000 y 60 000 plantas/ha. Durante el ciclo del cultivo, tienen lugar una serie de trabajos en las laderas donde se están desarrollando los cultivos; así, manualmente (con guataca) se realizan 2 o 3 deshierbes, rastrillado y amontone. Los agricultores utilizan en esta forma de cultivo más de dos semillas por hueco, con el propósito de obtener más plantas por unidad de área, para reducir el riesgo de pérdidas causadas por plagas o enfermedades y en forma indirecta reducir los costos de la siembra y mano de obra. En algunos casos se eliminan las flores masculinas parcialmente, dependiendo de la forma y el momento de la ejecución de esta práctica se induce la reducción de la dominancia apical y por consiguiente la translocación de las reservas fotosintéticas hacia la mazorca, con lo que se incrementa el follaje para uso forrajero.

La cosecha se realiza después que la mazorca está completamente seca, se seleccionan las mejores mazorcas, se desgranan y las semillas se almacenan en recipientes de vidrio, herméticamente cerrados para futuras siembras.

La duración del periodo vegetativo depende de varios factores: material genético, lluvias y tipo de suelo entre otros; pero, generalmente oscila entre 90 y 110 días.

Silva (1986) señala que a diferencia del color el tipo de grano es un factor importante en la selección varietal. Así, los granos cristalinos, tipo '*flint*', de endospermo duro, son los más apropiados (mayor rendimiento en el pilón) en la confección de "la cachupa", plato tradicional; sin embargo, los granos blancos predominan en la Isla de Fogos y los amarillos en Santiago.

La sequía durante la etapa de establecimiento del cultivo puede reducir la densidad de población. Además, la precipitación siempre es inferior a lo requerido por el cultivo durante su ciclo completo, unido a esto la baja humedad, la poca profundidad de los suelos de cultivo, la pérdida de agua por la escorrentía y la elevada evapotranspiración causada por las altas temperaturas conducen a rendimientos notablemente bajos.

Cuadro 1. Zonas ecológicas y sus caracteristicas.

Zonas ecológicas	Altura (m)	Precipitación (mm)	Tipo de agricultura
Humeda	500 - 900	> 600	Secano: Maiz, frijol, ganado, fruteras, forestales, guandul. Producción regular.
Sub-humeda	200-1800 *	400 - 600	Secano: Maiz, frijol, forestales, guandul. Producción irregular.
	500-1200	400 - 600	Secano: Maiz, frijol, Producción irregular.
Semi-árida	150 - 300 *	300 - 400	Secano: Maiz, frijol. Producción incierta.
	400 - 1500	300 - 400	Cultivos en suelos marginales Producción practicamente nula Pastos, forestales.
Arida	200 - 300	< 300	No aptas para cultivos. Algunos pastos nativos.

* - expuestos a vientos alisios, cargados de humedad.

Breve Descripción de las Evaluaciones del Cultivo del Maíz

En 1980 se inició el proyecto "Mejoramiento varietal de maíz, frijoles y otros granos alimentarios". Su principal objetivo fue inventariar, analizar y reproducir ecótipos locales de maíz. En 1981 fueron identificados cerca de 40 ecótipos de las islas de Santiago y Fogo. Sin embargo, se obtuvo número insuficiente de material para la multiplicación y en la isla de Santiago la investigación no se desarrolló de en mejor forma en las mejores condiciones debido a condiciones climáticas adversas y a la falta de entrenamiento del personal. En la isla de Fogo solo fue posible seleccionar el número reducido de 6 ecótipos. Finalmente, la preservación del material recuperado representó una dificultad, pues no se contaba con un banco de germoplasma y se perdió parte del material.

Se realizaron otros trabajos entre 1982 y 1989, fueron incluidos más de 120 cultivares mejorados, seleccionados por diversos programas nacionales e internacionales (CILSS, SAFGRAD, CIMMYT e IRAT), para un total de 24 ensayos en las islas de Santiago y Fogo. Unicamente en 4 ensayos se observaron diferencias significativas entre los testigos (ecótipos de Santiago, S. Nicolau, S. Antão, Fogo y Maio) y entre los mejores estuvieron: Jaune Flint de Saria, Jeka, Maka, IRAT 98,100, Pool 16, HVB 1, ZM 10, Jaune D. Bambey, J. Denté Bambey; de CILSS/IS; IRAT 178, Ferke 7622, Pool 34 QPM, Synthetic C, Capinopolis 8245, Across 8149, 8321-18(H) de SAFGRAD; Poza Rica 8126, Iboperenda 8035, Pirsabak 7980, Los Diamantes 7823, Ilonga 8032, Across 8126 y 8149, Capinopolis 8235, Suwan 8131, y Pirsabak 7930 del CIMMYT. Los cultivares mejorados respondieron mejor a las condiciones de intensificación; mientras que, el material local respondió mejor a las condiciones ambientales fuertemente desfavorables. Además, entre las poblaciones locales, la respuesta fue heterogénea y el maíz de la isla Maio reflejó una notable plasticidad, pero los ecótipos de Santiago se adaptaron mejor a las condiciones de esta isla.

Silva (1987) realizó tres ensayos de cultivo de maíz, en tres localidades de la isla Santiago, São Jorge, Serrado y São Domingos, con el objeto de identificar condiciones agronómicas críticas sin restricciones hídricas. En el estudio se incluyeron tres cultivares locales (Santa Catarina, Local Maio y Composto Blanco) de Fogo y uno de Mauritania (Maka). El citado investigador, no observó diferencias significativas entre los cultivares, al utilizar diversas dosis de N (0, 50, 100 y 150 kg/ha) y P (0, 40 y 80 kg/ha) y concluyó que la homogeneidad de la respuesta se debió al elevado contenido de nutrimentos en el suelo, aplicados en dos ensayos previos. El elevado rendimiento promedio obtenido (7.75 t/ha) fue atribuido a las condiciones excepcionales de manejo adecuado de las parcelas, fertilización, riego y control de insectos y enfermedades. Además, de lo anterior Silva (1987) observó diferencias significativas entre el cv. Maka y los locales en el ensayo de densidad por variedad, pero no entre los cultivares locales; pues el cv. Maka mostró mayor potencial productivo con la mínima densidad (26 650 plantas/ha), en cuanto que los cultivares locales mostraron mayor potencial para la densidad intermedia (39 975 plantas/ha). Además, los cultivares más precoces fueron Local Maio y Maka y el más tardío fue el cv. local Santa Catarina.

Conclusiones y Recomendaciones

Debido a la importancia del maíz en Cabo Verde es necesario continuar con las investigaciones relacionadas con este cultivo, pues de ello depende el bienestar de la población rural. Es indispensable evaluar y seleccionar genotipos con reconocida tolerancia al déficit hídrico, introducir cultivares precoces blancos y amarillos, en combinación con los trabajos de conservación del suelo y agua.

Agradecimientos

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Estimates of Yield Losses in Maize Production Due to Drought in Zimbabwe

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Abstract

Maize is the most important food crop in Zimbabwe and is widely grown. Two major sectors of agricultural production are recognized: the large-scale commercial farming sector (LSC) and small-scale communal farming sector or Communal Farmers (CFS). Most LSC maize growers are situated in the high rainfall areas, where average annual rainfall totals 800 mm or more (Natural Region II), while 91% of CFS maize growers are situated in semi-arid areas with average annual rainfall totals of 800 mm or less (Natural Regions III, IV and V). Rainy seasons dating back to 1970/71 were classified and grouped as either normal or drought seasons. The difference in average maize yields between normal and drought seasons was used to estimate yield loss due to drought in each farming sector. Estimated yield losses were 0.79 t/ha or 68% in the CFS, and 1.69 t/ha or 37% in the LSC. Yield differences between normal and drought seasons were highly significant (P£0.001) in both sectors. Mid-season drought was cited as the common form of drought responsible for substantial yield losses even during normal seasons in both sectors.

Zimbabwe is partitioned into five agricultural production zones referred to as natural regions (NR) I, II, III, IV and V (Fig. 1). NR I is for specialized farming, which excludes commercial maize (*Zea mays* L.) production. Maize productivity under dry-land conditions is highest in NR II, where rainfall is more reliable than in NRs III, IV and V. According to Vincent and Thomas (1960), cropping should be carried out in NR I and NR II with livestock becoming increasingly important in NR III, NR IV and NR V at the expense of crop production. Annual rainfall distribution is best in NR I and worst in NR V. Thus, high rainfall areas have better seasonal rainfall distribution than low rainfall areas.

Maize is the most important food crop in Zimbabwe. It is widely grown and generally two major groups of farmers are recognized based on their production systems and scale of operation. These are the large-scale commercial farming sector (LSC) and the communal farming sector (CFS). The CFS is mainly composed of small-scale farmers, and consequently the terms small-scale farming sector and communal farming sector are used interchangeably. There are several

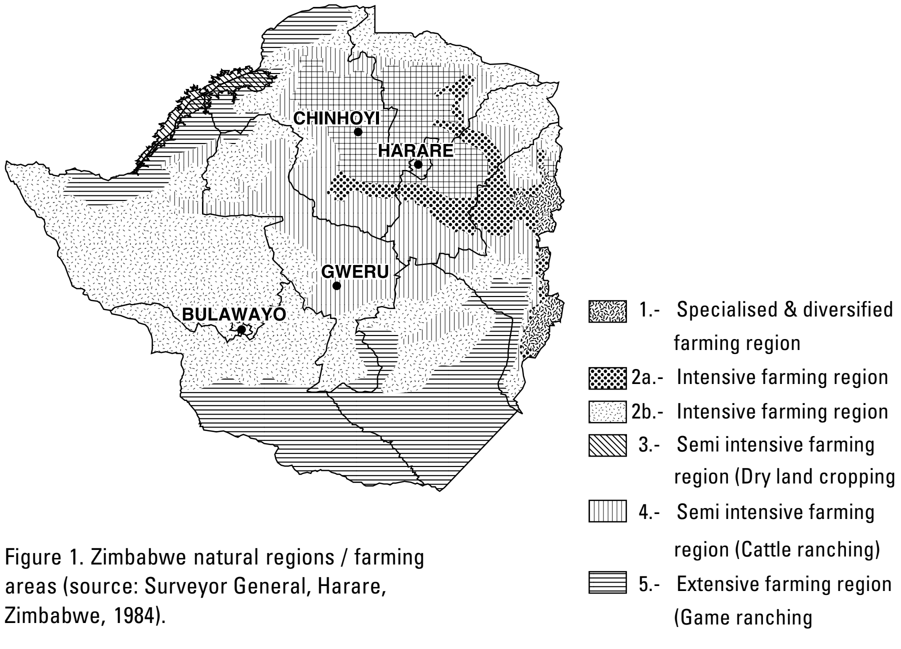

Figure 1. Zimbabwe natural regions / farming areas (source: Surveyor General, Harare, Zimbabwe, 1984).

basic differences between the LSC and CFS. Commercial farmers have privately-owned units averaging 2,500 ha (Rukuni, 1992). They rely heavily on machinery and can afford to use nitrogenous fertilizer, chemical pesticides and hired labor. Conversely, communal farmers have no title deeds. They have rights to the use of small holdings averaging one hectare per individual, and they rely heavily on animal draft power and family labor. Usually they cannot afford inputs such as nitrogenous fertilizer and chemical pesticides. Although farmers in both sectors are motivated by profits, commercial farmers can afford timely execution of farming operations whilst the communal farmers cannot. In the LSC, the rotation maize, soybeans/ groundnuts and wheat is generally practiced. In the CFS, there are efforts to rotate crops so as to maximize productivity, though these are limited by the constant need for each family to produce maize on their very small unit (less than 5 ha per family). The general tendency is to follow maize with maize and in occasional years to alternate with sunflower, groundnuts, cotton, or sorghum.

Table 1. Relative rainfall amounts and area utilized by the communal farming sector (CFS) and large-scale commercial farming sector (LSC) in Zimbabwe, by natural region.

	Area as a percent of total		
Natural region	Rainfall per annum (mm)	CFS (%)	LSC (%)
I	>1000	0.5	2.9
II	750-1000	8.9	26.8
III	650-800	16.4	22.1
IV	450-650	44.4	24.8
V	<450	29.8	23.4

Source: Adapted from Zimbabwe Rhodesia Science News (1979). 13:233.

An estimated 91% of the communal farming areas fall within NRs III, IV and V (Table 1). In addition to the low and erratic rainfall (Whitlow, 1980), communal area soils are deficient in available nitrogen, phosphorus, and sulfur, and have poor physical structure and low water-holding capacity (Mataruka, 1995). Although commercial farming areas are evenly distributed among NRs II, III, IV and V (Table 1), maize production by the large-scale commercial farming sector (LSC) is mainly practiced in NR II and to a lesser extent in NR III. The LSC emphasizes livestock production in NRs III, IV and V, as recommended by Vincent and Thomas (1960).

Total area, production and average yield levels in each of the two sectors for the period 1980/81 to 1994/95 are shown in Figure 2. On average, total maize area in the CFS is larger than that in the LSC. Average yield levels in the CFS are much lower than those obtained in the LSC.

Declining trends in rainfall during the 20th century in Zimbabwe have been reported by Barnes (1996) and Machida (unpublished, 1996). Severe droughts became more frequent from 1980/81 to 1994/95, and adversely affected maize yields. The objective of this study was to estimate average maize grain yield losses due to drought in the LSC and CFS sectors of maize production found in Zimbabwe.

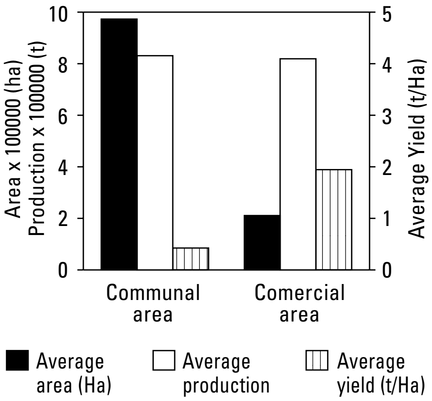

Figure 2. A summary of maize production statistics pooled across drought and normal seasons for the period 1980/81 to 1994/95 (source: adapted from statistics on maize production, Ministry of Agriculture, Zimbabwe).

Materials and Methods

Zimbabwean mean rainfall data from 1970/71 to 1994/95, summarized in Table 2, was used to categorize seasons as drought or normal rainy seasons; i.e., non-drought. All seasons with mean rainfall of less than 500 mm were considered drought seasons (Machida unpublished, 1996). This classification of years concurred with declarations by the Government of Zimbabwe. Maize yield data in both the LSC and CFS were categorized into data for normal or drought seasons, using the criterion mentioned above.

A t-test was performed to determine significance of differences in yield between normal and drought seasons within each sector (Clarke, 1980).

Table 2. A summary of annual rainfall data for Zimbabwe from 1970/71 to 1994/95.

	Drought seasons	Normal rainy seasons
Mean (mm)	408	712
Range (mm)	335 to 464	502 to 1004
Frequency	7 of 25 seasons	18 of 25 seasons

Source: Adapted from data obtained from the Department of Meteorological Services, Belvedere, Harare, Zimbabwe.

Yield differences between normal and drought seasons were taken as estimates of yield losses due to drought. For the purposes of this analysis, annual average yield data from 1980/81 to 1994/95 was used in both farming sectors. This was done because data before 1980 are unreliable due to factors other than drought (like the war of liberation which was fought mainly in communal areas, and lack of credit to acquire inputs) which strongly influenced maize yield.

Results

There were significant yield differences (P£0.001) between normal and drought seasons in both the CFS and LSC of 0.79 t/ha and 1.69 t/ha, respectively (Table 3). When expressed as percentages of average yield levels for normal seasons, the yield differences indicated yield losses of 68% for the CFS, and 37% for the LSC, respectively. About one out of every four years had a droughty growing season for the period 1970/71 to 1994/95. The frequency was higher for the period 1980/81 to 1994/95, with more than one out of every three years experiencing drought.

Table 3. Summary data and t-test results from the comparison of normal and drought seasons in both the communal and commercial sectors.

	Communal area (CFS), seasons 1980/81 to 1994/95	Commercial area (LSC), seasons 1980/81 to 1994/95
Normal rainy seasons (no.)	9	9
Drought seasons (no.)	6	6
Average normal yield (t/ha)	1.16	4.57
Average drought yield (t/ha)	0.37	2.88
Yield difference/loss (t/ha)	0.79	1.69
Pooled variance	0.042	0.355
Level of significance, t-test	P< 0.001	P< 0.001

Discussion

Although the 1.69 t/ha yield loss in the LSC is twice that of the 0.79 t/ha loss in the CFS, the percentage yield losses show that when drought occurs, the CFS loses proportionally more of its normal yield (68%), than the LSC (37%). Most communal farmers are 'obligate' maize growers and are situated in areas where the climate is less suitable for maize production even during normal seasons. The LSC areas are in the prime areas (NR II), and highly suitable for maize production. In the event of a drought, the CFS environment becomes harsh, whilst the LSC environment deteriorates but not to the same extent. The CFS area, therefore, is in greater need for drought tolerant maize varieties, and should get higher priority in targeting the breeding of such varieties.

Despite the average maize area in the CFS being four times larger than in the LSC, average yield levels are approximately five times larger in the LSC (Fig. 2). When average yield losses due to drought (Table 3) were computed together with average areas for the two sectors (CFS: 985,440 ha, and LSC: 211,020 ha, Fig. 2), average losses in production were 778,490 (CFS) and 356,620 (LSC) metric tons, respectively, giving a total average loss in production of 1,135,110 metric tons each time drought occurred. These are substantial yield losses which definitely warrant the breeding of maize varieties which tolerate drought better than currently existing varieties.

At present, the average frequency of severe drought in Zimbabwe is about once every four years (Table 2). However, the author has noted that even during normal seasons, maize in different parts of the country was subjected to mid-season drought which substantially reduced yield levels. These droughts generally coincide with the pre-flowering or flowering period, and the duration varies between years. Very long periods (three weeks and above) without rain reduce grain yield levels substantially or lead to a total loss of the maize crop.

Maize breeders should aim to reduce the adverse effects of this type of drought by breeding drought tolerant maize varieties. The public maize breeding program in Zimbabwe addresses this problem in several ways:

1. Developing drought tolerant inbred lines whose silks emerge before pollen shedding.
2. Constituting and evaluating experimental hybrids from these drought tolerant inbred lines.
3. Recycling drought tolerant inbred lines with inbred lines showing high yield potential.
4. Exchanging germplasm and information through regional trials.

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The Need for Genetic and Management Solutions to Limitations Imposed by Drought and Low N on Maize Production in Tanzania

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Abstract

Important constraints limiting maize production in Tanzania include both biotic to abiotic factors. The former, which covers pests and diseases, have received much attention. The latter, which includes drought and low soil nitrogen status, has received little attention. In most of the maize growing areas of Tanzania the maize crop is subjected to frequent drought due to erratic rainfall. Crop losses due to drought can be up to 50% in some seasons. The National Maize Research Program (NMRP) aims to overcome some of these effects of drought by providing an escape mechanism through development of early-maturing varieties and hybrids. Early maturing maize populations have been developed, targeted for the drought prone areas in the low and mid-altitude zones, and varieties with grain yields of up to 4 t/ha have been released. However, the early maturing varieties have been found to be very sensitive to early season stress, resulting in smaller cob and grain sizes, and hence lower yields. Nutrient deficiency, especially N, is a widespread problem in Tanzania because of low use of purchased fertilizers and lack of suitable crop rotations. Breeding for drought resistance and low-N utility is a feasible route towards increasing and stabilizing maize yields in moisture-stressed areas. NMRP plans to collaborate with CIMMYT, IITA and other national programs in the evaluation of resistant germplasm, and in agronomic work on soil fertility, soil enriching rotations and water conservation methods.

Maize is an important food crop for over 80% of Tanzania's 28 million people, both in rural and urban areas. It is also an important cash crop for rural people. According to data from the statistics unit, Ministry of Agriculture, maize occupied about 59% of total area under cereal crops in Tanzania between 1990 and 1995. In most of sub-Saharan Africa, and Tanzania in particular, maize is grown mainly under rainfed conditions, both in sole crop and mixed cropping systems. Intercropping reduces risks of crop failure. The average maize yield is low due to biotic, abiotic, institutional and socio-economic constraints, as well as under-utilization of improved germplasm. Although grain yields are highest in the southern highlands, where there is sufficient and reliable rainfall, production per unit area is still low (less than 1.5 t/ha). This is due to the fact that all Tanzanian agro-ecological zones are characterized by unpredictable dry periods of 1 to 3 weeks, an effect which is exacerbated by the relatively low water holding capacity of Tanzanian soils. In marginal rainfall areas, rainfall at the start of the season is erratic and unevenly distributed. Where rainfall is bimodally distributed, mid-season moisture stress results in considerable loss of yield, and in some cases complete crop loss. Production loss due to drought can be up to 50% in severe seasons, especially when drought coincides with flowering and early grain filling.

It has been reported that unpredictable periods of non-protracted drought throughout the humid lowland tropics are responsible for significant reductions in maize yields (Fischer et al., 1989; Shaw, 1983). The effect of drought cannot be entirely avoided by modifications to either genotype maturity or planting date because of the unpredictability in the timing of drought. However, maize cultivars that are better able to tolerate a reduced moisture supply, especially around flowering, would help stabilize grain yields and reduce farmers' risk. Turner (1979) suggested that drought tolerance involves mechanisms by which plant tissues escape, avoid or tolerate dehydration.

Nutrient deficiencies, especially nitrogen, are a widespread problem in Tanzania because of low use of purchased fertilizer, lack of crop rotation and soil degradation in maize producing areas. In the southern highlands, acidic and low fertility soils limit production when no fertilizer is used. In the western parts of Tanzania, soil fertility is generally low and poor rainfall distribution limits fertilizer response.

Early Maturity as a Drought Escape Mechanism

The National Maize Research Program (NMRP) aimed to partially overcome the effects of drought through escape, by developing early-maturing maize varieties and hybrids targeted to all agro-ecological zones of Tanzania. The main activities and objectives were to:

1. Collect and identify maize germplasm that is early maturing, hence, able to escape drought.
2. Form and improve early-maturing populations from germplasm collected, with consideration being given to desirable characters including resistance to leaf diseases (blight and rust), flint seed types, white seed color, etc.
3. Develop varieties and hybrids which mature early and produce reasonable grain yield.
4. Test the varieties and develop accompanying management practices on research stations and farmers' fields.

The program was designed to develop maize varieties that could be grown successfully in areas with short rainy seasons and uneven rainfall distribution during critical crop development stages. Table 1 shows the breeding populations, their origins and major selection criteria. Initially, materials were evaluated for adaptation and desirable characters at NMRP headquarters, Ilonga. After each selection cycle, progeny yield trials were conducted at three locations encompassing different zones. Rigorous testing of selections was then conducted in multi-location yield trials, and several varieties were released for commercial production (Table 2). Tables 3 and 4 show mean performance in grain yield, and days to 50% silking of released varieties tested in multi-location trials in several seasons.

Understanding farmer's circumstances through sharing previous results and experiences is essential in the development of appropriate varieties and management practices. Through on-farm research, NMRP realized that early-maturing varieties are not very acceptable to farmers. The farmers were concerned with the small cob size and lower yield associated with early maturity. Furthermore, early-maturing varieties have been found to be very sensitive to early-season moisture stress which in turn results in lower yields. Hence, the development of cultivars which are genetically tolerant to drought, but have larger cobs and higher yields is the longer term solution which NMRP breeders wish to pursue.

Table 1. Early-maturing breeding populations developed in Tanzania.

Pop. no.	Origin	Primary selection criteria	Selection method	Days to 50% silk	Grain type
11	Broadly based CIMMYT germplasm. Local streak resistant source used in recombination	Streak res., intermediate-maturity, low ear height, and flint grains	Full sib	55-58	White flint/dent
12	Broadly based CIMMYT germplasm. Local streak resistant source used in recombination	Streak res., intermediate-maturity, low ear height, and flint grains	Full sib	55-58	Yellow flint/dent
72	Crosses between Katumani, Lote 24, and Lote 81 recombined with CIMMYT materials Lote 88 and 89, Pop. 30, and other early maturing materials from Mexico.	Streak res., earliness, flint grains, and leaf blight resistance.	Full sib/ half sib	43-48	White/yellow Flint/dent
88	Developed from CIMMYT IPTT 30 (1979) tested at Ilonga Research Institute.	Larger grain size and streak tolerance.	Full sib	43-47	White flint
101	Developed from combination of crosses involving Pop. 88, 72, and 11, and CIMMYT Pop. 49 and EV8430SR from IITA.	Streak res., earliness, and larger grain and cob sizes.	Full sib	45-50	White flint/dent

Table 2. Released varieties developed from early-maturing maize breeding populations by the NMRP in Tanzania.

Pop. no.	Experimental/ variety name	Year released	Major attributes	Release name	Target zone
11	EV8311A	1987	Streak res., intermediate-maturity, and good yield.	TMV-1	Lowland and mid-altitude
88	EV8188	1983	Early-maturity	KITO	Lowland and mid-altitude
-	-	-	Early-maturity	KATUMANI	Lowland and mid-altitude
-	Chollima Hybrid	1992	Streak res. and early-maturity	CH1	Lowland
-	Chollima Hybrid	1992	Streak res. and early-maturity	CH3	Lowland
88	EV8188	1994	Early-maturity and streak tolerance	KITO-ST	Lowland and mid-altitude
-	-	1994	Early-maturity and streak tolerance	KATUMANI-ST	Lowland and mid-altitude

Table 3. Grain yield of released varieties developed from early-maturing populations in Tanzania.

Variety	1984/85	1985/86	1986/87	1987/88	1988/89	1989/90	1990/91	1991/92	1992/93
					(t/ha)				
TMV-1	4.4	4.6	4.9	4.9	6.1	4.1	6.1	5.8	4.9
Kito	3.3	3.8	2.0	3.1	4.1	3.2	4.0	5.8	-
Katumani	2.8	2.4	2.2	-	4.1	-	-	-	-
CH1	-	-	-	-	-	5.1	7.4	7.3	5.4
CH3	-	-	-	-	-	4.8	8.1	7.0	5.5
Number of locations	3	5	6	4	4	5	2	4	4

Table 4. Mean grain yield and days to 50% silking of early-maturing varieties evaluated in streak prone areas of Katrin, Selian, Maruku and Ukiriguru, Tanzania, in 1991-1993.

	Katrin '91	'92	'93	Selian '92	Maruku '92	Ukirigiru '91	Across locations	Days to 50% silk*
Variety					(t/ha)			
Kito	3.1	5.3	3.9	2.1	3.2	4.0	3.5	56
Kito-SR	6.7	4.3	-	3.5	3.0	4.6	4.4	56
Katumani	3.3	3.8	2.9	3.0	3.2	4.0	3.4	56
Katu-SR	5.8	3.2	4.0	3.5	4.0	5.3	4.3	56
TMV-1	7.1	7.4	5.5	3.8	3.5	6.6	5.7	65

* Means across 11 locations during 1992 and 1993.

Management Solutions to Low-N in NMRP

One important objective of the NMRP is the development of improved management practices for all the agro-ecological zones. Accordingly, studies have been conducted investigating the following topics:

1. Intercropping and related cropping systems.
2. Fertilizer response on-station and on farmers' fields.
3. Nitrogen x planting time interaction effects on maize yield.

The cumulative results of these studies led to publication of the "Maize Production Handbook" for Tanzania, and this year a maize production guide for the eastern zone was finalized. With the escalating price of chemical fertilizer and other inputs, there is a need for N-use-efficient genotypes which have high yield *per se* at both high and low N levels. As a complement to N-use efficient genotypes, new management strategies are required. The following studies need to be conducted to provide some management solutions to low levels of soil N:

1. On-farm trials using farm yard manure with or without mineral supplementation.
2. On-farm trials using rotational green manuring with *Crotalaria*, etc.

Future Plans

Due to various constraints, which include meager government research funds and a lack of proper facilities, the commencement of rigorous breeding programs for drought tolerance and N-use efficiency by NMRP is not possible in the near future. However, because drought is a serious problem mentioned in almost every farmer crop assessment study, NMRP plans to do the following:

- Collaborate with CIMMYT, IITA and other national maize programs in evaluating tolerant germplasm and superior varieties in order to identify drought tolerant varieties that could be released to farmers.

- Evaluate drought tolerant materials received from CIMMYT, Mexico, in 1994/95. These have been increased and included in the Tanzania Maize Variety Trials for lowland areas. Another small trial will be conducted under stress levels controlled by irrigation applications at Ilonga.
- Collaborate with CIMMYT, Abidjan and IITA in evaluation of materials selected for N-use efficiency and which also have streak resistance. A request for such germplasm has been made and evaluations will probably commence in 1996/97.
- Collaborate on agronomic studies evaluating soil fertility-enriching rotations and water conservation methods. The following trials will be conducted in collaboration with CIMMYT, Nairobi:

1. Influence of tillage and residue management on soil fertility and maize grain yield under low input levels.
2. Effect of herbicides and other management factors on weed control under reduced tillage.
3. Effect of maize/cowpea intercropping on the control of *Striga asiatica*.

Based on the efficient breeding schemes utilized by both NMRP breeders and CIMMYT scientists in Mexico, and sub-stations in Africa, it is hoped that high-yielding drought-tolerant varieties efficient in nitrogen use will be made available to farmers in Tanzania to increase and stabilize maize production.

Acknowledgments

On behalf of the NMRP, Tanzania, I am grateful to CIMMYT for inviting and sponsoring me to attend this important symposium. My participation will greatly enhance our breeding activities in general and drought/N-use efficiency activities in particular. The continued support and cooperation of CIMMYT and its sub-programs in Africa is highly appreciated.

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Drought and Low N in Zambia:
The Problems and a Breeding Strategy

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Abstract

Zambia is among the countries in the southern Africa region that has suffered from severe drought in three out of the last four seasons, the worst having occurred during 1991/92. The drought resulted in low production of maize, the staple food of the country, necessitating imports of the commodity. Low maize production was also exacerbated by a reduction in fertilizer usage, a result of removal of fertilizer subsidies. The solution in the agricultural sector has been to advocate crop diversification to encourage the growing of crops that are drought tolerant and those that can grow under low N or without additional fertilizer application. The latter can have detrimental effects of depleting soils through mining of nutrients. Since maize remains an important crop, efforts should be made to breed varieties that are drought tolerant or can use N efficiently. The Maize Research Program in Zambia has not initiated a breeding program for drought and nitrogen use efficiency (NUE) as such. The program uses earliness as a drought escape mechanism. Selection of drought tolerant genotypes has been done in drought years and areas because of the lack of controlled environments for drought work. Collaboration with CIMMYT has resulted in selection of material from its drought tolerant populations that are undergoing population improvement and are being used to develop inbred lines. Similarly, populations from the NUE project have been obtained recently from CIMMYT and are being used in the breeding program. As an additional strategy, the performance of finished products (including released varieties) is being evaluated under low and high N conditions, with the hope of identifying the most NUE varieties.

Maize is the most important cereal in Zambia. Per capita consumption of maize has risen from 145 to 170 kg per annum between the 1970s and the late 1980s (FAO, 1994). Almost 90% is for direct human consumption, with livestock and industry taking up the rest (CIMMYT, 1994). The area under production has fluctuated in the past 10 years between 500,000 and 800,000 hectares, except in 1991/92 when area went under 500,000 (Table 1). In general, production has declined since the late 1980s. Several factors are responsible for this, including poor rainfall and reduced fertilizer use – mainly N – due to high fertilizer prices.

Maize is grown in all three agro-ecological regions of the country. Region I has a mean annual rainfall between 600 and 800 mm (Government of the Republic of Zambia, 1991). It is characterized by short growing seasons due to low and poorly distributed rainfall. Some parts of the region can experience up to 50 days of drought. The soils have a high sodium and salt content, causing problems for agriculture. Other chemical limitations include acidity, low nutrient reserves and retention capacity.

Table 1. Area, production and fertilizer consumption figures for maize in Zambia.

	Area	Production	Fertilizer consumption
Year	(ha)	('000 t)	(t)
1984/85	576,000	1,214	
1985/86	532,000	1,427	198,633
1986/87	659,000	1,003	242,991
1987/88	692,000	1,834	229,931
1988/89	797,000	1,997	249,900
1989/90	668,000	1,464	234,640
1990/91	579,000	1,448	216,888
1991/92	477,000	515	
1992/93	623,000	1,160	
1993/94	679,000	1,021	
1994/95	520,000	737	172,274

Source: Central Statistics Office and Ministry of Agriculture, Food and Fisheries.

Region II receives between 800 and 1000 mm of rainfall annually. This is the major agricultural area of Zambia. Dry spells are, however, common and these reduce yield, especially in sandy soils. The soils are characterized by low nutrient reserves, low nutrient retention capacity, acidity, low organic matter and low N content, all limiting crop production.

Region III receives annual rainfall exceeding 1,000 mm. Although rainfall is adequate, crop production may be limited by the low number of sunshine hours. In addition, the soils are deficient in nutrients, and their capacity to retain nutrients is severely limited. These soils are generally high in exchangeable Al and Mn, which are toxic to most cultivated plants including maize. About 3% of the region, in scattered places, has soils that are relatively well supplied with exchangeable bases.

The objectives of this paper are to review the effects of drought and low N on maize production and to discuss breeding activities undertaken to ameliorate these problems.

Problems of Drought and Low N

Drought has had an adverse effect on the Zambian economy. In recent years, the country was severely hit by drought in 1991/92, followed by partial drought during 1993/94 and 1994/95 (Table 2). Reduced production and the importance of maize as a staple food necessitated imports of the commodity. In the 1994/95 season, the area harvested was reduced by 23% from 520,165 to 357,938 ha, primarily as a result of drought (CSO/MAFF, 1995). The drought also derailed maize market reform programs that were being implemented to avoid shortages and price increases (Howard and Mungoma, 1996).

Compared to other countries in the region, Zambia has had high adoption rates of fertilizer recommendations. A successful extension campaign on the use of improved seed (mostly hybrids) and fertilizer convinced farmers of the need to adopt these technologies (Howard and Mungoma, 1996). Trends in fertilizer use increased even more with the introduction of fertilizer subsidies in 1971/72 (Table 1), 90% of which was used on maize (Williams and Allgood, 1991). However, with the removal of subsidies between 1988 and 1993, a decline in fertilizer use and in the area planted to maize was observed. Planting maize with fertilizer was no longer profitable for some farmers and fertilizer applications to maize were either reduced or farmers planted other crops. Fertilizer:maize price ratios increased from 0.9:1 in 1986 to 2.7:1 and 1.9:1 in 1993 and 1994, respectively (Howard and Mungoma, 1996). During the 1994/95 season, estimated demand for fertilizer was 225,000 mt (CSO/MAFF, 1995). However, less than 172,000 mt were finally used because demand for fertilizer was less than predicted. The reduced demand was induced by the decline of the credit system, normally a sure source of capital for the purchase of fertilizer and other inputs. Rains in the current season 1995/96 have been very good, but severe shortage of finance for small holders has limited farmer access to seed and fertilizer and is expected to cut maize production significantly (Reuters, 20 December, 1995).

Breeding Strategies for Drought

Breeding for drought tolerance is one of the biggest challenges for any breeding program. The maize breeding program in Zambia has not used sophisticated methodologies to achieve this objective due to lack of resources. Nevertheless, four strategies have been used by the program, viz., the use of earliness as a drought escape mechanism, testing of material in drought prone areas, use of anthesis-silking interval as a

Table 2. Comparative annual rainfall figures (mm) for Zambia (1984-1994).

	Region I			Region II				Region III
Year	Livingstone	Gwembe	Siavonga	Golden Valley	Choma	Msekera	Nanga	Misamfu
1984/85				772	815	1044	639	1364
1985/86				989	1048	1130	769	1249
1986/87				687	712	925	644	1584
1987/88				748	726	1050	585	1427
1988/89				1040	1017	1180	1045	1267
1989/90				689	1067	1108	737	1314
1990/91	236			834	598	779	666	1323
1991/92†	509	475	433	633	723	825	507	1235
1992/93	666	916	308	950	791	1337	767	1344
1993/94†				614	537	545	555	1255

Source: Department of Meteorology. † Drought years.

trait for drought tolerance selection and collaboration with well established drought breeding programs such as those at CIMMYT to obtain drought tolerant material. A proposal under the Maize and Wheat Improvement Research Network (MWIRNET) for SADC on breeding for drought tolerance is under way and Zambia is one of the collaborating partners.

Use of Earliness

The program has released two open-pollinated varieties and five hybrids of early maturity (100 to 140 days). These are recommended for the drought prone Region I and Region II. These varieties have performed well during drought years as seen by the data from 1991/92 (Table 3).

Anthesis-Silking Interval (ASI)

Selection with an emphasis on short ASI has resulted in varieties that are more tolerant to stress, including drought stress. These late maturing varieties have the additional advantage to be less prone to lodging as compared to the check entry MM 752, a version of SR 52 (data not shown).

Table 3. Medium maturity maize trial, 1991/92 at Golden Valley. Rainfall: 633 mm.

Variety	Yield
	(kg/ha)
MM 501	2543
MM 502	3603
MM 504	2768
MM 441	4233
MMV 400	2237
Pool 16	1474
Mean	2810
CV	28
LSD (0.05)	1290

Source: 1991/92 Maize Program Annual Report.

Collaboration with CIMMYT

Collaboration on drought began during the 1989/90 season with the conducting of the International Progeny Testing Trial (IPTT) on DTP (Drought Tolerant Population) and evaluation of two Preliminary Evaluation Trials (late and medium maturity) of drought tolerant material. The trials were delivered late, consequently they were planted in early January. The recommended planting time is mid-November. However, the trials experienced a three-week dry spell which created good selection conditions for drought tolerance. Some S_1 progenies from the IPTT yielded as much as 3,000 kg/ha. Some of these progenies were later recombined to form the local DTP version which has since been undergoing population improvement. In addition, inbred lines are being developed from this population. More drought tolerant populations have been obtained from CIMMYT Mexico and Zimbabwe. These have been evaluated and some are undergoing population improvement, including ZM 601, Pop 101 and Pool 16 Sequía.

Table 4. Maize area in relation to other crops.

Crop	Area planted (ha) 1993/94	Area planted (ha) 1994/95
Maize	679,355	520,165
Sorghum	55,245	40,365
Millets	82,302	73,809
Paddy rice	7,177	9,746
Sunflower	31,079	32,433
Soybean	25,447	21,651
Mixed bean	48,599	41,462
Cotton	50,067	35,200
Tobacco	2,973	6,350

Source: Central Statistics Office and Ministry of Agriculture, Food and Fisheries.

Breeding Strategies for Low N

Breeding for low N environments is in the initial stages. Methodologies for breeding nitrogen use efficient (NUE) maize are now being developed. The program wishes to adapt practical methods that can easily be implemented. Complicated laboratory or greenhouse methods with results that cannot be replicated in the field will be avoided. Evaluation of all materials under both high and low fertility status is not practical either because fewer materials can be evaluated. The program has relied instead on the theory that the better performing selections at optimal fertility levels should be better performing at sub-optimal levels, too. Hence, the program concentrated on evaluating finished products (including released varieties) under high and low management levels. Collaborative work with the Soil Fertility group will determine which of the released varieties use N more efficiently, using the N^{15} technique.

Other strategies being employed include acquiring NUE populations from other programs and collaboration on NUE research. The program has obtained ZM 609 from CIMMYT Zimbabwe, which was developed as a NUE population. Finally, MWIRNET has begun a breeding project for NUE maize and Zambia will be collaborating.

Discussion

The two topics of this symposium could not have been discussed at a better time for Zambia. Despite the agricultural sector's call for more crop diversification as a mean of solving the problems of drought and low N, maize continues to be an important crop (Table 4). Breeding methods to obtain drought and low N tolerant material should be simple and easily adaptable. National programs that cannot successfully carry out such programs will have to rely on international organizations like CIMMYT that have more resources. The program in Zambia has tackled the problems of drought through the use of early-maturing material, drought tolerant material selected during drought years, introductions of drought tolerant material, and through selection for drought tolerance related traits and testing in drought prone areas.

Less work has been accomplished in the area of low N tolerance. New NUE breeding materials are being obtained. At the same time, finished products are being tested for their performance under low N and for their NUE. Through the MWIRNET, drought and low N tolerance are going to receive special attention.

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A Commercial Sector Approach to Developing Tolerance to Low Fertility and Drought in Maize Adapted to Kenya

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Abstract

Although the bulk of maize seed sales by Kenya Seed Company are for intermediate and late maturity maize hybrids, these are grown on only 20 to 30% of the land area. The rest of the area receives scant and irregular rainfall in seasons as short as 60 days. In 1985, the seed company initiated a breeding program to develop maize hybrids for the vast arid and semi-arid regions of Kenya, areas which support 50% of the population. This target environment receives 250 to 500 mm of rain per season. Since use of fertilizer was known to be low, selection and evaluation was done at fairly low fertility levels. Initial work involved screening of early maize varieties in dry areas, and later, evaluation of crosses among selected varieties. Selected S_1 lines from these varieties were used to form heterotic drought-tolerant populations KSDA and KSDB. The populations are being improved using S_1 reciprocal-recurrent selection. This selection system was ideal in terms of flexibility. It can be used to generate open-pollinated varieties, topcrosses, and assorted hybrid types. Selection emphasized grain yield, but other observable traits thought to reflect tolerance to moisture stress and low soil fertility were considered. Dryland hybrids DH01 and DH02 were recommended for release in 1995. The mean performance of DH01 was 4.8 t/ha, about 48% above Katumani Composite B (KCB), based on testing over six years in 36 sites. This hybrid took 56.8 days to flower, while KCB took 53.3 days. DH02 gave a mean grain yield of 4.5 t/ha at 57.0 days to flower. Results to date indicate good opportunity to develop even better varieties using this comprehensive breeding system. Water management of irrigated trials, though expensive, would offer more precise information.

The principal limitation to crop production in the arid and semi-arid areas of Kenya is water supply. About 70% of the maize area in Kenya suffers from moisture stress in addition to low soil fertility. The country can broadly be categorized as 20% non-arid, 30% semi-arid and 50% arid. A detailed agro-climatic zoning for maize was recently produced using geographic information systems (GIS). Long rains in the maize target environment begin March 20th and end May 30th. The rainy season is 60 to 70 days with stress periods occurring during crop germination and grain filling stages. The short rains begin October 20th and end December 25th and have a season duration of 60 to 65 days. Stress periods mainly occur during flowering and grain filling.

Mean annual rainfall (Fig. 1) ranges between 500 and 800 mm, while seasonal rainfall ranges between 200 and 400 mm. Seasonal variability is erratic and in some parts the seasonal rainfall does not exceed 250 mm. Severe drought occurs usually once in every three seasons. Knowledge of these probabilities has been useful for determining breeding and production strategies under drought conditions (Edmeades et al., 1989).

The following are two of Kenya Seed Company's objectives:

1. To establish a long-term selection strategy for developing early-maturing drought tolerant maize varieties.
2. To develop high yielding drought tolerant maize varieties for the arid and semi-arid regions of Kenya.

Materials and Methods

Early local germplasm and introduced germplasm, mainly from CIMMYT, was subjected to vigorous screening as shown below:

1985 season A
Screened germplasm for agronomic performance, especially days to flowering, disease and lodging resistance, leaf senescence, anthesis-silking interval, grain yield, etc. Identified 10 best populations.

1985 season B
Grew 5,000 plants from each selected population and selfed selected plants. Harvested the best 50 plants from each population, S_1 seed.

1986 season A
Evaluated these 500 S_1 lines under drought stress (used irrigated nursery at Sigor, 1 row plots and 2 replicates) and selected 250 S_1 lines tolerant to drought.

1986 season B
Topcrossed these 250 S_1 lines to two genetically-diverse locally-adapted synthetics (Katumani Synthetic VII and Katumani Synthetic VIII).

1987 season A
Evaluated the 500 topcrosses in two sets at 4 locations (1 row plots, 2 replicates, 16 × 16 lattice design with six checks). Identified 25 best S_1 lines in each tester group.

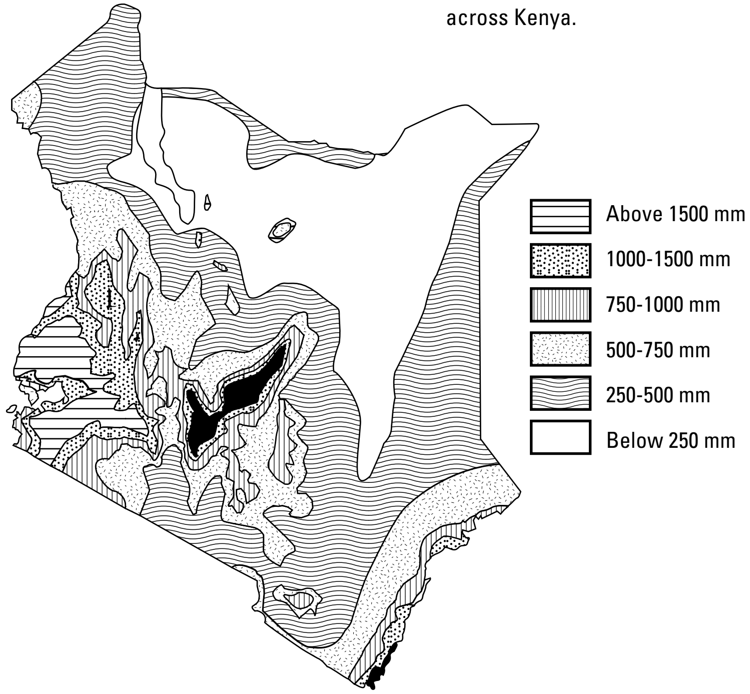
1987 season B
Recombined within each group forming two populations, Kenya Seed Drought Tolerant Populations A and B (KSDA and KSDB).

1989 season A
Using the comprehensive breeding system described by Eberhart et al. (1967) initiated a reciprocal recurrent selection program using S_1-testing. Established 5,000 plants from each population, KSDA and KSDB. Selfed 500 selected plants from each and identified the best 250 (5%), S_1 seed.

1989 season B
Testcrossed these 250 S_1 lines from KSDA to KSDB and 250 S_1 lines from KSDB to KSDA.

1990 season A
Evaluated the 500 testcrosses. Identified 25 best S_1 lines (10%) from each population. Recombined by random-mating among the selected lines to form cycle 1 of KSDA and KSDB. The better S_1 lines were saved and used for making topcrosses, double crosses, etc.
The testing sites most commonly used and most typical of the target environment were Katumani, Kitui and Kiboko. Their rainfall distribution and evapotranspiration (ET) are illustrated in Figure 2.

Figure 1. Mean annual rainfall distribution across Kenya.



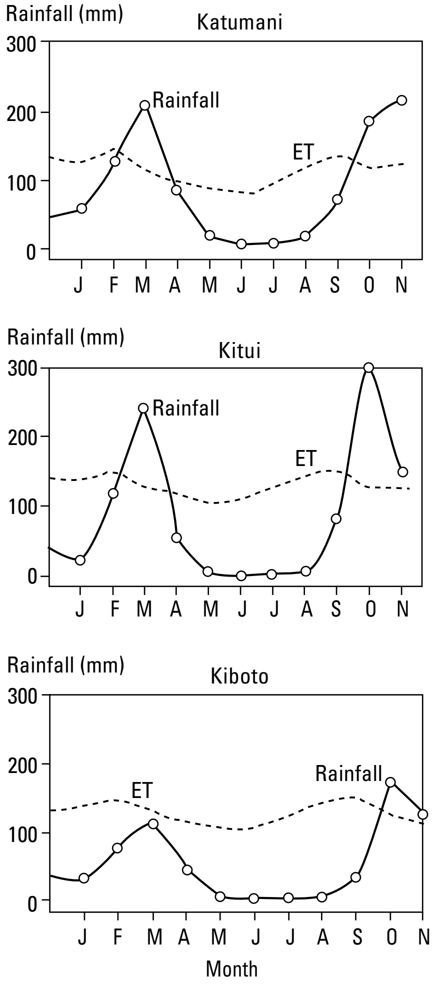


Figure 2. Annual rainfall distribution and evapotranspiration (ET) for three testing sites in Kenya.

Results

Mean grain yield and other agronomic characters of drought tolerant hybrids DH287SR and DH891SR and two commercial varieties are presented in Table 1. The six years of data ranked DH287SR first with a mean grain yield of 4.8 t/ha, followed by DH891SR with 4.5 t/ha. The best check, KCB gave a yield of 3.3 t/ha. DH287SR silked at 59.4 days, DH891SR at 61.0 days, KCB at 58.5 days and DLC1 at 58.3 days. Thus, the new hybrids were slightly later maturing and considerably higher yielding than the checks. Additionally, they were more resistant to leaf blight and rust and had less root lodging than the checks.

Grain yield and stability indicators of all 13 varieties tested in the Early Maize National Performance Trial during 1994 long rains are presented in Table 2 (on p. 90). DH891SR tended to be higher yielding and had a lower coefficient of variation than KCB, indicating that it was more stable across environments. DH287SR yielded slightly less than DH891SR, but had a lower regression coefficient, indicating that it was higher yielding under stress conditions.

Table 1. Mean grain yield and other agronomic performance of DH287SR and DH891 in advanced yield trials compared to DLC1 and KCB for six years in 36 environments.

Variety	1994	1993	1992	1991	1990	1989	Mean
DH287SR							
Grain yield (t/ha)	5.39	5.10	4.46	5.32	3.90	4.71	4.82
Root lodging (%)	14.2	12.4	21.8	9.2	3.9	11.1	12.1
Days to flower	52.3	55.9	61.5	54.2	61.5	55.2	56.8
Ear height (cm)	102		90	98	105	85	96
Blight score†	0.78	0.75	0.78	0.83	0.75	1.17	0.83
Rust score†	1.11	0.50	0.89	0.89	1.25	1.50	1.02
DH891SR							
Grain yield (t/ha)	5.34	4.92	3.86	5.14	3.36	4.51	4.52
Root lodging (%)	15.3	19.0	26.7	9.0	5.3	11.4	14.4
Days to flower	54.7	55.1	61.8	54.2	60.7	55.3	57.0
Ear height (cm)	83		83	96	104	83	90
Blight score†	0.78	0.83	0.89	0.89	0.58	1.25	0.87
Rust score†	1.22	0.58	1.00	0.78	1.08	1.67	1.06
KCB (check)							
Grain yield (t/ha)	3.53	3.65	2.79	3.67	3.22	2.64	3.25
Root lodging (%)	24.5	18.2	27.5	13.1	8.9	25.4	19.6
Days to flower	48.8	50.8	58.4	51.5	57.3	52.7	53.3
Ear height (cm)	89		81	95	104	77	89
Blight score†	0.61	0.67	1.00	3.67	0.75	1.50	1.37
Rust score†	1.06	0.50	0.83	0.87	1.33	1.67	1.04
DLC1 (check)							
Grain yield (t/ha)	2.38		1.74	3.21		2.67	2.50
Root lodging (%)	35.3		20.5	21.8		27.0	26.1
Days to flower	47.6		57.8	49.9		51.7	51.8
Ear height (cm)	84		68	81		73	76
Blight score†	0.83		1.33	1.00		1.00	1.04
Rust score†	0.94		0.78	1.17		1.58	1.12
Number of test sites.	7	6	6	7	5	5	36

† 0 to 5 scale; 0 is excellent and 5 is poor.

Discussion

The comprehensive breeding system adopted offered opportunities for the exploitation of heterosis existing within and among local and exotic germplasm. The system also offered a wide range of possible hybrid types. The first dividend was the release of DH287SR (as DH01) a varietal cross hybrid and DH891, a topcross hybrid (released as DH02). It was observed that the commercial checks used, KCB and DLC1 were earlier maturing and lower yielding. The new maize hybrids were more stable across environments and were higher yielding under stress.

In conclusion, these results indicate that the breadth of opportunity to develop drought tolerant maize varieties in Kenya is high. A more efficient approach would be desirable; i.e., approaches that include soil-water management techniques in irrigated nurseries, selection focused on genotypes with short anthesis-silking interval (Edmeades et al., 1990) and a way of monitoring levels of available soil nitrogen. Finally, introgression of CIMMYT germplasm tailored to challenge both biotic and abiotic stresses is expected to result in better hybrids.

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Table 2. Stability parameters of 13 early-maturing maize varieties tested in the semi-arid regions Katumani, Kiboko, and Kitui in the 1994 Long-Rains National Performance Trial.

Variety	Grain yield (t/ha)	CV (%)	b	sd	R^2
DH891SR	3.17 a	5.86	1.17	+0.11	0.99
DH287SR	2.87 ab	19.17	0.74	+0.32	0.84
DH194SR	2.78 ab	24.71	0.40	+0.40	0.49
DH394SR	2.77 ab	4.26	1.48	+0.07	0.99
IC 25	2.62 abc	2.79	1.09	+0.05	0.99
KAAP 3DR	2.46 abc	4.44	1.07	+0.06	0.99
KCB Commercial	2.29 abc	24.84	1.13	+0.33	0.92
KVC 4522	2.27 abc	11.70	0.85	+0.16	0.97
KAVC 9034	2.21 abc	13.46	1.37	+0.17	0.98
IC23	2.20 abc	12.63	1.16	+0.16	0.98
KATC9024	1.91 bc	11.10	1.06	+0.12	0.99
Makueni Comp.	1.90 bc	3.51	0.64	+0.04	0.99
Kat. Mpya	1.70 c	19.50	0.86	+0.19	0.95

Means within a column followed by the same letters are not significantly different according to SNK ($P \leq 0.05$)

Fertilizer Nitrogen Recovery Efficiency in the Sub-Humid Highlands of Central Kenya

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Abstract

Nitrogen is one of the major soil nutrients limiting maize production in the sub-humid highlands of Central Kenya. A field experiment was designed to determine fertilizer N recovery by maize, measured by the ^{15}N isotope technique in two major soil types. Fertilizer N recovery in above-ground parts was low, less than 20% in both soil types. The presence of farmyard manure tended to increase fertilizer N recovery in the acidic andic humic Nitisol but had no effect on fertilizer N recovery in near neutral humic Nitisol. Less than 3% of N applied in the first season was recovered in the second season. There is evidence of N leaching to the lower soil horizons. In the first 0.5 m of top-soil, there was approximately 25 kg N ha^{-1} in the acidic andic Nitisols, while between 0.5 and 2.5 m there was an accumulation of more than 450 kg N ha^{-1}. In view of low N recovery and high N leaching, it is important to design strategies for more efficient N utilization by maize and recycling of the large quantities of N accumulated in lower soil horizons. Leaching of N to lower soil horizons may be a greater problem than anticipated by researchers and farmers, or conversely may constitute a large reserve of N.

The sub-humid highlands of central Kenya are characterized by a diversity of farming systems, with coffee, tea and dairying being the major cash enterprises. The area has a bimodal rainfall distribution, with long rains (LR) from mid-March to July and short rains (SR) from October to December. Annual rainfall ranges between 1250 and 1740 mm, with 65% of this rainfall occurring during the LR and the rest during the SR. Seasonal precipitation varies between years, and its distribution also varies within the highlands. There are two major soil types in the region: ando-humic Nitisol and humic Nitisol. In the USDA classification system, these soils represent orthoxic Palehumult and typic Palehumult, respectively (Siderius and van der Pouw, 1980). Both are derived from rich basic igneous rock (FURP, 1987). The two constitute more than 70% of the soils in Kenya's central highlands (Jaetzold and Schmidt, 1983).

Maize is the main food crop grown in this area. One of the major nutrients limiting maize production is nitrogen. Farmers use very low rates of inorganic fertilizer N to improve crop productivity. One survey revealed that less than 30% of farmers interviewed use N fertilizer on maize, applying it at rates between 15-25 kg N ha^{-1}, while farmyard manure (FYM) is being used by more than 75% of farmers (Hassan et al., 1993). The average maize grain yield is approximately 1.2 t ha^{-1}. The region is a net importer of maize, importing from other parts of the country. Acidic soils of Kavutiri are characterized by low pH (less than 4.5) and low exchangeable bases, and the application of lime and/or FYM may therefore improve N use efficiency.

This study analyzes the effects of N fertilizer, farm manure and lime application on maize yields in the sub-humid highlands of Central Kenya over nine years. It further assesses N uptake, fertilizer N recovery efficiency, the distribution of mineral N in the soil and long-term changes in soil organic carbon to better understand effects of N fertilization and manure application on the sustainability of maize production systems.

Materials and Methods

The experiment was conducted on the eastern slopes of Mount Kenya in Embu district using two trial sites: Kavutiri and Embu. It was conducted for nine years starting in 1987 and the same treatments were applied to the same plots in each of the nine years. The Kavutiri trial site is located at 0° 25´ S. and 37° 30´ E., at an elevation of 1,700 masl. Mean annual rainfall is 1,736 mm, and mean annual temperature is 18 °C. Soils are acidic (pH < 4.5); low in exchangeable potassium, calcium and magnesium; high in exchangeable aluminum; and high in organic carbon. They are classified as ando-humic Nitisols. The site is typical of the tea and coffee agro-economic zone (Jaetzold and Schmidt, 1983).

The Embu trial site is located at 0° 30´ S. and 37° 27´ E., at 1500 masl, and has a mean annual rainfall of 1252 mm and a mean annual temperature of 20 °C. Soils are near neutral in pH (pH 5.8-6.6); moderate in exchangeable potassium, calcium and magnesium; and high in organic carbon. They are classified as humic Nitisols, and are representative of soils in the main coffee zone (Jaetzold and Schmidt, 1983).

Different factorial experiments were conducted at the two sites. The factors under study at Kavutiri were nitrogen fertilizer (N) at 0 or 50 kg N ha^{-1}, agricultural lime (L) at 0 and 1.0 t ha^{-1}, and air-dried farmyard manure (FYM) at 0 and 5.0 t ha^{-1}. At Embu, N was applied at the same rates and FYM was applied at four rates, 0, 2.5, 5.0 and 7.5 t ha^{-1}. Treatments were arranged in a randomized complete block design with two replications per site.

Maize hybrids H614 and H512 were used at Kavutiri and Embu, respectively. They were grown during the short and the long rains. Plants were separated by 0.75 m between rows and by 0.25 m within rows. An experimental plot consisted of eight 6 m rows with a harvested area of four 5 m rows. Lime was broadcast and worked into the soil 4 weeks prior to planting. Farmyard manure was applied in the planting holes at sowing time. Two weeks after crop emergence the N fertilizer was applied beside the hills using a calibrated measure.

Within the 50 kg N ha^{-1} plots and during the 1994 LR season, labeled ^{15}N fertilizer was applied on 2.25 m^2 microplots at the same rate and time that the macroplots received unlabelled N fertilizer. The unlabeled fertilizer was in the form of calcium ammonium nitrate. The labeled ammonium nitrate fertilizer had a ^{15}N enrichment of 5.3 atom %. At harvest of the 1994 LR and 1994 SR crops, total above-ground dry matter was determined, samples of plant fractions (grain, cob and stover) from the microplots were dried, and total N concentration and ^{15}N abundance were measured by mass spectrometry.

Nitrogen uptake was computed as the product of N concentration and total dry matter for a particular plant fraction. Nitrogen recovery efficiency for applied N fertilizer was estimated using the following relationship (Rao et al., 1992).

$$\text{N recovery efficiency (\%)} = \frac{\text{atom \% excess in plant}}{\text{atom \% excess in fertilizer}} \times \frac{\text{N uptake (kg N ha}^{-1}\text{)}}{\text{N rate applied (kg N ha}^{-1}\text{)}} \times 100$$

At the end of the 1994 LR season soil samples were taken, and at Kavutiri, soil pH in the topsoil was determined. In plots that received N fertilizer, concentrations of soil mineral N were determined from soil samples taken at 0.12 m intervals down to a depth of 2.5 m. At Kavutiri and Embu, soil organic matter concentration was determined in the topsoil in 1987, 1993 and 1996.

Results

Application of fertilizer N increased maize grain yield significantly ($P \leq 0.05$) at both Embu and Kavutiri (Table 1). It is important to note that whereas the increase in grain yield at Embu was 38%, the increase in the acidic soils of Kavutiri was about 120%.

Application of 5.0 t ha^{-1} of FYM did not significantly increase grain yield at Embu, but a combination of

Table 1. Effect of nitrogen fertilizer (N) application on maize grain yield (nine-year means; kg ha^{-1}).

Treatment	Embu	Kavutiri
0 kg N ha^{-1}	2039	1467
50 kg N ha^{-1}	2810	3219
SE	109	156

fertilizer N at 50 kg ha^{-1} and 5.0 t ha^{-1} of FYM improved maize yield by 51% over the FYM treatment and by about 18% over the N fertilizer treatment (Table 2). In the acidic Kavutiri soils there was an increase of 1.2 t ha^{-1} in grain yield due to the FYM application, and when FYM and N fertilizer were applied together there was an increase of 1.6 and 1.0 t ha^{-1} above the FYM and N fertilizer treatments, respectively (Table 2).

Lime was applied only to the acidic soils of Kavutiri. Liming alone increased maize grain yields by more than 200% (Table 3). A combination of lime and N fertilizer increased the grain yield by 105% and 142% over the individual lime and N fertilizer treatments, respectively. Application of lime also increased the soil pH by 1.5 units in the plots where no N was applied. Soil pH increased by 1.2 units where lime and N fertilizer were applied together.

Table 2. Effect of nitrogen fertilizer (N) and farmyard manure (FYM) application on maize grain yield (nine-year means; kg ha^{-1}).

Treatment	Embu	Kavutiri
0 kg N ha^{-1}	1648	878
0 kg N ha^{-1} plus 5 t ha^{-1} FYM	2009	2056
50 kg N ha^{-1}	2560	2675
50 kg N ha^{-1} plus 5 t ha^{-1} FYM	3026	3673
SE	153	219

Table 3. Effect of nitrogen fertilizer (N) and lime (L) application on maize grain yield (kg ha^{-1}) and soil pH on an acidic humic Nitisol at Kavutiri, Kenya.

Treatment	Maize grain yield	Soil pH
0 kg N ha^{-1}	715	4.2
0 kg N ha^{-1} plus 1 t ha^{-1} L	2218	5.7
50 kg N ha^{-1}	1882	4.7
50 kg N ha^{-1} plus 1 t ha^{-1} L	4556	5.4
SE	219	

There was no significant difference between the total above-ground plant N in plots receiving fertilizer N alone or in combination with FYM at Embu (Table 4). In both treatments, total N uptake of the above-ground plant parts was approximately 100 kg N ha^{-1}. In the acidic Kavutiri soils, there were differences ($P \leq 0.05$) in N uptake between plots that received N fertilizer alone and those that received a combination of fertilizer N and FYM. Farm yard manure increased N uptake by more than two fold.

Fertilizer N recovery efficiency in the above-ground plant parts of maize was low, being less than 20% at both trial sites (Table 4). At Embu, N recovery efficiencies were 18 and 16% in the N fertilizer and N fertilizer plus FYM treatments, respectively. The Kavutiri site had lower N recovery efficiencies of 6 and 13% for the N fertilizer and N fertilizer plus FYM treatments, respectively. Only 2% of the labeled fertilizer applied during the LR was recovered during the SR (data not shown).

Nitrogen was apparently leached to lower soil horizons (Fig. 1). At Kavutiri in plots that received N fertilizer, there was approximately 25 kg N ha^{-1} in the first 0.5 m of top soil. Between 1.0 and 2.5 m there was an accumulation of about 450 kg N ha^{-1}. Ten percent of the labeled fertilizer was present in the soil between 1.0 and 2.0 m in depth.

Table 4. Total N uptake and N recovery efficiency from the application of 50 kg N ha^{-1} and either 0.0 or 5.0 t ha^{-1} of farmyard manure (FYM). Data are from the 1994 long rains season in Kenya.

	Embu		Kavutiri	
FYM =	0 t ha^{-1}	5 t ha^{-1}	0 t ha^{-1}	5 t ha^{-1}
Mean ^{15}N (atom % excess)	0.44	0.38	0.39	0.33
Total plant N(kg N ha^{-1})	101.1	99.4	37.0	95.5
Fert. N recovery efficiency (%)	17.9	16.1	5.9	12.8

Soils at Embu and Kavutiri were fairly high in soil organic matter. At the time of the trial's inception, soil organic carbon was 2.42 and 3.75% for the Embu and Kavutiri sites, respectively (Table 5). Six years later, there was a mean decrease in soil organic carbon of 13% and 31% at Embu and Kavutiri, respectively. By the end of nine years of experimentation, the mean decrease in soil organic carbon was 16% for Embu and 41% for Kavutiri. For each sampling period there were no significant differences amongst the treatments.

Discussion

Nitrogen is one of the major soil nutrients limiting maize production in the humid highlands of central Kenya. Application of N fertilizer has been shown to increase maize grain

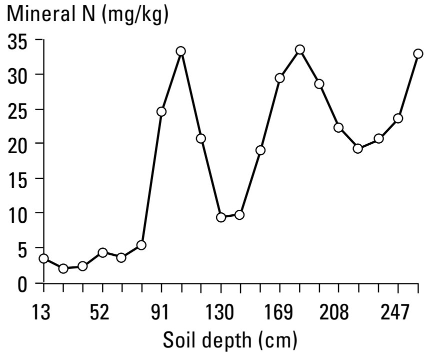

Figure 1. Mineral N at various soil depths in Kavutiri.

yield in the area (Jaetzold and Schmidt, 1983; Qureshi, 1990; Ayaga and Heinzamann, 1992; Woomer, 1992). In the current experiment, increases in maize grain yield of up to 120% clearly demonstrate the importance of soil N in increasing maize production.

The use of farmyard manure can be viewed as an important pathway for recycling soil nutrients. Its usefulness as a source of N is mainly determined by its quality, which in turn governs the rate of N mineralization, and hence the N released to the growing crop (Swift et al., 1979; Murwira et al., 1993). In the present study, the large increases in maize grain yield in the acidic soils of Kavutiri could have been due to one or more of the following factors: the manure may have provided N directly through mineralization; provided other nutrients which are low in these soils, or may have reduced exchangeable aluminum to less toxic levels. Most likely a combination of these factors was responsible.

The benefits accrued from lime application to acidic soils have been adequately demonstrated by several researchers (Kihanda and Ransom, 1988; Lungu et al., 1993). The more than three-fold increase in maize yield in the current study shows the importance of liming acidic soils in the region. This increase in grain yield may have been due to a reduction in exchangeable aluminum to less toxic levels, and therefore the creation of a more favorable environment for microorganisms to mineralize the soil organic matter (Lungu et al., 1993).

The low N fertilizer recovery compared to the high total plant N implies that more than 80% of the plant N is derived from other N sources. Nitrogen fertilizer recovery efficiencies of less than 25% have been reported for Kiboko (Pilbeam et al., 1995) and Kabete, Kenya (G.O. Ayaga, personal communication). One of the reasons advanced for the observed low fertilizer N recovery efficiency was the rapid mineralization of soil organic N with the onset of the rainy season. This quickly dilutes the contemporaneous addition of ^{15}N label, leading to poor fertilizer recovery efficiencies (Pilbeam et al., 1995).

The large quantities of mineral N accumulated below 0.5 m is likely to have been derived from N fertilizer applied in the nine years of experimentation and also from the mineralization of soil organic matter. In view of the low fertilizer N recovery and high N leaching, it is important to design strategies for more efficient N utilization and recycling of the large quantities of N accumulated in the lower soil horizons. Leaching of N to lower soil horizons may be a greater problem than anticipated by researchers and farmers, or conversely may constitute a large reserve of N.

Intensive agriculture has led to continuous cultivation of the land, and this has led to accelerated nutrient depletion, decline in soil organic matter, loss of physical structure and reduced crop productivity (Swift et al., 1989). In the present study, it was observed that during the nine years of experimentation, there was a decline in soil organic carbon of 16% and 41% at the Embu and Kavutiri trial sites, respectively. Larger decreases in soil organic carbon after several years of continuous cultivation have been reported in Kabete, Kenya (Qureshi, 1990; Swift et al., 1994), northern Zambia and the Mbeya region of Tanzania (Singh and Goma, 1993). These results suggest that there is an urgent need to focus our attention on soil organic matter maintenance and its improvement, which should lead to more sustained or increased crop productivity.

Table 5. Changes in percent soil organic carbon with years of cropping at Embu and Kavutiri, Kenya.

	Embu				Kavutiri			
Treatment	1987	1993	1996	Percent decrease	1987	1993	1996	Percent decrease
0 kg N ha^{-1}	2.45	1.99	1.93	21	3.76	2.61	1.99	47
0 kg N ha^{-1} plus 5 t ha^{-1} FYM	2.39	2.17	2.07	13	3.69	2.73	2.35	36
50 kg N ha^{-1}	2.48	2.12	2.03	18	3.74	2.67	2.30	39
50 kg N ha^{-1} plus 5 t ha^{-1} FYM	2.37	2.14	2.08	12	3.78	2.33	2.20	42

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Use of Simulation Models to Predict the Optimum Duration of Maize Cultivars Adapted to the Rift Valley of Ethiopia

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Abstract

Maize has become one of the most important food crops in the Rift Valley region of central Ethiopia. Due largely to drought stress, maize yields are usually less than 1 t/ha. This region has a bimodal rainfall pattern which is characterized by a short season with erratic rainfall beginning in early April, followed by the main rainy season starting in late June or early July. Farmers traditionally plant long duration local varieties during the short rains which must survive the drought stress in June and then mature during the main season. Early maturing varieties have been developed or introduced which can be planted at the beginning of main rains, thereby avoiding the prolonged period of stress between the two rainfall periods. CERES maize, a crop simulation model, was used to simulate the relative productivity of using a late maturing variety planted early and an early maturing variety planted late. Simulations were run using 8 years of weather data from Adamitulu and 10 years from Melkasa, both within the Rift Valley. Of the treatments simulated, planting an early-maturing variety like Katumani at the beginning of the long rains is the most stable for yield across years and sites. The long duration cultivar A210 planted early was not stable for yield but frequently out-yielded the other treatments by a significant margin. Germplasm development for the rift Valley should continue to focus on improving early-maturing types which can be planted at the beginning of the long rains, but should also look at developing later maturing, drought tolerant genotypes and improving management practices for early plantings in the short rainy season.

Maize has become one of the most important cereal crops in Ethiopia, where it is currently cultivated on more than 1 million ha (CIMMYT, 1994). Although second to teff (*Eragrotis teff*) in area planted, maize ranks first among the cereals in yield and production (Mulatu et al., 1993). Moisture stress is a significant constraint to production on about 40% of the area cropped to maize (Mohammed and Mulatu, 1993).

Within the moisture stress zone, the greatest research effort on maize has been carried out in the Rift Valley region of central Ethiopia. This zone is characterized by erratic rainfall which falls within two relatively distinct seasons. Katumani, an early-maturing maize cultivar is currently recommended for planting at the beginning of the long-rainy season (June - September). Research is continuing on developing other early-maturing varieties (Mohammed and Mulatu, 1993). Although the rainfall within the short-rainy season (March - May) is limited, farmers in the Rift Valley often plant longer-season maize varieties during the short-rains so that they can mature during the long rains. In most years, these plantings suffer severe stress. Longer season cultivars normally have greater yield potential in stress free environments than early-maturing varieties, and can provide extra production in stressed environments if the stress is not excessive.

Simulation models have been developed to allow testing of the effects of a range of management practices on crop growth using historical weather data, thus allowing multiple management options to be simulated without the expense of multiple years of field testing (Tsuji et al., 1994). Keating et al. (1992) used a modified CERES Maize model to predict the optimum duration of maize cultivars adapted to the semi-arid regions of Kenya. The objective of our study was to simulate the effect on yield and yield stability of maize cultivars with differing relative maturities planted at two dates using historical weather data from the Rift Valley region of Ethiopia. This information can help elucidate management and breeding strategies that can be deployed to optimize yield in this moisture-stress prone zone in Ethiopia.

Materials and Methods

The weather data used in this study were obtained from Melkasa, a major research station of the Institute of Agricultural Research (IAR) near the town of Nazret and from Adamitulu, about 70 km south of Nazret. Both sites are located in the Rift Valley (approximately 1650 m elevation). Ten years of weather data were used for the Melkasa site and eight years for Adamitulu. The CERES maize model within the DSSAT3 shell (Tsuji et al., 1994) was used to simulate the effect of length of maturity and planting date on maize yield and yield stability. A moderately deep (90 cm) sandy soil (IB00000011, from the soil catalog within the DSSAT3 program) was used to represent the soils of the Rift Valley. Two planting dates and two cultivars were compared in this study. The automatically determined planting dates were when the top 30 cm of the soil reached 50% moisture after April 19 and after June 18. It was assumed that there was no water in the profile prior to beginning the simulation.

The planting dates were similar to those that have been observed in the region of this study (Tilahun, 1995). The two maize cultivars used in the simulations were 'Katumani', an early-maturing variety developed and recommended for planting at the beginning of the long rains, and 'A210', an intermediate-maturing variety for which genetic coefficients are available and which has a similar growing cycle to that of 'A511', an open pollinated variety used in early plantings within the Rift Valley. All treatments received 50 kg of N as urea just prior to planting. The plant population used was 3.8 plants/m^2 in a 90 cm row spacing. Harvesting occurred automatically upon maturity of the crop. The water and nitrogen routines were turned-on during the simulation. It was also assumed that there was no residue application.

Results

Rainfall during the crop's growing cycle was on average greater at Adamitulu for the various planting dates and cultivar combinations (Table 1), the difference between the two sites tended to be larger for the early planted treatments. More precipitation was available for the later planted treatments at both sites, in comparison with the earlier planted treatments. In the early plantings, there were large differences in available seasonal precipitation between cultivars, with the later maturing A210 receiving significantly greater rainfall than Katumani. Averaged over seasons, the least precipitation (315 mm) occurred with Katumani planted early at Melkasa.

The highest average yield at Adamitulu, based on the simulations, was obtained with A210 planted early (Table 2). Moreover, A210 planted early most often out-yielded Katumani planted early, yielding substantially more in highly productive years like 1988 and 1989.

Table 2. Simulated grain yield (kg/ha) for two cultivars planted on approximately April 19 (early) and June 18 (late) using weather data from Adamitulu, Ethiopia.

	Early planted		Late planted	
Year	Katumani	A210	Katumani	A210
1983	760	790	3940	2900
1984	5820	6360	1820	1210
1985	1760	1790	4750	3140
1986	3840	3020	4790	2570
1987	1300	1240	3210	3250
1988	4450	6610	5220	6880
1989	4160	5000	380	570
1990	4937	3950	3590	2890
Mean	3380	3595	3463	2925
SD	1857	2262	1648	1868

Table 1. Seasonal precipitation during the simulation of two cultivars planted on two dates at Adamitulu and Melkasa, Ethiopia.

	Adamitulu				Melkasa			
Year	Katumani Early	A210 Early	Katumani Late	A210 Late	Katumani Early	A210 Early	Katumani Late	A210 Late
1982					198	448	575	661
1983	659	834	857	889	394	655	802	813
1984	438	566	566	566	242	369	499	499
1985	394	511	548	548	261	662	775	776
1986	444	549	619	620	410	531	627	637
1987	479	572	598	608	380	599	675	687
1988	232	367	486	555	279	448	623	638
1989	726	928	995	1011	333	614	673	683
1990	613	787	876	876	291	542	683	697
1991					365	631	720	728
Mean	498	639	693	709	315	549	665	681
SD	160	188	190	185	72	100	90	85

The lowest standard deviation for yield was achieved with Katumani planted late, suggesting that this treatment was more stable for yield. Compared to A210 planted early, Katumani planted late was more productive in four of the eight years. Late planted A210 had the lowest overall yield, only exceeding late planted Katumani in three seasons, and in two of these the advantage was very small.

Although average rainfall was less at Melkasa than at Adamitulu (Table 1), yields were generally higher (Table 3). The highest and most stable yield, based on the lowest standard deviation, was obtained with Katumani planted late. A210 planted early had the largest standard deviation for yield, probably as a result of the extremely low yield in 1991, and the extremely high yield in 1984. Nevertheless, A210 planted early had the highest yield of the four treatments in four of the ten years, a higher frequency than any other treatment. Although A210 planted late had a higher mean yield and a lower standard deviation than A210 planted early, it only outperformed Katumani planted late in three of the ten years.

Table 3. Simulated grain yield (kg/ha) for two cultivars planted on approximately April 19 (early) and June 18 (late) using weather data from Melkasa, Ethiopia.

	Early planted		Late planted	
Year	Katumani	A210	Katumani	A210
1982	2640	3800	4500	5160
1983	2780	2480	3120	3410
1984	5090	8430	5330	4100
1985	2360	2730	2170	1640
1986	3760	3440	2060	1810
1987	3460	2820	4770	4730
1988	4520	5130	4130	3600
1989	4500	5610	4660	4220
1990	1330	1430	5320	6420
1991	480	530	2720	2210
Mean	3090	3640	3879	3724
SD	1466	2274	1256	1525

Discussion

The yields arising from the simulations conducted in this study were generally quite high, considering the low rainfall at these two sites, and may indicate that the model may over-predict growth under extremely dry conditions. Validation of these results with field experimentation is needed. The early-maturing cultivar Katumani planted at the beginning of the long rainy season produced on average the highest grain yield across the two sites. This treatment combination is being recommended by researchers for this area, and the maize breeding program currently focuses on selecting and improving early-maturing germplasm targeted for planting at the beginning of the long rainy season.

Data from these simulations suggest that, although more risky, there is a reasonably good chance of obtaining greater yields by planting an intermediate maturing cultivar during the short rainy season, particularly at Melkasa. In a few seasons, this strategy would result in a substantial yield increase over planting Katumani later. This coupled with the fact that staggering planting dates helps to spread out labor demands may explain why farmers in the Rift Valley grow both intermediate and short season cultivars on their farms (Tilahun, 1995).

There has been little investment in the development of intermediate type germplasm for these zones in Ethiopia. These data suggest that a modest effort directed towards developing drought tolerant, intermediate-maturing genotypes would be justified.

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Drought in Ethiopia and the Potential of Maize under Water Stress

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Abstract

The effects of drought in Ethiopia in the last two decades have been drastic (10 to 100% yield loss). Prolonged drought has lowered production of major food crops, resulting in an acute and recurrent shortage of food. The farmers' ability to adjust to droughts depends upon available technology and the production systems in use. Agriculture is the mainstay of the Ethiopian economy, accounting for 41% of GDP, 90% of foreign exchange, and 85% of employment. The agricultural potential to overcome food shortages remains high. Chronic food insecurity however, characterizes the arid and semi-arid regions, which comprise nearly 55% of the total cropped area. Here shortage of rainfall is the most important limiting factor to agricultural production. In these zones irrigation and the development of relatively drought-tolerant staple crops are the best options for sustained agricultural output without further damage to the environment. Among the major food crops grown in Ethiopia, maize ranks first in total production and yield per hectare. It is a well-adapted Ethiopian priority food crop grown in almost all ecological zones. Its yield in drought-prone areas is primarily limited by shortage of rainfall and absence of drought-tolerant varieties. Two open-pollinated maize varieties, 'ACV3' and 'ACV6', both early-maturing and relatively drought-tolerant, have been recently proposed for release. These varieties have proved to be significantly higher yielding than local check varieties, showing the potential for improving the performance of maize under conditions of water stress through plant breeding.

Ethiopia's economy is highly affected by the performance of the agricultural sector, which itself is subject to vagaries of natural and man-made factors. As a result, national gross domestic product (GDP) growth has registered year-to-year fluctuations which are strongly linked with variations in the output of the agricultural sector.

Despite its high agricultural potential, Ethiopia has been experiencing chronic food shortages for the past several years. Gross per capita food production in 1980 was 224 kg grain equivalent. It declined sharply in subsequent years, reaching a low of 121 kg in 1985. The situation in the 1990s has not been any more promising (Transitional Government of Ethiopia, 1993).

Chronic food insecurity characterizes the arid and semi-arid (drought prone) regions, estimated to occupy 452,000 km^2 (Table 1). Here shortage of rainfall is the most limiting factor to agricultural production and irrigation use and technology is the least advanced. In moist and humid agroecological zones, covering about 666,000 km^2, food security is becoming increasingly precarious, largely because of serious land degradation and unpredictable

Table 1. Major agroecological zones identified in Ethiopia.

Major zone	Climate	Area ('000 ha)	Agricultural suitability	Major limiting problem
Arid	Hot, arid	41,272	Pastoral	Rainfall
Semi-arid	Arid	2,900	Pastoral & cultivation	Rainfall
Semi-moist	Warm, semi-arid	18,963	Annual crops	Erosion
Moist	Cool, semi-humid	24,540	Annual crops	Erosion
Semi-humid	Cool, semi-humid	16,844	Annual & perennial crops	Erosion
Humid	Cool and humid	6,358	Annual & perennial crops	Erosion
Per-humid	Cool and moist	669	Perennial crops	Frost/cold
Total =		111,546		

Source: Transitional Government of Ethiopia, 1993.

weather. In these areas structural and transitory food shortages are widespread and threatening (Transitional Government of Ethiopia, 1993). A more unpleasant element is the emergence of chronic food insecurity. Areas, which in the past had only passing food shortages, are today experiencing chronic food deficits as a result of prolonged drought. Recurring droughts have caused serious failures in agricultural production (10-100% yield loss) that have resulted in mass starvation and loss of life (Yitbarek, 1993).

If conservation and natural resources management activities continue in their present manner, a national ecological crisis may not be averted. An ecological catastrophe already exists in some areas and in drought years this contributes to the death of thousands of people and creates debilitating conditions for those who survive. The need for a greatly increased effort to improve land use and natural resource management is clear and of extreme urgency as one means of alleviating drought-related problems (Table 2).

A more satisfactory outcome can be achieved through the development of the country's water resources for irrigation and/or the development of stress-tolerant stable varieties wherever such opportunities exist. The arid and semi-arid lowlands offer tremendous opportunities for increasing agricultural production if resources are directed towards them. Agriculture in water deficit areas can be made more independent of nature's vagaries through water management; diversion of perennial rivers, water harvest and storage from the frequent flash floods, and the development of deep wells for irrigation-based intensive agriculture.

Among the major food crops grown in Ethiopia, maize ranks first in total production and yield per hectare, both with and without fertilizer (Table 3). It is a well-adapted priority food crop grown in almost all ecological zones of Ethiopia. It is the major staple and supplementary dietary food crop of millions of people. Maize is used in various ways: direct consumption as roasted or boiled grain, bread, porridge or soup, and for local beer production. It is also an important source of animal feed, fuel and construction material (Yitbarek, 1996). Because of these multiple and widespread uses of maize it is important to design improvement projects so that they include consideration of yield, grain quality and other factors.

Maize yield in drought-prone areas is primarily limited by shortage of rainfall and absence of drought-tolerant varieties. The Maize Improvement Program has 10 trial sites in the drought-prone areas of Ethiopia (Table 4). In these areas the identification and development of drought tolerant varieties and the establishment of irrigation programs seem the best choices for successful crop production. The Maize Improvement Program for Low Rainfall Areas of Ethiopia was initiated with the following major objectives:

1. Develop stable, early maturing varieties that are relatively drought-tolerant.
2. Identify germplasm with special qualitative and quantitative characters related to drought tolerance and escape.
3. Assess optimum cultural practices for the improved varieties.

Table 2. Current land use in Ethiopia.

Land use	Area (000' ha)	Area (%)
Cultivated Land	16,509	14.8
Annual crops	14,613	13.1
Perennial crops	1,896	1.7
Grazing and browsing land	56,888	51.0
Forest, shrubs, etc.	13,051	11.7
Forest	4,016	3.6
Shrubs and others	9,035	8.1
Currently unproductive	4,239	3.8
Currently not utilizable	20,859	18.7
Total =	111,546	100.0

Source: Transitional Government of Ethiopia, 1993.

Table 3. Grain yields obtained from fertilizer (N and P only) application trials on the major cereal crops of Ethiopia.

		With fertilizer			No fertilizer	
Crop	No. of trial sites	N	P_2O_5	N & P_2O_5	Control	National
		Average grain yields (t/ha)				
Maize	262	2.98	3.03	3.83	2.52	1.69
Sorghum	44	1.74	1.79	2.23	1.46	1.36
Wheat	539	1.72	1.61	2.21	1.29	1.33
Barley	198	1.20	1.55	2.02	0.96	1.25
Teff	876	1.20	0.88	1.29	0.69	0.88

Source: National yield trials conducted by the Agricultural Development Department, Ministry of Agriculture, 1988-1991. The amount of fertilizer applied varied depending on the soil status of the trial site.

Materials and Methods

Germplasm composition

Germplasm sources used to develop the variety 'ACV3' were early maturing collections from North America and Europe. Using a half-sib family selection scheme, recombination of components was made for four cycles. Performance evaluation and selection (selection intensity of 10-25%) of families were conducted under rainfed conditions. Progeny tests took 1 to 2 crop seasons to complete. The best 10% of families from the last selection cycle were then bulked to produce the variety ACV3.

Germplasm sources for variety ACV6 were maize collections from the USA and from southern, central and eastern Africa. These collections had been improved using an S_1 recurrent selection scheme with a selection intensity of 5-15%. In each cycle more than 200 S_1 families per collection were evaluated at a minimum of two locations under rainfed conditions. The best families were recombined in all possible combinations by hand pollination, and a new set of S_1 progenies were formed for the next selection cycle. The variety ACV6 was formed after several cycles of S_1 selection by recombining an elite fraction of S_1 families from the latest selection cycle and advancing the crosses to F_2. The local check used in most locations was Katumani Composite. It is an open-pollinated early-maturing maize variety that has been under production for more than two decades. This variety has lost its trueness to type and is now relatively low yielding under water-deficit conditions.

Experimental design

The following experiment was conducted in the 1995 crop season:

Treatments/
Varieties: ACV3, ACV6 and the local check
Design: RCBD with three replicates on-station, and a single replicate on-farm
Locations: Zewai, Tuka, Hidi Ale, Nazareth, Yavello, Dhera, Bidre and Mega (on-station and on-farm trials)
Plot size: harvested area = 10 x 10.5 m = 105 m^2 (on-station)
harvested area = 50 x 50 m = 2500 m^2 (on-farm)

Spacing between plants and rows was 25 and 75 cm, respectively, giving a target plant density of 53,000 plants/ha.

Table 4. General environmental conditions at the Awassa College of Agriculture maize trial sites.

Location	Region	Altitude (m)	Mean daily temp. (^{o}C)	Mean annual rainfall (mm)	Rainy season Small	Rainy season Big
Awassa	Sidamo	1650	26	950	Mar.-May	Jun.-Oct.
Bidre	Bale	1500	28	760	Sept.-Nov.	Mar.-Jun.
Dhera	Shewa	1565	29	575	Feb.-May	Jun.-Sept.
Hidi Ale	Sidamo	1412	29	650	Sept.-Nov.	Mar.-Jun.
Mega	Sidamo	1300	26	800	Sept.-Nov.	Mar.-Jun.
Mieso	Hararghe	1400	29	675	Feb.-May	Jun.-Sept.
Nazareth	Shewa	1650	28	675	Feb.-May	Jun.-Sept.
Tuka	Sidamo	1300	29	600	Sept.-Nov.	Mar.-Jun.
Yavello	Sidamo	1650	28	650	Sept.-Nov.	Mar.-Jun.
Zewai	Shewa	1380	28	700	Feb.-May	Jun.-Sept.

Source: Awassa College of Agriculture, 1995.

Table 5. Grain yield (t/ha) of improved maize varieties and a check entry grown at eight different on-station locations in the 1995 crop season.

Variety	Zewai	Nazareth	Dhera	Yavello	Hidi Ale	Mega	Tuka	Bidre	Mean
ACV3	1.96	4.21	1.74	2.54	3.27	2.24	5.45	4.97	3.30
ACV6	2.08	4.25	1.94	2.32	3.14	1.99	5.42	5.12	3.28
Local check	1.44	3.85	1.53	2.19	2.52	1.00	1.24	4.96	2.34
LSD$_{(0.05)}$	0.24	NS	0.19	NS	0.20	0.26	0.19	NS	
CV (%)	6.8	7.3	5.4	12.6	3.5	7.5	2.4	3.0	

Results

Grain yield obtained under on-station conditions ranged from 1.00 t/ha at Mega to 5.46 t/ha at Tuka. Grain yields obtained at Dhera, Mega and Zewai were very low because of severe water stress at flowering. Improved varieties were superior across and within locations, compared with the local check (Table 5). Under water stress the performance and yield of ACV3 was better than that of ACV6, though differences between them were not significant at most locations in 1995. Physiological maturity of the varieties was from 95 (ACV3) to 121 d (local check) and plant height was from 164 (ACV3) to 219 cm (local check) (Table 6). Diseases and insects were not problems for any entry.

At the eight locations under on-farm conditions, ACV3 and ACV6 had yields of 2.56 and 2.39 t/ha, compared with 1.59 t/ha yield for the local check (Table 7). Part of the superiority of the improved varieties could be due to their relative earliness, resulting in a capacity to escape drought.

Conclusion

The varieties ACV3 and ACV6 are early and relatively drought tolerant when compared to the local checks. It was possible to harvest reasonable yield under extreme stress conditions, when farmers were experiencing near 100% crop failure. There is high potential for genetic gains in maize performance under water stress with substantial benefits and little cost to farmers.

Acknowledgments

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Table 6. Agronomic data of two improved varieties and a check variety in the crop season of 1995. Means over eight locations in Ethiopia.

	Disease and insect scores[†]			Days to			Height (cm)	
Variety	Blight	Rust	Borers	Tassel	Silk	Mature	Plant	Ear
ACV3	1.6	1.5	1.2	42	47	95	164	70
ACV6	1.5	1.5	1.0	45	50	105	173	77
Local check	1.4	1.3	1.1	53	59	121	219	112

[†] Disease and insect scores: 0 = no incidence and 9 = extreme susceptibility.

Table 7. On-farm grain yield of two improved varieties and a check variety at nine different drought-prone locations in Ethiopia during the crop season of 1995.

	ACV3	ACV6	Local check[†]
Location		(t/ha)	
Bidre	4.49	3.33	1.90
Dhera	1.85	2.20	1.70
Hidi Ale	0.07	0.04	0.01
Mega	2.88	2.62	0.00
Nazareth	2.50	2.70	1.90
Tuka	3.74	3.36	2.61
Yavello	2.88	3.00	2.85
Zewai	2.10	1.90	1.71
Mean	2.56	2.39	1.59

[†] In most locations the local check was Katumani Composite.

Maize Losses Due to Drought in Indonesia and Sources of Drought Tolerance and Escape

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Abstract

The maize area harvested in Indonesia is about 3 million ha with an average yield of 2.2 t/ha. Most of the maize area is in rainfed uplands and lowlands, with only about 11% in irrigated lowlands. About 74% of maize area is grown in the rainy season and the rest in the post-rainy season and dry season. The yields of maize planted in the post-rainy or dry season with limited irrigation are about 73% and 63% of the yield under full irrigation for early and late maturing varieties, respectively. An estimated 69% of maize area grown in the rainy season is in areas with erratic rainfall. Maize frequently suffers from drought during early plant development and flowering. The estimate of maize production loss due to drought is about 15%, approximately 1.2 million tons annually. Some local varieties are early-maturing and may escape drought. A local variety 'Cetek' from Mojosari, East Java is drought tolerant. The yield reduction due to drought at flowering of a population developed by crossing this variety with the improved variety 'Arjuna' was 16%, while other populations ranged from 27 to 51%. Pool 2, a population developed by crossing local varieties with 'Suwan 2', has been improved for drought tolerance using a full-sib family procedure. Five cycles of selection have resulted in yields increasing from 4.44 to 6.08 t/ha under full irrigation and from 2.68 to 3.90 t/ha under drought at flowering.

Maize Production Systems in Indonesia

In Indonesia, maize is second in importance as a staple food crop after rice. Maize area harvested in Indonesia has varied from 2.44 million ha in 1985 to 3.05 million ha in 1994, but averages about 3 million ha. Yield has been increased from 1.8 t/ha in 1985 to 2.2 t/ha in 1994 (CBS, 1987, 1994).

The largest maize cropping system in Indonesia, which comprises about 79% of the maize area planted, is 'tegal' (rainfed dryland). The remainder is planted in rainfed (11%) and irrigated (10%) 'sawah' (wetland), respectively. The tegal system covers a large area and is quite heterogeneous. Multiple (55% of the total maize area) or single maize crops (24%) are grown each year. It differs from sawah in the frequency of maize harvests. The sawah system is sub-divided according to the degree of water control, the irrigated sawah having a permanent irrigation infrastructure and the rainfed sawah being irregularly flooded by rainfall runoff (Mink, 1984; Subandi et al., 1988).

Maize is planted throughout the country, but around 70% of total production comes from Java (4 million tons in 1993). East Java alone produces more than 40% of the total national harvest. The remaining areas, such as Sumatra, Sulawesi, and other islands, produce about 29%.

Maize productivity in Java is higher than that of outer Java (Table 1), mainly due to the adoption of newer technologies and more intensive management (Subandi et al., 1988; CBS, 1994). Average fertilizer

Table 1. Maize area, production and average yield in Indonesia, 1993.

	Production (t)	Yield (t/ha)	Area harvested (ha)
Sumatra	1,033,722	2.22	465,640
Java	3,956,658	2.39	1,655,505
Bali and Nusa Tenggara	628,279	1.84	341,456
Kalimantan	57,946	1.34	43,243
Sulawesi	754,046	1.82	414,311
Maluku and Irian Jaya	29,086	1.33	21,869
Outer Java	2,503,079	1.95	1,283,630
Indonesia	6,459,737	2.20	2,939,135

Source: CBS, 1994.

application is about 205 kg of total nutrients/ha in Java and Sumatra and 48 kg nutrients/ha in the other areas.

Maize Losses Due to Drought

Maize production varies in Indonesia due mainly to abiotic constraints. The exception being the irrigated wetlands, where maize often grows in favorable conditions with high soil fertility and adequate water supply. Two important problems related to the soil and to crop water supply exist in Indonesia (Subandi, 1984; Subandi et al., 1988). The major soil groups in the maize growing area include alluvial, grumusol, latosol, regosol, mediterranean, andosol, and red/yellow podzolics (59% of total maize area). Their low phosphorus status, low organic matter content, and low pH are important constraints to production (Subandi et al., 1988). Secondly, the crop is often subjected to periods of severe moisture stress because of marked variation in timing and intensity of rainfall. Moisture stress occurring during flowering or during early plant development and flowering can cause severe yield losses (Fischer et al., 1983; Subandi et al., 1988). Evaluations in several locations showed that the maize variety 'Arjuna' planted in dryland areas yielded only 3.04 t/ha, while in rainfed and irrigated wetlands its yield was 4.14 and 5.07 t/ha, respectively (Sudjana, 1990).

About 74% of maize is grown in the rainy season, and the rest in post-rainy and dry seasons. For maize grown in the rainy season about 69% is in areas with erratic rainfall, of which 49 and 20% occur in the climatic zones D and E, respectively. A D2-D3 zone typically has 3 to 4 consecutive wet months with more than 200 mm rainfall and 4 to 6 dry months with less than 100 mm rainfall, whereas, an E zone has less than 3 consecutive wet months and 2 to 6 dry months (Oldeman, 1975). About 20% of the maize area in East Java has a favorable water supply, and the rest is classified as D to E with low yield potential. Crops suffer from drought during early development stages or flowering, though sometimes water deficits extend to include the grain filling period.

Based on multi-location trial data (1991 to 1993), the average yield of standard varieties planted in post-rainy and dry seasons with limited irrigation was about 73% and 63% of the yield in fully irrigated land for early and late maturing varieties, respectively. The average yield of standard varieties planted in an E climatic zone was 42 and 28% of the yield in fully irrigated land for early and late maturing varieties, respectively. From these data we estimate that the total maize grain losses due to drought are about 25%, if Arjuna (a recommended early-maturing variety) is planted in erratic rainfall areas. However, only about 25% of these areas are planted to Arjuna, and the rest is planted to local varieties which are more successful at escaping drought through early maturity. The estimated yield loss of local varieties is about 10% in climatic zone D and 15% in climatic zone E. Considering the different rates and zones, total grain losses are about 15% of total production or about 1.2 million tons annually.

Sources of Drought Tolerance and Escape

Genetic resources

Some local varieties (landraces) are early-maturing and are thus good drought escapers. These landraces can be separated into two groups, one with 36 to 42 d to silk and the second with 43 to 50 d. The first group includes varieties Cetek, Krasekan, Burdek, Impa-Impa, Medok, Goter, Tongkol, and Warangan, and the second includes Penjalinan, Genjah Kertas, Genjah Randu, Putih Nusa, Penjalinan, and Sili. Although the yield will be low, varieties from the first group are still likely to produce grain under severe drought and short season conditions in which Arjuna may produce no grain.

A local variety Genjah Randu from Mojosari, East Java was crossed with Arjuna. The resulting population has been selected for early maturity using ear-to-row breeding methodology. The cultivar 'Abimanyu' resulted from this selection. The yields of Arjuna and Abimanyu under water-stress were both 63% of their yield under no stress (Sudjana, 1989). Another population, 'AC', was formed from the cross and backcross of Arjuna to Cetek, and selection has emphasized early maturity.

Breeding methodology for drought tolerance

Pool 2 was developed by crossing local varieties with 'Suwan 2', and has been improved for drought tolerance using a full-sib selection scheme. The evaluation of full-sib progenies was conducted at Mojosari Research Station during the dry season on regosol soil after rice. A total of 250 families were evaluated under two environments, namely four and six irrigations. A total of 190 and 120 families were evaluated in selection cycles 4 and 5 using a simple lattice experimental design. Each family was planted in a single 5 m row with rows spaced 75 cm apart and two plants/40 cm, under 140 kg N urea and 90 kg P_2O_5/ha.

Two sub-populations were developed in each selection cycle. One consisted of 15 progenies selected for good performance under water-stress and the other five progenies chosen for good performance under no stress; i.e., families with a drought index greater than 1.0 (Fischer et al., 1983). This sub-population was named Pool 2 (FSD)-Cn. The second sub-population consisted of 20 progenies selected for good performance under well-watered conditions, and was named Pool 2 (FSI)-Cn. Only the population that included water-stress-selected progenies was used for the next cycle of selection. Hence, Pool 2 (FSI)-C_5 was selected for drought tolerance for the first four cycles and the fifth for performance under no stress, while Pool 2 (FSD)-C_5 was selected under water-stress for all five cycles.

Evaluation of Improvement in Drought Tolerance

The experimental varieties from C_3 were evaluated at 14 locations in East Java and West and East Nusa Tenggara for adaptation and performance in the rainfed dry land areas. The experiment was arranged in a randomized complete block design with four replications. Grain yield was expressed at 15% grain moisture content.

Average yields of Pool 2 (FSD)-C_3 and Pool 2 (FSI)-C_3 were 11% and 8% higher than Arjuna, the recommended early-maturing variety (Table 2). Population AC 9 (FSD)-C_3 and AC 9 (FSI)-C_3 did not differ for yield, and both yielded 6% more than the check entry Rama.

Cycles 0 to 5 of Pool 2 selected under drought-stress and non-stress conditions and AC selected for early maturity were evaluated at Mojosari Substation during the 1994 dry season. Each entry was evaluated in three environments created using different irrigation regimes, as follows:

1. Six irrigations: full irrigation was applied until grain filling was complete.
2. Four irrigations: no irrigation applied from 50% flowering.
3. Two irrigations: no irrigation applied from 21 d after sowing.

The yield reduction due to drought at flowering for AC was only 16%, while the other populations showed yield reductions ranging from 27 to 51%. Selection in Pool 2 (FSD) for five cycles has increased yield from 4.44 to 6.08 t/ha, when evaluated at full irrigation , and from 2.68 to 3.90 t/ha when evaluated under four irrigations (Table 3). Selection in AC has increased yield from 4.23 to 5.67 t/ha when, evaluated under full irrigation.

Table 2. Grain yield of sub-populations selected from Pool 2 C_3 and MC 9 C_3, and two check varieties when evaluated at 14 locations in Indonesia during 1991/92.

Pedigree[†]	Range (t/ha)	Mean (t/ha)	Percent of Arjuna (%)	Percent of Rama (%)
Pool 2 (FSD)-C_3	1.96 - 6.41	4.94	111	109
Pool 2 (FSI)-C_3	2.73 - 7.00	4.84	108	107
Arjuna	2.27 - 6.34	4.45	—	97
MC 9 (FSD)-C_3	2.55 - 7.12	4.76	107	106
MC 9 (FSI)-C_3	2.68 - 6.97	4.77	107	106
Rama	2.23 - 6.71	4.51	101	—

[†] (FSD) = population selected in its latest selection cycle under a drought condition, (FSI) = population selected in all cycles under a well-watered condition. Source: Slamet, 1992.

General Discussion

Variety trials conducted in different agroecological zones may be good indicators of the effect of climatic differences between locations and years, but estimates of yield losses based on these trials contain some bias, if different local varieties are used at the different sites. Normally each variety trial should be grown using the same rate of fertilizer, soil preparation, weeding, pest and disease control, etc., and comparisons made between sites and years using standard varieties.

Indonesian local varieties are mostly extra early-maturing, and can often escape drought. When the crop suffers drought at an early growth stage, however, these local varieties have poor recovery and consequently high yield reduction compared to later-maturing varieties. They are, however, a useful source of genes for drought escape, and possibly for tolerance.

Selection for drought tolerance gives modest progress under stress, as demonstrated by our results. Selection for specific characters may also diminish yield reduction under drought, for example the anthesis-silking interval. The drought selection index (Fischer et al., 1983) and minimum yield under stress appear useful when selecting for tolerance. Populations formed using families selected under stress and under no stress showed improved yields in both stressed and non-stressed conditions (Table 3), but it is not known if selection under only favorable conditions would result in yield improvement under stress.

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Table 3. Grain yield (t/ha) of populations derived from five cycles of selection in populations Pool 2 and AC, when evaluated at Mojosari Research Station, DS, 1994. Selection was under drought and irrigated conditions for Pool 2 (see text for explanation), and emphasized early maturity for AC.

Pedigree	Number of irrigations			Mean	Days to 50% silk
	2	4	6		
Selected under irrigated conditions					
Pool 2 (G12)- C_0	1.50	2.68	4.44	2.87	57
Pool 2 (FSI)- C_1	1.50	2.80	5.04	3.11	55
Pool 2 (FSI)- C_2	1.22	2.69	3.53	2.48	55
Pool 2 (FSI)- C_3	1.76	3.51	5.09	3.45	56
Pool 2 (FSI)- C_4	1.90	3.04	5.13	3.35	55
Pool 2 (FSI)- C_5	2.10	3.68	5.84	3.87	53
Selected under drought conditions					
Pool 2 (FSD)- C_1	1.51	2.83	4.93	3.09	57
Pool 2 (FSD)- C_2	2.10	3.95	6.17	4.07	55
Pool 2 (FSD)- C_3	2.00	4.00	5.76	3.34	56
Pool 2 (FSD)- C_4	1.98	3.57	5.09	3.55	56
Pool 2 (FSD)- C_5	2.04	3.90	6.08	4.01	53
Selected for earliness					
AC- C_0	1.58	3.55	4.23	3.12	57
AC (S1)- C_1	1.84	3.06	4.20	3.03	56
AC (S1)- C_2	1.53	2.84	4.08	2.82	55
AC (S1)- C_3	1.54	2.72	2.78	2.35	55
AC (S1)- C_4	1.72	2.66	4.20	2.86	55
AC (S1)- C_5	1.92	3.93	5.67	3.84	56
Arjuna (check)	1.57	3.91	5.71	3.73	56
Mean	1.71	3.31	4.99	3.34	55
LSD 5%	0.48	0.72	1.11	0.47	2
CV (%)	19.9	15.5	15.8	17.6	5.7

Source: Suyamto, 1994.

Morpho-Physiological Basis for Breeding Drought and Low-N Tolerant Maize Genotypes in India

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Abstract

Development of drought and low-N tolerant maize genotypes serves more than one purpose. It not only reduces the cost of cultivation but is also an effective way of sustaining maize production in drought prone areas. For the last 25 years, the area under maize in India has stagnated at around 6 million ha. India is currently producing about 10 million tons per year of maize, but productivity is low compared to most temperate countries - partly because of drought and low soil fertility. More than 80% of the maize area is rainfed and almost all the Indian soils where maize is grown are poor in indigenous N. India has set a target of 18 million tons of maize production per annum by the year 2000. There is little scope for increasing area under irrigation, so maize will continue to be grown in rainfed conditions. Hence, productivity has to be improved in order to meet the increasing demand for maize. This may be possible by developing short duration, drought and low-N tolerant hybrid varieties of maize. Hybrids are not only high yielding but tend to be more stable and tolerant to drought and infertility than open-pollinated varieties. Only limited research has been conducted on drought and low N tolerance in India. Studies normally consider these two factors separately, but efforts have been made to combine both stresses to obtain more comprehensive information. Selection for stress tolerance is difficult due to inconsistent expression of genetically controlled characters in stress environments. Some studies conclude that higher yielding genotypes under normal conditions will also be the better yielders under drought and sub-optimal nitrogen, so breeding for high yield may be the most appropriate approach for developing drought and low N tolerance. Screening germplasm under artificially created stress conditions can be expected to enhance gains derived from normal testing. Testing under both conditions may attain more quickly the goals of high yield and stress tolerance.

Status of Maize in India

Maize is grown in almost all parts of India, occupying 6 million ha or about 4% of the total cultivated area. Maize production in India has increased from 5 million tons in 1966-67 to 10.6 million tons in 1994-95. This is more than a 100% increase (Fig. 1) and largely results from an increase in mean yield from 1.0 to 1.7 tons/ha. However, maize contributes only 5.2% of total food grain production. The annual growth rate of maize productivity from 1966-67 to 1994-95 has been merely 1.8% as compared to 2.4 and 3.5% for rice and wheat (Table 1), suggesting that there is considerable potential for enhancing maize productivity in India.

Geographical Distribution of Rainfed Area

Annual rainfall in India ranges from about 200 mm to more than 3000 mm. Fluctuation in the quantity of monsoon rainfall over different parts of India has an important bearing on agriculture. The Indian Institute of Tropical Meteorology (Pune, Maharastra) has divided the country into five climatic macro-regions based on analyses of the monsoon rainfall from 1871 to 1990 (Table 2).

Table 1. Annual growth rates of maize, rice and wheat area, production and yield in India from 1967 to 1995.

	Maize (%)	Rice (%)	Wheat (%)
Area	0.28	0.63	2.21
Production	2.11	3.02	5.65
Yield	1.84	2.38	3.45

An analysis of rainfall data from a number of locations throughout the country indicates that:

1. There is considerable variability in the date of onset and cessation of rainy seasons.
2. The monsoon rainfall within the season is cyclical in nature with dry spells, lasting a month or more, interspersed between wet spells.
3. The coefficient of variation of rainfall increases with decreases in monsoon rainfall.
4. High intensity rainfall often occurs, resulting in sizable loss of water through runoff and deep drainage.

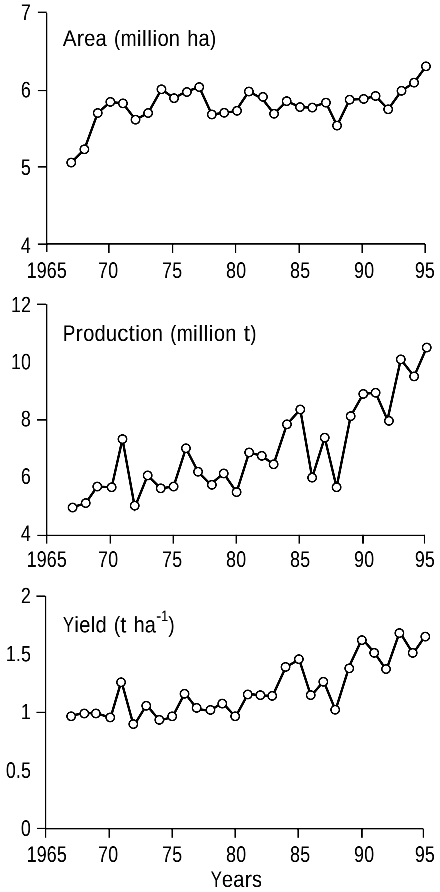

Figure 1. Trends in area, production and productivity of maize in India.

Drought and Maize Production

Moisture stress is the environmental factor most adversely affecting maize production in India. Maize plants under drought stress show stunted growth, wilting, top-firing, tassel blast, silk delay, poor seed set, barrenness and eventually low grain yield. In India, drought has substantially reduced maize production over the years; e.g., maize production declined from 7.4 million tons in 1970-71, when there was a slight drought, to 5.1 million tons in 1971-72, a severe drought year.

Table 2. Statistical details of climatic regions of India, based on data from 1871 to 1990 (Indian Inst. Trop. Meteorol., Pune, Maharastra, India).

Region	Area of India (%)	Mean rainfall (mm)	CV (%)
Northwest	22.0	490	27.0
West Central	33.4	933	13.5
Central Northeast	19.9	1002	11.2
Northeast	9.3	1419	8.6
Peninsular	15.4	659	14.9

Table 3. Maize production and drought in India.

Year	Maize production (million t)	Drought category
1965	4.8	Moderate
1966	4.9	Moderate
1968	5.0	Slight
1969	5.7	Slight
1971	7.4	Slight
1972	5.0	Severe
1974	5.6	Moderate
1979	6.2	Moderate
1982	6.8	Moderate
1985	8.4	Slight
1986	6.0	Severe
1987	7.4	Moderate
1988	5.7	Severe
1991	9.1	Slight
1992	8.0	Severe
1993	10.2	Slight
1994	9.6	Moderate

Similarly maize production was drastically affected in 1987-88 (Table 3). In some areas, rainfall for the crop season may be adequate, but a reduction in water availability around a critical growth stage may have a marked effect on grain yield.

Nitrogen Status of Indian Soils

Indian soils have been characterized as being low in organic matter and nitrogen. The nitrogen map of Ghosh and Hasan (1980) shows that except for 15 districts of the Northeastern Hills and Himalayan regions, covering 4.9% of total cultivated area, all have either low (62.5% of the area) or medium (32.6% of the area) nitrogen levels. Furthermore, tropical rainfed soils in semi-arid regions are typically low in organic matter, often containing less than 1% organic matter with a total N generally not exceeding 0.1%. Deficiency of N is very common, and about 77% of these rainfed soils are classified as low to very low in available N (Katyal, 1994).

Role of N in Maize Production

Nitrogen affects photosynthetic rate, leaf surface area, size of the sink, and thus yield. Each ton of maize grain production requires about 16 kg N in the grain. Application of N to maize during grain filling normally results in an increase in grain protein production (Deckard et. al., 1973). N fertilizer use in India has increased several-fold for some crops, raising environmental concerns. This is not yet the case for maize, where N supply usually constrains yields. About 3% of N fertilizer use in India is on maize (M.K. Chaudhary; pers. comm.), only a fraction of it being in rainfed areas. Nonetheless, maize yields in India have shown a linear response to increased N fertilizer use over the past several years (Fig. 2). Nitrogen recommendations for maize in India are specific for location and crop rotation, and vary from 80 to 150 kg N ha^{-1}, depending upon plant spacing and moisture conditions of the area. In irrigated areas, N rates up to 150 kg ha^{-1} have proved economical, whereas in rainfed areas economic rates of N application are around 80 kg N ha^{-1} (Fig. 3). In practice, farmers often use less than half of the recommended N rate. In general, N is applied in three equal splits: planting, knee height and at silking stages. The use of both N and water would be more efficient if irrigation were synchronized with the rate and timing of N application.

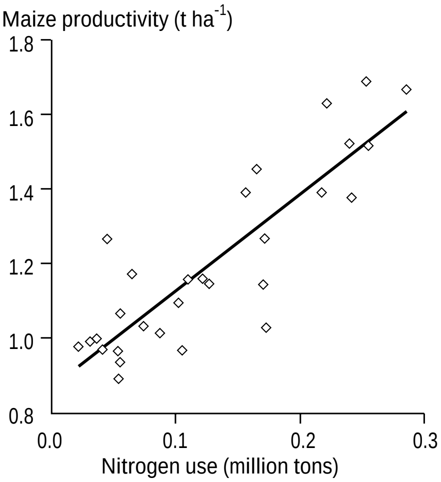

Figure 2. Relationship between nitrogen use in maize in India and maize productivity.

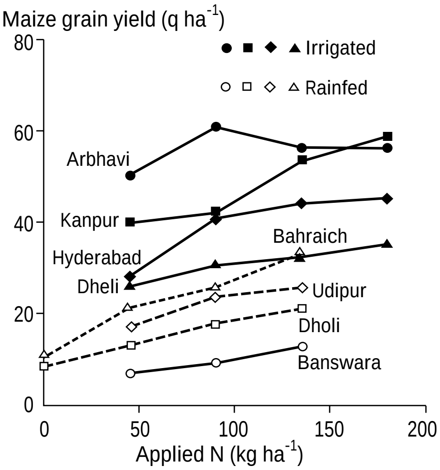

Figure 3. Responses of applied nitrogen on maize grain yield under limited and optimum moisture conditions.

Breeding for Drought and Low-N Tolerance

Grain production is adversely affected by stress conditions that occur during the onset and the early phases of reproduction. Breeding for drought tolerance is difficult because it is a complex character like grain yield, and many traits affect the outcome. Initially, the breeder should start working with only a few of the most important characters. Some known indicators of drought tolerance include days to 50% silking, days to 50% pollen shedding, the interval between the two, plant height, ear length, ear girth, number of kernels row^{-1}, and 1000 kernel weight. Tollenaar (1977) suggested that sink capacity rather than source capacity commonly limits maize grain yield. He further suggested that where sink limitations exist, improved grain yield could be achieved by selecting for factors that influence photosynthate supply to the ear during the flowering period.

Morphological Characters

Flowering date

Maize is sown in June and harvested in October in drought prone areas of India. Sowing is dependent on the monsoon, which starts by the end of June or beginning of July, but rainfall distribution is erratic and can result in drought conditions at critical crop stages, particularly flowering. Drought is often experienced during the last week of August or first fortnight of September, often coinciding with flowering. Robins and Domingo (1953) reported that if drought conditions continue for a week, losses in grain yield may exceed 50%. Even drought lasting 1 to 2 days at pollination can reduce grain yield by up to 22% (Fischer et. al., 1983).

The date of 50% silking is commonly delayed under stress conditions. Delays of up to 9 d in silking have been reported under Indian conditions (Subramanyam, 1992). The timing of pollen shed appears to be less affected under stress conditions (although delays can occur under N stress), leading to an increase in the interval between pollen shedding and silking. In general, anthesis-silking interval (ASI) is 2 to 4 d under irrigated conditions, but under stress conditions it increases to 4 to 5 d, and intervals up to 13 d have been reported for highly drought susceptible genotypes. The importance of a short ASI has been documented by Fischer et. al. (1989) at CIMMYT, and by Singh and Sarkar (1991) and Subramanyam (1992) in India. There is a direct correlation between this interval and maize grain yield, and genotypes with a short ASI tend to suffer less yield reduction under drought.

Plant height

The maize crop approaches knee height about 30 to 35 d after sowing. If there is insufficient moisture during this time (a common condition in India), plant height is reduced. However, drought usually has a limited affect on plant height, especially for drought tolerant genotypes. Subramanyam (1992) reported a study involving Harsha (an India variety), La Posta (from CIMMYT) and a cross between two Indian maize varieties. Harsha and Navjot had almost the same plant height under both no-stress and stress conditions when grown at Hyderabad.

Test weight-grain filling

Rather limited genetic variation has been reported for kernel weight under drought. It is assumed that if there is poor grain filling then the test weight is likely to decrease, though conflicting reports exist in the literature. However, complete grain filling is essential for higher yield in maize.

Ear length and girth

These traits are often reduced under drought, but little reduction in these measurements was observed in the drought tolerant genotypes Navjot, Harsha, La Posta, and Tuxpeño Sequía C_8. It was also observed that wherever a cross involved at least one of these as a parent, the length and girth measurements under stress were comparable to those under normal conditions (Subramanyam, 1992).

Physiological and Biochemical Factors

Studies point to parameters that may prove useful when selecting for drought tolerance. These include:

1. The ability of leaves to increase abscisic acid concentration, which leads to stomatal closure, is genetically controlled and is variable (Larque-Saavedra and Wain, 1976).
2. Under water stress conditions, a 42% increase in sugar (Barlow et al., 1976) has been reported in maize.
3. Pinter et. al. (1978) reported that free proline content of plant tissue subjected to drought increased, and was positively correlated with drought tolerance.
4. A relatively more drought tolerant line of maize had a higher cuticular resistance to water diffusion than a less tolerant line (Dube et al., 1975).
5. A slow rate of leaf senescence and a high degree of chlorophyll stability are criteria which may also be used during selection.
6. Subramanyam (1992) concluded that a combination of characters such as high stomatal diffusive resistance, low transpiration rate and high nitrate reductase activity can be used for selection of drought tolerant genotypes. High heritability values for nitrate reductase have been reported by Mishra et al. (pers. comm., 1978).

Gene Action for Drought and Low-N Tolerance

Limited information is available regarding gene action and combining ability for different characters under water deficit or low N conditions. Martiniello (1983) suggested that while breeding for drought tolerance only morphological characters which are less sensitive to genotype by environment interaction (G x E) should be utilized. The Indian varieties Harsha and Navjot have been identified as good general combiners for a number of characters, and this likely explains their stable performance across a large number of locations.

Studies reported in the literature do not agree on the importance of additive and dominance gene action under drought. Hemlata et al. (1989) observed a preponderance of dominance variance for grain yield, though Subramanyam's (1992) results were inconsistent perhaps because of a large G x E caused by fluctuations in drought conditions at the different locations and years. Similar observations have been reported by Seetharama et al. (1983), who noted that inconsistent trial results are one of the major problems when breeding for drought tolerance.

Breeding Strategy

Some of the G x E for various traits under stress can be reduced by the use of managed drought stress or low N environments during testing of progenies and varieties. Repeatability of trial results depends heavily on good execution of screening techniques. In general, most physiological traits (those discussed above) are sensitive to environmental fluctuations and some may require special screening nurseries. The testing of germplasm under drought conditions however, should be done at more than one environment to identify tolerant genotypes with stable performance across environments, and identify drought tolerant genotypes targeted for a specific set of environmental conditions.

Germplasm that is a source of favorable expression of only one character has limited value when developing gene pools or especially when developing hybrids or composite varieties, and it is more important to identify genotypes possessing favorable expression for several characteristics. Once the hybrid, composite or gene pool is developed, its should be screened under both normal and stress conditions. Genotypes giving high yield under normal conditions are also expected to give high yield under stress. Evaluation under both conditions provides an opportunity to eliminate those genotypes that do not.

Several physiological and biochemical traits responsible for drought tolerance — proline content, sugar content and chlorophyll stability — could be used to identify drought tolerant genotypes under laboratory conditions, but only if a clear association between these traits and yield under drought in the field can be demonstrated. Similarly, parameters desirable for improving N use efficiency include: high rate of N uptake and assimilation during the grain filling period, high rate of N movement to developing grain, and retention of green leaf area and efficient C assimilation during grain filling. For convenience when incorporating drought and low N-tolerance traits, a hybrid breeding methodology will be the simplest approach, since heterosis is associated with stress tolerance. Single-cross hybrids having short ASI under drought, early maturity and high yield under stressed and well-watered or high N conditions should be selected.

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Maize Breeding for Tolerance to Low Soil Fertility and Drought in Guizhou Province

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Abstract

Maize is one of the main cereal crops in Guizhou Province, and plays an important role in farmers' lives and in farm income. However, yield is very low, with drought and low soil fertility among the principal factors influencing maize production. Two years ago we began a special program working with drought and low soil fertility. Three basic methods for developing tolerant hybrids have been used in our breeding program. They include: using crosses of lines from local populations x temperate lines; tropical lines x temperate lines; and developing broadly adapted three-way, double, and topcross hybrids. These methods have lead to the release of some hybrids tolerant to drought or low soil fertility. In 1993, the low N-tolerant population 'Across 8328-BN' was introduced from CIMMYT. We have begun to improve it per se and use it for inbred line development. In the future, our drought and low soil fertility program will get increased attention with the objectives: 1) to adapt high yielding germplasm to the stress conditions in Guizhou Province, 2) to develop inbred lines tolerant to drought and low soil fertility, and 3) to identify hybrids with broad adaptation to the highly variable growing conditions in Guizhou, concentrating on three-way and double cross hybrids.

Guizhou is a plateau and mountainous province in southwest China. It is situated between 103º36'-109º35' E longitude and 24º37'-29º31'N latitude and has an area of 176,100 km^2. Sichuan Province borders Guizhou on the north, Guangxi Autonomous Region on the South, Yunnan Province on the west, and Hunan Province on the east. Guizhou has a varied topography, with about 87% of its area mountainous, 10% hilly land, and only 3% flat ground. Its altitude varies from 147 to 2,903 masl, and the terrain slopes from west to east. Its weather is warm and humid, classified as a subtropical-humid-monsoon climate.

Both total maize growing area and production take second place to those of rice (Table 1). In 1994, the last reporting year, maize growing area was 644,020 ha and production 2,525,700 tons. Maize is planted from 250 to 2,200 masl in environments which include mountainous, hilly, and flat lands. It is used for food and feed. Maize is the staple food for about 40% of the people and plays an important role in rural economies, especially in mountainous areas.

Table1. Maize area planted and total maize production in Guizhou Province.

	Year							
	1991		1992		1993		1994	
Crop	Area ('000 ha)	Production ('000 tons)	Area ('000 ha)	Production ('000 tons)	Area ('000 ha)	Production ('000 tons)	Area ('000 ha)	Production ('000 tons)
Rice	720	4140	745	3833	714	3836	735	4204
Maize	662	2190	602	1848	605	2178	644	2526
Wheat	484	827	508	846	551	906	563	954
All Cereals	2642	8855	2635	7889	2697	8695	2697	9311
Maize† (%)	23.7	25.8	22.9	23.4	22.5	25.1	23.9	27.1

† Maize as a percentage of all cereals.

Factors Influencing Maize Grain Yield in Guizhou Province

Compared with the mean grain yield across China or in Jilin Province, maize yields are still very low in Guizhou Province (Table 2). Drought is one of the most important factors influencing maize production. Maize is planted on dry land, principally on sloping fields and land that can not be irrigated during the growing season (Fig. 1). Precipitation is abundant, but rainfall distribution is irregular with spring and summer droughts occurring regularly (Figs. 2, 3). On sloping fields and hilly land, water-holding capacity is low, consequently, we call maize production 'drought agriculture' or 'rainfed agriculture'.

Soil fertility is low in Guizhou Province. Most soils are low in available nitrogen and phosphorus, and have moderate levels of potassium (Table 3). Soils devoted to maize can be characterized as 10% rich-fertile flat land, 50-70% moderately-fertile hilly and sloping lands and 20-30% highlands with low fertility. The quantity of applied organic manure and chemical fertilizer is not enough to build up soils to the required nutrient levels. Farmers, especially those living in mountainous areas, are poor and cannot buy enough chemical fertilizer and hybrid seed for their maize production needs. In addition to poor fertility, soil erosion is a very serious problem on the hilly and sloping lands.

Hybrid use is low in Guizhou Province; about 40% of the maize was planted to hybrids in 1989. In 1994, this came up to about 60%, with the release of a series of three-way and double cross hybrids.

Guizhou Province is short of sunshine during the maize growing season (Table 4). It is often cloudy and rainy. In valleys and sloping lands, maize has sunshine for only half of the day (Fig. 1).

Maize breeding in China has the general objective of selecting for high yield, high quality, and resistance to diseases and insects. But in Guizhou Province, we also need to select for adaptation to the many different growing conditions. As a result, the most important factors in maize are tolerance to drought, low soil fertility and low radiation.

Maize Breeding Methods Related to Drought and Low Soil Fertility

Much research on maize physiology and agronomic characters relating to drought has been done in China, and most maize breeders in Guizhou Province test their inbred lines,

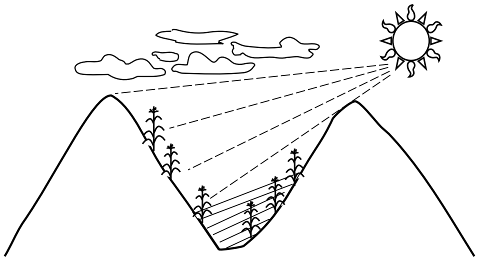


Figure 1. Maize production situation in Guizhou Province.

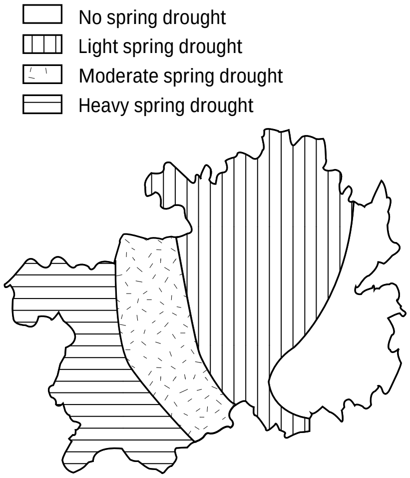


Figure 2. Distribution of spring drought in Guizhou Province (Source: General Division of Agriculture, Guizhou Province).

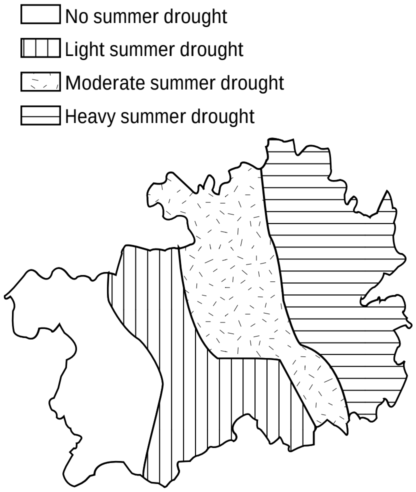


Figure 3. Distribution of summer drought in Guizhou Province (Source: General Division of Agriculture, Guizhou Province).

Table 2. Average maize grain yields (t ha^{-1}) for Guizhou and Jilin Provinces and across China.

	Year				
	1980	1983	1985	1987	1990
Guizhou	2.955	3.120	2.670	3.225	2.955
Jilin	3.015	6.045	3.735	5.805	6.900
China	3.075	3.630	3.615	3.945	4.620

Table 3. Available soil nitrogen, phosphorous, and potassium (N, P, and K) in Guizhou Province.

	Soil grade											
	Rich			Moderate			Low			Very Low		
	N (%)	P (ppm)	K (ppm)	N (%)	P (ppm)	K (ppm)	N (%)	P (ppm)	K (ppm)	N (%)	P (ppm)	K (ppm)
Concentration	>0.2	>20	>150	0.1-0.2	10-20	100-150	0.05-0.1	5-10	50-100	<0.05	<5	<50
Frequency[†] (%)	10.8	10.2	37.3	35.9	20.3	33.1	49.2	30.9	23.8	4.1	38.6	5.8

[†] Percent of the 820 samples analyzed that occur within the given range.

hybrids, and other germplasm for drought tolerance. Equipment for field and laboratory testing is in short supply, so these evaluations can only be done under naturally stressed conditions. Research for tolerance to low soil fertility seldom occurs. Despite these limitations, some good hybrids with tolerance to drought or low soil fertility have been released to farmers (Fig. 4).

General Methods Used by the Breeders

One method has been to cross inbred lines from local germplasm with temperate lines. The local populations have good adaptation to low soil fertility, low radiation levels, and to the humid climate resulting from natural selection. Their leaves are thin, narrow, light in color, and hang down loosely, and their internode length is long so that photosynthesis is more effective in these growing conditions. The temperate lines used contain germplasm from northern China and the USA. These inbred lines have good characters for yield and agronomic performance, as well as good combining ability. When combining these two kinds of lines, we are able to select hybrids that have good adaptation to Guizhou Province. This method has led to the release of hybrids including Qiandan-4 (Guanhua x zi330), Xingyu-1, etc. Qiandan-4 is grown widely in Guizhou.

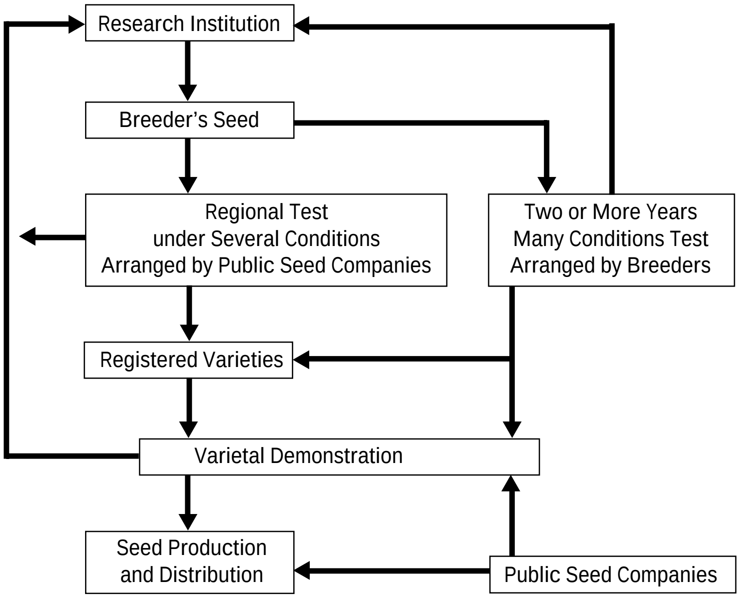
Another method has been to cross tropical lines with temperate lines. Some tropical lines have good resistance to drought, especially those selected from Tuxpeño-1 and Suwan-1. Tuxpeño-1 and Suwan-1 are grown widely in Guizhou, and they have been used extensively by breeders. Inbred lines have been developed directly from them or from materials containing this germplasm. For example, 3012 was selected from Suwan-1 and is used in the hybrid Qiandang-9 (478 x 3012). Inbred line 449 was selected from Tuxpeño-1 and is used in the hybrid Bidan-3 (411 x 449). From the Guizhou Academy of Agricultural Sciences (GAAS), new hybrids Qiandan-10 (zhongxi140 x 3502, 3502 is from Tuxpeño-1) and 9504 (QA02 x FS1, FS1 was selected from Suwan-1 for tolerance to low radiation) are ready for release. These hybrids appear to have good tolerance to drought.

The third method is to develop three-way, double, and topcross hybrids. Natural soil and climate conditions are very complex in Guizhou Province, with multiple ecological environments and adverse growing conditions. For the components of phenotypic variation, environmental effects and genotype x environment interaction effects are more important than genotypic effects. Three-way, double, and topcross hybrids have a wider germplasm base, and are expected to be more broadly adapted than single-cross hybrids under stress conditions. A series of Guibi three-way and double cross hybrids are being used successfully in Guizhou's

Table 4. Hours of sunshine per month at Guiyang, Guizhou Province as compared to Beijing in 1993.

	Month							
	March	April	May	June	July	August	September	Total
Guiyang	112.6	88.7	87.6	114.0	93.5	82.8	97.0	676.2
Beijing	247.2	263.0	287.5	252.2	180.8	234.8	255.4	1720.9

Figure 4. Maize Breeding System in Guizhou Province.



mountainous areas and are spreading into Sichuan and Yunnan Provinces. Examples of this type of hybrid include Guibi 301, Guibi 302, Guibi 402, and Xinyu-1 X Suwan1. In GAAS, a new three-way hybrid (53 x 8112) x Jiao 51 is ready for release. Its yield is 5-8% higher than the check Jiaoshandanjiao (a single cross widely grown in Guizhou, Sichuan, and Guangdong Provinces).

Research for Drought and Low N Tolerance in Maize

We have just begun our drought and low N tolerance work and have only a few results to date. In 1993, a low N-tolerant population Across 8328-BN was introduced from CIMMYT. Initially, we developed inbred lines from it. We used alternate seasons at Guiyang and Nanning, and now have a group of S_3 and S_4 lines. In 1995, we began to use S_1 recurrent selection to improve this population. We tested S_1 progenies at Guiyang, Kunming, and Nanning. In 1995, we also tested for drought-tolerance in S_1 progenies from the Guangxi Maize Institute, and plan to use these materials for inbred line development.

We chose Across 8328-BN as the basic population for our tolerance work because of our experience with Across 8328. It has performed well for farmers and is an important germplasm in the Guangxi breeding program. The shortcomings of Across 8328-BN include a sensitivity to light and temperature, and that its relative maturity is late for Guizhou. We will cross it to local materials and then use S_1 recurrent selection to improve the resulting population for yield and adaptation to low soil fertility.

Inbred lines will continue to be developed from drought and low N-tolerant populations, and to be tested in several stress environments. Attention will be given to developing lines from different germplasm sources, and to acquiring new populations (from CIMMYT or other research institutions) to incorporate into our breeding program. Inbred lines from drought and low N-tolerant populations will be used in our maize hybrid breeding program to meet the need for maize production under stress condition in Guizhou province. Our special emphasis on three-way and double-cross hybrids will continue.

Conclusions

Drought and low soil fertility are two important factors influencing maize production in Guizhou Province, and it is envisaged that even more attention will need to be directed towards them in the future. Some tropical germplasm has good tolerance to drought. Guizhou local populations have good tolerance to low soil fertility, and some temperate materials have good agronomic characters and high yield potential and combining ability. Combining these three kinds of germplasm may be one way to reach our maize breeding objective, to continue to release successful three-way and double-cross hybrids for the Guizhou Province.

Importance of Drought and Drought Tolerance Research on Maize in Guangxi Province, China

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Abstract

Drought is one of the most important abiotic stresses affecting maize production in Guangxi Province, China. Area sown to maize is about 0.5 m ha annually and 90% of this is grown under rainfed conditions. Total production obtained during 1992 was 1.22 mt from 0.52 m ha, with an average yield of 2.37 t/ha. Guangxi experiences a subtropical monsoon climate with an annual rainfall of 1250 to 1750 mm. About 75% of this precipitation is received during the monsoon season from May to September. Variation in rainfall among years and regions results from fluctuations in the monsoon, and spring and fall droughts commonly occur. Most maize is either spring, summer or fall-sown. In the main production regions of western Guangxi, spring drought occurs in 60 to 90% of years, and affects germination, early plant development, silking and pollination of spring-sown maize. In eastern Guangxi fall drought occurs in 50 to 70% of years, affecting grain filling of fall-sown maize. Droughts may also be regionwide. Drought stress is also thought to limit the adoption of hybrids, especially single crosses and three-way crosses. Plastic mulching and irrigation can be used to reduce the effects of drought, but these cannot be used extensively. The development of drought tolerant hybrids represents an important method for reducing the effect of drought stress on maize production.

Maize is the second most important food crop after rice in Guangxi Province. Maize occupies 14% of the total food crop area and contributes about 10% of total crop production. Average yields are low and unstable because most maize is grown under rainfed conditions with fluctuating rainfall patterns. Average yields ranged from 1.63 to 2.01 t/ha during the 1970s and 1980s. Although average yields have increased with time, the lowest mean yield in recent times, 1.35 t/ha, was observed in 1988 (Fig. 1). Total production obtained during 1992 was 1.22 mt from 0.52 m ha with an average yield of 2.37 t/ha. Maize production statistics for Guangxi demonstrate that drought is one of the most important abiotic stresses affecting maize in this province, and a shortage of maize varieties and hybrids with adequate levels of drought tolerance results in fluctuating maize production from year to year.

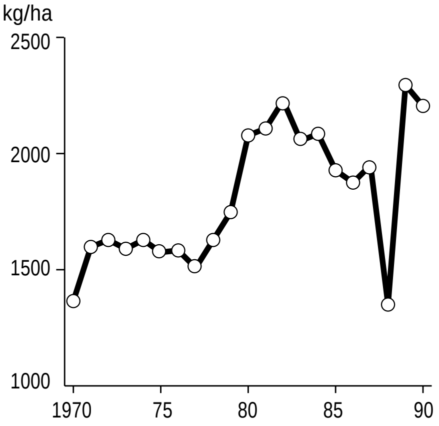

Figure 1. Average maize yield during 1970 to 1990 in Guangxi, P.R. China.

About 90% of the total maize area is in mountainous and hilly regions. Fields here are rainfed with shallow and infertile soils having a loose structure, low organic matter, and low water and fertilizer holding capacities. In this situation maize suffers severely when dry spells occur. Edmeades et al. (1990) reported that drought on average reduces annual grain yield by 10 to 50% on 80% of the area sown to maize in the lowland tropics. Claasen and Shaw (1970) pointed out that grain yield is the character most influenced by drought. They observed that grain yield reduction is largest (50%) when stress is imposed at the silking stage. In contrast the reduction in grain yield at the vegetative and grain filling stages was 25% and 21%.

Rainfall Characteristics: Drought Stress as a Constraint to Maize Production

Guangxi has a subtropical monsoon climate suitable for growing maize. Annual rainfall ranges from 1250 to 1750 mm in normal years, but fluctuations in precipitation are large among years, seasons and regions. More than 75% of rainfall is received during the monsoon season from May to September. A higher percentage is received during the monsoon in the southern, northern and eastern regions than in the central, western and northwestern regions. The latter are the main production regions where only about 1000 mm of rainfall is received during the monsoon.

Drought stress is one of the most important environmental factors reducing maize yield in Guangxi. Fu et al. (1992) reported 18 occurrences of drought during 1949-1985. Individual episodes affected cropping areas of 330,000 to 1,550,000 ha. For example, in 1963, 670,000 ha of maize was affected and average maize yields reduced by 0.30 t/ha from the long-term average yield of 1.95 t/ha. In 1988 the total maize area affected by drought was 470,000 ha and the average maize yield dropped to 1.35 t/ha, a reduction of approximately 0.60 t/ha (or 31%).

Maize is threatened frequently by spring and fall drought because of the lack of concurrence of maize seasons with monsoon rains. The season for spring maize is from early February to late July. Fall maize is grown from mid-July to mid-November. The monsoon season is from May to September. Meteorological data show that the frequency of spring drought in the western hilly regions is 60-90%, and that of fall drought in the east is 50 to 70%. Regionwide drought may even occur in 'normal' years. CIMMYT's (1988) empirical study of maize growing environments suggests that there are around 500,000 ha of maize (that is, almost all the planted area) under some moisture stress in Guangxi Province in an average year.

Most maize in Guangxi is sown in the spring and fall seasons (Table 1). Spring maize is usually planted from early to mid-February, and the first monsoon rains do not normally come until the end of April or early May. As a consequence, germination, early plant development, silking and pollination are commonly affected by water deficits. Fall-sown maize is sown from the end July to early August, and drought usually affects silking, grain filling, and occasionally vegetative development. Normally fall maize is exposed to higher temperatures and matures more quickly than spring maize, and this likely accounts for the generally lower yield of fall versus spring maize.

In addition to drought's direct affect on production, it also discourages the adoption of hybrids. In China, the area planted with hybrids was about 70% of the total maize area in 1980 and had risen to 90% by 1991. In Guangxi Province the area sown to hybrids remained at 45% over this same period. Most released hybrids were double topcross hybrids that occupied 35% of the area. The other 10% was planted to either topcross, single-cross, three-way cross, or intervariety cross hybrids. The yield potential and yield advantage of hybrids is not easily observed given drought, low soil fertility and inadequate chemical fertilizer use in this province. These three abiotic factors appear to have contributed substantially to the lower hybrid utilization. Yang Huaquan (1994) reported the average yield of single-cross, three-way cross and double-topcross hybrids and of open pollinated varieties (OPVs) as 4.84, 4.84, 4.87 and 4.53 t/ha, respectively, in the Guangxi Elite Variety Multilocation Test from 1980 to 1993. The average yield did not differ by hybrid type but all hybrids outyielded the OPVs by 7%.

Commercial seed is produced during the fall to winter season. Fall drought usually results in very low seed yield when producing single- and three-way crosses. If the parental lines are vulnerable to drought stress, seed production can fail completely.

Table 1. Area and yield of maize sown in the four production seasons, Guangxi Province, 1989.

Growing season	Area (ha)	Total area (%)	Production (t)	Production (%)	Average yield (t/ha)
Spring	327,800	61.5	841,370	68.8	2.57
Summer	67,333	12.6	137,500	11.2	2.04
Fall	138,200	25.9	243,460	19.9	1.76
Winter	87	<0.1	120	<0.1	1.38

The Possibility and Importance of Breeding for Drought Tolerance

Improved moisture availability through plastic mulching and better irrigation management are important management approaches to solving the problem of chronic low yields and yield fluctuations in farmers' fields. Unfortunately, given the economic and geographic conditions in the maize production regions of Guangxi and the costs associated with these practices, their use is strictly limited. A more cost-effective method would therefore be to develop hybrids with drought tolerance.

Elite lowland tropical maize germplasm contains considerable genetic variability for yield, anthesis-silking interval (ASI), and morphological and physiological traits indicative of improved plant water status under drought (Edmeades et al., 1990). By careful management of stress levels, it is possible for the breeder to observe and exploit this variability. Full-sib recurrent selection for drought tolerance in the lowland tropical maize population 'Tuxpeño Sequía' resulted in a significant improvement in grain yield (Edmeades et al., 1990).

Heterosis utilization has proved to be an efficient and economical way for increasing maize yield. Several single-cross and three-way cross hybrids with good yield potential were developed or introduced to Guangxi. At present they are only grown in areas where irrigation is available, mainly because the seed is costly and there is the risk of low yield under rainfed conditions. The development of drought tolerant hybrids could lower this risk and improve the adoption of hybrids, and is therefore a high research priority.

Tentative Project of Breeding for Drought Tolerance

Three basic approaches are proposed for the development of drought tolerant varieties and hybrids:

1. Characterize lines developed in China or introduced from abroad for drought tolerance, combining ability and yield potential, with the objective of developing new hybrids and composites from these sources.
2. Select locally-adapted germplasm containing genetic variability for high yield potential, short ASI and morphological and physiological traits associated with drought tolerance. In Guangxi there is considerable local maize germplasm which has been grown under drought conditions for a long time and which presumably has acquired some drought tolerance. This germplasm will be combined with materials known to have high combining ability to develop new populations. The new populations will be improved for drought tolerance, yield potential and combining ability using recurrent selection methods under controlled levels of drought stress.
3. Develop elite inbred lines from new and improved drought tolerant populations and composites (developed in 2, or identified in 1, above), and use these in the hybrid breeding program.

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Influence of Drought in Maize Fields in South China: Strategies to Overcome these Constraints

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Abstract

South China has a predominantly subtropical seasonal climate, and drought stress is one of the most important constraints to maize production in this region. Spring and summer drought results in poor seedling establishment and development, leading to 10-30% yield loss. Autumn drought prolongs the anthesis-to-silking interval, resulting in poor seed set, and can lead to 10-40% yield reductions, or in some cases complete crop loss. Four strategies are being pursued in South China to improve and stabilize maize production in drought prone areas. These are the use of improved maize varieties, agronomic practices, water management, and soil management. The main technical approaches include breeding maize hybrids that are tolerant to drought and responsive to water and fertilizer, seedling transplanting and plastic-film seed-bed mulching, water harvesting, and better crop rotation, irrigation and soil management.

Maize ranks behind rice and wheat in importance as a cereal crop in China. In the early 1990s the maize growing area was around 20 million hectares, with a total production of about 100 million tons. Today it accounts for 22% of the total food grain production.

Maize production contrasts with rice in that over 95% of the area devoted to rice is irrigated, whereas 90% of the maize area is rainfed and subject to yield loss due to drought. Based on statistics for the last four decades, maize yield losses due to drought have averaged 1.8 million tons per year (Lu and Zhang, 1991). Occurrences of below-average maize yield are correlated with the maize area under weather stress (r = -0.62**) (Liu et al., 1989).

Annual rainfall distribution can be used to categorize the maize production area into two main climate zones in China — the northern arid and southern seasonally arid zones. In the former, annual precipitation is 400-600 mm per year. In the latter, annual rainfall may reach 800-1600 mm per year, with more than 80% of it occurring during the summer months (May to October). The aim of this paper is to discuss the influence of drought on maize production in this southern seasonally arid zone, and the appropriate strategies to overcome its effects.

The Influence of Drought on Maize Production

In southern China, maize production is concentrated in the hilly and mountainous regions of Sichuan, Yunnan, Guizhou and Guangxi provinces. During recent years, their average annual maize area has been 3.9 million ha, representing 20% of the total area under maize production in China. Total production in these four provinces has been about 14.5 million tons per year.

This zone is made up of three different geographic sub-zones: north-tropical (I8), south-subtropical (I6) and mid-subtropical (I5). The southern zone is characterized by a range in altitude from 70 to 3,300 masl, average annual temperatures of 12-18 ºC, 240-360 frost free days, 3,500-6,500 growing degree days (GDD, using 10ºC as a base) annually, and 800-1600 mm of annual precipitation. In principle these climate conditions are well suited to maize production. Annual variation in maize production is relatively low, the coefficient of variation for mean grain yield being 8.2-13.1% as compared to 14.0-20.6% in the northern zone. Nevertheless, the standard deviation (SD) of annual rainfall is quite large, being as high as 156 mm in some areas. During a typical 10-year period, the southern zone has two rainy and two dry years, two years with rainfall levels more than one SD above the mean, and two years with rainfall more than one SD below. More important than annual differences is the monthly and even weekly variation in rainfall. These variations generate four types of drought stress during the maize growing season, and the frequency of occurrence of each of these has been observed over a 12-year period (Table 1).

Spring drought

The frequency of occurrence of spring drought was 35% during the period 1981 to 1992 (Table 1). Because it coincides with the planting season, it can result in poor seedling establishment or planting delays. This type of drought reduces maize yield by 5-20%.

Summer drought

The frequency of occurrence of summer drought was 32% (Table 1). Its effect on maize production is greater than that for spring drought, partly because it usually occurs in combination with spring drought.

Early autumn drought

The frequency of early autumn drought was 19% (Table 1). It occurs during the flowering stage, resulting in prolonged anthesis-to-silking intervals and poor seed-set. It reduces yield by 20-40%, but in some severe cases it results in complete crop loss.

Late autumn drought

The frequency of late autumn drought was 13% (Table 1). It occurs during the grain filling stage, resulting in poor grain and seed quality, and leading to a 10-20% yield loss.

Estimated losses of maize yield due to drought in southern China during the last decade have averaged 460,000 tons per year. The yield potential of maize has been increasing with the adoption of improved varieties and agronomic practices, and with increases in yield potential the losses due to drought have increased in absolute terms.

Strategies to Overcome the Constraints

There are four strategies widely used in southern China to alleviate drought's effect on maize production.

Breeding for drought tolerance

Drought tolerance breeding is the primary strategy used for improving maize yield. The major objective is to select maize hybrids that are tolerant to drought and highly responsive to water and fertilizer. Among the elite, high-yielding hybrids developed by our program, there are examples of hybrids that also do well under drought. Jindan8, Huidan2 and 128 x 133 , with yields ranging from 9.1-10.0 t/ha, performed better under normal growing conditions than Chiyin1, Lodan2 and Huidan4 with yields from 7.7-9.6 t/ha (Table 2). The advantage of this high yielding group appears to be even greater under drought. Their yields ranged from 5.3-5.7 t/ha during the dry year, while yields for the other three ranged from 2.7-4.5 t/ha. Chiyin1 appears to have good yield potential, giving 9.6 t/ha in normal year, but it has poor yield stability. It produced only 3.0 t/ha in the dry year, leading to a high SD for yield (3.5 t/ha). Lodan2 was selected in a high rainfall environment (annual rainfall of 1400 mm) and yielded only 2.7 t/ha in the dry year.

Improved agronomic practices

Seedling transplanting and plastic film mulching are two very popular practices in southern China. Transplanting is used to help avoid periods of drought and/or cold stress. Plastic-film mulching helps reduce drought, increases soil temperatures, and helps control

Table 1. Season of occurrence, severity and frequency of drought in Yunnan Province, China, based on 12 years of data from 1981-1992.

Season	Months	Frequency of drought			Frequency (%)
		Slight[†]	Moderate	Severe	
Spring	Mar. to April	3	5	3	35
Summer	May to June	4	4	2	32
Early Autumn	July to Aug.	2	2	2	19
Late Autumn	Sept. to Oct.	3	0	1	13
No. of occurrences during the 12 years		12	11	8	
Frequency %		39	35	26	

[†] slight = 7-14 days, moderate = 15-24 days, and severe = more than 24 days without rain.

weeds, thereby further reducing water losses.

Plastic film mulching prevents soil water evaporation. Soil moisture under a film is maintained 2-7% higher than in an open field and soil temperatures are also higher. This technology is an effective tool to attenuate the stress of drought and cold, especially in marginal regions. It increases maize production to a significant extent. In recent years, over 600,000 ha/year of maize was mulched with plastic in the region comprising the four provinces.

Transplanting has two main advantages for rainfed maize production. Seedlings can be raised in a small nursery and later moved to the field. Transplanted seedlings are less apt to be in the field during periods of cold stress, and can be expected to be larger and less vulnerable to spring and summer drought, as compared to seedlings raised from seed planted in the field. Transplanting also results in a more uniform plant stand and potentially better yields. Since the late 1980s, 350,000 ha/year of maize has been transplanted in these four provinces.

Water management

As mentioned above, total rainfall during the maize growing season usually exceeds the demands of maize growth and development. Seasonal drought is generated by aberrant distribution of rainfall within the season, and heavy rains can lead to severe water erosion in hilly areas. 'Water harvest' (water capture and storage) and supplementary irrigation techniques that efficiently redistribute water within the season can be used to overcome the problem of erratic distribution. Terrace cropping, contour farming, stripe intercropping, and water storage pits and tanks built on the corners of maize fields are widely used to reduce erosion and to increase water harvest. Soft-pipe siphon irrigation is feasible in hilly areas, and is being used effectively.

Soil management

Soil can be thought of as a container for holding rainwater. The soil's water holding capacity depends on its texture, profile thickness and organic matter content. Subsoiling, organic manure application and crop residue mulching are conventional practices for improving soil water holding capacity, thereby helping to alleviate drought's effects.

References

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Table 2. Yield performance (t/ha) of six elite hybrids under different rainfall patterns.

Year	Rainfall pattern	Hybrids					
		Jindan8	Huidan2	128x133	Chiyin1	Lodan2	Huidan4
1990	Normal	9.11	10.00	9.13	9.55	7.68	8.48
1991	Rainy	8.74	9.23	7.16	8.49	8.11	8.35
1992	Dry	5.72	5.31	5.73	2.98	2.72	4.46
Average		7.85	8.18	7.34	7.00	6.17	7.10
SD		1.86	2.52	1.71	3.53	3.03	2.28

Development of Ciba's Drought Tolerant Maize Hybrids in Thailand

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Abstract

All grain maize growing areas in Thailand are rainfed. Nearly every year it is normal to have severe drought stress resulting in crop damage or failure in many of the major production areas. One of Ciba's research objectives is to develop hybrids that yield well under both normal and drought stress conditions. To meet this objective, various practices and selection criteria have been employed during the breeding and evaluation of inbred lines and hybrids. During inbred line development, breeding materials are grown at high plant densities in nurseries with different soil types, both during the rainy season and the dry season under irrigation and high temperatures. Selection criteria include characters related to drought tolerance: synchronization of male and female flowering, prolificacy, heat stress damage, etc. Experimental hybrids are evaluated in yield trials sown in a wide variety of environments, using two plant densities, different sowing dates, and different soil types and fertility levels at various locations, including drought-prone areas. Locations are separated into groups, stress or non-stress, according to their rainfall and its distribution during various plant development stages. After harvest, average yield for each entry is calculated for each location group and the averages are used in a drought index. The index is used together with the performance data for other agronomic traits to select promising hybrids for further testing or commercialization. Hybrids G-5431 and G-5440, also called Hercules 31 or Hercules 40, are examples of Ciba's success in developing drought tolerant hybrids. They were released in 1987, and are still important commercial varieties for drought-stressed areas.

Rainfed grain maize is grown in many provinces in Thailand's northern, northeastern, eastern and central regions. These regions have quite different amounts and distribution of rainfall, though their distributions have a common bimodal pattern (Fig. 1). In all regions the rainy season is normally interrupted by a 2-6 week dry spell occurring during the period June to August.

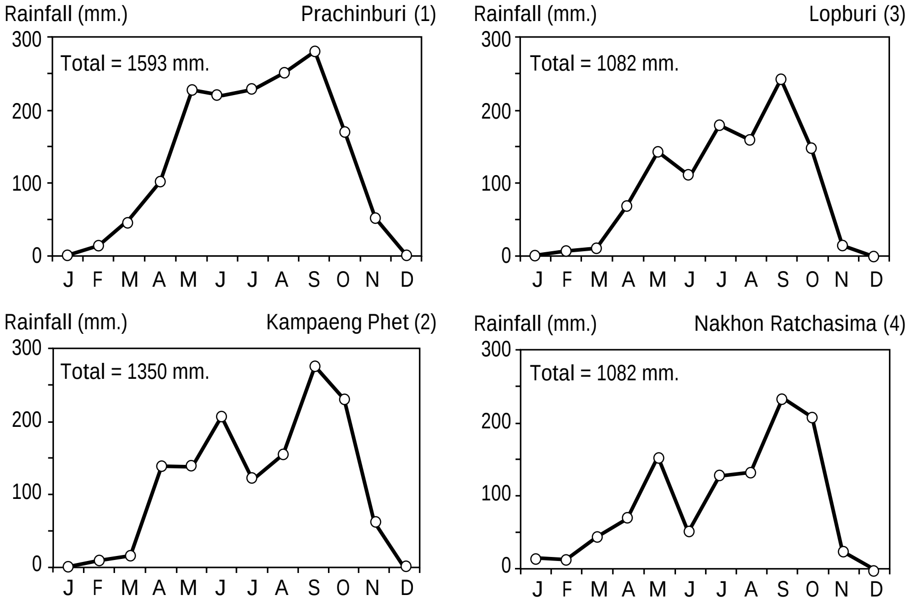

Figure 1. Average amounts of rainfall in different months during 1985-1989 of four major corn growing provinces in the eastern (1), northern (2), central (3), and northeastern (4) regions of Thailand.

The rainy season is rather long (5-6 months), and as a result the majority of farmers grow two crops using various rotation patterns, e.g., legumes and maize, maize and maize, and maize and sorghum. Depending on farmers' practices and climatic conditions, maize can be planted anytime from April to August. During April to June, there is a high probability of having unfavorable growing conditions due to relatively low amounts of rain, high temperatures and low humidity. Consequently, the maize crop may encounter drought stress at any stage from sowing to post-flowering. It is most likely, however, that drought will occur during the seedling to flowering stage. Effects of drought stress vary from little damage to total crop failure. Because of this potential for loss, drought tolerance is a major variety requirement for most farmers, second in importance to high and stable yielding ability. Drought tolerance has been one the main objectives of Ciba's R&D Department since 1981, when Ciba began its seed business in Thailand.

Approach Used in Developing Drought Tolerant Hybrids

Two factors should be considered during the development of drought tolerant materials. The first factor concerns the agro-ecological conditions suitable for expression of the various traits related to a plant's ability to withstand stress. The proper choice of environments enables differences to be observed amongst genotypes at various plant growth stages. A second factor involves appropriate selection criteria — selection should include certain traits related to drought tolerance in addition to general agronomic traits. The drought tolerance traits should be easily observed or evaluated, and involve different stages of plant growth. Additionally, a drought tolerance index can be developed using available yield data, and this allows the selection criteria to vary and be adapted for use at any point in a breeding and testing program.

In this paper, we describe our two phase approach for the development of drought tolerant hybrids, i.e., that used during inbred line and during hybrid development.

Inbred line development

Ciba's R&D Station in Nakhon Sawan Province has four soil types with varying degrees of acidity or alkalinity (pH from 4.5 to 7.5). These soils are similar to those in the major corn growing areas of Thailand. Our irrigation facilities allow us to establish breeding nurseries at any time during the year. Breeding materials and inbred lines are normally grown at 67,000 to 74,000 plants/ha. Most breeding projects are carried out in both the dry and rainy seasons. Dry season breeding nurseries are normally established during December-April. It is usual for breeding materials and inbred lines to encounter strong wind, intense sunshine, high temperatures and low humidity in this season, facilitating selection for drought tolerance related traits. Such traits are leaf wilting and recovery, heat stress damage, prolificacy, synchronization of male and female flowers, seed set, etc.

In the rainy season, we normally plant breeding materials periodically from May to August. Our selection criteria concern mostly plant and ear traits, and disease and insect resistance. It is normal, however, to have drought stress occurring for 2-6 weeks in the period June to August, so it is possible to add selection criteria based on the plant's response at various growth stages to this adverse growing condition.

Hybrid development

Many experimental hybrids are formed from the inbred lines developed. They are arranged group-wise with appropriate checks and evaluated in yield trials using either a 7x7 partial balanced lattice or a randomized complete block design, with three to four replications. These yield trials are grown under two plant populations (53,000 and 67,000 plants/ha) on different soil types, and using either 63:63:0 or 126:126:0 kg/ha N:P_2O_5:K_2O as 20-20-0 fertilizer. Testing sites include our research station, as well as farmers' fields representing most major corn growing areas. Plantings are made periodically from May to August, following farmers' practices in the individual regions. During this evaluation period all experimental hybrids are exposed to environmental conditions that vary from very favorable to very unfavorable due to moisture stress at different plant growth stages and to rather low soil fertility at the lower fertilizer application rate.

Besides taking notes on performance traits for each trial entry, we also record daily rainfall received from sowing until harvest at each location. In addition, each location is assessed using a 1-9 scoring system (1 is favorable or non-stressed and 9 is least favorable or most severely stressed). This overall environmental condition is largely a function of rain received and its distribution.

After harvest, agronomic performance data are analyzed separately for each location. Combined analyses over locations are made using only locations providing quality data. In addition, these acceptable locations are further divided into two groups, stressed and non-stressed locations, based on their environment scores. The average yield of individuals and all hybrids are used to calculate drought indices following the formula proposed by Fischer et al. (1983). The drought index for any one genotype is the ratio of its yield under stress to non-stress, relative to the ratio of the mean yield of all genotypes under stress to non-stress. A drought index > 1.0 suggests relative drought resistance, and a drought index < 1.0 suggests relative drought susceptibility.

Selection of the promising experimental hybrids for further testing or for commercialization is normally based on their yielding ability and other important agronomic traits. Drought indices are also seriously considered, especially if we want to position the hybrid in drought prone areas.

Ciba’s Success in Developing Drought Tolerant Hybrids

Hybrids G-5431 and G-5440, also called Hercules 31 and Hercules 40, are good examples of Ciba’s success in using the above approach. These two hybrids were first evaluated in a preliminary yield trial in 1986. They were selected for further testing in an advanced yield trial grown the following year. This yield trial consisted of 39 Ciba hybrids, nine competitive hybrids and one open-pollinated variety, Suwan 1. The 49 entries were arranged in a 7x7 balanced lattice design, and planted at 10 locations. Two locations were discarded due to severe drought stress. The remaining locations were divided into two groups, non-stressed and stressed locations. Average yields for individuals and all entries were used to calculate drought indices. Indices were considered together with yield and other agronomic performance data. Table 1 shows average yields and drought indices of the six selected Ciba experimental hybrids, nine competitive hybrids and Suwan 1. G-5431 and G-5440 had the highest average yields under non-stressed and stressed conditions. They also

Table 1. Average yields (t/ha) and drought indices of 15 selected entries in the advanced yield trial grown at eight acceptable locations in 1987. Locations were separated into two groups: those experiencing drought stress, and those experiencing no drought stress.

Hybrid/ variety	Non-stressed locations					Aver. (5 locs)	Stressed locations			Aver. (3 locs)	All locations		Drought index
	loc.1	loc.2	loc.3	loc.4	loc.5		loc.6	loc.7	loc.8		Aver. (all locs)	% of check	
CGx14435	5.08	4.26	4.31	5.53	5.34	4.86	4.18	2.38	4.00	3.61	4.39	139	1.01
CGx14446	4.73	4.67	4.62	5.24	5.56	4.93	4.07	1.94	4.50	3.56	4.42	139	0.98
G-5431	4.95	4.39	4.54	5.21	5.32	4.93	3.97	2.85	4.64	3.73	4.48	141	1.03
G-5440	4.98	4.92	4.41	5.51	5.28	4.97	3.83	2.36	4.68	3.70	4.50	142	1.01
G-5401	4.65	4.48	4.32	4.68	4.86	4.50	3.51	2.14	3.96	3.38	4.08	129	1.02
G-5402	4.74	4.28	4.66	4.41	4.87	4.51	3.01	2.13	3.88	3.14	3.99	126	0.95
Commercial 1	4.60	4.51	4.57	4.47	5.12	4.41	2.93	1.99	3.28	3.14	3.93	124	0.97
Commercial 2	4.57	4.68	4.25	4.66	5.26	4.38	3.72	1.78	3.16	3.39	4.01	127	1.06
Commercial 3	4.08	4.17	3.96	4.67	4.67	4.11	2.18	2.09	3.17	2.81	3.62	114	0.93
Commercial 4	3.92	4.21	3.16	4.57	4.08	3.86	2.73	3.01	3.56	3.32	3.65	115	1.17
Commercial 5	4.48	4.36	4.23	4.76	5.18	4.54	3.60	2.50	4.04	3.50	4.14	131	1.05
Commercial 6	4.09	3.86	3.40	3.87	4.02	3.70	2.97	1.51	3.12	2.78	3.36	106	1.02
Commercial 7	4.41	3.75	4.56	3.86	4.82	4.18	3.45	2.01	3.23	3.07	3.76	119	1.00
Commercial 8	3.73	3.83	3.64	4.49	4.36	3.85	2.68	2.37	2.82	2.96	3.49	110	1.05
Commercial 9	5.12	4.25	4.55	4.64	5.36	4.71	3.90	2.44	3.90	3.53	4.27	135	1.02
Suwan 1 (check)	4.11	3.51	3.27	3.56	4.33	3.75	2.96	1.08	2.55	2.52	3.17	100	0.96
Mean	4.56	4.33	4.28	4.89	5.00	4.49	3.35	2.20	3.77	3.29	4.04		
$LSD_{(0.05)}$	0.60	0.65	0.65	0.66	0.57		1.04	0.51	0.72				
CV (%)	9.27	10.5	10.7	9.38	7.97		21.8	16.3	13.3				

had drought indices higher than 1.00, indicating that they were relatively tolerant to moisture stress. Consequently, both hybrids were launched into the market in 1988 and were positioned for early planting in most major growing areas. They were well accepted by farmers due to their high yielding ability and outstanding drought tolerance.

G-5431 and G-5440 were evaluated in multi-location yield trials together with other hybrids and new experimental hybrids in subsequent years. Fourteen entries, including G-5431 and G-5440, 11 hybrids and Suwan 1 were included in the same trials over locations and years, and were used to calculate new drought indices. Table 2 shows average yields obtained from two groups of yield trials conducted over three years, 1987 to 1989. G-5431 and G-5440 were the top yielding varieties among these 14 common entries, and they also had high drought indices. Feedback received from farmers has confirmed our results. To date, these hybrids are still important hybrids for drought-prone areas.

Conclusion

When developing drought tolerant hybrids, it is important that all breeding materials are grown and evaluated under stress conditions similar to the actual agro-ecological conditions in farmers' fields, before they are advanced and tested further. We believe that this approach is a practical means to generate suitable drought tolerant hybrids because it is relatively easy to execute, and can (and should) be practiced at the different stages of hybrid development. Furthermore, except for the need for irrigation facilities, this approach does not require additional equipment to evaluate characters related to drought tolerance.

Reference

Fischer, K.S., E.C. Johnson, and G.O. Edmeades. 1983. Breeding and selection for drought resistance in tropical maize. CIMMYT, Mexico D.F., Mexico.

Table 2. Average yields (t/ha) in 26 non-stressed locations, 15 stressed locations, and across locations; and drought index estimates for 14 entries common to various yield trials grown from 1987 to 1989 in Thailand.

	Non-stressed locations		Stressed locations		All locations		
Hybrid/ variety	Aver. (26 locs)	% of check	Aver. (15 locs)	% of check	Aver. (41 locs)	% of check	Drought index[†]
HB 87279	5.71	109	4.12	118	5.13	112	1.01
HB 86197	6.27	120	4.63	133	5.67	124	1.03
HB 85166	6.36	122	4.39	126	5.64	123	0.96
HB 86534	5.59	107	4.23	121	5.09	111	1.05
HB 86554	5.83	111	4.08	117	5.19	113	0.98
G-5431	6.42	123	4.79	137	5.83	127	1.04
G-5440	6.49	124	4.82	138	5.88	128	1.04
Commercial 1	5.91	113	4.07	117	5.24	114	0.96
Commercial 2	5.84	112	3.99	114	5.16	112	0.95
Commercial 3	5.48	105	3.85	110	4.89	106	0.98
Commercial 4	5.66	108	4.19	120	5.12	112	1.03
Commercial 5	5.85	112	4.19	120	5.25	114	1.00
Commercial 6	5.80	111	4.31	123	5.25	114	1.04
Suwan 1 (check)	5.23	100	3.49	100	4.59	100	0.93
Mean	5.89		4.23		5.28		1.00
Minimum	5.23		3.49		4.66		0.93
Maximum	6.49		4.82		6.01		1.05

[†] Estimated by using average yields of 14 entries

Management and Breeding Approaches to Alleviate the Effect of Drought on Maize in Vietnam

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Abstract

Vietnam is traditionally a rice-eating country and favorable irrigated land is reserved for rice production. Maize is planted mostly as an upland crop where drought is more common. Average rainfall is 1,500 - 2,000 mm per year but rainfall distribution is irregular in some regions and seasons, leading to drought. The National Maize Research Institute's research has led to the adoption of new management practices and varieties to alleviate the effect of drought on maize. Widely adapted early-maturing maize varieties are used to escape periods of low moisture availability during critical development stages. Early-maturing open-pollinated varieties (OPVs) 'TSB-2', 'MSB-49', and 'MSB-49B' are widely grown, and new OPVs are being developed. Intercropping maize with legumes (soybean, groundnut and mungbean) appears to reduce evaporation from the soil surface, increases profits and improves soil condition and water holding capacity. Transplanting winter maize takes advantage of adequate temperatures, humidity and sunlight during the early stages of plant development and helps avoid drought and low temperatures that are common at the end of the rainy season. Crop duration in the field is being reduced by harvesting the maize for fresh consumption as glutinous, sweet, or baby corn, thereby avoiding late season drought. Another focus is the development of short-stature erect-leaf hybrids for planting at high densities and in intercropping systems. A few such hybrids — 'LVN-20', 'EE-1', and 'HTD-5' — have been widely disseminated. Prolific maize is being selected to reduce drought-induced barrenness, and is being used in an effort to develop more prolific baby corn hybrids. 'NN-1' is one such promising hybrid. Drought-tolerant germplasm from CIMMYT, including 'Tuxpeño Sequía', 'Pool 26 Sequía', 'Pool 18 Sequía', and wide crosses between teosinte and maize are being used as genetic resources in our breeding program for drought tolerance and prolificacy.

Vietnam is located in southeast Asia ($8^0$10' - $23^0$30' latitude), and experiences seasonal tropical weather. Average rainfall is between 1,500-2,000 mm per year, but its distribution is irregular in some regions and seasons, causing drought. Vietnam is traditionally a rice-eating country, as its land and irrigation systems are suited to rice cultivation. Maize is a secondary upland crop, prone to drought when planted in rainfed areas. The maize growing area in Vietnam is divided into eight ecological regions:

1. In the Northeastern Mountainous region, 113,000 ha of maize are grown during the spring season (January-June). Drought often occurs at the beginning of the season.
2. In the Northwestern Mountainous region, 43,000 ha of maize are grown in the spring-summer season (April-August). Again, drought occurs at the beginning of the season.
3. The Red River Delta has three different seasons supporting a total of 220,000 ha of maize. The seasons are spring (February-June), autumn (July-October), and winter (September-January). The alluvial soil on river banks is subject to drought which often occurs at the end of winter and during the early part of spring.
4. In the Northern-Central region, 45,000 ha of maize are sown during two seasons, winter-spring (November-April) and spring (January or February-May). Drought often occurs at the beginning of the spring season and the middle of the winter-spring season.

5. The Central Highlands has 46,000 ha of maize under production during its spring-summer season (April-August). This region is prone to drought at the start of the season.
6. The Central-Coastal region produces maize on 28,000 ha during two growing seasons, winter-spring (November-April) and spring-summer (April-August). Drought often strikes at the beginning of the spring season.
7. The Southeastern region supports 48,000 ha of maize during its spring-summer season (April-August). Drought occurs at the beginning of the season.
8. The Mekong River Delta has 11,000 ha of maize during two seasons, winter-spring (November-April) and spring-summer (April-August).

In general for all ecological regions in Vietnam, maize is usually prone to drought at the beginning of the main season and the end of secondary seasons where irrigation is not available.

Main Objectives of the National Maize Research Institute (NMRI)

The NMRI conducts research on management and breeding approaches to reduce the effects of drought and on intensive technologies and high-yielding hybrids. Drought research in maize is somewhat limited by a lack of equipment. In light of this constraint the NMRI has developed additional research objectives:

1. To find effective and applicable management methods that help avoid or reduce drought's effects.
2. To develop high-yielding maize varieties for each region using indirect selection for characteristics which are easily observed and thought to be related to drought tolerance (reduced leaf area index and barrenness, and short plant height).
3. To incorporate into our breeding program drought-tolerant germplasm from CIMMYT and other institutions or countries.
4. To introgress traits indicative of drought-tolerance into improved maize using wide-hybridization techniques.

Results

Results obtained from variety trials and evaluations of various agronomic technologies in different ecological regions from 1985 to present have been used to identify methods which limit the effect of drought on maize production. Results related to a few of these methods are discussed in the following sections.

Adapted early-maturing maize varieties

These are widely used to escape drought effects during critical development stages, and their importance is well known (e.g., Edmeades et al., 1990). Early-maturing OPVs such as 'TSB-2', 'MSB-49', 'MSB-49B' (a yellow version of MSB-49), and 'Q-2' have been adopted by farmers. MSB-49, MSB-49B and Q-2 were released in 1986, 1992 and 1990, respectively. MSB-49 is derived from CIMMYT's Population 49, which originated from Tuxpeño germplasm. At present they are used in areas with unfavorable growing conditions, resulting in yields comparable with some hybrids (Table 1). NMRI is also developing new early-maturing hybrids. Multi-year testing has identified promising hybrids 'EET-1', 'LVN-20', 'LVN-4' and 'LVN-5'. Among these, LVN-20 appears to be the most promising. It has been widely adopted by farmers in Vietnam's northern provinces. It is a short-statured erect-leaved hybrid, and has been planted for testing in several different ecological zones.

Intercropping maize with legume crops

Intercropping with legumes (soybean, groundnut, and mungbean) reduces evaporation from

Table 1. Yields and yield components of early-maturity OPVs grown under unfavorable conditions, i.e., low temperatures at the beginning of the season and drought. Data are three year (1992-4) means from the Northeastern Mountainous region of Vietnam.

		Yield				Physiological maturity	Ear length	Ear diameter	Kernel row no.	Kernels row^{-1}
		1992	1993	1994	Mean					
	Varieties	(t ha^{-1})				(d)	(cm)	(cm)	(no.)	(no.)
1	TSB-2	2.96	3.48	3.06	3.16	116	12.1	4.0	13.3	27
2	Q-2	3.66	3.46	3.59	3.57	118	13.5	4.5	13.8	28
3	MSB-49	2.82	3.00	2.65	2.82	117	11.5	4.3	13.2	29
4	MSB-49B	2.74	2.99	3.12	2.95	117	11.7	4.2	13.0	28
5	P-11 (DC) Check	3.15	3.53	3.62	3.43	120	12.0	3.8	13.0	26
	LSD $_{(0.05)}$	0.76	0.54	0.55						

the soil surface, increases profit, and improves soil conditions and water holding capacity. Vietnamese farmers have practiced intercropping for a long time, but their success has been limited when unsuitable combinations of species were planted together, or when they were planted at inappropriate intercropping ratios. In general NMRI research shows that intercropping has advantages over maize and legume monoculture. This advantage is greatest when maize and *Phaseolus* are grown together and diminishes for maize with groundnut, maize with mungbean and maize with soybean, in that order. Nonetheless, because of the economic importance of groundnut and soybean, they are the main crops being intercropped with maize.

NMRI research results indicate that high leaf area index (LAI) of maize, when it is intercropped, is the main factor limiting yields of both component crops. As a consequence NMRI's recommendation is that farmers plant a two-eared hybrid like LVN-10 at a lower density, or an erect-leafed hybrid (e.g., LVN-20 or HTD-5) at a normal density. Maize/legume intercropping using more than one row of each crop tends to give better results than intercropping alternating single rows of each crop, or when monocropping the component crops. The following row ratios have given good results:

Intercropping row ratio	Value of returns over maize monoculture
1 maize to 1 (or 2) soybean	1,000,000 Vietnamese dong (VND)/ha (US $90/ha)
1 maize to 2 (or 3) groundnut	1,300,000 VND/ha (US $110/ha)
2 maize to 2 mungbean	2,000,000 VND/ha (US $180/ha)

Soil fertility is often better following intercropping. Humus content, total nitrogen (N), and soil pH all tend to increase with intercropping, P_2O_5 and K_2O remain largely the same, and a particular benefit is the reduced concentration of Al cations (Table 2).

Transplanting maize

This is practiced at increasing levels across several regions of Vietnam. Transplanted winter maize takes advantage of adequate temperatures, humidity and sunlight during the early stages of plant development, helping to avoid drought and low temperature towards the end of the rainy season. Traditionally two rice crops (spring and summer) were planted on the Red River Delta's 1.2 million hectares. Summer rice is harvested at the end of September or early October, and spring rice is transplanted at the end of January or in early February. More recently either a winter crop of maize, sweet potato, or a vegetable or legume crop has been added to the crop rotation during the October-January period. Maize is planted on about 120,000 ha out of the 1.2 million ha available. It needs to flower in November when the daily average temperature is above 17 ºC. If it flowers in December when temperatures are lower, yield potential is much lower and the farmer may not be able to wait for it to mature and could lose the crop. Transplanting winter maize helps avoid these problems. Seven to 10 d before rice harvest, maize is planted along the edges of fields and canals. After harvest, the maize seedlings are transplanted into soil still wet from the rice crop. Thanks to the additional winter maize crop, a farmer can produce 15 tons of grain/ha/year, assuring enough food for his family and for feeding his animals. The winter maize growing area is expected to expand in the future. This transplanting technique is also being practiced in several mountainous provinces.

Harvest of fresh maize

Maize is being harvested fresh as glutinous, sweet, or baby corn, thereby avoiding drought at later stages of plant development. Traditionally, glutinous maize was most often cultivated and consumed by farmers in the marginal mountainous regions. Nowadays glutinous maize is more commonly planted near suburban areas and is harvested just before physiological maturity and consumed after either boiling or roasting. Glutinous maize requires from 70 to 90 d from planting to harvest. This short season can easily be timed to avoid weather

Table 2. Changes in soil fertility associated with maize monocropping and maize/soybean intercropping. Data are from Bac Thai in northeastern Vietnam.

				Concentration		
Farming system	pH_{KCl}	Humus (%)	N (%)	P_20_5 (%)	K_20 (%)	Al (mg/100g of soil)
Maize monoculture						
Pre-planting	5.6	2.07	0.13	0.06	0.42	0.16
Post-harvest	5.8	2.03	0.12	0.04	0.40	0.13
Intercropping						
Pre-planting	5.6	2.07	0.13	0.06	0.42	0.16
Post-harvest	5.9	2.11	0.14	0.04	0.42	0.11

stress. Glutinous maize varieties are abundant in Vietnam. The NMRI has collected and is preserving 42 samples of white, 11 of yellow, and 10 of violet glutinous maize varieties, all originating from several locations in the mountainous regions. NMRI is conducting an improvement program to increase yield of these varieties and their stress tolerance. Some white glutinous synthetics were released in 1990. NMRI is currently improving earlier-maturing white glutinous varieties and some good quality yellow varieties.

Sweet corn production is new to Vietnam. It has been quickly adopted by the farmers located near suburban areas. To support this recently developed industry, NMRI has developed two sweet corn varieties, yellow sweet variety 'TSB-3' and a white sweet variety. Baby corn is also new in Vietnam. This industry is developing quickly, largely because of advantages associated with its short duration in the field (50 to 70 d). Like other fresh-maize crops, its crop cycle is easily managed to avoid times when drought is likely. A farmer can raise 4 to 5 crops per year on the same land, if irrigation is available. NMRI research results show that under Vietnamese conditions, one hectare of baby corn can produce on average 1 ton of ears and 25 tons of fresh green biomass. To meet the need of the baby corn industry, NMRI has developed early-maturing prolific hybrids such as 'NN-1' and 'LVN-17'.

Indirect selection for drought tolerance

Early-maturing hybrids with erect leaves and short plant height are being developed for the dual purposes of drought tolerance/ avoidance and their value in intercropping systems. Due to inadequate means for selecting directly for drought tolerance, NMRI is selecting indirectly for tolerance using several morphological traits. The selected traits are those thought by several scientists (Fischer et al., 1983) to be related to drought tolerance, including short-plant height, narrow leaves, and dark green color. A number of promising hybrids which have both the desired set of traits and high yield potential have been identified. Their descriptive characteristics and relative yield are presented in Table 3. Among them is the early-maturity hybrid LVN-20, discussed above.

Prolific maize

Prolific maize is being selected for reduced barrenness as a means of improving drought tolerance, and is also being used to develop more prolific baby corn hybrids. The relationships between prolificacy, resistance to barrenness and drought tolerance of maize have been discussed by others (Hallauer and Troyer, 1972; Guei and Wassom, 1992). NMRI is using two main breeding approaches to develop prolific parents. Inbred lines are being extracted from prolific germplasm by sib-mating plants expressing the character. Presumably there is more opportunity for recombination and accumulation of desired genes and less opportunity for inbreeding depression when using this breeding method compared with others.

The second approach is the use of wide hybridization with teosinte, followed by cycles of backcrossing to develop prolific lines. NMRI research

Table 3. Relative yield and descriptive morphological characteristics of a group of early-maturing hybrids identified for their potential value in drought-prone environments and in intercropping systems in Vietnam.

Hybrid pedigree	Yield ($t\ ha^{-1}$)	Physiological maturity (d)	Plant height (cm)	Ear height (cm)	Leaf no.[†] (no.)	Leaf angle	Plant color	Ear length (cm)	Ear diameter (cm)	Kernel row no. (no.)	Kernels row^{-1} (no.)
TF-1 X 137/2649	6.52	100	155	66	17.0	Erect	Dark green	13.4	5.4	15.0	29.5
LVN-20	6.73	100	172	88	17.2	Erect	Dark green	15.3	5.2	13.4	33.7
TF-1 X 454/2649	6.08	98	164	73	17.5	Erect	Dark green	14.1	4.8	13.2	30.8
UT-436 X 137/2649	7.68	102	158	70	16.7	Erect	Dark green	14.4	5.2	14.4	32.4
235/2649 X UT-436	7.40	101	163	80	17.1	Erect	Dark green	15.7	4.7	12.8	35.2
UT-436 X 275/2649	5.92	105	144	72	17.5	Erect	Dark green	12.8	4.7	14.8	40.4
Check mean	6.72										
$LSD_{(0.05)}$	0.47										

[†] Determined from 10 plants, early senescence leaves not included.

shows that it takes only one or two backcross cycles to recover the desired agronomic performance (Table 4), though with further cycles of backcrossing the desired prolificacy may be lost. Several promising prolific hybrids contain parental lines that trace to this germplasm. They include hybrids used in the baby corn industry, such as NN-1, and hybrids used for grain production.

Drought tolerant source populations

Drought-tolerant source populations from CIMMYT and other countries are being incorporated into NMRI's breeding program to augment drought tolerance. CIMMYT's drought-tolerant populations 'Pool 16 Sequía', 'Pool 26 Sequía C_3', 'Pool 18 Sequía', 'Tuxpeño Sequía' and 'La Posta Sequía' (and others) have been evaluated in the laboratory for water-holding capacity (percent water in tissue after drought) and ability to recover turgor after drought. La Posta appears to have the highest leaf water-holding capacity (44.8%), considerably higher then the check Q-2 (13.7%). Tuxpeño Sequía had the highest ability to recover leaf turgor (41.2%), followed by La Posta Sequía (40.9%). Pool 26 Sequía had the highest ability to recover root turgor (70.6%). The tests were used to identify a group with superior drought tolerance. Field evaluation of this germplasm in Vietnam's more drought-prone regions has been started, and have shown that these materials exhibit 'strong' plant type — dark green leaves, good synchrony between pollen shed and silking and high grain yields. They are being used to develop drought-tolerant composites and for inbred line development in the hybrid breeding program.

Conclusions

Drought affects maize production to varying degrees depending on ecological region and soil type. It is probably the leading cause of lost maize production in Vietnam. NMRI is developing both improved maize management techniques and maize varieties to help alleviate these effects. Widely-adapted early-maturity varieties have been developed and are being used to avoid drought effects during critical development stages. Intercropping maize with legumes (groundnut, soybean, mungbean) is used to reduce evaporation from the soil surface and increase profits and soil conditions. Transplanting winter maize shortens the crop season and thereby takes advantage of adequate temperatures, humidity, sunlight during the early stages of plant development and helps avoid drought. Fresh maize crops like glutinous, sweet, and baby corn are short-season crops whose sowing dates can be managed to avoid drought. In NMRI's breeding program for drought tolerance attention is being paid to early maturity, short plant height, erect leaves, prolificacy and resistance to barrenness. At the same time the best performing germplasm from CIMMYT and wide hybridization with teosinte are being used to introduce higher levels of drought-tolerance into the germplasm used by NMRI.

Table 4. Descriptive characteristics of teosinte (donor parent of the prolificacy trait), JV-2 (recurrent parent), F_1, BC_1, and BC_2. Data are from 1987-1989.

Source	Physio-logical maturity (d)	Plant height (cm)	Ear height (cm)	Leaf no. (no.)	Stalks plant^{-1} (no.)	Ears plant^{-1} (no.)	Ear length (cm)	Ear diameter (cm)	Kernel row no. (no.)	Kernels row^{-1} (no.)	Kernel weight (mg)
Teosinte	90	132	66	12.8	2.3	4.7	-	-	-	-	126
JV-2	115	182	76	17.0	1.0	1.0	12.6	3.7	12.3	17.5	222
JV-2 x Teosinte (F_1)	100	160	67	14.9	1.1	3.0	6.8	1.8	6.9	10.2	136
BC_1	113	178	79	15.5	1.0	2.1	10.2	2.4	9.6	14.2	150
BC_2	113	179	79	15.5	1.0	1.3	10.8	3.3	13.5	24.7	220

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Constitutive Traits Affecting Plant Performance Under Stress

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Abstract

The final integrated plant response to drought stress in terms of total biomass or economic yield is conditioned by genes which are expressed constitutively and genes which are stress-responsive and stress-adaptive. Genes expressed constitutively may be stress-responsive, but they are not, by definition, stress adaptive. This brief review discusses the impact, whether positive or negative, of several major plant constitutive traits on plant production under drought stress. For most crop plants there is a genotype x drought stress interaction for yield which is expressed when stress is severe enough. Besides well-watered conditions, a high yield potential is expressed also under moderate levels of stress. However, a high yield potential may be negatively affecting yield under severe stress. The possible reasons for this negative association are discussed. Plant phenology has been widely implicated in plant production under drought stress. Phenology determines plant characters which may impact plant water-relations, crop assimilation and reproductive integrity under drought stress. The roles of plant size, vigor and potential growth rate in affecting productivity under stress are not well resolved. Some of the positive and negative implications of plant size towards plant productivity under drought stress are considered. Carbon assimilation, storage and utilization are expressed constitutively and their impact on stress adaptation is becoming evident, such as the case of plant reserve utilization. Finally, molecular techniques are now used to achieve the constitutive overexpression of stress adaptive genes. The few available examples and their implications are mentioned.

When an organism is subjected to environmental stress its function may depend on two genetic systems. One system involves genes which are expressed constitutively irrespective of the stress situation. These genes are not stress responsive in the sense that they do not require stress in order to be expressed. The other system is comprised of those genes which are stress responsive and stress adaptive. This discussion is limited to those genes and those traits which are expressed constitutively, but are still very valuable in sustaining plant productivity under stress.

Yield Potential

This trait is at the top of the agenda in most plant breeding programs. Ceccarelli and Grando (1991) divergently selected barley lines for yield under non-stress and under stress conditions and compared them in different environments as expressed by the ‘environmental index’. When tested, the two groups of lines presented a crossover (interaction) in yield with respect to the environment, whereas lines selected under high yield conditions yielded relatively better in the high yield environments and lines selected under low yield (stress) conditions were relatively superior to the other group in low yielding environments. The crossover occurred at a mean yield of about 250 to 300 g m^{-2}. Very similar results were obtained for various wheat varieties by Blum and Pnuel (1990). It was seen that varieties selected for higher yield potential yielded relatively well also under moderate stress conditions as expressed by mean yields of about 400 g m^{-2}. Only when mean yields were reduced to below 250 to 300 g m^{-2}, the more stress-adapted lines were superior to the high yielding ones.

Hybrid sorghums, by the token of their high yield potential, have been repeatedly shown to yield better than their parental lines or open-pollinated varieties also under moderate and even more severe stress. Heterosis appears to act constitutively, and does not seem to constitute a stress adaptive feature. Blum et al. (1992) showed that yield reduction with increasing drought stress was proportionally the same in sorghum hybrids and open-pollinated varieties. However, at all levels of plant stress the hybrids yielded relatively better, most probably because of their higher potential productivity.

On the physiological level, leaf carbon exchange rate (CER) was found to be higher in a sorghum hybrid than its two parental lines, because of hybrid vigor (Blum et al., 1990a). As environmental stress increased and CER declined, the hybrid maintained its relative advantage in CER. Only when mean CER was reduced to about 1/5 of its potential, one of the parental lines became superior to the hybrid, evidently because of its specific stress adaptation.

The same conclusion on the importance of potential productivity under stress has been reached also for salinity stress. Kapulnik et al. (1990) showed that alfalfa lines selected for high vigor were yielding better than lines selected for low vigor over a range of salt concentrations, until yields of all lines converged to a very low value at the highest salinity stress. Similarly, Shannon and Noble (1995) demonstrated that subterranean clover varieties of high potential biomass production yielded better than less productive lines under a wide range of salinity levels. A crossover may have been observed only at a high salt stress when yields were very low. This is culminated by Richards's (1992) conclusion that the most important trait for breeding towards saline conditions is high yield potential.

There is therefore a wide range of stress conditions where high yield potential supports plant production and specific adaptation per se is not required and sometimes even not effective. If stress adaptive genes exist in the breeding material they are expressed only when stress becomes sufficiently severe.

Plant Size and Growth Rates

The role of plant size and growth rate in plant performance under stress has not been studied very extensively. It is generally thought that large size and high growth rates involve a large demand for environmental resources. When these resources are not available in the quantities required, a large reduction in growth would occur as compared with inherently more moderate and less demanding genotypes. However, this is in conflict with the concept that the non-competitive (smaller) plant commensurate with a high yielding ideotype (e.g. Reynolds et al., 1994).

In a preliminary study we have tested the response of the *Rht* height isogenic lines of wheat (in two backgrounds) to stress. These genes affect juvenile plant size (in terms of total dry matter weight at about 3 weeks after emergence), which declines from *rht* to Rht_3. While absolute plant mass under stress was highest in the largest (*rht*) plants, the rate of reduction in growth rate under stress as compared with controls clearly declined with potential plant size from *rht* to Rht_3. Similar results were obtained also under heat and abscisic acid (ABA) stresses, both of which reduced plant growth relatively more in the largest than in the smallest plants.

Thus, while a small size may be counter productive, it seems to suffer less reduction under stress. As with potential yield, while potentially high growth rates are relatively susceptible to reductions by stress, they still support productivity under stress, as long as stress is not too severe.

Plant Phenology

Plant phenology and phasic development are constitutive traits controlled by genes affecting basic development, photoperiod and vernalization responses. The advantage of short growth duration under conditions of late-season (terminal) drought and heat stress is well documented. It is also recognized that short-season varieties generally express lower yield potential than longer season varieties. However, while longer growth duration does not allow escape of late-season (terminal) stress, it should not be equated with greater drought susceptibility. This was well represented in work with peanuts

(Nageswara Rao et al., 1989). Early peanut varieties had an advantage under terminal drought stress while late flowering varieties had a relative advantage under mid-season stress. The advantage of late flowering varieties under mid-season stress stems from their better recovery capacity. At the same mid-season date, late flowering varieties will be more juvenile and thus generally more tolerant than earlier varieties. Furthermore, a longer growth duration is often associated with greater root growth and deeper soil moisture extraction (e.g. Blum and Arkin, 1984; Matthews et al., 1990).

The Root

While root growth, depth and length-density are strongly affected by soil and atmospheric environments, some basic constitutive features of roots can be sustained under stress and impact plant performance. Inherent and consistent differences in root attributes are known to occur and have been repeatedly documented for many crop species. At the same time we must recognize that while roots are genetically controlled by some specific genetic systems, they are also shaped by genes which are not directly involved with the root, such as genes which control shoot growth, tillering and phenology. Thus, it is difficult to predict root size under stress in any given genotype, only that genotypes of potentially large roots under non-stress conditions will most likely sustain a relatively large root under stress. Problems of soil barriers to root growth are excluded.

The late Charles Sullivan and I grew a high yielding variety and a landrace of spring wheat in 150 cm long PVC tubes. The controls received normal and frequent irrigation while the stress treatment tubes received limited irrigation through the bottom of the tube. Thus, the stressed plants had to rely on deep soil moisture (Fig. 1). Under non-stress conditions the high yielding variety and the landrace did not differ in biomass, water-use and water-use efficiency (WUE). Under the designed stress conditions the landrace produced more biomass than the high-yielding variety. It produced more biomass with relatively greater water-use because it could reach the deep moisture due to its longer roots. While the landrace produced more biomass under stress it had a lower WUE than the high-yielding variety. It used more deep soil moisture to produce a little more biomass, as compared with the high yielding variety. While there is a lesson to be learned here about the utility of WUE as a comparative measure of crop performance under dryland, the role of the root as a constitutive trait is well emphasized. A proper root as a constitutive trait serves well across many environments to allow better resource capturing with respect to water and minerals, if there are resources to capture in the deep soil.

Photosynthetic Capacity

Photosynthesis is an important component of the plant's potential capacity and it has a bearing also on its performance under stress. The issue warrants a few comments here, without getting lost in the maze of available data on the subject. Plant assimilation under drought stress is largely controlled by two main features. One is the impact of stress on the effective leaf area. Stress reduces leaf area and light interception by the canopy. Leaf area

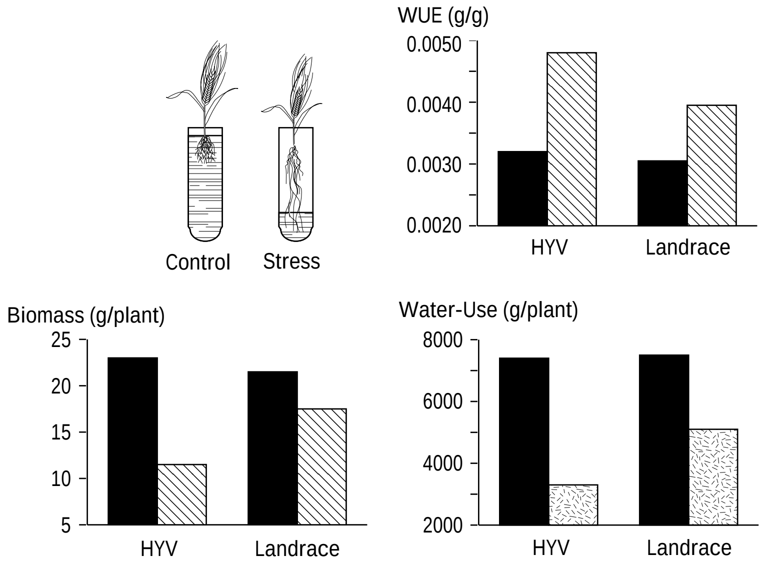

Fig. 1. The comparative biomass, water-use and water-use efficiency (WUE) of a landrace and a high yielding variety (HYV) of durum spring wheat grown under stress and non-stress (control) conditions. Plants were grown in the greenhouse in soil filled PVC tubes 150 cm deep. Control tubes received normal and frequent irrigation. Stressed plants received limited irrigation from the bottom of the tubes (Blum and Sullivan, unpublished).

may be reduced reversibly (e.g. leaf rolling) or irreversibly. Secondly, stress reduces photosynthesis per unit leaf area by affecting stomatal conductance and photosystem function. Severe stress affects also photosystem structure.

It is now almost a consensus that the photosystem is relatively desiccation-tolerant, while most of the variation in photosynthetic activity in plants under drought stress can be ascribed to modulated stomatal conductance. Stomata do not only respond to hydraulic and hormonal signals from root and soil, but they also constitute a sensitive and an effective interface between the plant and the atmosphere.

In 1975 Shimshi and Ephrat working at Gilat Experiment Station in Israel, found that yield of different wheat varieties under irrigation was positively related to their leaf permeability as measured with the pressure-drop porometer. In our own work, we later found that the drought susceptibility index for yield was positively related to mid-day canopy temperatures of different wheat breeding materials subjected to drought stress (Blum et al., 1990b) and that such canopy temperature variation was a reflection of variations in stomatal conductance. Stable-yielding varieties had cooler leaves and higher stomatal conductance under drought stress. More recently, the positive relationship between stomatal conductance, low canopy temperatures and high yield was confirmed for irrigated wheat growing in a warm and dry climate (Rees et al., 1993). These results lead to the conclusion that a high yield potential is associated with high stomatal conductance and efficient leaf cooling, especially in warm and high irradiation conditions. In certain wheat environments, such as the low altitude Mediterranean region or parts of Mexico, the latter half of the growing season may involve supra-optimal (>30^0 C) leaf temperatures due to high solar irradiance and air temperatures during midday. Under such conditions leaf cooling specifically serve to reduce leaf temperature back to the optimum 'thermo-kinetic window' (Burke et al., 1988).

High stomatal conductance as a constitutive trait of high yielding wheat varieties may serve well also under moderate drought stress conditions as long as water is available at least in deep soil. When stress becomes severe and water is very limited, other type of stomatal responses would be required, and such specific adaptive responses take control over plant performance and later over plant survival. Stomatal conductance is therefore a physiological mechanism underlying some of the above discussion of potential yield and crossover.

Plant Reserves

The plant stores carbon in various organs at various stages of development. Some of this storage is designated for attaining stability and homeostasis under stress. Cereals store carbon in the stem before and during flowering. Depending on the species, most storage is in the form of fructans and/or starch. Stem storage is affected by the conditions for assimilation before flowering, the demand for carbon by various sinks and by the developmental or morphological features of the stem. For example, height genes, which affect stem length, have an important effect on storage and its subsequent utilization for grain filling in small grains (Borrell et al., 1993) and sorghum (Blum et al., in preparation).

When a demand for storage develops during grain filling, the large carbohydrate molecules are broken into simple sugars which are mobilized to the grain. The demand for storage usually develops when current photosynthesis during grain filling is inhibited by stress such as drought, heat, leaf disease or shading. There are, however, cases where the utilization of stem reserves for grain filling is constitutive, irrespective of the environmental conditions during grain filling (Blum et al., 1994).

Information in maize on the importance of stem reserves in sustaining kernel growth under stress is not conclusive (Kiniry et al., 1992; Lafitte and Edmeades, 1993) and in view of the large diversity in this species, the issue warrants further investigation. The role of reserve carbon in maize may be peculiar or even unique, in view of the grain position on the plant. Furthermore, the evidence on the effect of stem infused sugar on grain setting in drought stressed maize (Zinselmeier et al., 1995) may suggest perhaps a possible involvement of stored stem carbon in grain setting. High stem sugar content may act at least as well as infused sugar. This hypothesis should be tested.

The general capacity for stem reserve utilization for grain filling can be easily evaluated experimentally by comparing grain filling in intact plants with plants in which leaves were removed or desiccated at the onset of the exponential phase of kernel growth. At that point stem reserve accumulation has reached its peak while the demand for carbon by the grain is maximal.

Conclusion

Various constitutive (and often simple) plant traits have an important effect on plant performance under stress. However, when stress intensifies, genes which express adaptive features become crucial for production and survival. It is important to recognize and differentiate between the two systems and the environments in which they impact plant productivity the most. It is essential to be able to define and genetically improve the constitutive traits affecting plant performance under stress - before the more complex and often elusive ‘stress responsive’ and ‘stress adaptive’ genes are targeted for genetic manipulations.

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Physiology of Flowering in Maize: Identifying Avenues to Improve Kernel Set During Drought

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Abstract

Asynchronous floral development and abortion of fertilized ovaries are responsible for much of the kernel loss caused by drought during flowering in maize. Inhibition of silk elongation and ear growth at low water potential both contribute to the failure of silks to emerge during pollen shed. Because this delay in silk emergence, rather than loss of pollen availability, pollen viability, or silk receptivity generally limits kernel set, selection for genotypes which exsert silks in advance of pollen shed (protogyny) should be beneficial. Modern maize genotypes tolerate up to 6 days of protogyny without loss of silk receptivity. Rapid and sustained ovary growth also is essential to maintain kernel set during drought. A decrease in assimilate production in droughty plants coupled with inhibition of carbohydrate metabolism within the ovaries leads to a dramatic decrease in carbohydrate partitioning to the ear, and ultimately, kernel abortion. While it has been possible to reverse the effect of drought on kernel abortion by supplying sucrose via stem infusion, attempts to increase kernel set in droughty plants by increasing assimilate supply per kernel naturally under field conditions have not proven successful. The ear of maize competes poorly for available assimilates. Selection for genotypes with rapid ear growth relative to vegetative growth at anthesis is a practical method to improve ear sink strength. Current research on the molecular basis for inhibition of ovary carbohydrate metabolism and the role of cytokinins in controlling ovary growth may provide new molecular targets for improving drought tolerance in maize.

Large yield losses occur when maize is exposed to drought conditions during flowering; losses are due primarily to a decrease in ears per plant and kernels per ear. When we examine the many ways reproductive development and function are affected by drought, this vulnerability is not surprising. Asynchrony in flower development, loss of pollen viability, loss of silk receptivity, failure of fertilization, as well as embryo abortion all contribute to the reproductive failure caused by drought.

Much of the problem stems from maize having separate staminate and pistillate flowers. Drought inhibits ear and silk growth causing the delay in silk emergence relative to pollen shed (protandry). The typical breeding strategy to minimize this problem has been to select against protandry and for high yield across environments. Selection under controlled drought conditions for a minimum anthesis-silking interval (ASI) by scientists at CIMMYT has also proven successful. Both approaches assume that development and fecundity of staminate and pistillate flower types must be synchronized for optimum kernel set. We will explore the possible benefits of selecting for silk emergence prior to pollen shed (protogyny) as an additional method to improve the drought tolerance of maize.

The second major problem caused by drought is an increase in kernel abortion. Zygotes formed in pollinated ears abort within a few days of pollination (Westgate and Boyer, 1986). Ear and early kernel development are highly dependent on the flux of assimilates which is severely limited during drought due the inhibition of photosynthesis and poor ‘sink strength’ of the ear prior to and during pollination. Selecting for prolificacy has been correlated with improved drought tolerance; in part, because it effectively increases the demand for assimilates by developing ears (Hallauer and Troyer, 1972; Arihara and Watanabe, 1985; Schoper et al., 1987). We will examine how direct selection for rapid ear growth prior to and during anthesis may be useful in increasing drought tolerance in maize.

Benefits of Selecting for Protogyny

Under well-watered conditions, silks emerge at about the same time pollen is shed (Fig. 1). In this particular hybrid (Pioneer Brand 3790), the ASI between 50% of plants shedding pollen (anthesis) and 50% of plants having some silks emerged (silking) is one day, (i.e. ASI=1). Of course, synchrony in floral development is not fixed since silk emergence can be delayed or accelerated relative to pollen shed by selection or environmental conditions. Using a quantitative approach, we determined whether kernel loss due to asynchrony was a consequence of failure of silks to emerge, loss of silk receptivity, or lack of sufficient pollen (Bassetti and Westgate, 1994b).

Distinguishing between these possibilities is important because modifying the pattern of pollen shed or improving ear/silk growth to improve drought tolerance would require markedly different selection strategies. In the field, pollen shed follows a skewed distribution with a maximum two or three days after anthesis (Fig. 2). We imposed asynchronous ear development on this pattern of pollen shed by varying the planting date of small detasseled plots within a large field. This approach allowed us to examine kernel set as affected by pollen supply within a range of ASIs, both positive and negative. As expected, maximum kernel set was obtained on ears whose silks first appeared within two or three days of anthesis (Fig. 3). Percent set decreased rapidly on ears with later-emerging silks. Progressively more kernels were lost from tip to basal floral positions as asynchrony increased (data not shown). To determine when pollen amount became limiting, it was necessary to match kernel set on ears with a known number of receptive silks exposed on a day when the density of pollen shed was also known. Figure 4 shows kernel set was nearly perfect in florets with silks exposed on any day when pollen density was at least 100 grains cm^{-2} d^{-1}. Considering the seasonal pattern of pollen shed (Fig. 3), there must have been sufficient pollen available in the field for nearly perfect kernel set of all florets whose

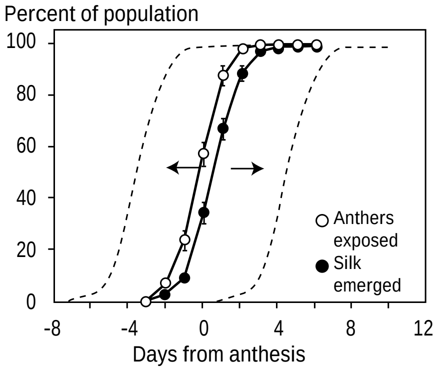

Figure 1. Close synchrony in flower development in maize. Percent of plant population with anthers exposed or silks emerged is plotted relative to anthesis, the day 50% of the population has begun to shed pollen. The anthesis-silking interval is 1 day. Arrows indicate a delay or acceleration of silk emergence relative to pollen shed. Adapted from Bassetti and Westgate (1993a).

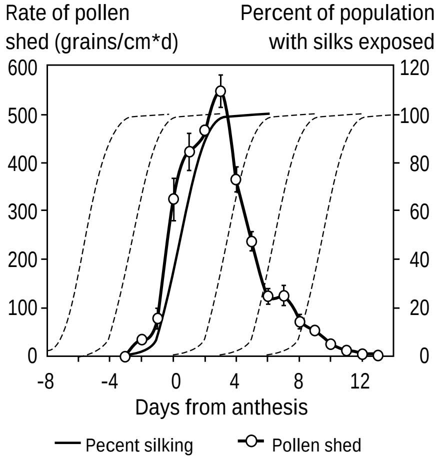

Figure 2. Seasonal pattern of pollen shed in the field plotted relative to anthesis. Percent silking curves indicate various anthesis-silking intervals imposed artificially by varying planting date in the same field. Adapted from Bassetti and Westgate (1994).

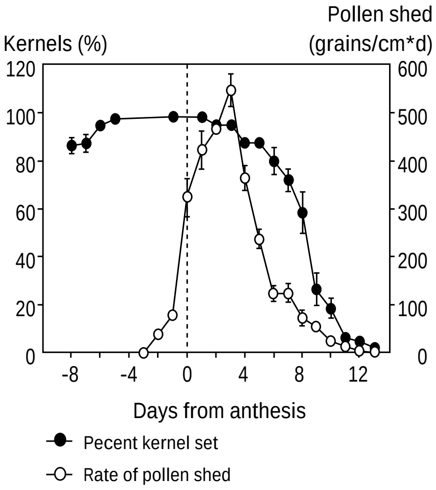

Figure 3. Percent kernel set on ears with silks emerged at various times relative to anthesis. The seasonal pattern of pollen shed is plotted for comparison. Adapted from Bassetti and Westgate (1994).

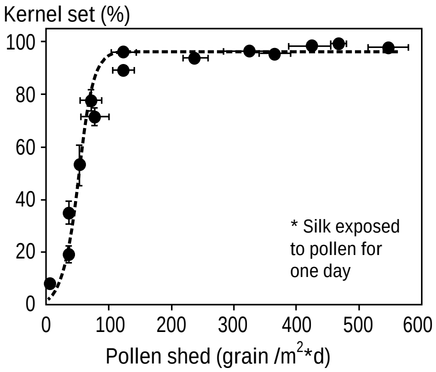

Figure 4. Effect of pollen shed density on kernel set. Receptive florets were exposed to pollen for one day when rate of pollen shed was known. Adapted from Bassetti and Westgate (1994).

silks had emerged one day prior to anthesis to eight days after anthesis. With greater asynchrony, kernel set decreased throughout the ear, indicating that both silk emergence and pollen shed limited kernel set. These results confirm pollen amount does not limit kernel set in maize under favorable growing conditions. Initial silk emergence must lag behind pollen shed by many days (about 8 d for Pioneer 3790), before pollen amount begins to limit kernel set. This value may vary for other hybrids with their inherent pattern of pollen shed and ear development (Bassetti and Westgate, 1993a).

How does this information help us to overcome the problem of silk delay relative to pollen shed? While selection for a short ASI in droughty environments undoubtedly will continue to prove beneficial (Edmeades et al., 1997), selecting against a delay in silk emergence does not take full advantage of the floral biology of maize. Maize silks remain ‘receptive’ to pollen for many days after they emerge from the surrounding husks (Bassetti and Westgate, 1993, 1994b). This same field study with Pioneer 3790 indicates a negative ASI as great as -6 days would cause no loss in kernel production under favorable conditions (Fig. 3). Selecting for silk emergence prior to pollen shed (protogyny) would effectively shift ASI to negative values. A large negative ASI could be advantageous under drought because any delay in silk emergence would only improve the synchrony between maximum pollen shed and silk emergence and lead to more stable kernel production. This conclusion is supported by the results of Moser et al. (1997), who associated high kernel number per ear during drought in La Posta Sequía C_4 with an ASI of -2.5 days under well-watered conditions. Together, these results suggest further improvements in drought tolerance of maize may result from direct selection for protogyny under well-watered conditions. The results of Moser et al. (1997) also indicate that selection for short ASI under drought conditions will lead to negative ASI. Unfortunately, selecting plants for a negative ASI alone will not guarantee high kernel set if drought occurs during the critical pollination period.

Selecting for Increased Carbohydrate Supply Prior to Anthesis

Under severe drought, newly formed zygotes abort within a few days of pollination (Westgate and Boyer, 1986). Several lines of evidence indicate reproductive abortion results from a lack of carbohydrate supply to the developing ear coupled with an inhibition of carbohydrate metabolism at low ovary water potential (Boyle et al., 1991; Schussler and Westgate, 1991; Zinselmeier et al., 1995a,c). Table 1 shows that drought during pollination can eliminate kernel development almost completely in plants grown in a controlled environment chamber. Shading well-watered plants to inhibit leaf photosynthetic rates to the same extent as occurred in these droughted plants (Fig. 5) decreased kernels per ear by nearly 70%. Similarly, infusing a solution containing sucrose into stems of growth-chamber plants can recover about 70% of the kernels lost to drought during pollination (Fig. 6).

Table 1. Effect of water-deficit and light-reduction treatments at pollination on silk water potential (Ψw) and kernel set.

Treatment	n	Silk Ψw (MPa)	Kernel number/ear
Control	5	-0.41 ± 0.03	598 ± 17
-Light	11	-0.40 ± 0.04	222 ± 72
-H_2O	8	-1.00 ± 0.02	15 ± 6

These studies underscore the importance of maintaining the supply of photosynthate to the developing ovaries during drought. This situation is very problematic because it has not been possible to improve drought tolerance in maize by selecting for decreased sensitivity of the photosynthetic machinery to low leaf water potentials. A possible alternative to selecting for higher photosynthetic rates during drought is to select for increased carbohydrate reserves in the plant prior to anthesis,

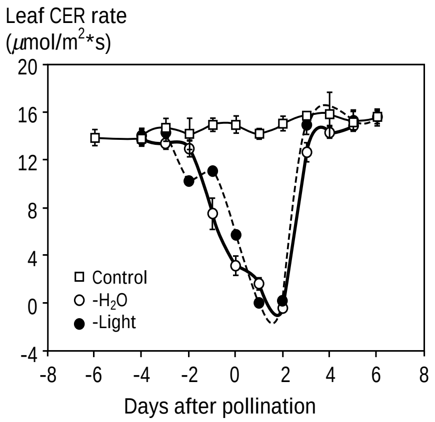

Figure 5. Leaf Carbon Exchange Rate (CER) for well-watered (control), water stressed, and shaded plants growing in a controlled environment chamber. Water was withheld at silk emergence and plants were pollinated four days later. Shaded plants were similar to controls except light intensity was varied to match the photosynthetic rates of the droughty plants. Adapted from Schussler and Westgate (1991).

provided these reserves can be utilized to support ear and kernel development during a temporary loss of concurrent photosynthate supply. Increasing the level of reserves might translate into greater kernel production during drought. We tested this possibility on two hybrids in the field by shading and spacing plants prior to and during anthesis (Schussler and Westgate, 1994). The shade treatment decreased incident sunlight by about 50% and decreased total extractable carbohydrates relative to unshaded 'control' plants at the same population density (5.4 plants m^{-2}) (Fig. 7). Wide spacing (0.7 plants m^{-2}) increased carbohydrate reserves, presumably due to the genetic potential of the crop under the conditions of this experiment. All three pre-treatments were exposed to a drought of similar duration and intensity during pollination and were pollinated with excess pollen. The results were essentially the same for both hybrids. Drought during pollination caused abortion of about 50% of the kernels in the control treatment (Fig. 8). The shaded plants with less reserves were more sensitive and aborted about 80% of their kernels. The widely spaced plants with increased carbohydrate reserves aborted as many kernels as the 'control' treatment. Thus, it was possible to make early kernel development more sensitive to drought by decreasing reserve levels and the concurrent rate of photosynthesis, but it was not possible to decrease the sensitivity by increasing the level of reserves. These results lead us to two important conclusions about the maize plant. First, early reproductive development depends strongly on the concurrent supply of photosynthate to the ear. Second, reproductive success (i.e., kernel set) is not modulated directly by carbohydrates levels in reserve pools accumulated at some time earlier in development. This latter conclusion has a very practical implication for breeding programs aimed at improving drought tolerance in maize. It is very unlikely that selection for greater stem reserves of carbohydrate at flowering will lead to improved kernel set during drought. In fact, selection for such a trait may decrease drought tolerance because the developing ear competes so poorly for available photosynthate. Selection for greater partitioning of carbohydrate to the stem may put the ear at an even greater disadvantage. This conclusion is supported by concurrent reductions in plant height in breeding populations selected for improved drought tolerance (Edmeades, pers. comm.).

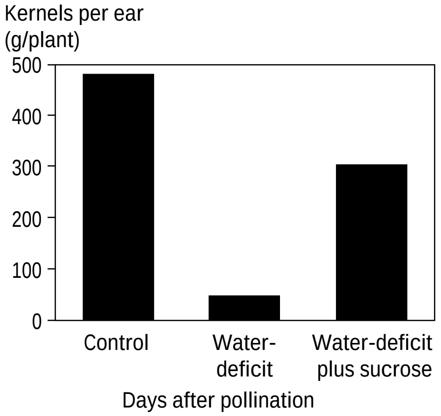

Figure 6. Kernel number per ear in control, water-stressed, and water-stressed + sucrose infused plants. Water was withheld at silk emergence and plants were pollinated four days later. Stem infusion began on the day water was withheld and continued for five days. Approximately 35 g of sucrose was infused during this time. Adapted from Zinselmeier et al. (1995a).

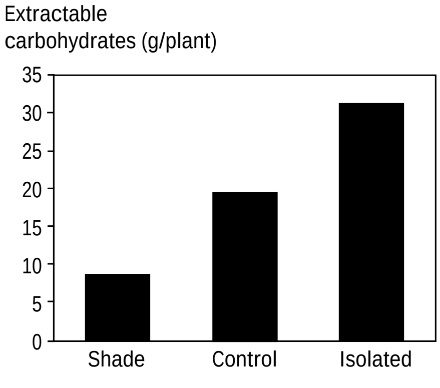

Figure 7. Total reserve carbohydrates (sucrose + glucose + fructose) in shaded, control, and isolated plants at anthesis. Plants were grown in pails in the field. Shade treatments, which decreased incident radiation by 50%, were imposed at the 6th leaf stage and maintained until maturity. Adapted from Schussler and Westgate (1994).

Selecting for Rapid and Sustained Ovary Growth

Not all kernel abortion due to drought can be accounted for by a lack of concurrent photosynthate supply to the ear (Schussler and Westgate, 1991; Zinselmeier et al., 1995b). This discrepancy led us to examine whether some aspect of carbohydrate metabolism had been impaired in ovaries of droughty plants.

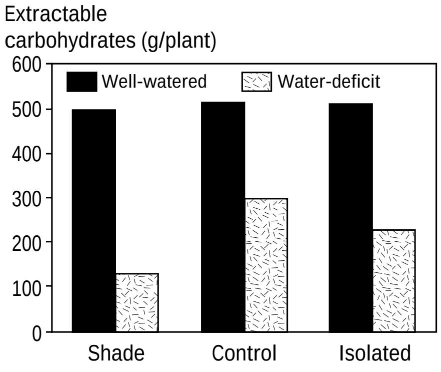

Figure 8. Kernel numbers per primary ear in shaded, control, and isolated plants. All three treatments were exposed to a water deficit of similar intensity and duration during pollination. Adapted from Schussler and Westgate (1994).

The plant normally supplies sugars to developing sinks in the form of sucrose, but sucrose is not necessarily the form of sugar the ovaries can utilize for metabolism. While examining the sugar content in the cell wall space surrounding the ovary, we found most of the sugar was monosaccharides, glucose and fructose (Fig. 9). Only a small amount of sucrose was present. This pattern of sugar distribution is consistent with the action of cell-wall bound acid invertase, which cleaves sucrose to glucose and fructose. This cleavage may be necessary for the ovary to utilize the sugar supplied by the plant. In severely droughted plants, the amount of sucrose in the cell-wall pool was much greater and there was a corresponding decrease in glucose and fructose levels. Measurements of acid invertase activity confirmed that drought severely decreased the activity of this enzyme within the ovaries (Fig. 10). These results indicate drought caused a metabolic lesion within the ovaries which may have decreased their capacity to incorporate sugars supplied by the plant. In other words, maize ovaries, which were poor competitive sinks under favorable conditions, became even poorer sinks for assimilates during drought. During drought, available assimilates are partitioned to other sinks, particularly the stem (Schussler and Westgate, 1991, 1994; Zinselmeier et al., 1995b). The most important consequence of this metabolic lesion is an inhibition of ovary growth. In all our studies examining why drought increases kernel abortion, final kernel number per ear is directly correlated with the inhibition of ovary growth regardless of genotype, potential kernel number per ear, culture conditions, or plant pre-treatment (Fig. 11). Whether accomplished artificially (Boyle et al., 1991; Zinselmeier et al., 1995a), culturally (Schussler and Westgate, 1994; Zinselmeier et al., 1995b), or genetically (Edmeades et al., 1993, 1997), improvements in seed set under drought conditions have been coupled closely with the maintenance of ovary growth. The practical conclusion from all these studies is that selection for rapid and sustained ovary growth during drought will lead to improved drought tolerance.

The work by Edmeades et al. (1993) at CIMMYT to improve performance of maize in droughty environments provides direct support for this conclusion. Eight cycles of selection for a shorter ASI in Tuxpeño Sequía under controlled drought have resulted in a dramatic increase in kernel production under drought. The decrease in ASI was associated with greater biomass per spikelet at anthesis (Fig. 12). It also reflected a greater rate of biomass accumulation in the ear prior to and during anthesis (Fig. 13). Since selection resulted in fewer spikelets per ear, with no change in rate of spikelet initiation, each spikelet must have been growing at a faster rate as well. Therefore, recurrent selection for a shorter ASI under severe drought

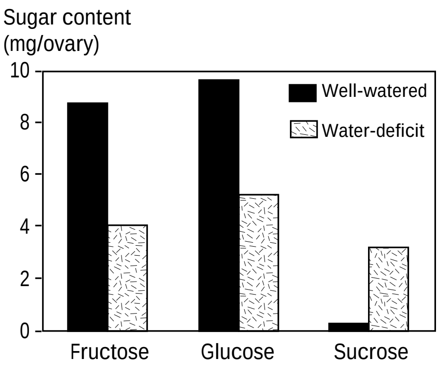

Figure 9. Sugar content in the cell-wall free space of maize ovaries at pollination. Water was withheld at silk emergence, and ovaries were sampled four days later. Kernel set would be decreased by 50 to 75% in the droughty plants compared to the controls (Westgate, Jones, and Hampton, unpublished data, 1996).

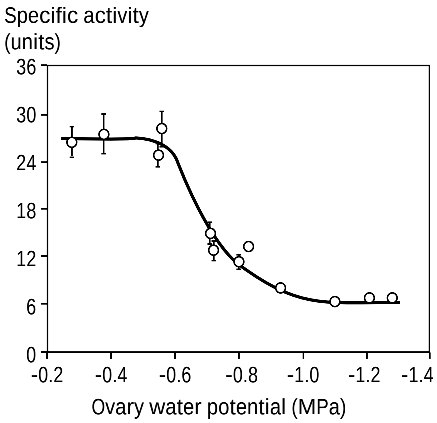

Figure 10. Specific activity of cell-wall bound acid invertase in maize ovaries at various ovary water potentials. Ovary water decreases with increasing severity of plant water deficit. Kernels fail to develop in ovaries pollinated at -1.0 MPa or lower (Westgate, Jones, and Hampton, unpublished data, 1996).

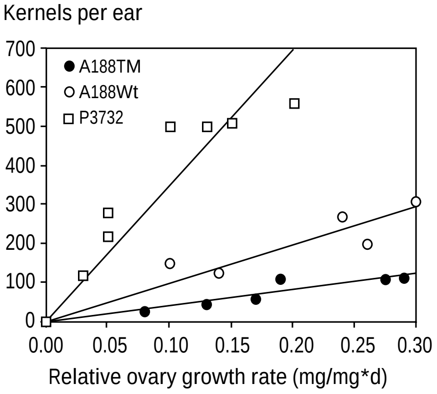

Figure 11. Correlation's of kernel number per ear with relative ovary growth rate during pollination in a maize hybrid (Pioneer Brand 3790), an inbred (A188WT), and a translocation mutant of that inbred (A188TM). Data are pooled from several studies in which kernel number varied with drought or shade treatment. Adapted from Schussler and Westgate (1991), Schussler and Westgate (1994), Zinselmeier et al. (1995b, c).

conditions effectively increased the average spikelet sink strength in C_8 relative to C_0.

These physiological studies suggest further progress towards improving drought tolerance of maize can be made by incorporating two selection criteria into current breeding programs. One is protogyny (i.e., a negative ASI). Current breeding programs emphasize close synchrony between anthesis and silk emergence, but do not take advantage of maize's tolerance for up to six days of protogyny without loss of flower function. A shift in ASI to negative values under well-watered conditions has accompanied eight cycles of selection for shorter ASI under drought in Tuxpeño Sequía (Edmeades et al., 1997). Similar progress has been possible in other breeding material in response to selection for short ASI and should be possible in response to direct selection for protogyny (Edmeades et al., 1977). A second trait of importance is rapid ear growth prior to anthesis. Maintenance of ovary growth rate is critical for high kernel set under drought. Selecting for larger ears at anthesis and/or negative ASI are practical approaches to increase biomass partitioning to the pistillate flowers, especially when assimilate supplies become limiting under severe drought conditions.

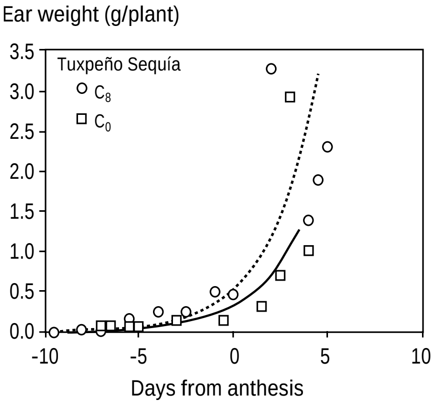

Figure 12. Increase in ear biomass during anthesis in C_0 and C_8 of Tuxpeño Sequía. Adapted from Edmeades et al. (1993).

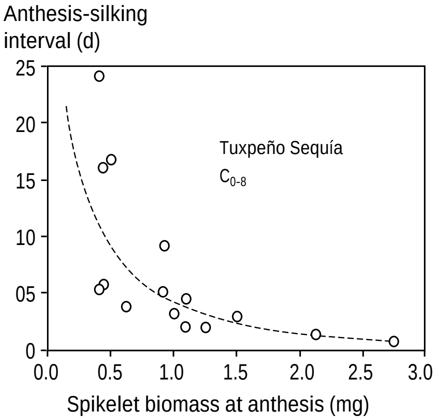

Figure 13. Relationship between anthesis-silking interval (ASI) and spikelet biomass at anthesis in Tuxpeño Sequía. Populations were selected through eight cycles for a short ASI and high grain yield under controlled drought conditions. Adapted from Edmeades et al. (1993).

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Role of the Phytohormone ABA in Drought Tolerance: Potential Utility as a Selection Tool

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Abstract

Knowledge concerning the physiology and molecular biology of abscisic acid (ABA) responses in plants has advanced considerably in recent years. This information has shown that ABA has numerous roles in stimulating adaptive responses to water deficit and other stresses. Methods for ABA assay have improved so that they are now sensitive and economical for large-scale use. Several features of the ABA-mediated response to drought suggest that ABA assay might be a useful selection tool in breeding for drought tolerance. ABA stimulates several processes that conserve water and induce desiccation-protective cellular changes, including stomatal closure, increased root:shoot ratio, osmolyte accumulation, and accumulation of substances that stabilize cellular structures. ABA is also involved in developmental responses that alter plant ontogeny and partitioning of resources in ways that could improve plant adaptation to drought. Such responses include induction of leaf senescence, inhibition of leaf and stem growth, and abortion of reproductive organ development. Although these responses may confer improved plant survival in severe drought, they may decrease yield performance in less stressful environments. Furthermore, because ABA synthesis dramatically increases in response to loss of tissue water, the extent to which a genotype accumulates ABA during mild water deficit may indicate its degree of failure to adequately employ stress avoidance responses. Thus, the use of ABA assay as a selection tool may require careful choice of the selection environment in relation to breeding objectives.

Introduction: The Central Role of ABA in Adaptation to Drought

Increases in our understanding of plant adaptive responses to water-limited environments in recent years have strengthened the view that the phytohormone abscisic acid (ABA) plays a central role in stimulating a concerted set of drought adaptations (Quarrie, 1993). For the most part, roles for ABA that were postulated in the past have been supported, further clarified, and expanded upon by recent studies. Study of ABA is an active area of research, employing contemporary tools of molecular and developmental biology, membrane transport, and discovery of single-gene mutants. Such research indicates that ABA is involved in stimulating many processes within both of the two functional categories of drought adaptation: drought escape and drought tolerance.

Drought Escape

ABA confers drought escape by altering the plant in such a way that less water is lost through transpiration and more water is obtained by the roots. Several processes are involved. First, we now know that the most important water-conserving response, stomatal closure, involves a complex series of events triggered by ABA (Ward et al., 1995). ABA initiates a signal cascade in guard cells that alters the membrane transport of several ions, and as a result guard cells lose their turgor and the stomatal pores close. Second, ABA provides improved water transport between plant parts by increasing the hydraulic conductance for water movement from roots to leaves (Ludewig et al. 1988, Zhang et al., 1995). Third, ABA alters the relative growth rates of various plant parts. It is well known that plants subjected to water deficit increase their root:shoot dry weight ratio. Evidence now indicates that ABA has a role in inducing this response. ABA inhibits leaf area development by decreasing the rate of cell proliferation in the leaf meristem and by decreasing cell wall loosening activities that are necessary for cell-wall plastic deformation and leaf elongation (Lecoeur et al., 1995). Such inhibition limits the formation of evaporative leaf surface, and hence, transpiration. Furthermore, by limiting the sink strength of leaves, inhibition of leaf growth facilitates a shift in assimilate partitioning in favor of root growth. ABA at high concentrations inhibits root growth via mechanisms similar to those described above for leaves. But at moderately elevated concentrations, ABA elicits growth promoting events in roots that serve to maintain or enhance root growth at much higher rates than what they would be without ABA intervention (Sharp et al., 1994). The overall effect, then, is to stimulate root growth, particularly deep rooting, that enhances water acquisition from drying soils.

Drought Tolerance

The second category of adaptation, drought tolerance, involves cellular changes that confer an ability to maintain cell turgor and withstand the damaging forces associated with lowered water potential and desiccation. Although a plant might withstand a mild drought by employing the drought escape processes described above, a more severe drought requires the development of tolerance. ABA plays a role in stimulating numerous drought tolerance processes. First, ABA stimulates osmotic adjustment by altering membrane transport and enhancing the synthesis of osmotically active compounds (osmolytes) (Ober and Sharp, 1994; Bohnert et al., 1995; Orr et al., 1995). During soil drying, plant total water potential must decrease to provide the gradient necessary to sustain water transport from soil to root to shoot. By stimulating the accumulation of osmolytes, such as sugars and ions, ABA provides the means by which tissue water potential can decrease while positive turgor is maintained. Accumulation of certain osmolytes, notably, sucrose and other nonreducing sugars, proline, and glycine betaine, provide additional protective benefit in that they stabilize proteins, membranes and other components when water potentials decrease (Bray, 1993; Bohnert et al., 1995). ABA is also responsible for inducing the synthesis of a second category of protective substances: the *LEA* and related proteins (Bray, 1993; Chandler and Robertson, 1994). These protective proteins have enhanced water binding and ion-sequestering properties that allow them to interact with enzymes and other cell constituents in such a way that their critical functions are preserved during drought.

Growing evidence indicates that osmoprotectant substances are highly effective and could be valuable traits for crop improvement. For example, by using molecular biology techniques to create transgenic plants that overexpress just one of these osmoprotectant substances, growth in water stress environments was substantially improved (Tarczynski et al., 1993; Xu et al., 1996). These results suggest that such methods might provide a powerful tool for genetic improvement of crops. However, a dilemma with using these nontraditional methods is that they are feasible for transfer of only a single or small number of genes, whereas the number of desirable drought-adaptive traits is very large. It should be noted that maize and other species already possess the capability for synthesis of these substances and for expressing the drought adaptive traits mentioned above in regard to drought escape. An alternative strategy, then, is to devise a selection scheme whereby the expression of many drought-adaptive traits are enhanced or optimized, or both simultaneously. Given that ABA is involved in stimulating the expression of most of these traits, selection for genotypes that accumulate ABA during drought is a plausible approach.

Genetic Differences in ABA Accumulation

In maize, studies indicate that there are genotypic differences in the accumulation of ABA in response to low water potential (Pekic and Quarrie, 1987; Ivanovic et al., 1992; Tuberosa et al., 1992; Conti et al., 1994; Tuberosa et al., 1994; Lebreton et al., 1995; Pekic et al., 1995). Pekic and Quarrie (1987) found a 3-fold range in leaf ABA concentrations for 10 maize inbreds in the field, while Tuberosa et al. (1992) and Conti et al. (1994) reported a 2- to 3-fold range in leaf ABA concentration among 11 early and 23 medium-maturing maize inbreds. Estmates of broad sense heritability (h^2) of leaf ABA accumulation, evaluated in water-limited field conditions using a range of inbreds, has provided encouraging values of 21 to 78% (Conti et al., 1994; Ivanovic et al., 1992; Tuberosa et al., 1992). But each of these studies involved growth of plants at a single location and hence, in each of these studies the range of environments to which the genotypes were exposed was narrow, i.e., essentially including only replicate differences at one location. So these h^2 estimates may have been high because environment effects and genotype by environment interaction were correspondingly small. Ivanovic et al. (1992) estimated additive, dominance and interaction parameters for leaf ABA accumulation by measuring ABA in two parental inbreds differing in this trait and in F_1, F_2's, and backcrosses of F_1 to each parent. In a water-limited field environment, additive effects were significant at $P<0.01$, while dominance effects were significant at $P<0.05$. Thus it appears that genetic selection for ABA accumulation is feasible.

Methods of ABA assay

Two general approaches toward ABA assay are currently used: physicochemical and immunological (Hedden, 1993). Physicochemical methods involve chromatographic separation of ABA from other substances in extracts followed by detection with a physical/chemical methods such as mass spectrometry coupled to gas chromatography. Although such methods can provide quantitative estimates without incurring errors due to contamination with other compounds, these methods require investment in costly equipment, large amounts of labor by trained technicians, and are not amenable to scale-up for large scale screening. Immunoassay methods involve the use of highly specific antibodies whose binding to ABA can be employed in low cost, high throughput assays that lend themselves to large scale screening applications.

Immunoassays are made possible by the remarkable ability of animal immune systems to produce highly specific antibodies to virtually any antigen, when the antigen is conjugated to a carrier protein. For ABA immunoassays, mouse antibody-producing cells have been cloned so that monoclonal antibodies directed toward a specific epitope of the ABA molecule have been obtained (Walker-Simmons and Adams, 1993). This provides a continuous supply of identical monoclonal antibody that has the desired specificity toward ABA and lack of cross-reactivity toward other substances in a plant extract. High specificity allows assay of tissue extracts with a minimum of 'cleanup'. A second advantage of immunoassays is their ability to detect extremely small amounts of antigen. For example, although 1 cm^2 of a well-watered maize leaf typically has about 2.5 picomoles of ABA, only 1/25th of this is needed for an ABA immunoassay; for leaves from plants subjected to water deficit the ABA levels rise so that typically only 1/300th of a cm^2 is needed per assay.

Two types of ABA immunoassay are available: radioimmunoassay (RIA) and enzyme linked immunosorbant assay (ELISA). Both involve the same basic antibody-antigen binding reactions and therefore they can provide equivalent results. They differ in that RIA uses a radioactive ABA tracer, whereas ELISA uses a non-radioactive enzymatic tracer. Although both types of ABA immunoassay can be used for mass screening, the ELISA method is particularly well suited for such applications because it employs standard 96-well plates that lend themselves to handling large numbers of samples. The following section briefly describes the steps involved in an ABA ELISA.

ABA ELISA

In ELISAs, one of the reagents is permanently coated onto the inner surface of plastic vessels while other reagents are suspended in solution and participate in reversible antibody/antigen binding reactions. For the sandwich ABA assay described here, the coated reagent is a conjugate between ABA and a protein (ABA-protein); the protein serves to attach ABA to the plastic (Ober et al., 1991). Coating with this reagent is accomplished by incubating it in the wells overnight. Next, a mouse monoclonal antibody that specifically binds ABA (anti-ABA mAb) and a sample or standard containing free ABA are incubated in the well. At this step, two pools of ABA compete for binding by the anti-ABA mAb: 1) the immobilized ABA that is coated onto the plastic surface and 2) the free ABA in solution. After binding reaches equilibrium, the wells are washed thoroughly to remove that portion of the mAb that is not bound to immobilized ABA-protein. To detect how much mAb had bound to the well, a secondary antibody which specifically recognizes certain epitopes on monoclonal antibodies from mouse is added. The secondary antibody has an enzyme, alkaline phosphatase, covalently conjugated to it, serving as a label. After secondary binding is complete, the unbound antibody is washed away and the amount of bound secondary antibody is measured by adding a reagent that forms color in accordance with the amount of enzyme present. Intensity of the pigment is measured in a 96-well colorimetric reader. Output from this instrument goes directly to a computer so that a spreadsheet macro can automatically perform regression to establish the standard curve and to calculate amounts of ABA in unknowns.

Although the ABA ELISA has many steps, it is not labor intensive because its use of 96-well plates facilitates bulk handling of many samples at a time. In practice, the most time consuming steps are sampling specimens from plants and initial dispensing of sample extracts into wells. For sampling leaves in the field, two representative disks, 5 mm in diameter, are cut with a cork borer and immediately placed into a pre-labeled 1.5-mL plastic tube containing 0.4 mL of extraction solvent (80% methanol, 0.2 M acetic acid). Samples can be stored at -20° C. Extraction from nonpulverized whole leaf disks is adequate if residence time is long enough and tubes are vigorously spun to create a turbulent vortexing action. For handling large numbers of samples, it is advantageous to assay the extracts directly without chromatographic cleanup or drying. If cross-reacting substances or substances that interfere with antibody/antigen interaction are present, they should be removed before assay; so whenever immunoassay is used with a new tissue preliminary tests are needed to determine whether interfering substances are present. Certain plant species contain substances that interfere with ABA immunoassay (Ryu et al., 1992). In red maple, my colleagues and I have found that interfering substances can be removed by suspending insoluble polyvinyl pyrilidone (PVPP) into extracts prior to centrifugation. This treatment removes phenolics and related compounds. But for maize leaves, satisfactory ABA immunoassay has been achieved by direct assay of extracts (Quarrie et al., 1988). To avoid interference, it is necessary to increase the stringency of the wash, and antibody/antigen interaction, by including detergent in all wash solutions (Ober et al, 1991). By including these precautions, 5 to 20 mL of maize leaf extracts, prepared as described above, can be directly assayed without drying.

Problems with ABA as a Breeding Tool

Despite some promising features of ABA assay as a breeding tool, investigators who have used ABA assays to characterize maize genotypes have encountered potential problems that may be a forewarning of weaknesses in the general approach. Studies have indicated that the method of imposing water stress affects the outcome (Pekic and Quarrie, 1987; Tuberosa et al., 1992). When plants were grown in the field, a consistent ranking of leaf ABA content was observed, but a test of ABA synthesis by detached leaves dehydrated to zero turgor did not reveal any genotypic differences. Furthermore, xylem ABA content had a higher correlation with drought adaptation traits, such as stomatal closure, than it did with the more easy-to-sample leaf ABA content (Lebreton et al., 1995; Tuberosa et al., 1994). These results suggest that an understanding of environmental and physiological factors that affect ABA content in a tissue may be needed to wisely employ an ABA selection scheme.

Many Factors Affect ABA Accumulation

As a phytohormone, ABA is a signal or mediator between sensing of a tissue's physiological state and response in that same plant part or some other distant plant part. Hence, in a breeding program, although we might wish to improve drought response, genetic control of ABA content primarily resides in the processes involved in sensing of water status and synthesis of ABA.

ABA synthesis is not only stimulated by water deficit — other stresses such as chilling (Lee et al., 1995) and flooding-induced O_2 deficit (VanToai et al., 1995) can be involved, as well. Furthermore, ABA synthesis is a normal event in the developmental program of some plant organs, notably the late stages of seed formation, where ABA stimulates the accumulation of certain proteins and confers dormancy to embryos in advance of tissue desiccation (Bray, 1993). Thus, interpretation of data on ABA accumulation needs to be done with an awareness of these other situations that can give rise to ABA accumulation.

ABA Synthesis, Catabolism, and Transport

Studies indicate that in droughted plants, the physiological state that initiates an increase in ABA synthesis is loss of cell turgor to the point of wilting (Bray 1993). Increased synthesis of ABA involves transcription and translation of one or more key enzymes in the pathway, but the response is rapid — usually a rise in ABA can be detected in 30 minutes. Accompanying a rise in ABA synthesis are rate increases of two other processes that tend to limit the extent of ABA accumulation: catabolism and export. When ABA concentrations increase in tissue, activities of enzymes involved in catabolizing ABA to compounds that lack biological activity also increase. The rise in rate of ABA catabolism is such that when water stress is relieved by rewatering, ABA levels usually decline rapidly as well, returning to levels found in well-watered controls within 24 hours. Thus, the extent of ABA accumulation is strongly affected by rates of both synthesis and catabolism. The second process that limits the extent of ABA accumulation in tissue is export. A substantial flux of ABA that is produced in roots is exported to shoots via the xylem. And, ABA produced in leaves is exported to sink organs via the phloem. As with catabolism, ABA export diminishes the magnitude of ABA accumulation in an organ that is synthesizing ABA, and so makes it more difficult to detect ABA accumulation. Another more important consequence is that plant parts that are not sites of ABA synthesis can accumulate and respond to ABA that is imported from other plant parts. This phenomenon is the basis of recent findings, at least for the environments of Northern Europe, that water deficit leads to root-produced ABA at an early stage of soil drying, and such ABA is transported via xylem to leaves where it closes stomates, thereby decreasing transpiration and preventing leaves from ever being subjected to a perceptible decline in water potential (Davies and Zhang, 1991; Davies et al., 1994). Such a drought response might be advantageous in environments that have short-term, mild water deficits. In this case, genotypes with root systems that substantially increase their ABA synthesis in response to slight decreases in soil water potential might close their stomates and increase their root:shoot ratio, thereby escaping more serious drought consequences. Indeed, studies of field-grown maize indicated that genotypic differences in stomatal conductance had substantially higher correlations with xylem ABA than with whole-leaf ABA concentration (Tuberosa et al., 1994; Lebreton et al., 1995).

Rate of Soil Water Depletion

From the arguments presented above, one would conclude that a genetic selection program based on identification of genotypes with high xylem ABA concentrations at initial stages of soil dry-down might identify genotypes that will perform well in environments with mild, short-term drought. But there is a potential pitfall with this scheme. It is plausible that large, rapidly growing lines will have higher rates of transpiration and will deplete soil water more quickly than smaller plants with less transpiration. Studies have indicated that within an environment, transpiration is usually well correlated with rates of photosynthesis (Wong et al., 1985). If xylem ABA were sampled at a fixed time after withholding irrigation water, those with highest ABA might be the most rapidly growing lines. In this case, the ABA data serves as an indicator of rapid soil water depletion, but not necessarily an indicator of more favorable drought adaptation. It is also possible that if the soils in which genotypes are being evaluated have moisture at depth, faster growing genotypes might correspondingly develop a deeper root system. By accessing an amount of water in the soil profile proportional to root-system size, the time between withholding irrigation water and depletion of soil water may not differ between rapidly growing and slow growing genotypes. It is even possible that certain fast-growing genotypes will partition a larger proportion of their assimilates into deep root growth. These will be slower to deplete the soil water their roots come in contact with and hence may have lower levels of xylem ABA at the time of sampling. Thus, genotypic comparisons of ABA levels need to be carefully interpreted with respect to the above factors which might affect the timing of soil water depletion relative to the date of ABA sampling.

ABA and Developmental Regulation of Senescence

The above description of ABA assay as a selection trait was limited to situations where drought escape alone is desired. For situations where drought tolerance is needed to withstand more severe drought, additional issues need to be considered. Because ABA plays a role in stimulating both drought escape and drought tolerance traits, it is conceivable that selection for genotypes that accumulate very high levels of ABA would be a productive approach. However, ABA is also involved in eliciting developmental traits that alter plant ontogeny and partitioning of resources in ways that could decrease yield performance. For example, ABA inhibits growth of new leaves (Hoffmann-Benningard and Kende, 1992; Jacquard et al.,1995) and stimulates leaf senescence (Smart, 1994). Induction of senescence may be desirable if it is limited to lower leaves such that it decreases the evaporative surface area and, through remobilization, provides nitrogen to sustain kernel growth. But, if senescence is excessive, photosynthesis of upper-canopy leaves will decline and yield potential will decrease.

Abortion of Reproductive Development

Abortion of a portion of the reproductive capacity in response to drought may be a valuable attribute to the extent that it adjusts sink capacity downward and restores the balance between capacities for photosynthate production and utilization. But if abortion is excessive, yield potential may suffer unnecessarily. In addition to abortion *per se*, plants also adjust their development of sink capacity at numerous other stages, such as by adjusting the extent of tillering, number of flowers produced, and percentage of flowers that are successfully pollinated. In maize, researchers at CIMMYT have shown that an exceedingly important indicator of yield capacity in drought environments is the anthesis silking interval (Bolanos and Edmeades, 1993). Bassetti and Westgate (1994) have shown that one aspect of this is the timing of silk growth relative to ovule fertility. To the extent that such timing is controlled by genetically programmed partitioning of assimilate and rate of tissue growth, these aspects of reproductive development might also be a part of the genetic control of source/sink balance during drought. Although these processes can be adaptive, if they restore the balance between source and sink capacities when photosynthesis is decreased in response to stress, excessive downward adjustments are maladaptive and yield limiting.

In wheat, studies indicated that increases in ABA can abort pollen development during pollen mother cell meiosis (Zeng et al., 1985). In maize, Cheikh and Jones (1994) have show that disruption of kernel growth by a short-term high-temperature treatment involved decreases in endogenous cytokinin levels and increased accumulation of ABA. In our research group, we have also investigated an aspect of reproductive development that appears to be regulated, in part, by ABA: maize kernel cell division.

ABA and Endosperm Cell Division

We have examined endosperm cell division that occurs after pollination. Because each endosperm cell has a limited capacity for growth and storage-material accumulation, the number of cells per endosperm limits the kernel growth capacity. At the initial stage after fertilization, endosperm cell division is extremely sensitive to water deficit. Aborted development at this stage decreases kernel set and is responsible for much of the yield loss attributable to water deficit (Zinselmeier et al., 1995). At later stages of endosperm development, water deficit decreases endosperm cell division, small shriveled kernels are produced. In our model system, the effect is largely localized to the apical regions of the ear, while kernels in the middle and basal regions are affected to a lesser extent (Ober et al., 1991). We have found that ABA accumulation is also localized to the kernels in the apical regions of ears (Ober et al., 1991). Studies with exogenously applied ABA have indicated that ABA is capable of inhibiting endosperm cell division (Myers et al., 1990). Although a substantial part of the loss in cell division is likely related to diminished supply of photosynthate (Zinselmeier et al., 1995), the above evidence indicates that the accumulation of ABA may have a regulatory role.

The specificity of increase in ABA within apical regions is a puzzle that our ongoing research seeks to address; it also may point the way to possible uses of ABA assay in a genetic selection program. The ABA source in our drought treatments is the maternal plant parts, probably via the phloem (Ober and Setter, 1992). Since a common, interconnected phloem system serves apical and all other regions of the ear, we postulate that apical/basal differences in ABA accumulation may be due to differences in rate of ABA catabolism; whereas basal and middle-ear kernels may have high ABA catabolic activity, apical kernels may not have sufficient catabolic activity to prevent a rise in ABA level. A working model that summarizes our findings is shown in Figure 1.

A potential outcome of our research is that measurement of ABA accumulation in maize kernels may provide an indication of the degree to which a genotype to adjusts sink capacity downward. Desired genotypes are predicted to employ ABA signalling to induce drought escape and tolerance traits, yet have high rates of ABA catabolism in ear-shoot and kernel tissues so that they are able to avoid reproductive failure. Such ABA catabolism could be viewed as one kind of mechanism by which a decrease in sensitivity to ABA is achieved. Some researchers have developed methods to identify plant genotypes with differing sensitivity to exogenously-applied ABA (Lu et al., 1989; Blum and Sinmena, 1995). A problem with using kernel ABA assay for selection decisions is that decisions are made regarding which lines to pollinate before assay results are available. Of greater value would be an ability to evaluate ABA catabolism in relevant reproductive tissue at an earlier developmental stage so that assay results could guide decisions as to which lines should be crossed and/or carried forward in a breeding program.

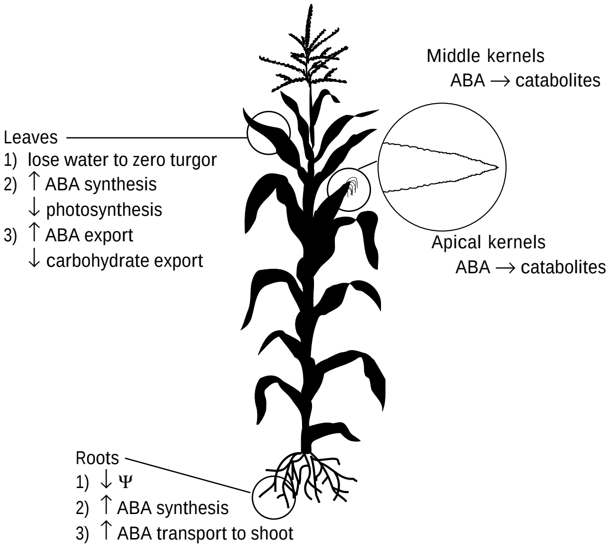

Figure 1. Postulated events during a drought episode that lead to selective abortion or down regulation of kernel growth in apical regions of maize. As soil water is depleted, root water potential (Y) decreases and root-produced abscisic acid (ABA) increases; leaf ABA synthesis also increases and photosynthesis decreases; leaf phloem export of ABA increases and photosynthate decreases. Middle kernels are postulated to have a high rate of ABA catabolism so that steady-state ABA levels in middle-kernel endosperms are kept low; apical kernels are postulated to have a low rate of ABA catabolism, so ABA accumulates to levels that inhibit kernel growth and development.

Conclusion

Use of ABA assay as a selection tool requires careful consideration of the physiology of ABA accumulation relative to breeding goals. It is a mediator of stress responses, rather than a cellular property that in itself provides adaptation to drought. The information it provides on adaptive genetic attributes is indirect. Choice of the selection environment, which tissue to sample, and timing of sampling will depend on the target environment's climate and whether drought escape or tolerance is to be improved. Nevertheless, assay methods for ABA have reached a point where it is feasible to perform large scale screening, and ABA is involved in a wide range of water deficit responses, so it offers the potential to impact several adaptive traits simultaneously. Perhaps the day is at hand when we will see this tool contribute toward genetic improvement of maize.

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Modeling the Consequences of Water Limitations at Flowering and Nitrogen Shortage in Tropical Maize Germplasm

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Abstract

The ear of the maize plant at flowering has a relatively weak sink capacity. When this is coupled with low current carbohydrate availability, due, for example, to limited water availability, it leads to reduced ear growth, low number of grains per ear, or completely barren plants. Low grain yield is the consequence. One symptom of these reductions in the flux of assimilates to the ear is delayed silking, and an increase in the anthesis-silking interval (ASI). Our working hypothesis is that the length of the ASI can be related to the photosynthetic rate or growth rate per plant at flowering, and that this is modified by genetic parameters. Quantification of this relationship would enable explanatory simulation of ASI of a maize crop that experiences some sort of growth limitation, especially drought, but also low nitrogen or low amounts of intercepted radiation per plant (as in high plant density). Various simulation approaches, varying in the level of detail with which underlying physiological processes are treated, can be chosen. Detailed photosynthesis modules, and modules that convert intercepted photosynthetically active radiation with a light use efficiency coefficient to crop growth rate, are readily available. However, these rely on accurate simulation of leaf area development, which is often problematic. In addition, existing phenology modules for temperate maize need testing and parameterization. Realistic modelling furthermore depends on the accuracy of the soil description, simulation of root growth, and quantification of water supply and demand. Simpler models that use a coefficient that relate crop growth to water availability may have greater utility in studies of some types of drought. Simulation studies are performed to investigate sensitivity, in terms of phenology, growth and production, to changes in the model's integration level, and to its input parameters. Modules describing specific functions can then be developed. This leads to an assessment of the module's validity domains, and to a prioritization of research needs.

Simulation approaches to the growth of a field crop differ in the level of detail with which physiological processes are treated. This varies from simple conversion of solar energy to plant biomass through a light use efficiency coefficient, to incorporation of basic plant metabolic, soil, and micro-environmental processes. A decision regarding the appropriate level of detail must address a basic question: how many levels of organization can be bridged to combine an optimal causal insight into the system while maintaining the possibility of returning to the desired level of organization (Leffelaar, 1990)? National or continental studies of production levels or variation in maize grain yield due to variation in rainfall distribution can be conducted by assuming a crop that is characterized by realistic standard leaf area development and light use efficiency for the available levels of soil N and moisture. Studies regarding processes such as sink-source balance, however, require more detailed crop growth and development information.

This text explores some approaches to modeling the consequences of water shortage at flowering and of nitrogen deficiencies during the entire growing period in tropical maize germplasm, making use of experimentally-obtained crop growth data. Simulation of crop growth on the basis of light and nitrogen use efficiencies and complex photosynthesis modules are compared. We refer frequently to the CERES Maize model (Jones and Kiniry, 1986) and the SUCROS model (Spitters et al., 1989) which are commonly-used modeling standards against which comparisons can be made. A simple approach to simulation of preanthesis development is presented. Known effects of growth reduction on kernel set are used to quantify sink capacity.

Field Experiments

Five tropical maize genotypes, viz., open-pollinated varieties La Posta Sequía C_4, Across 8328 BN C_6 (both late maturing), PR 8330, Pool 16 C_{20} (both early maturing), and the late-maturing hybrid CML254xCML247 were evaluated in three experiments at Poza Rica (tropical lowlands, 60 masl) and one at Tlaltizapan (mid-elevation tropics, 940 masl) during the 1995 summer cycle. Both locations are CIMMYT experimental stations in Mexico. Experiments 5620, 5621 and 5622 at Poza Rica differed only in soil N availability. Exps. 5620 and 5621 were conducted on fields that had not received artificial nitrogen for 9 and 6 years, respectively. Exp. 5622 received 75 kg N ha^{-1} at sowing and 125 kg N ha^{-1} one month after sowing. Exp. 6609 at Tlaltizapan received 150 kg N ha^{-1} at sowing, but unfortunately this did not meet the crop's demand for nitrogen as leaf N contents and crop growth rates remained relatively low (data not shown). Experimental design for each trial was an RCBD with three replications. Plot size was 10 rows 5.25 m in length, 0.75 m apart, with a plant density of 5.3 plants m^{-2}. Periodic harvests of plants from well-bordered areas 1.5 m^2 in size were taken at approximately 14 d intervals throughout the life of the crop, and plant parts separated and dried to constant weight at 80 °C. Radiation interception was measured at 14 d intervals from 10 well-bordered locations in each plot, using a Ceptometer (Delta T Devices, Pullman, WA) light bar. Leaf nitrogen content was determined using the micro-Kjeldahl technique.

Simulation of Crop Growth

Radiation use efficiency (RUE)
Crop growth is approximately linearly related to absorbed photosynthetically active radiation (PAR_a) (Monteith, 1977; Biscoe and Gallagher, 1977) under conditions of non-limiting moisture and nutrient supply and in the absence of pests and diseases. This results in an almost constant RUE (Waggoner and Berger, 1987). Daily growth rate can be described by

$$G = RUE \times PAR_a \tag{1}$$

In our experiments, RUE remained stable during a substantial part of the season before declining (Table 1). At low soil N availability (Exp. 5620), RUE remained stable up to anthesis. At higher soil N levels (Exps. 5621, 5622 and 6609), RUE remained stable up to 3 to 4 weeks after anthesis. RUE declined gradually afterwards, in some cases reaching negative values at the end of the season as a consequence of decline in total aboveground biomass.

Higher soil N availability often leads to higher crop RUEs, which is demonstrated by the differences in RUE between Exps. 5620, 5621 and 5622 (Table 1). Wide variation among genotypes and experiments makes it difficult to compute meaningful averages of RUE in relation to growth stages. Average values of RUE between the onset of the decline in RUE and final harvest are presented in Table 2. Higher soil N availability also leads to a lower end-of-season RUE .

The relationship between leaf N content (N_L; kg ha^{-1} ground surface area) and RUE was relatively consistent for Exps. 5620, 5621, and 5622 in Poza Rica (data not shown). The relationship between N_L and RUE for the Poza Rica environments can be described by:

$$RUE = 3.26 \times (1\text{-}e^{(-0.1172 \times NL)}) \tag{2}$$

Table 1. Level and duration (dur.; d after sowing) of stable radiation use efficiency (RUE; g MJ^{-1}) and days to anthesis (anth.; d after sowing) for four experiments conducted in Mexico during the 1995 summer cycle under varying level of nitrogen.

	Exp. 5620			Exp. 5621			Exp. 5622			Exp. 6609		
Germplasm	RUE	dur.	anth.	RUE	dur.	anth.	RUE	dur.	anth.	RUE	dur.	anth.
La Posta Sequía C_4	2.38	61	55	3.06	81	54	3.48	70	55	1.84	85	64
Across 8328 BN C_6	2.64	49	55	2.83	81	54	3.13	81	53	2.13	85	64
PR 8330	2.84	49	49	2.78	60	49	3.10	70	49	1.92	76	56
Pool 16 C_{20}	2.60	49	47	2.47	81	47	3.28	70	47	1.99	76	54
CML254xCML247	2.09	67	58	2.53	87	56	3.26	87	56	2.16	100	67
Average	2.51			2.73			3.25			2.01		

The Tlaltizapan environment was not well managed with regard to N, which resulted in low RUEs. With the exception of the hybrid, there were few differences among genotypes. The hybrid had a relatively low RUE at low N_L (data not shown). All five genotypes had accumulated 15 kg leaf N ha^{-1} by about 4 to 5 weeks after sowing in all experiments.

Sinclair and Horie (1989) argued that during early vegetative growth a number of field crops, including maize, show a great responsiveness of RUE to changes in N_L at low levels of N_L, while at higher levels of N_L RUE approaches a maximum value. Our data confirm these trends: four genotypes at Poza Rica reached a RUE of about 2.7 g MJ^{-1} at 15 kg leaf N ha^{-1}, whereas at the highest N_L levels, RUE was 3.26 g MJ^{-1} (Fig 1.). Maximum RUE in Tlaltizapan was less however, at about 2 g MJ^{-1}, a value slightly lower than the 2.4 g MJ^{-1} reported at that same location by Bolaños and Edmeades (1993a).

Modeling biomass accumulation in tropical maize can be based on the constant utilization of intercepted radiation at least until anthesis, or 3 to 4 weeks later, depending on the growing conditions. After that point, a reduced value should be used. This requires, however, that light interception and, therefore, leaf area development are estimated This is difficult to do accurately, especially under growth-limiting conditions. Since RUE is related to N_L levels, soil nitrogen processes and N uptake and distribution within the plant should be described and estimated as well. Inadequate soil characterization may result in under- or over-estimation of leaf nitrogen content.

Nitrogen use efficiency (NUE)

NUE is defined here as kg aboveground dry matter per kg leaf N. This definition is preferred over one based on total N recovered by the plant, or one based simply on the amount of applied N. The latter approach introduces soil-related variation in N supply, including the effects of applied fertilizer N, soil N naturally available, denitrification, N uptake, and N allocation within the plant, and does not lead to accurate quantification of the relevant processes. In a similar way to the radiation use efficiency model, daily growth can be described by:

$$G = NUE \times N_L \qquad (3)$$

NUE usually decreases over time. Average NUEs during the period of stable early-season RUE are presented in Table 3. NUE is highest at lowest levels of N availability, as demonstrated by differences among Exps. 5620, 5621, and 5622.

When modeling the growth of tropical maize on the basis of leaf N utilization, one can assume either a continuously decreasing crop NUE or a constant NUE up to anthesis followed by a decreasing NUE. The choice will depend on the sort of

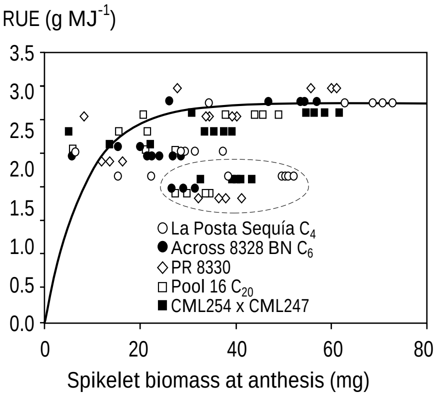

Figure 1. Radiation use efficiency (g MJ^{-1}) in relation to leaf N content (kg ha^{-1} ground surface area). The regression is based only on Poza Rica data.

Table 2. End-of-season radiation use efficiency (RUE; g MJ^{-1}) calculated as the average RUE from the onset of RUE decline to final harvest, days to onset of decline (decl; d after sowing) and days to harvest (harv; d after sowing) for four experiments conducted in Mexico during the 1995 summer cycle. A negative RUE was considered zero in computation of the averages.

	Exp. 5620			Exp. 5621			Exp. 5622			Exp. 6609		
Germplasm	RUE	decl	harv	RUE	decl	harv	RUE	decl	harv	RUE	decl	harv
La Posta Sequía C_4	0.73	61	104	-0.65	81	109	0.98	70	104	0.85	85	125
Across 8328 BN C_6	1.14	49	104	1.06	81	104	0.48	81	104	0.47	85	125
PR 8330	0.86	49	104	1.18	60	104	0.53	70	104	0.94	76	112
Pool 16 C_{20}	0.71	49	104	0.21	81	104	0.27	70	104	0.84	76	112
CML254xCML247	0.61	67	115	0.84	87	119	0.43	87	119	-0.10	100	133
Average	0.81			0.66			0.54			0.62		

Table 3. Nitrogen use efficiency (NUE) calculated as the average aboveground dry matter per kg leaf N (kg kg^{-1} leaf N) during the early plant development period that is characterized by stable radiation use efficiency; data from four experiments grown in Mexico under varying levels of nitrogen during the 1995 summer cycle.

Germplasm	Exp. 5620	Exp. 5621	Exp. 5622	Exp. 6609
La Posta Sequía C_4	10.07	5.86†	4.99	2.21†
Across 8328 BN C_6	8.93	5.80	4.33	2.20†
PR 8330	8.53	7.21	5.25	1.66
Pool 16 C_{20}	7.84	6.36	4.57	1.76
CML254xCML247	7.08	5.21	3.91	2.52†
Average	8.49	6.09	4.61	2.07

† Calculated for a time period somewhat shorter than mentioned in Table 1 for stable RUE.

application, and validity of calibration data. In any case, a site-genotype specific calibration factor must be introduced into the model, and N uptake and allocation must be simulated accurately.

More complex models

Complex photosynthesis models are, for example, described in Goudriaan and van Laar (1994). Net leaf photosynthesis can be described by an asymptotic exponential, i.e., the photosynthesis light response curve is

$$A_{net} = A_{max} \times (1 - e^{-PAR_a \times \varepsilon / A_{max}}) - R_d \qquad (4)$$

This approach requires estimates of initial radiation use efficiency at a very low radiation intensity (e), maximum rate of CO_2 assimilation at high light intensities (A_{max}), dark respiration rate (R_d), the light extinction coefficient, and the effect of leaf nitrogen content on A_{max}. High values of A_{net} were measured on young well-fertilized plants grown in pots at the experimental station in Tlaltizapan. A_{net} varied between 71.8 (CML254 x CML247) and 79.6 (La Posta Sequía C_4) with an average of 75.7 kg CO_2 ha (leaf)$^{-1}$ h^{-1}. Field observations on leaf area index and intercepted radiation led to a calculated value for the light extinction coefficient of 0.53 across the five genotypes. As little data are available on the relationship between leaf nitrogen content and A_{max} for tropical maize, standard relations must be used (see, for example, van Keulen and Seligman, 1987).

This detailed modeling approach is suitable if a high level of precision is required, or if growth limiting effects or reducing factors can not be explained adequately at a lower integration level, e.g., if leaf senescence high in the canopy needs to be accounted for through its effect on light availability low in the canopy. However, detailed parameterization is required, and N uptake and leaf area dynamics must be simulated accurately.

The effect of limited water supply

Simulation of crop growth under water limited conditions requires modules which describe soil water processes and compute evapotranspiration. Water use efficiency (WUE) can be calculated in a similar manner to RUE and NUE if simplified computations are adequate. Experimental data under differing moisture levels are currently unavailable, so the effects of limited water supply will be addressed later with regard to kernel set.

Comparative simulations

Growth of the five genotypes under the three growing conditions at Poza Rica was simulated in two ways, viz. using complex photosynthesis modules and the relation between N_L and RUE. A number of additional modules were incorporated into SUCROS for this purpose. RUE was multiplied by 0.5 for development stages beyond 50% grain filling. The rationale behind this is that RUE was computed on the basis of early vegetative growth which is not representative for the lower radiation and nitrogen use efficiencies that may develop during reproductive growth. Results are depicted in Figure 2. Use of RUE procedures caused slight over-estimates. Use of photosynthesis modules caused a limited under-estimation of aboveground biomass, and some estimates were less than 10 t ha^{-1}. In general, at higher production levels both approaches caused limited over- and under-estimates, but on the whole their simulation results were acceptably accurate.

Simulation of Pre-anthesis Development

Preliminary phenology modules for tropical maize have been developed, and are linked directly to leaf number, implying a constant amount of thermal time per additional leaf formed (e.g., Kiniry, 1991). They assume that embryos need 75 d°C (4 to 5 d under tropical conditions) to germinate and emerge. The juvenile phase is characterized by leaf initiation that progresses unaffected by daylength. This is followed by the inductive photoperiod-sensitive phase. During this phase additional

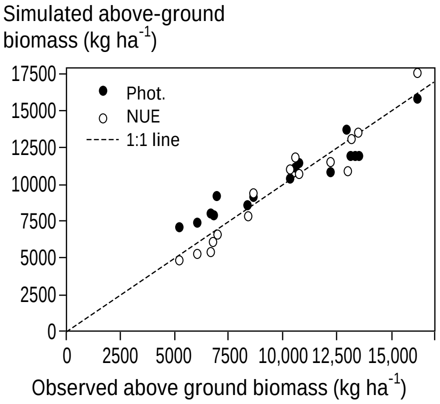

Figure 2. Observed and simulated above-ground biomass (kg ha^{-1}) for the five genotypes at three levels of soil N availability at Poza Rica, summer cycle 1995. Simulations were carried out using complex photosynthesis modules (Phot.), and using a N-based light use coefficient (NUE).

leaves are initiated, and the number formed is influenced by daylength. The juvenile phase ends about 70 d°C before tassel initiation, at this stage a daylength longer than the critical daylength (P_c) leads to additional leaves. Genotypes can be characterized by the total number of leaves (L_{cd}) that form under critical daylength. The value of P_c under tropical summer conditions is estimated to be 12.5 h, and L_{cd} is on average 19.2 leaves for tropical maize (Edmeades et al., 1994). When daylengths exceed a ceiling photoperiod (P_{ce}, often around 16-17 h), no further increase in leaf number occurs.

Daylength sensitivity is expressed as an additional number of leaves per hour extra photoperiod between P_c and P_{ce}, and averages around 2.3 additional leaves h^{-1} for tropical maize (Edmeades et al., 1994). A temperature x daylength interaction exists however, since low night temperatures reduce sensitivity, increase the thermal time to tassel initiation, and increase L_{cd}. However, this interaction is commonly ignored because the majority of tropical maize is grown in the summer when nights are warm.

The advantage of the above phenology module is that parameterization requires only two genetic inputs, viz. L_{cd} and daylength sensitivity. The former can be determined by growing the genotype under a daylength $< P_c$ (e.g., in the tropical winter), and the latter by growing the genotype under two contrasting daylengths such that P_c <daylengths $< P_{ce}$. The dependence of these parameters on temperature is more difficult to quantify and remains to be parameterized.

Other traits have been used to characterize preanthesis development. Various researchers have observed leaf tip appearance rates (LAR) of between 0.0176 and 0.0333 leaves $[d^oC]^{-1}$ (Tollenaar et al., 1979; Warrington and Kanemasu, 1983; Picard et al., 1985; Hesketh and Warrington, 1989; Zur et al., 1989). The CERES Maize model assumes a value of 0.0257 leaves $[d^oC]^{-1}$ (Kiniry, 1991). Differences in this value may also reflect how thermal time has been calculated, since several different computational approaches have been used. At CIMMYT's Poza Rica and Tlaltizapan stations, calibration against field observations leads to a value LAR of 0.024 leaves $[d^oC]^{-1}$. On average, anthesis occurred 12 d°C (less than one day) after the appearance of the last leaf (observations based on visible leaf number). However, we noted large genotype x experiment interactions with this thermal time requirement.

Under favorable growing conditions, silking and anthesis commonly occur at the same time, and for this reason they are not treated separately in the CERES Maize model. If growth rate is reduced then the rate of carbohydrate supply to the young ear, a relatively weak sink at that stage, is reduced. Reduced carbohydrate supply can be due to low radiation per plant (as in the case of high plant density), or low water or nitrogen availability, and can lead to kernel abortion, barren plants, and ultimately reduced grain yield. Reduced supply also leads to delayed silking and an increased anthesis-silking interval (ASI). Plant factors determining ASI have not been fully explained to date, but we hypothesize that ASI is related to ear growth rate at flowering and are pursuing research to quantify this relationship. The trait is especially attractive in that it is easy to measure, highly heritable and highly correlated with grain yield (Bolaños and Edmeades, 1993b).

Postanthesis development is tentatively treated as in the CERES Maize model, and is not discussed here.

Simulation of Grain Set and Growth

Simulation of preanthesis growth and development must be followed by simulation of grain growth to obtain grain yield estimates. Growth limitations have serious consequences for the number of kernels per plant and therefore for grain yield. Consequently, a fairly detailed approach is required. Grain set and subsequent grain growth are the two main processes considered here.

Grain set

Kernel number per plant (KPP) appears to be related to plant growth rate around anthesis and silking, based on experiments using differing plant densities. Edmeades and Daynard (1979) observed a maximum of about 680 kernels ear^{-1} at a plant growth rate of 6 g CH_2O $plant^{-1}$ d^{-1}, and described the relationship between growth rate and KPP with a hyperbola. At rates higher than about 6.5 g CH_2O plant^{-1} d^{-1}, a second ear forms in semi-prolific genotypes, and KPP is described by a second hyperbola (Fig. 3, Tollenaar et al., 1992). Tollenaar et al. developed the following equations that describe the relationship when two ears develop:

for the first ear:

$$y = y_0 + \frac{\alpha(x - x_0)}{1 + \beta\,(x - x_0)} \tag{5a}$$

for the second ear:

$$y = y_r + \frac{\alpha x_F}{1 + \beta x_F} \tag{5b}$$

in which

$$x_F = x + - \frac{\alpha x_{int}\,(\beta x_{int})\,(y_{int} - y_r)}{\alpha - \beta(y_{int} - y_r)} \tag{5c}$$

and the variables are defined as:

y: number of kernels per plant
y_0: number of kernels per plant at zero plant growth (usually 0)
$y_{r:}$ kernels per plant at a plant growth rate of 6 g d^{-1}
y_{int}: kernels per plant when a second ear begins forming
x: plant growth rate (g CH_2O plant^{-1} d^{-1})
x_0: highest plant growth rate at which y is 0 (g CH_2O plant^{-1} d^{-1})
x_{int}: plant growth rate at which kernels begin forming on a second ear (g CH_2O plant^{-1} d^{-1})
α: initial slope of kernels per plant per unit plant growth rate (g CH_2O plant^{-1} d^{-1})$^{-1}$
β: an empirical coefficient that determines the maximum kernel number on a first ear

The three genotypes (Pioneer 3978 and 3851 and Funks 280) included in the Tollenaar study were prolific and could be characterized by relatively similar parameters. The mean parameter values were: $\alpha = 513$, $\beta = 0.713$, $y_r = 566$, $x_0 = 0.77$, and $x_{int} = 6.49$. We calibrated our model with these values for α, y_r, x_0, and x_{int}, and derived values for β from the number of kernels per ear at high N availability. CML254 x CML247 was characterized by a β of 0.75, Across 8328 BN C_6 and La Posta Sequía C_4 by a β of 1.05, Pool 16 C_{20} by a β of 1.20, and PR 8330 by a β of 1.50.

Kernels per plant can also be related to ASI. Bolaños and Edmeades (1993b) found an exponential relationship between ASI and KPP that was based on data collected under both well-watered and water deficit conditions (see Fig. 4):

$$KPP = e^{7.08 - 0.82(ASI+1.1)^{0.5}} \tag{6}$$

Fractional reductions in KPP can be computed for given changes in ASI. The maximum KPP at simultaneous male and female flowering is 503, suggesting that this model describes KPP for genotypes with only one ear per plant. For this equation, the strongest KPP response is at low ASI values, which normally coincide with high ear growth rates. In the two-ear per plant model (Tollenaar et al., 1992), the KPP response to growth rate is strongest at low growth rates. The two models appear to describe fundamentally different responses to the amount of intercepted radiation per plant and water availability at flowering, though the quantitative response of ASI to ear growth rates has still to be determined. Both equations have been introduced into a grain growth module in which modeled KPP is the minimum value determined by the two approaches.

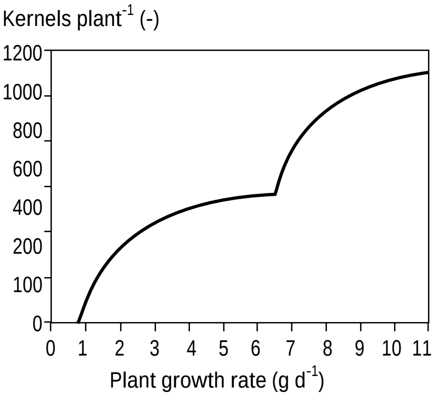

Figure 3. The relationship between plant growth rate (g CH_2O plant^{-1} d^{-1}) and kernels per plant (after Tollenaar et al., 1992).

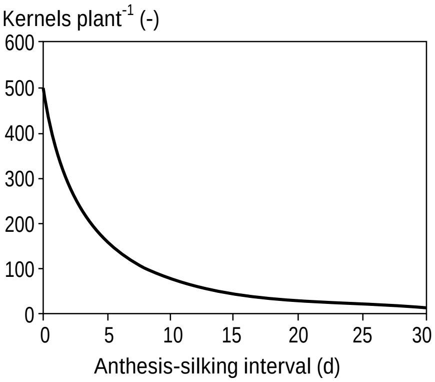

Figure 4. The relationship between ASI (d) and kernels per plant (after Bolaños and Edmeades, 1993b).

Grain growth

Lafitte and Edmeades (1995) found a mean individual grain growth rate of 3.22 mg d^{-1} during the lag phase of grain filling for two genotypes grown in normal and low nitrogen conditions. Average grain growth rate during the linear phase of grain filling was 8.50 mg d^{-1} (9.64 mg d^{-1} under normal and 7.53 mg d^{-1} under low nitrogen conditions). Maximum grain weight averaged 0.192 g at low N and 0.269 g at high N availability.

Sensitivity analysis

The consequences of variation in ASI were simulated for three levels of N availability at Poza Rica for PR 8330 and hybrid CML254 x CML247. The hybrid gave the highest simulated grain yield, 9 t ha^{-1}, at the high soil N level (Fig. 5). At low N availability, its simulated grain yield was 3.5 t ha^{-1}. Grain yield of PR 8330 varied between 2 and 4 t ha^{-1} over a range of

N availability's. An increase in ASI led to reduced grain yield. The yield response was strongest for ASI's between 3 to 10 d in the highly productive high soil-N environment. For the other production levels, grain yield decreased more gradually with increases in ASI. In these simulation studies green leaf area was kept constant. Under field conditions green leaf area is less in lower production environments, suggesting that reductions in grain yield will be larger than those in the simulations. Most conditions that cause an increase in ASI will also cause a reduction in green leaf area and duration, with consequent yield reductions.

This simple model shows some instability. An ASI of 1 d can result in a greater simulated grain yield than simultaneous male and female flowering. This is because this small increase in ASI leads to a greater time interval when growth rate is related to KPP. Resulting variation in growth rate causes the variation in KPP.

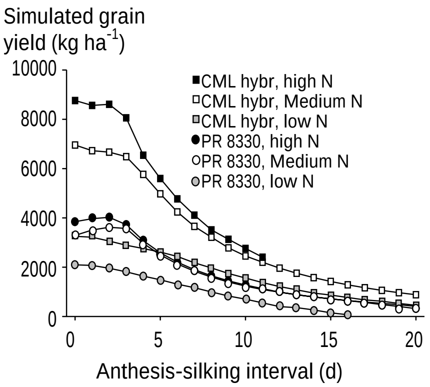

Figure 5. Variation in simulated grain yield as a consequence of increased ASI for PR 8330 and CML254xCML247 when grown at three soil N levels at Poza Rica, summer cycle of 1995.

Conclusions

- The use of complex photosynthesis models are most appropriate for studies that require detailed canopy description. However, the use of a RUE coefficient linked to leaf N content per ground surface area appears sufficient for more general purposes. In either case, it is critical to accurately simulate N uptake from the soil.
- Grain set and growth can be related to plant growth around flowering, but available equations that relate plant growth rate (radiation growth limiting) and the length of the anthesis-silking interval (moisture growth limiting) to kernel number per plant do not lead to satisfactory results in all cases. The equations need further refinement, especially for simulations at lower production levels, and this will require better quantification of underlying processes.

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Tropical Maize Under Pre-Anthesis Drought and Low Nitrogen Supply

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Abstract

An estimated 50% of tropical lowland maize grown in Southeast Asia is reported to suffer substantial grain yield reduction because of drought stress and low soil fertility. Field trials were conducted in the tropical lowlands of Thailand during the dry season to determine the extent to which water stress and nitrogen limit maize growth and yield. Water stress was established during the vegetative period in combination with three nitrogen fertilization levels. Two hybrids (KTX2602, DK888) and two OPVs (Suwan1, La Posta Sequía) were grown; DK888 and La Posta Sequia were assumed to be relatively drought tolerant. Morpho-physiological traits (including leaf rolling and anthesis-silking interval) were evaluated and biomass accumulation was observed during the vegetative period and at maturity. Shoot and grain were analyzed for nitrogen and mineral element concentrations. Soil water content was measured using time domain reflectrometry (TDR) and tensiometers.

Maize is often grown in drought-prone and marginal areas with low soil fertility in Southeast Asia. An estimated 50% of tropical lowland maize grown in the region is reported to suffer substantial grain yield reduction because of periodic drought stress and low N supply. Probability of drought is highest at the beginning and end of the growing season. In Thailand, less than one fifth of the cropped land (4 million ha) can be irrigated. The remainder is vulnerable to drought periods lasting several weeks, especially in the early rainy season (April to July). In some parts of the country even the beginning of the rainy season (August) shows irregular patterns of precipitation which may affect the vegetative growth of crops because plant roots are mainly confined to the topsoil at that growth stage. Continuous maize cultivation on recently cleared land rapidly depletes nitrogen and may cause erosion. Economic constraints often restrict farmers from applying fertilizer in adequate amounts, and under these circumstances the only affordable option for many small farmers may be the cultivation of drought tolerant and nitrogen (N) use efficient varieties (Bolaños and Edmeades, 1993). Many studies have focused on either water or N deficits but ignored the complex interactions between these factors. Dry soil conditions severely reduce the supply of mobile ions to roots and impede transformation of soil nutrients to plant-available forms. Nitrogen fertilizer applied under drought stress seems to have a positive effect on maize yield (e.g., Eck, 1984). In the present study, the combined effects of N and preanthesis drought on dry matter (DM)-related traits (preanthesis DM accumulation, grain yield, harvest index), ASI, and leaf rolling were investigated.

Materials and Methods

The field study was conducted at the National Corn and Sorghum Research Center, Suwan Farm, Thailand (latitude 14.5 °N; altitude 360 masl). The climate is semi-arid, the soil is a dark reddish brown Oxisol, consisting mainly of kaolinite. The soil properties of the experimental field are presented in

Table 1. Water permeability is moderately high. Treatments were arranged in a split-split-plot design with six replications. Water regime was the main plot, rate of N application the subplot and variety the sub-subplot. Two different water regimes were used before anthesis: the control treatment received weekly applications of about 40 mm, while the water stressed plots were watered at 4 wk intervals until anthesis, both by graded furrow irrigation; thereafter the whole field was irrigated weekly in order to avoid any water deficiency in the period from anthesis to maturity. Three levels of N were supplied to plots, either 0 kg, 80 kg, or 160 kg N/ha. The 160 kg N rate was split; 80 kg N was applied at planting and the remaining 80 kg N was applied 40 d after planting. Two open-pollinated varieties, Suwan1 C_{11} (Thailand) and La Posta Sequía C_4 (CIMMYT), and two hybrids, KTX2602 (Thailand) and DK888 (Thailand/US) were chosen to represent a wide spectrum in grain yield potential, and in grain mineral and N content. La Posta Sequía and DK888 are thought to have good drought tolerance, and KTX2602 shows a high grain N content (Feil et al., 1993). Both KTX2602 and Suwan 1, the latter released in 1975, are traditional check varieties at Suwan Farm. The established plant density was 53,000 plants/ha. Plots consisted of 8 rows and measured 54 m^2. The trial was planted on December 22, 1994, i.e., at the beginning of the dry season. The following traits were determined before anthesis (about 9 wk after emergence): shoot fresh- and dry matter (DM) (weekly sampling of 12 plants per plot), number of green and dead leaves (counted weekly), leaf rolling index (measured twice a week), and soil water content measured with time domain reflectrometry (TDR) and tensiometers. Days to anthesis, silking, and time to 50% black layer (i.e., physiological maturity) were recorded. Plant and ear height were measured shortly after anthesis and at black layer. Total shoot DM, grain yield, grain yield components (thousand kernel weight (TKW), and kernels per ear) and harvest index (HI, ratio of grain to total above-ground biomass) were determined on 30 plants per sub-subplot. Shoot samples taken at four dates before anthesis and at harvest will be assayed for concentrations of N, phosphorus (P) and potassium (K), and grains will be analyzed for the concentration of N, P, phytate-P, K, Ca, Mg, Fe, Mn, Zn, and Cu. Soil mineral N contents were measured immediately prior to sowing, at four dates before anthesis, and at physiological maturity.

Table 1. Soil properties from two depths (0-30 cm, 30-60 cm) of the experimental field in Thailand, 1995. Data are means of 20 samples.

Parameter	Unit	0 - 30 cm	30 - 60 cm
Clay	g kg^{-1}	550	740
Silt	g kg^{-1}	220	130
Sand	g kg^{-1}	230	130
pH		6.9	6.5
Organic matter	g kg^{-1}	21	12
P[†]	ppm	97	40
K[‡]	ppm	100	60

[†] P assessed with the Bray II method

[‡] Exchangeable K extracted with 1 mmol l^{-1} ammonium acetate at pH 7.0

Results and Discussion

The first results of the 1994-95 experiment are shown in Figures 1, 2, and 3. Other data are still being recorded in the laboratory. In the meantime, the 1995-96 experiment has been finished successfully, but the data have not been analyzed yet. The experiment will be repeated a third time in 1996-97.

The general impact of water supply on shoot DM accumulation is depicted in Figure 1. The development of DM showed a sigmoidal growth curve. As expected, less DM was accumulated over the season under water-stress conditions, with 58% less shoot DM/plant for the water-stress treatment by week 10; i.e., shortly after flowering. In the second half of the stress period, plants suffered more heavily from water deficit than during the first half: seven and eight weeks after emergence, growth depressions of 65% and 63%, respectively, were observed. Thus, in contrast to reports by Ackerson (1983) or Neidhart (1994), the relative difference in DM accumulation between well-watered and water-

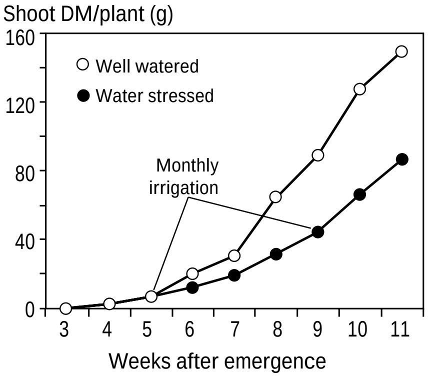

Figure 1. Effect of water supply on shoot dry matter accumulation. Values are means of three N levels and four varieties.

stressed treatments increased at advanced stages of growth. At maturity, total above-ground DM in droughted conditions was reduced by 54.5% compared to well-watered conditions. Averaged across the rates of N application and cultivars, water stress reduced grain yield by 30% (Fig. 2). Under both treatments, DK888 performed much better (+32%) than the other three varieties. The percentage reduction in grain yield of the two hybrids (KTX2602 and DK888) under drought was significantly higher than that of Suwan 1 and La Posta Sequía. Water stress did not affect the ranking of the varieties. Analysis of variance did not show significant varietal differences in the response to water supply. The three-way interaction between water supply, N level and variety was non-significant for yield (P=0.20). The decrease in grain yield from water stress was clearly lower than that for total DM at maturity. This indicates that maize can compensate for early stress to a certain extent during the grain filling period. This is not surprising because it has been reported that most assimilates contributing to grain yield are formed after silking (Simmons and Jones, 1985). Consequently, an increase in harvest index from 0.44 under well-watered conditions to 0.54 under reduced water supply was found (values are means over all varieties and rates of N application; data not shown). Thus the adverse effect of drought on biomass accumulation during vegetative growth stages can be partly compensated for by an increased HI. The HI found under drought is surprisingly high for tropical germplasm (Feil et al., 1992). Experiments with drought at or after flowering, however, usually result in a stable or decreasing harvest index (Sinclair et al., 1990; Bolaños and Edmeades, 1993).

The effects of variety, water, and N supply on the anthesis-silking interval (ASI) are shown in Figure 3. ASI is considered to be an indicator of drought tolerance (Fischer et. al., 1989; Bolaños and Edmeades, 1993) and is, therefore, used as selection criterion in breeding programs. In experiments reported by these authors the drought period was usually initiated just before or at the beginning of tasseling, and resulted in an ASI of up to 18 d or more. In contrast, in the present study, the drought stress ended at the beginning of flowering. As a result, when averaged across the rates of N application and varieties, variation in ASI was limited (0 to 5 d).

Data for KTX2602 show that, under well-watered conditions, low N supply caused ASI to increase by more than 2 d, indicating that ASI responses of maize to N and water deficiency are similar (Fig. 3A). Under drought, however, ASI was shorter under low N supply than under high N supply (Fig. 3B). The interaction between variety, water supply, and N level was significant at P=0.05. There were significant differences in ASI among cultivars. The CIMMYT variety La Posta Sequía C_4 had a negative ASI when well-watered, while ASI was about zero under drought. This may have contributed to its significant advantage in yield behavior over the hybrid KTX2602.

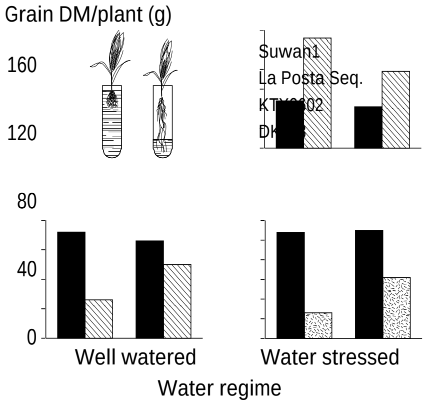

Figure 2. Effect of water supply on grain yield of four maize cultivars. Data are means of three levels of N supply. Depicted values represent percentage reduction of each variety under drought, compared with well-watered conditions.

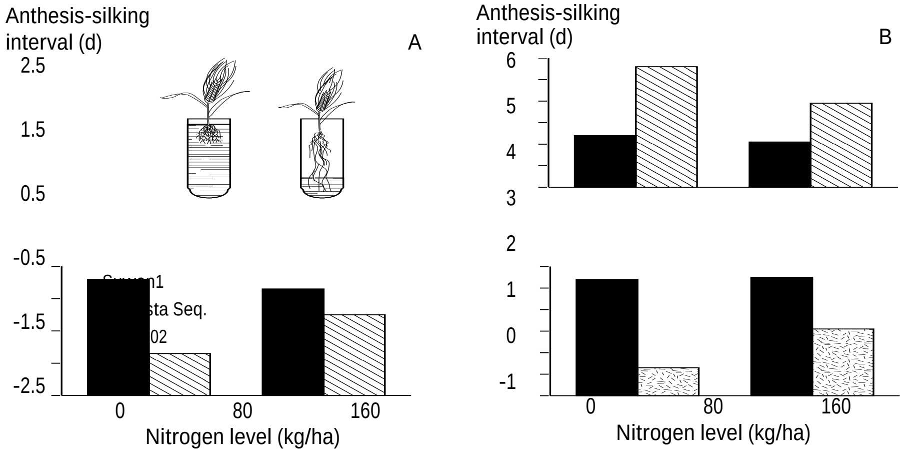

Figure 3. Effect of water supply (A=well watered; B=water stressed), N level and variety on the anthesis-silking interval.

Acknowledgments

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Biochemical Characterization of Drought Tolerant and Susceptible Young Maize Plants Under Well-Watered Conditions

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Abstract

Selected biochemical traits were evaluated in various sections of developing leaves of a drought susceptible population, Tuxpeño Sequía C_0*, and of a drought-tolerant selection from the same population, Tuxpeño Sequía* C_8*. Both populations were grown in the greenhouse under full sunlight and well-watered conditions. Photosynthetic and transpiration rates, a and b chlorophyll content, total protein, dry matter and specific weight were measured in five 2 cm sections along the second leaf when it was 10 cm long. Chloroplasts from mesophyll cells were also isolated from each section and photochemical activities were measured. Finally, ultrastructure organization of the chloroplasts in leaf tissue was observed by electron microscopy. Tuxpeño Sequía* C_8 *had a higher photosynthetic rate (30%), accumulated more dry matter per leaf segment (5%), and had a higher specific leaf weight (10.5%) than* C_0*. Although total protein and chlorophyll a contents were similar in both populations,* C_8 *had 19% less chlorophyll b. With respect to photochemical activities of isolated chloroplasts, values for proton pumping, photophosphorylation and basal phosphorylating and uncoupled electron transport rates were 60 to 80% lower in* C_8 *than in* C_0*. Electron microscopy showed that chloroplasts of both bundle sheath and mesophyll cells differed somewhat morphologically between the populations.*

Maize is one of the three most important cereals of the world, and is consumed as food by millions of people especially in developing countries. Per capita consumption of maize in some countries exceeds 100 kg per year (Paterniani, 1990; Pandey and Gardner, 1995), and the crop is probably the most widely distributed of any in the world.

Maize is often grown in environments with between 250 and 1000 cm rainfall, and in the tropics about 95% of the maize area suffers from erratic rainfall distribution (Hallauer and Miranda, 1988; Edmeades et al., 1989). It has been estimated that 80% of maize planted in lowland tropical environments suffers periodic yield reduction ranging from 10 to 50% as a result of water-limited conditions. Many national and international programs around the world are breeding genotypes improved for drought tolerance. Significant improvements have been obtained in experimental plots, but no related increase in productivity has yet been observed at the farm level. Under adverse environments, many physiological and morphological traits have been presumed to have adaptive value. A better understanding of the biochemical and physiological characteristics — such as those related to photosynthesis — and how they differ among stress sensitive and tolerant cultivars, may be essential for further maize improvement.

The International Maize and Wheat Improvement Center (CIMMYT) has been doing recurrent selection for improved maize population performance for almost three decades (Pandey and Gardner, 1995). Using a selection index comprised of relative leaf and stem elongation rate, anthesis-silking interval, delayed foliar senescence, grain yield, and canopy temperature, eight cycles of full-sib recurrent selection under drought were carried out in the maize population Tuxpeño Sequía (Bolaños and Edmeades, 1993a, 1993b; Bolaños et al., 1993). Agronomic, physiological and morphological differences between Tuxpeño Sequía C_0 and C_8 have been evaluated under well-watered and drought conditions (Bolaños and Edmeades, 1993a, 1993b; Bolaños et al., 1993). These studies show an increase in grain yield due to a higher harvest index in both wet and dry environments, thus indicating that drought improvement may be due to improved partitioning of biomass toward the female inflorescence at flowering. The characterization of drought-tolerant cultivars under favorable environments could also be important, since it has been suggested that some drought tolerant genotypes may not have the capacity to exploit good environments (Edmeades et al., 1987).

The present work was devoted to the study of the effects of selection for drought tolerance on leaf gas exchange related processes (net photosynthesis and transpiration rate), leaf chlorophyll and protein content, and some photochemical activities of isolated chloroplasts (light induced proton pumping, photophosphorylation and electron transport rate) during the early growth of Tuxpeño Sequía C_0 and the drought tolerant C_8 selection from that same population under well watered conditions.

Materials and Methods

Plant material and growth conditions

Two versions of the same maize population, Tuxpeño Sequía, were used for this study: C_0, considered to be drought sensitive, and C_8, known to be tolerant to drought that coincides with flowering and grain filling (Bolaños and Edmeades, 1993a). Seeds were soaked in water for 24 h at 22ºC. Plastic boxes (38 cm x 25 cm x 10 cm) were filled with a greenhouse soil mixture and 25 soaked seeds were equidistantly planted in each. Germination and plant development was allowed to continue normally in a greenhouse at Chapingo, Mexico (19º29′ N, altitude 2250 m) under natural daylight, and with an average daytime temperature of 27.6°C and night temperature of 15°C. Light intensity in the greenhouse was 60% of the outdoor natural light (midday light intensity in May was 2,000 mmol m^{-2} s^{-1}). Twice each week both cultivars were watered to field capacity.

Evaluations

The second fully expanded leaf with an exposed ligule was used for this study, normally when it reached 10 cm in length. The leaves were cut into 2 cm-long segments, and all evaluations were carried out on these. Net photosynthesis and transpiration rate were measured in intact leaf segments immediately after they were harvested, so each leaf segment belonged to a different plant. A portable infrared gas analyzer system (ADC, LCA-2; Analytical Development Co.) was utilized in the open system mode of operation. The measures were taken under full sunlight outside the greenhouse. Light-dependent proton uptake (proton pump activity), light-dependent ATP formation (photophosphorylation) and whole-chain electron transport rates (including basal, phosphorylating and uncoupled rates) were measured in isolated chloroplasts as described previously (Peña-Valdivia et al., 1994; Peña-Valdivia and Torres V., 1995). Total, *a* and *b* chlorophyll content of the tissue and isolated chloroplasts were quantified according to the method described by Arnon (1949). Nitrogen content was determined by the micro-Kjeldahl method, and crude protein was calculated as N x 6.26 (Bateman, 1970).

Ultrastructure

Samples for electron microscopy were obtained as described previously by Crespo et al. (1979).

Statistical design and analysis

The experimental design was an RCBD. Treatments were arranged as a factorial in four replications, the factors being cultivars and leaf sections. All assays were replicated four times within an experimental unit consisting of 20-25 plants. Analysis of variance and Tukey's HSD test were determined using the SAS computer package (SAS Institute Inc., Cary, NC).

Results

Photosynthetic and transpiration rates

Net photosynthesis increased lengthwise along the second leaf in both cultivars. A maximum rate was obtained in the lamina segments most distant from the leaf base (Table 1). The negative values in the region nearest the ligule, observed in both cultivars, indicate that the respiratory rate was slightly higher than the photosynthetic rate in this region. Leaves of C_8 were 30% more active than those of C_0. In contrast, transpiration rate increased from leaf base to tip only in C_0 (Table 1). In C_8 the highest transpiration rate was recorded for the central lamina sections, situated between 4 and 8 cm from the ligule. The highest transpiration rate attained by C_8 was 36.2% lower than the highest recorded for C_0 (22.5 vs. 30.6 µmol m^{-2} s^{-1}).

Chlorophyll content

In both cultivars a gradient of increasing chlorophyll content was observed from the base to the tip of the leaf, with chlorophyll *a* and total chlorophyll concentration being 17 and 26 times higher in the leaf tip than in the section nearest the ligule (Table 2). Although chlorophyll *a* and total content were similar for both cultivars, a significant difference was observed in the content of chlorophyll *b* in the region nearest the ligule (first 4 cm). In the first two sections, chlorophyll *b* was noticeably lower in C_8 than in C_0 (0.02 to 0.2 µg mg^{-1} fresh weight vs. 0.4 to 0.85 µg mg^{-1}).

Dry weight, specific leaf weight and protein content

Dry weight of individual sections increased lengthwise along the leaf in both cultivars, with the maximum value attained in the distal section of leaf where it was almost twice that of the basal section. Conversely, fresh leaf weight per unit leaf area of basal sections of laminae was almost 50% larger than for distal sections, which indicates that basal tissue had a higher water content (Table 3). Total foliar dry weight of C_0 was only slightly higher (4%) than that of C_8, though this difference was statistically significant (Table 3). In contrast, specific leaf weight, on a fresh weight basis, of C_8 laminae was 10.5% greater than C_0, indicating that the blade of the latter was thinner. Variation for both dry weight and specific leaf weight along the lamina was dependent on the cultivar, and the cultivar x section interaction for these traits was significant (Table 3). Contrasting with these two parameters, differences in total crude protein concentration were non-significant between cultivars and

Table 1. Photosynthetic and transpiration rates of leaf lamina sections from along the length of the second leaf of drought susceptible (C_0) and tolerant (C_8) Tuxpeño maize populations. Data were collected under well-watered conditions.

Distance to ligule (cm)	Photosynthesis C_0 (μmol m^{-2} s^{-1})	Photosynthesis C_8 (μmol m^{-2} s^{-1})	Transpiration C_0 (μmol m^{-2} s^{-1})	Transpiration C_8 (μmol m^{-2} s^{-1})
0 to 2	-3.45 d	-1.31 dc	20.36 bcd	11.44 e
2 to 4	3.51 dc	12.04 bc	19.99 bcd	16.56 de
4 to 6	18.74 ab	22.95 ab	27.77 abc	22.47 abcd
6 to 8	24.54 ab	32.54 a	30.60 a	21.75 abcd
8 to 10	29.98 a	29.14 a	29.50 ab	18.68 cde
Mean	14.66	19.07	25.64	18.18

Source	*P*-values from F-tests	
Cultivar	0.0004	0.0001
Section	0.0001	0.0001
Cultivar x Section	0.0092	0.3957

Different letters indicate statistically significant differences for multiple comparisons within a parameter for both cultivars and the five leaf sections.

Table 2. Content of chlorophyll *a*, *b*, and *total* of leaf sections from along the length of the second leaf of drought susceptible (C_0) and tolerant (C_8) Tuxpeño maize populations. Data were collected under well-watered conditions.

Distance to ligule (cm)	Chlorophyll a C_0 (μg mg^{-1} of fresh tissue)	Chlorophyll a C_8 (μg mg^{-1} of fresh tissue)	Chlorophyll b C_0 (μg mg^{-1} of fresh tissue)	Chlorophyll b C_8 (μg mg^{-1} of fresh tissue)	Chlorophyll total C_0 (μg mg^{-1} of fresh tissue)	Chlorophyll total C_8 (μg mg^{-1} of fresh tissue)
0 to 2	1.23 e	0.97 e	0.40 f	0.02 g	1.70 f	0.99 f
2 to 4	4.60 de	4.35 de	0.85 d	0.20 e	5.30 ef	4.00 f
4 to 6	9.35 d	9.07 d	2.30 c	1.68 c	12.20 cd	10.72 ed
6 to 8	16.20 bc	14.67 c	4.03 b	3.22 b	21.27 b	17.90 cb
8 to 10	21.45 ab	23.47 a	5.48 a	5.42 a	29.38 a	28.90 a
Mean	10.57	10.51	2.61	2.11	13.97	12.75

Source	*P*-values from F-tests		
Cultivar	0.9375	0.0241	0.1684
Section	0.0001	0.0001	0.0001
Cultivar x Section	0.6091	0.8157	0.6959

Different letters indicate statistically significant differences for multiple comparisons within a parameter for both cultivars and the five leaf sections.

among sections, although there was a tendency for protein content to increase towards the lamina tip (a 10% increase in C_8 and 21% in C_0).

Photosynthetic activity of isolated chloroplasts

Large differences in photosynthetic activities of the isolated chloroplasts were observed (Tables 4 and 5). The differences were dependent on both the position along the leaf and on the cultivar, and the cultivar x section interaction for this trait was significant. In general, relative activities were lower in the distal regions of C_0 leaves for light-dependent proton uptake (proton pump activity) and whole-chain electron transport rates (including basal, phosphorylating and uncoupled rates). In contrast, rates for these activities in C_8 leaves were uniform across leaf segments. For light-dependent ATP formation (photophosphorylation), the relative activity tended to be lower in the distal segments of C_8 leaves, whereas C_0 leaves had similar rates in all regions, although the cultivar x section interaction effect was not significant in this case. Differences between the two cultivars were highly significant for the five photochemical activities. Proton pump activity in C_0 was 45% higher than for C_8. The differences were much larger for the other photochemical activities; i.e. photophosphorylation and the three electron transport rates were two or more times larger in C_0 than in C_8.

Ultrastructure

The ultrastructures of chloroplasts at different points along the lamina

Table 3. Dry weight, specific leaf weight (on a fresh weight basis) and crude protein concentration of leaf sections from along the length of the second leaf of drought susceptible (C_0) and tolerant (C_8) Tuxpeño maize populations. Data were collected under well-watered conditions.

Distance to ligule (cm)	Dry weight C_0	Dry weight C_8	Specific leaf weight C_0	Specific leaf weight C_8	Protein C_0	Protein C_8
	(mg 100 mg^{-1})		(mg cm^{-2})		(mg 100 mg^{-1})	
0 to 2	8.97 gf	7.97 g	0.019 d	0.025g	32.07 a	34.09 a
2 to 4	10.45 de	9.50 ef	0.014 c	0.014 c	33.09 a	32.57 a
4 to 6	10.87 d	11.17 d	0.012 ab	0.014 c	34.52 a	32.41 a
6 to 8	12.95 bc	12.87 c	0.011 a	0.013 bc	34.47 a	33.41 a
8 to 10	14.95 a	14.12 ab	0.014 c	0.013 bc	35.46 a	41.31 a
Mean	11.64	11.13	0.0133	0.0147	33.92	34.76

Source	P-values from F-tests		
Cultivar	0.0037	0.0001	0.6418
Section	0.0001	0.0001	0.2785
Cultivar x Section	0.0547	0.0006	0.6354

Different letters indicate statistically significant differences for multiple comparisons within a parameter for both cultivars and the five leaf sections.

Table 4. Light-dependent proton uptake (proton pump activity) and light-dependent ATP formation (photophosphorylation) in isolated chloroplasts of leaf sections from along the length of the second leaf of drought susceptible (C_0) and tolerant (C_8) Tuxpeño maize populations. Data were collected under well-watered conditions.

Distance to ligule (cm)	Proton pump C_0	Proton pump C_8	Photophosphorylation C_0	Photophosphorylation C_8
	(hmol mg^{-1} chlorophyll h^{-1})		(hmol mg^{-1} chlorophyll h^{-1})	
0 to 2	50.33 a	27.39 de	83.44 a	54.70 ab
2 to 4	38.00 bc	21.30 e	69.84 a	24.45 bc
4 to 6	30.64 cd	20.19 e	54.98 a	25.75 bc
6 to 8	32.81 cd	19.08 e	63.40 a	26.62 bc
8 to 10	43.89 ab	19.74 e	63.10 a	15.91 c
Mean	39.13	21.54	66.93	29.49

Source	*P*-values from F-tests	
Cultivar	0.0001	0.0001
Section	0.0001	0.0007
Cultivar x Section	0.0040	0.5137

Different letters indicate statistically significant differences for multiple comparisons within a parameter for both cultivars and the five leaf sections.

Table 5. Whole-chain electron transport rates (including basal, phosphorylating and uncoupled rates) in isolated chloroplasts of leaf sections from along the length of the second leaf of drought susceptible (C_0) and tolerant (C_8) Tuxpeño maize populations. Data were collected under well-watered conditions.

Distance to ligule (cm)	Basal C_0	Basal C_8	Phosphorylating C_0	Phosphorylating C_8	Uncoupled C_0	Uncoupled C_8
	(hmol mg^{-1} chlorophyll h^{-1})					
0 to 2	788 a	316 bd	820 a	286 cd	884 b	294 c
2 to 4	565 ab	154 cd	768 ab	223 d	1378 a	220 c
4 to 6	414 bc	159 cd	615 b	213 d	899 b	262 c
6 to 8	271 cd	142 d	422 c	243 cd	828 b	281 c
8 to 10	113 d	91 d	237 d	196 d	678 bc	242 c
Mean	430	173	572	232	933	260

Source	*P*-values from F-tests		
Cultivar	0.0001	0.0001	0.0001
Section	0.0001	0.0001	0.0242
Cultivar x Section	0.0011	0.0001	0.0081

Different letters indicate statistically significant differences for multiple comparisons within a parameter for both cultivars and the five leaf sections.

from both cultivars were broadly similar. Mesophyll and bundle sheath cell chloroplasts of the basal leaf section of C_0, however, possessed rudimentary grana with little starch, though in general chloroplasts of C_8 had less starch than those of C_0 (data not shown). Chloroplasts of mesophyll and bundle sheath cells from along the C_8 leaf were shaped like biconvex lenses, while those from C_0 were more spherical or irregular in shape. In chloroplasts of several leaf sections of C_0 the membrane system called the peripheral reticulum was observed (data not shown).

Discussion

Photosynthetic and transpiration rates

Changes in yield and its components resulting from eight cycles of recurrent selection for drought-tolerance in the Tuxpeño Sequía population have been previously reported (Bolaños and Edmeades, 1993a, 1993b; Bolaños et al., 1993). The present work shows that characteristics of gas exchange processes have also been modified, and that these differences can be detected at an early phenological stage. The fact that net photosynthesis of C_8 was 30% greater than that of C_0 (Table 1) may have implications for ear growth at flowering, though Bolaños and Edmeades (1993a) did not observe differences for total biomass among selection cycles of this population when measured at flowering or maturity. They did however detect a significantly greater radiation use efficiency in later selection cycles during grain filling. Differences in photosynthetic rate between different segments of the same leaf in the present study however, were often greater than differences between cultivars.

Mean transpiration rate was also modified by the selection process, the value for C_8 being 30% less than that of C_0. This indicates that stomatal behavior and / or stomatal frequency differ between C_0 and C_8, at least during this early development stage and under well-watered conditions. Stomatal aperture is controlled by a complex mechanism which operates to maintain a variable balance between CO_2 uptake and water vapor loss (Schulze and Hall, 1982). Thus, these differences in net photosynthetic and transpiration rates between C_0 and C_8 suggest that eight cycles of full-sib recurrent selection have improved stomatal function and perhaps water use efficiency. The higher photosynthetic rate accompanied with the lower transpiration rate could explain, at least partially, the higher grain yield of C_8 under water-stressed conditions (Bolaños and Edmeades, 1993a), provided these differences are maintained under water deficit.

Chlorophyll content

The large increases in total *a* and *b* chlorophyll content per unit of fresh weight from the ligule to leaf tip in both cultivars (Table 2) show the progressive development of the photosynthetic apparatus along the blade's length. This contrasts with photosynthetic rates which attained maximum values between 6 and 8 cm from the ligule (Table 1). Photosynthetic and transpiration rate differences described above may be due to C_8's greater concentration of chlorophyll *b*, which could support a more efficient energy transduction into useful chemical forms, i.e., ATP and NADPH. Concomitantly, there would be an increase of carbon reduction processes which use ATP and NADPH to build carbohydrates from CO_2.

Gummuluru et al. (1989) showed that drought tolerant wheat (*Triticum turgidum* L.) varieties had a higher total chlorophyll content (*a* + *b*) than susceptible ones during early development stages (25 d after planting). Their results suggested that differences for chlorophyll content could diminish during growth and development to the point that cultivars would have the same chlorophyll content when evaluated at a late development stage. Bolaños et al. (1993) found that chlorophyll concentration of Tuxpeño Sequía C_0 and C_8 ear leaves during mid to late grain filling were statistically similar under field conditions. If chlorophyll content in the second fully-expanded leaf relates to that observed in ears leaves, then the results of Bolaños et al. (1993) and our study taken together appear to support the conclusion of Gummuluru et al. (1989).

Dry weight, specific leaf weight and protein content

Dry weight of leaf sections of C_0 was greater than that of the drought tolerant C_8. Additionally, the greater specific leaf weight of C_8 and the absence of differences in protein percentage are consistent with the greater photosynthetic rate observed in that cultivar (Tables 1 and 3).

Photosynthetic activity of isolated chloroplasts

The differences observed in photosynthetic activities of isolated chloroplasts indicated that C_0 possessed greater photosynthetic electron transport capability and thus a greater rate of light-dependent ATP formation (photophosphorylation). The cultivar C_0 is apparently less efficient at using chemically reduced forms of light, since its carbon reduction rate *in vivo* was lower than that of C_8.

Ultrastructure

Differences between chloroplasts of C_0 and C_8 could help explain the observed differences between their physiological, biochemical and biophysical properties. The rudimentary grana in C_0 chloroplasts of basal leaf sections suggest slow chloroplast development in this cultivar. Additionally, the larger amounts of storage starch in C_0 chloroplasts, especially in distal leaf sections, suggests a less efficient translocation process for the products of photosynthesis that probably affects the allocation patterns of carbohydrates (Daie, 1988). Further, the observation of peripheral reticulum exhibited in cells of C_0 but not in C_8 suggests additional differences in chloroplast activity (Laetsch, 1974).

In conclusion, this work demonstrates that eight cycles of recurrent selection for drought tolerance in a Tuxpeño maize population have resulted in changes in several biochemical, biophysical, and physiological traits. Additionally, it was shown that evaluation at early phenologic stages is effective at exposing these differences, while observations made at later stages may be less effective and less useful in the process of selecting parental genotypes for crossing. Similarly, leaf lamina sections that contrast in age should be utilized to ensure that differences are detected, since some of these may not be observed in mature tissue of the type often used in studies of this kind.

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Procesos Bioquímicos-Fisiológicos del Maíz Involucrados en la Tolerancia a la Sequía

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Abstract

This work was done to determine whether the drought tolerance obtained in maize through recurrent selection is closely related to biochemical and physiological activities starting at early development stages. From the maize population, 'Tuxpeño Sequía', which underwent extensive selection for drought tolerance, seed of original population (C_0) *prior to selection and of* C_8 *was grown in the greenhouse and submitted to drought beginning three weeks after emergence until permanent wilting occurred, at which point one irrigation was applied. Under drought, photosynthetic electron transport* in situ *was significantly reduced in* C_0 *plants. In* C_8 *plants, there was a reduction in photosynthetic pigments per unit dry weight and in variable and maximum chlorophyll flourescence emissions (induced with 450 and 630 mmoles of photons/*m^2 *s)* in situ. *Although relative water content was reduced 23% in* C_0 *and 18% in* C_8 *plants under early drought, as drought became severe differences between the experimental plants and the checks were non-significant. A similar result was observed for dry weight of tops and total root dry matter, which on average diminished 30% due to drought in plants from* C_0*, a non-significant change. The 34% reduction in total dry weight of* C_0 *plantlets was however significant. Drought also changed slightly the electrophoretic pattern of plants from both cycles. Drought and subsequent watering generally affected both maize populations equally, although it is possible that the traits measured do not adequately represent the effects of drought.*

La importancia de la obtención de materiales tolerantes a la sequía es evidente, ya que a nivel mundial el principal factor limitativo para el aumento de las cosechas es precisamente el déficit hídrico en México, además de la presencia de zonas áridas y semiáridas en gran parte del país la incidencia de la sequía intraestival merma considerablemente los rendimientos; aproximadamente 930,000 ha de riego y siete millones de ha de temporal se siembran con maíz y la irregularidad de las lluvias ocasiona que los rendimientos promedio fluctúen entre 200 kg/ha y 8 t/ha (González et al., 1994).

El uso de cultivares tolerantes a la sequía es una alternativa viable ante el problema de disponibilidad de agua; aunque, no es fácil la selección de materiales que se desarrollen y produzcan buenos rendimientos en condiciones adversas, ya que cuando se ha logrado la tolerancia a la sequía la producción disminuye considerablemente cuando el temporal es adecuado (Blum, 1989).

Actualmente, el rendimiento de la semilla es el principal criterio de selección; sin embargo, está influenciado por multitud de procesos fisiológicos, bioquímicos y metabólicos y en condiciones hostiles su grado de hereditabilidad disminuye (Blum, 1989; Bolaños et al., 1993). Además, aunque como resultado del efecto ambiental adverso se alteren los procesos metabólicos (reducción de la fotosíntesis) la relación exacta entre éstos y la caída del rendimiento, particularmente de semilla, se desconoce.

Por lo anterior, sería deseable realizar la selección basándose en una o unas cuantas características cuya relación con el estrés estuviera completamente comprobada, desde las primeras etapas del desarrollo y en ambientes controlados. De esta forma, se podría evaluar un mayor número de materiales, en tiempos más cortos, y con poca cantidad de semillas.

El presente trabajo se realizó con el objeto de caracterizar algunas modificaciones bioquímicas y fisiológicas del maíz involucradas en la tolerancia a la sequía. La hipótesis es que la tolerancia a la sequía que expresa el cultivar Tuxpeño Sequía C_8 está íntimamente relacionada con diversas modificaciones en las actividades bioquímicas y fisiológicas, que se manifiestan desde las primeras etapas del desarrollo.

Materiales y Métodos

Material biológico

Se utilizaron dos ciclos de selección de la población de maíz, Tuxpeño Sequía, el denominado Ciclo Original (C_0) que es sensible a la sequía, y uno derivado de éste, que es resistente a la sequía (C_8). Este último fue obtenido en el CIMMYT después de ocho ciclos de selección recurrente (Bolaños y Edmeades, 1993a, b; Bolaños et al., 1993).

Diseño estadístico

El diseño experimental utilizado fue un modelo factorial 2 x 2 completamente al azar, en el que los factores fueron dos cultivares y dos regimenes hidricos, con tres muestreos y cuatro repeticiones. Los factores de estudio fueron: los dos cultivares de maíz (Tuxpeño Sequía C_0 y C_8) y cuatro condiciones de riego: a) riego adecuado, b) sequía incipiente, por suspensión del riego durante 6 d, tres semanas después de la emergencia, c) sequía severa, por suspensión del riego durante 13 d, 7 d más que el tratamiento anterior y d) riego postsequía, aplicado después de la sequía severa. Se muestrearon entre ocho y diez plantas para cada ensayo.

Protocolo experimental

La siembra de ambos materiales se realizó el 25 de marzo de 1994 en un invernadero en Chapingo, México. Las temperaturas medias en el invernadero oscilaron entre 27.6 °C durante el día y 15 °C durante la noche. La intensidad luminosa dentro del invernadero correspondió al 60% de la intensidad luminosa externa (máxima intensidad luminosa de un día del mes de mayo, sin nubosidad @ 2 000 mmoles de fotones m^{-2} s^{-1}).

Las plantas se desarrollaron en bolsas de plástico (negro), de 50 cm de altura y 10 cm de diámetro, con 3 kg de una mezcla de suelo para invernadero (dos partes de tierra de monte y una de arena de río). Se mantuvo una planta por bolsa y la parcela útil estuvo constituida por 136 plantas (68 de cada cultivar) por cada repetición. Para mantener la homogeneidad de las condiciones de desarrollo, las plantas se cambiaron de lugar aleatoriamente, una vez por semana, sobre la superficie utilizada dentro del invernadero.

Tratamientos

Para tener las cuatro condiciones de riego tres semanas después de la emergencia de las plántulas la población de cada cultivar se dividió en dos lotes, uno recibió riego adecuado (agua corriente) cada dos o tres días durante todo el tiempo que duro el experimento. Al segundo lote de cada cultivar se le suspendió el riego y se mantuvo así hasta que mostraron síntomas evidentes de marchitez; esto último, correspondió al momento en el que las plantas no recuperaron la turgencia durante la noche. Se mantuvieron así durante 24 h más y finalmente se aplicó riego adecuado. Debido a que los ensayos se realizaron siempre en la quinta hoja (hoja más reciente y completamente expuesta cuando se inició la suspensión del riego) y en la mayoría de las evaluaciones se destruía el tejido, se utilizaron plantas diferentes en cada ensayo.

Evaluaciones

El transporte fotosintético de electrones y la fluorescencia de la clorofila se evaluaron *in situ* con un oxímetro-fluorómetro para fase gaseosa (Hansatech LC1), equipado con fuente de iluminación integrada que emite luz con longitud de onda de 635 nm (Walker, 1987); la señal se registró con un graficador LKB Bromma 2210. Para la evaluación de la fluorescencia, las plantas (ocho por tratamiento) intactas se mantuvieron en penumbra antes del inicio del ensayo (aproximadamente 1 h). Se cortaron cuadros de 0.5 x 0.5 cm (con tijeras) de la región central de la quinta hoja de cada planta. Se colocó un segmento (con el haz hacia arriba) en la cámara del fluorómetro manteniéndose en obscuridad 3 min. La fluorescencia se evaluó por inducción con tres intensidades: 450, 630 y 900 mmoles de fotones m^{-2} s^{-1}.

El contenido de clorofilas y feofitinas se cuantificó con el método descrito por Arnon (1949) y el contenido relativo de agua del tejido foliar según lo descrito por Beadle et al. (1988). La extracción de proteína foliar soluble, su separación por cromatografía en geles de poliacrilamida y su análisis densitométrico se realizó de acuerdo con lo descrito por Velasco (1994).

Resultados

Transporte fotosintético de electrones

En este trabajo, el transporte fotosintético de electrones se evaluó *in situ*, transporte que podría ser equivalente al tipo fosforilante, pues, en condiciones naturales, en los cloroplastos del tejido intacto el transporte de electrones y la fotofosforilación están acoplados. En ambos cultivares la sequía drástica indujo el enrollamiento de las hojas, pero sólo en el C_0 el transporte de electrones disminuyó drásticamente (51%) respecto al de las plantas bien hidratadas; mientras que en el C_8 la disminución no fue estadísticamente significativa (Cuadro 1). El riego de recuperación revirtió totalmente el efecto de la sequía en el transporte de electrones del C_0, pero en el C_8 incrementó la caída (Cuadro 1).

Cuadro 1. Transporte de electrones fotosintético (mmoles de oxígeno min^{-1} cm^{-2}) en plantas de maíz Tuxpeño Sequía sensible (C_0) y tolerante (C_8) a la sequía.

	Cultivar	
Tratamiento	C_0	C_8
Riego (testigo)	1.15b	1.00b
Sequía incipiente	1.19b	1.44a
Riego (testigo)	1.28b	1.41a
Sequía severa	0.64c	1.08b
Riego (testigo)	1.28b	1.41a
Riego postsequía	1.31b	0.97b

Letras diferentes dentro de columnas y entre cultivares indican diferencias estadísticamente significativas con una α=0.05

Clorofilas y feofitinas

Previamente, se ha demostrado que el estrés hídrico en maíz (Sánchez et al., 1983), frijol (Peña-Valdivia, 1994) y trigo (Gummuluru et al., 1989) podría modificar el peso seco, el peso fresco o el área foliar. Como resultado de esto las modificaciones del contenido de los pigmentos fotosintéticos podrían enmascararse. Para evitar esto, en el presente trabajo el contenido de pigmentos se calculó con base en esas tres variables (Cuadro 2).

Con excepción del contenido de feofitina *a* calculada con base en el peso fresco el contenido de pigmentos fue semejante entre los cultivares. Por otro lado, en el C_0 sólo el contenido de feofitina *a* por unidad de peso seco y la relación feofitina *a/b* disminuyeron con la edad de la planta (comparación entre los testigos, Cuadro 2) y ni el déficit hídrico ni el riego postsequía modificaron estadísticamente el contenido de esos pigmentos en el C_0. Sin embargo, aunque no resultó estadísticamente significativo, en este cultivar sometido a sequía los contenidos relativos de las clorofilas y las feofitinas por unidad de peso fresco representaron 13% más que en las plantas con riego adecuado (Cuadro 2).

En contraste, en el C_8 se observó un aumento significativo de las clorofilas y feofitinas por unidad de área con la edad de la hoja (comparación entre los testigos, Cuadro 2). Las clorofilas *a*, *b* y *total* incrementaron 20%, 34% y 24%, respectivamente, entre los 21 y los 36 d después de la emergencia. Además, el contenido de feofitinas incrementó en proporciones similares a las indicadas para las clorofilas.

Cuadro 2. Contenido de clorofilas y feofitinas *a*, *b* y *total* en la quinta hoja de maíz Tuxpeño Sequía sensible (C_0) y tolerante (C_8) a la sequía.

	a	b	total	a	b	total	a	b	total	Relación
Pigmentos	($\mu g\ cm^{-2}$)			($\mu g\ mg^{-1}$ pf)			($\mu g\ mg^{-1}$ ps)			a/b
Clorofila: C_0										
Riego (testigo)	40.3a	15.8a	56.2a	2.3ab	0.89a	3.1ab	13.0ab	5.0ab	18.0ab	2.55a
Sequía incipiente	41.1a	16.2a	57.3a	2.6a	1.00a	3.6a	13.0ab	5.0ab	18.0ab	2.55a
Riego (testigo)	39.5a	16.3a	55.8a	2.3ab	0.94a	3.2ab	10.0b	4.0b	14.0b	2.40ab
Riego postsequía	35.8a	15.4a	51.2a	2.0b	0.88a	2.9b	10.0b	4.0b	14.0b	2.32b
Feofitina: C_0										
Riego (testigo)	51.5a	36.3a	87.8a	2.9ab	2.0a	4.9ab	16.0ab	11.0a	28.0ab	1.45a
Sequía incipiente	52.5a	37.4a	89.9a	3.3a	2.3a	5.6a	16.0ab	11.0a	28.0ab	1.45a
Riego (testigo)	49.5a	38.8a	88.2a	2.8ab	1.9a	5.0ab	13.0c	9.0ab	23.0b	1.26b
Riego postsequía	45.1a	35.9a	81.0a	2.6bc	2.1a	4.6b	13.0c	9.0ab	23.0b	1.28b
Clorofila: C_8										
Riego (testigo)	35.7b	13.9c	49.6b	2.2ab	0.8a	3.0a	14.0a	5.0a	19.0a	2.52a
Sequía incipiente	40.3ab	15.8bc	56.1ab	2.3ab	0.9a	3.2a	11.0b	4.0b	15.0b	2.55a
Riego (testigo)	42.9a	18.5a	61.4a	2.3ab	1.0a	3.4a	10.0b	4.6ab	15.0b	2.30b
Riego postsequía	39.1ab	17.0ab	56.2ab	2.1ab	0.9a	3.0a	11.0ab	4.9ab	16.0ab	2.27b
Feofitina: C_8										
Riego (testigo)	45.7b	32.2c	77.9b	2.3d	2.2a	4.7a	18.0a	12.0a	30.0a	1.43a
Sequía incipiente	51.8ab	36.5bc	88.3ab	2.3cd	2.0a	5.0a	14.0bc	9.7b	24.0b	1.43a
Riego (testigo)	53.5a	42.3a	95.8a	1.9d	2.3a	5.2a	13.0bc	10.4ab	24.0b	1.25b
Riego postsequía	48.8ab	38.8ab	87.7ab	2.1d	2.1a	4.8a	14.0bc	11.9ab	25.0ab	1.28b

Letras diferentes dentro de columnas, para cada tipo de pigmento, indican diferencias estadísticamente significativas ($P < 0.05$); pf: peso fresco; ps: peso seco.

Como resultado de estos aumentos inducidos por el desarrollo de la hoja la relación clorofila *a* / *b* también se modificó en este cultivar. Lo anterior contrasta con la disminución de los mismos pigmentos cuando el cálculo se basó en el peso seco (Cuadro 2). Podría decirse que en el C_8 las modificaciones de la concentración relativa de los pigmentos está íntimamente relacionada con las modificaciones del área foliar, el peso seco y el peso fresco de la lámina durante su desarrollo.

En el Tuxpeño C_8 sometido a sequía también se observó 13% de aumento no significativo de todos los pigmentos cuando se expresaron por unidad de área. Además, aunque tampoco resultó estadísticamente significativo, después del riego postsequía todos los pigmentos fotosintéticos de ambos cultivares disminuyeron 8-9% respecto a sus propios testigos (Cuadro 2).

Emisión de la fluorescencia

La selección de las intensidades luminosas se realizó después de observar que con intensidades menores de 450 o mayores de 900 mmoles m^{-2} s^{-1} la fluorescencia resultó tan pequeña o tan grande que no era posible evaluarla con el equipo utilizado.

En ambos cultivares los valores de la fluorescencia inicial (Fo), máxima (Fm) y variable (Fv) se incrementaron proporcionalmente con la intensidad luminosa y resultaron semejantes entre los dos cultivares (Cuadro 3).

Cuadro 3. Fluorescencia inicial (Fo), máxima (Fm) y variable (Fv) de la clorofila, inducidas por iluminación, con intensidades luminosas (IL) de 450, 630 y 900 mmoles de fotones m^{-2} s^{-1}, de las hojas de maíz Tuxpeño Sequía sensible (C_0) y tolerante (C_8) a la sequía.

		C_0			C_8		
Tratamiento	IL	Fo	Fm	Fv	Fo	Fm	Fv
Riego (testigo)	450	4.97a	8.07a	3.10a	5.12a	8.47a	3.35ab
Sequía incipiente		4.95a	8.37a	3.42a	4.97a	8.02ab	3.05ab
Riego (testigo)		5.17a	8.32a	3.15a	4.65a	8.17a	3.52b
Sequía severa		4.75a	8.07a	2.55a	5.10a	7.22b	2.40a
Riego (testigo)		5.17a	8.10a	3.10a	4.62a	8.18ab	3.40ab
Riego postsequía		5.32a	8.00a	3.25a	4.82a	8.27ab	3.18ab
Riego (testigo)	630	7.42b	11.35b	3.92b	7.95b	11.85c	3.90c
Sequía incipiente		7.52b	11.70b	4.17b	7.32b	11.22bc	3.90c
Riego (testigo)		7.72b	11.75b	4.02b	7.47b	11.55c	4.07c
Sequía severa		7.40b	11.22b	3.77c	8.00b	10.10b	2.50a
Riego (testigo)		7.72b	11.70b	4.00b	7.47b	11.50bc	4.00c
Riego postsequía		7.45b	11.27b	3.87b	7.62b	11.70c	3.72bc
Riego (testigo)	900	10.58c	15.84c	5.26c	11.14c	16.60d	5.46d
Sequía incipiente		10.78c	16.72c	5.94c	10.64c	15.82d	5.18d
Riego (testigo)		11.00c	16.74c	5.74c	10.84c	16.54d	5.70d
Sequía severa		10.96c	15.58c	4.86c	11.30c	15.54d	4.56d
Riego (testigo)		11.00c	16.70c	5.50c	10.84c	16.54d	5.40d
Riego postsequía		10.72c	16.10c	5.14c	10.96c	16.98d	5.68d

La diferencia significativa honesta (DSH) entre tratamientos para el Tuxpeño C_0 y para el C_8 con cada una de las intensidades fue: 1.00 y 1.72; 1.42 y 1.76; y 1.72 y 1.13, para la Fo, respectivamente; 1.52 y 1.22; 2.14 y 1.61; y 2.71 y 2.46, para la Fm, respectivamente; y 1.00 y 1.05; 1.04 y 1.40; y 1.42 y 1.22, para la Fv, respectivamente. Letras diferentes dentro de columnas indican diferencias estadísticamente significativas con una $\alpha = 0.05$.

En el C_0 los tres tipos de fluorescencia fueron semejantes entre los tratamientos riego-sequía. En contraste, la sequía severa en el C_8 disminuyó 12% la Fm, respecto a su testigo, con 450 y con 630 mmoles m^{-2} s^{-1} y también la Fv inducida con las mismas intensidades luminosas disminuyó 28% y 36%, respectivamente (Cuadro 3).

Contenido relativo de agua, materia seca, peso fresco y seco

El contenido relativo de agua fue semejante entre los cultivares cuando se mantuvieron con riego adecuado; con la sequía incipiente, disminuyó 23.3% y 18.4% en el C_0 y en el C_8, respectivamente. Sin embargo, con la sequía severa y con el riego postsequía las diferencias respecto a los testigos perdieron significancia (Cuadro 4).

El porcentaje de materia seca en las hojas de ambos cultivares resultó semejante (Cuadro 5). Entre las

Cuadro 4. Contenido relativo de agua en plantas de maíz Tuxpeño Sequía sensible (C_0) y tolerante (C_8) a la sequía.

	Cultivar	
Tratamiento	C_0	C_8
Riego (testigo)	83.0a	88.5a
Sequía incipiente	63.7c	72.3b
Riego (testigo)	72.7bc	77.5ab
Sequía severa	77.5ab	70.5b
Riego (testigo)	72.7bc	77.5ab
Riego postsequía	78.0ab	80.0ab

La diferencia significativa honesta (DSH) entre tratamientos para el Tuxpeño C_0 y para el C_8 fue: 10.2 y 14.7, respectivamente. Letras diferentes dentro de columnas indican diferencias estadísticamente significativas con una $\alpha = 0.05$.

tendencias interesantes destaca el hecho de que tanto la raíz como el vástago del Tuxpeño C_0 resultaron más ligeros que los del C_8; además, la raíz del C_0 resultó notablemente más afectada por la sequía (un tercio más ligera que su testigo) que la del C_8, aunque, estas diferencias no resultaron estadísticamente significativas. En el peso húmedo del vástago se observaron tendencias semejantes a las descritas para la raíz y únicamente en el peso seco total del vástago del C_0 se detectó una caída significativa (33.6%) como resultado de la sequía (Cuadro 6).

Electroforésis de las proteínas foliares solubles

En ambos cultivares se detectó la presencia de un nuevo polipéptido de peso molecular mayor a los 56 kDa y la disminución o eliminación de algunos otros de peso molecular menor a 18 kDa (resultados no mostrados). Además, en las diferentes repeticiones se observó que la definición de las bandas en los geles y por lo tanto de las curvas de los densitogramas correspondientes fue mayor en las muestras correspondientes al Tuxpeño Sequía C_8; esto, podría estar relacionado con una mayor estabilidad de las proteínas de este cultivar.

Discusión y Conclusiones

Transporte fotosintético de electrones

En ambos cultivares con déficit hídrico la actividad del transporte de electrones fotosintético permaneció relativamente elevada (Cuadro 1). Lo anterior significa que bajo esas condiciones de estrés los fotosistemas (PSI y PSII) y los transportadores de electrones eran funcionales y que la concentración de CO_2 en los espacios intercelulares era elevada, aún cuando los estomas estuvieran cerrados. Esto último podría deberse a que el gas se difunde al interior de la hoja como consecuencia de su elevada concentración en la cámara del oxímetro (Hsiao, 1973). Como consecuencia, si la reducción del carbono está activa requerirá equivalentes reductores (NADPH) y equivalentes químicos (ATP) generados por la cadena transportadora de electrones y la ATP sintetasa.

La disminución lenta de la actividad del transporte de electrones en el C_8 como efecto del déficit hídrico y aún después del riego postsequía podría ser reflejo de su capacidad de aclimatación al estrés. Lo anterior contrasta con la respuesta del C_0, que parece no expresar esa aclimatación (Cuadro 1). Al respecto, se ha señalado que una disminución gradual de las actividades como respuesta al déficit hídrico representa una mayor oportunidad para que las plantas se aclimaten (Ludwig y Matthews, 1993).

Meyer y Yaroslav (1993) indicaron que como resultado de la sequía en *Lupinus* podría haber daño en el PSII, sin que se afecte la actividad de la ATP sintetasa. De acuerdo con esto, es conveniente evaluar más de una variable a la vez, pues, aunque hay una estrecha interacción entre las diversas actividades fotoquímicas y la reducción del CO_2, la alteración de alguna no siempre es correspondiente con la alteración de las otras. Lo anterior se ha demostrado en *P. vulgaris* donde la reducción del CO_2 es prácticamente inhibida por la sequía y por bajas temperaturas, pero la tasa de fotólisis del agua se mantiene en niveles relativamente altos, con lo que se deduce que el PSII se mantiene activo

Cuadro 5. Contenido de materia seca (%) en hojas de maíz Tuxpeño Sequía sensible (C_0) y tolerante (C_8) a la sequía.

Tratamiento	Cultivar C_0	Cultivar C_8
Riego (testigo)	16.0b	18.0ab
Sequía incipiente	21.6ab	21.9a
Riego (testigo)	21.0ab	21.9ab
Riego postsequía	18.9ab	20.3ab

La diferencia significativa honesta (DSH) entre tratamientos fue: 5.9. Valores seguidos por distinta letras son estadísticamente diferentes con una α = 0.05.

Cuadro 6. Peso fresco y contenido de materia seca (g) en plantas de maíz de 36 días de edad Tuxpeño Sequía sensible (C_0) y tolerante (C_8) a la sequía.

		Raíz		Vástago	
Tratamiento	Cultivar	Peso húmedo	Peso seco	Peso húmedo	Peso seco
Riego (testigo)	C_0	36.94a	3.54d	19.75b	2.71e
Riego postsequía		23.75a	2.69de	13.50b	1.80f
Riego (testigo)	C_8	38.25a	4.22d	24.75bc	3.43d
Riego postsequía		26.50a	3.43d	21.00c	2.86de

La diferencia significativa honesta (DSH) entre tratamientos para peso húmedo y peso seco de raíz y vástago, del C_0 y del C_8 fue: 10.7 y 12.6; 1.4 y 1.23; 6.7 y 6.6 y 0.76 y 0.66, respectivamente. Letras diferentes dentro de columnas indican diferencias estadísticamente significativas con una α = 0.05.

(Peña-Valdivia, 1994; Peña-Valdivia et al., 1994). Esto último coincide con los resultados del presente trabajo.

Clorofilas y feofitinas

Los resultados de las concentraciones de los pigmentos en los dos cultivares de maíz Tuxpeño Sequía indican que durante el desarrollo en condiciones adecuadas de riego, iluminación y temperatura existen pequeñas diferencias en la síntesis, acumulación o degradación de las clorofilas y las feofitinas (Cuadro 2). Esas diferencias fueron documentadas para los mismos cultivares por Peña-Valdivia et al. (1996), pues observaron que durante el desarrollo inicial, cuando la segunda hoja tiene sólo 10 cm de longitud el C_8 acumula cantidades ligeramente mayores, pero significativas, de clorofila *a* por unidad de tejido fresco a lo largo de la lámina, respecto al C_0.

Por otro lado, la respuesta casi homogénea a la sequía y al riego postsequía, de ambos cultivares, sobre el contenido de los pigmentos fotosintéticos (Cuadro 2), podrían ser reflejo de las tenues diferencias entre los cultivares cuando se desarrollan con regímenes adecuados de riego. También, podría considerarse la posibilidad de que el estrés inducido no haya alcanzado el nivel en el que se expresa su efecto sobre los pigmentos fotosintéticos, pues, se ha observado que la caída lenta del contenido de la clorofila en plantas de maíz sometidas a estrés hídrico se hace más evidente cuando el déficit hídrico se agudiza (Demmig et al., 1988; Ludwig y Matthews, 1993). Otra posibilidad es que la metodología utilizada no tenga la sensibilidad requerida para detectar las pequeñas alteraciones inducidas en la síntesis, acumulación o degradación de esos pigmentos como resultado de los tratamientos.

Además de la evaluación directa del contenido de clorofilas se ha sugerido la cuantificación de las feofitinas, que son producto de degradación de las clorofilas (por pérdida del magnesio de su molécula), como indicador de la alteración del aparato fotosintético. Sin embargo, como en el caso de las clorofilas, en el presente trabajo la metodología utilizada aparentemente fue poco sensible para evidenciar las diferencias entre los dos cultivares de Tuxpeño Sequía o el estrés no fue suficientemente drástico para que se expresaran contrastes sobresalientes (Cuadro 2).

Emisión de la fluorescencia

Demmig et al. (1988) mencionan que cuando las plantas pierden agua Fm y Fv caen. Esto coincide con lo observado en el C_8, y podría representar el ajuste de la maquinaria fotosintética de este cultivar, mediante el incremento de los centro de reacción inactivos del PSII o por la migración lateral del LHCII, que conduciría más energía hacia PSI, todo como respuesta al estrés (Krause y Weis, 1991).

Los cambios del contenido de clorofila también podrían utilizarse para explicar las modificaciones de la fluorescencia en el C_8, de acuerdo con lo observado en un mutante de *Nicotiana*, aunque, con la acumulación de clorofila, por enverdecimiento, no hay aumento de la fluorescencia (White y Hoober, 1994).

En el presente trabajo, se observó que no hubo inhibición del transporte de electrones como resultado de la sequía, por lo que la caída de la emisión de Fv en el C_8 podría ser efecto del apagamiento q_N (apagamiento no fotoquímico de la fluorescencia), pues, según Krause y Weis (1991) la energización del tilacoide puede apagar hasta el 90% de la fluorescencia variable. Además, el maíz alcanza valores elevados de q_N, que evitan la reducción química completa de los transportadores de electrones y la fotoinhibición, aunque, el flujo de electrones esté inhibido hasta en 40% por el déficit hídrico (Scheuermann et al., 1991). Por otro lado, es difícil indicar si la energización del tilacoide fue resultado del flujo de electrones pseudocíclico o cíclico, o de la asimilación neta de carbono, pero se ha observado la caída de Fm por la activación del transporte de electrones (Krause y Weis, 1991). Es probable que el apagamiento de Fm, sea reflejo de los ajuste bioquímicos y biofísicos en el C_8 para mantener la integridad del aparato fotosintético durante el estrés.

Las diferencias en el apagamiento de la fluorescencia entre los dos cultivares de maíz Tuxpeño Sequía (Cuadro 3) reflejar las diferencias biofísicas en el funcionamiento de su cadena transportadora de electrones, ya que, la inhibición del lado foto-oxidante del PSII, como resultados de la acumulación de $P680^+$ (centro de reacción oxidado del fotosistema II) o Z^+ (donador primario oxidado del PSII, Krause y Weis, 1991) podría ser otro motivo de la caída de la emisión de la fluorescencia en el C_8, pero no en el C_0. Lo anterior indica que probablemente los mecanismos de control que operan para que haya un ajuste entre las diferentes funciones y reacciones en los tilacoides, a nivel de los fotosistemas o complejos antena, deben ser mecanismos específicos y precisos que eviten el daño y mantengan un adecuado balance de la energía en los cloroplastos del C_8.

La elevada reducción química de la cadena transportadora de electrones, que conduce a la disminución de la energización de la membrana tilacoidal podría explicar por que la Fv y la Fm disminuyeron en menor grado con alta intensidad luminosa (900 mmoles cm^{-2} s^{-1}) en comparación con las intensidades menores (450 y 630 mmoles cm^{-2} s^{-1}) el C_8.

Contenido relativo de agua, materia seca, peso fresco y peso seco

Las fluctuaciones en el contenido relativo de agua son sin duda de gran importancia, pues podrían tener efecto prácticamente sobre todos los procesos fisiológicos y bioquímicos de la planta. Aunque, al parecer si hay una relación positiva entre la respuesta a la sequía por el C_8, y su mayor contenido relativo de agua, Bolaños et al. (1993) no encontraron diferencias en el potencial hídrico en plantas adultas de los mismos cultivares utilizados en el presente estudio.

Un efecto evidente de la sequía sobre las plantas es la caída de la acumulación de la materia seca, reduciéndose concomitantemente su altura y su desarrollo general; además, el peso fresco también se modifica, aunque no siempre en proporciones equivalentes.

El uso del peso seco como característica para seleccionar cultivares tolerantes a algún tipo de estrés ha sido documentado (Peña-Valdivia et al., 1994). Aquí, se demostró la superioridad del C_8 para acumular más peso, tanto húmedo como seco, en la planta completa, respecto al C_0 (Cuadro 6). Esto fue documentado previamente por Bolaños y Edmeades (1993a). Además, en otro experimentos realizados por nuestro grupo, se demostró que el C_8 se recupera después de una serie de dos y hasta tres tratamientos consecutivos de sequía (drástica) que lo conducen hasta marchitez permanente después de cada tratamiento en invernadero y continúa acumulando mayor peso que el C_0 (datos no publicados).

Patrón electroforético de las proteínas foliares

Es obvio el interés por avanzar en el conocimiento del efecto del estrés sobre las proteínas, debido a sus funciones fundamentales en todas las células vivas; sin embargo, actualmente se desconoce el papel real que juegan algunas proteínas en la resistencia al estrés. Los resultados obtenidos con el maíz Tuxpeño Sequía (no mostrados) concuerdan parcialmente con los obtenidos por Ranieri et al. (1989), quienes evaluaron los patrones electroforéticos unidimensionales de hojas de maíz sometidas a estrés hídrico, y observaron que las proteínas de alto peso molecular aparentemente disminuyen por efecto del estrés y las de bajo peso molecular parece que aumentan.

El diferente grado de tolerancia entre los cultivares de maíz Tuxpeño Sequía C_0 y C_8 ha sido ampliamente documentado en trabajos previos. En conclusión, los resultados de la presente investigación indican que las diferencias bioquímicas, biofísicas y fisiológicas son exiguas y que algún(os) mecanismo(s) de respuesta a la sequía podrían localizarse a nivel de los tilacoides, en los procesos fotoquímicos y de transducción de energía. Además, las pequeñas diferencias metabólicas, podrían ser acumulativas a lo largo del desarrollo y conducir a mayores diferencias en el crecimiento de los dos cultivares, al final del desarrollo, tanto con riego adecuado como con sequía. Finalmente, existe la posibilidad de que las variables seleccionadas en el presente estudio no sean las que verdaderamente reflejen los efectos diferenciales de la sequía entre los dos cultivares.

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Effects of Transplanting Shock on Maize Root Growth

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Abstract

A field experiment was conducted in 1993 involving three maize genotypes - a drought-sensitive hybrid, a drought-tolerant hybrid and an open-pollinated variety (OPV). Results show that the response of the maize plant to transplanting shock depended on its genetic background. Compared with direct-seeding, root initiation in the two transplanted hybrids was stimulated by the shock. For the hybrid tolerant to drought, the root initiation stimulus started earlier than for the drought-sensitive hybrid, but in the OPV root initiation seemed to be generally depressed. Prior to the 5-leaf stage the root dry weights of the three genotypes following transplanting were all lower than expected. The stimulus for increased rooting took place from the 6-leaf stage through to the silking stage. In the hybrid sensitive to drought this stimulus came much later than for the other two genotypes.

Maize transplanting is a popular agronomic practice in southwestern China. It is used to reduce drought and / or cold stress damage during seedling establishment. The physiological mechanisms associated with transplanting shock and their effect on maize growth and development are not well understood. This study examines the effect of transplanting shock on maize root development.

Three maize varieties and two treatments were evaluated using a split-plot restriction in a randomised complete block design. Whole plots were direct-seeding and transplanting treatments, while subplots were three maize varieties: hybrids Chinsan and Kundan-1 and the open-pollinated variety (OPV), Suwan 8363. The varieties were sown 15 April, 1993, and transplanted 3 May, 1993 (3 leaf stage) at a density of 67,500 plants / ha.

Results

Effect of transplanting on root number

Transplanting shock appeared to stimulate root initiation at an earlier growth stage in Chinsan, since the root number of transplanted Chinsan was 90% higher than the direct-seeded equivalent at the five leaf stage (Fig. 1). Chinsan is a single-cross hybrid tolerant to drought. For Kundan-1, a single-cross sensitive to drought, an increased rate of root initiation did not take place until the 10 leaf stage. Root initiation appeared to be unaffected by transplanting in the tropical OPV Suwan 8363.

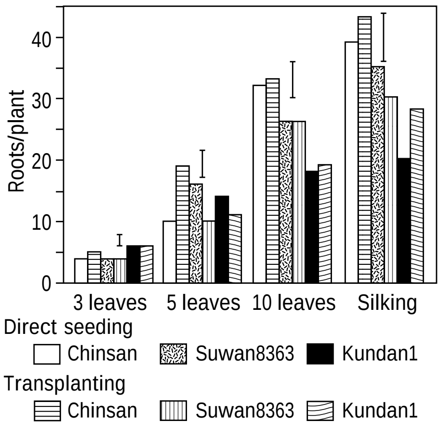

Figure 1. Effect of transplanting shock on root number at different growth stages.

Effect of transplanting on root biomass

At the five-leaf stage, root biomass was less for the transplanting treatment than for direct seeding in all three genotypes (Fig. 2). This reduced growth was likely due to

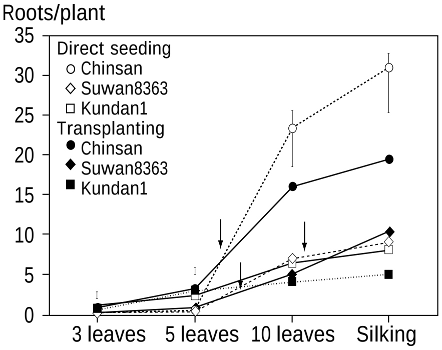

Figure 2. Effect of transplanting shock on root dry matter at different growth stages.

transplanting shock. By silking the opposite was the case. Biomass accumulation for the transplanted treatment consistently surpassed that for direct seeding. It appears that transplanting shock stimulates later growth in some compensatory manner. Biomass accumulation for transplanted Chinsan and Suwan 8363 overtook that for the direct seeded treatment shortly after the five-leaf stage (note the arrows pointing to the crossover points on Fig. 2). For Kundan-1, this crossover occurred after the ten-leaf stage, suggesting that the genotypes differ in the timing of their response to transplanting shock. Chinsan displayed the greatest response to transplanting. Biomass at silking was 12.5 g / plant (63%) higher for the transplanted treatment than for direct seeding. Kundan 1 showed the smallest response, giving an increase of only 3.5 g / plant in biomass at silking.

Conclusions

Initially, transplanting shock reduces root growth, but by silking transplanted maize has a higher root biomass than direct seeded maize. Maize genotypes differed in the magnitude and timing of this response. Further study in this area is needed to help understand the physiological mechanisms associated with transplanting shock and to improve the transplanting practices used by farmers.

Increased Water Use Efficiency and Grain Yield by Transplanting Maize

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Abstract

Transplanting techniques have been used successfully in our institute since 1981 to increase maize grain yields. Seeds of variety H-30 were sown using three procedures: 1) seeds sown in sterile soil with seedlings transplanted to the field 15 to 20 days after emergence; 2) seeds sown directly into a wet field; and 3) seeds sown in a dry field where germination started after rainfall. Using the transplanting technique, the time required to reach flowering stage was 67 d. When seeds were sown directly in wet soil the time required was 89 d, and 109 d when the seeds were sown in dry soil. Transplanted plants took 134 d to reach maturity, while those sown in wet soil required 151 d, and those sown in dry soil required 180 d. Statistical analyses showed significant differences in grain and cob yield for the treatments. In all cases, transplanted plants produced more grain and cob. Transplanting increased the water use efficiency by 66% or more over the other two treatments.

Many inputs important for Mexican agriculture, such as seed, fertilizer, herbicide and water, are becoming either more expensive or less available (Larqué-Saavedra, 1981; Hibon et al., 1992). In Mexico 7 million ha of maize is sown annually, 95% under rainfed conditions and the remaining portion with irrigation. In rainfed soils lack of water is frequent because precipitation is either insufficient or erratic. Even irrigated soils may suffer from a lack of water, because reservoir water may be insufficient to meet demand (SARH, 1994a). Mexican agriculture therefore needs alternative techniques to achieve more efficient and rational use of limiting inputs.

The problem of drought in Mexico has been studied for many years, but recently suggested strategies for dealing with it have included selection of plant varieties with high drought tolerance and improved irrigation management systems (SARH, 1994b). In prehispanic Mexico, the technique of transplanting was used to produce maize (De la Rosa, 1846; López, 1973; De Gortari, 1980; Peña, 1981), a crop which was as important then as a staple food as it is in modern Mexico. Traditionally used to good effect with vegetables, flowers, rice, etc., transplanting has more recently been tried with maize in various parts of the world; e.g., Vietnam (Houg and Quoc, 1988) and China (Jingxiong, 1990). Since 1981, a group of Mexican researchers has been gathering information regarding yield response and quantifying water use efficiency (accumulated biomass per quantity of rain water) to help facilitate farmer adoption of this technique and improve the efficiency of use of Mexico's water resources. Results from these studies are reported here.

Materials and Methods

The maize variety H-30, a hybrid recommended for highland regions of Central Mexico, was used throughout the present study to minimize the sources of variation. Seed from H-30 was sown using three different procedures:

1. Seed sown in sterile soil with seedlings transplanted to the field 15 to 20 d after emergence.
2. Seed sown directly in a wet field (DSW).
3. Seed sown in a dry field (DSD), where germination began after rainfall.

Treatments were applied to plots 5 m long and 4 m wide, with each treatment replicated four times. Dry-seeded (DSD) plots were sown in the second week of April, the usual maize sowing time at these sites. Five seeds were planted at 25 cm intervals in rows 80 cm apart. The transplant nursery was established on May 15 (a date by which the rainy season has normally started and after which rainfall is relatively secure, although occasionally it may occur in small amounts) using a wooden frame measuring 1.0 x 0.5 x 0.25 m with a plastic sheet at the bottom (Larqué-Saavedra, 1981). The wooden frame was filled with fertilized soil (three parts black soil and one part manure), which was then sterilized by adding Foximal powder (2.5%) at a rate of 50 kg m^{-3} of substrate dissolved in 2.5 l water. The soil was then leveled and watered to field capacity. Furrows were created and 600 seeds were sown in each seedbed. Irrigation was applied until the seedlings were slightly hydrated. The seedbed was covered with mesh to protect against rodents, birds and weather stress such as hailstorms or low temperatures. When the third leaf appeared, usually 15-20 d after sowing, seedlings were transplanted into the field. Prior to transplanting the field was prepared using fallow, harrowing, leveling and ploughing. Furrows ran north-south and were 80 cm apart. To avoid damaging seedling roots and stems, the protective mesh and plastic sheet were carefully removed to loosen the seedlings but not too much of the soil surrounding the roots. The seedlings were then transferred to furrows with a spade and immediately covered with soil from both sides of the furrow. The field was fertilized using 80-60-00, applying half of the nitrogenous fertilizer with the phosphorus and the remainder 50 days later. One or two weedings were performed after transplanting and pests were controlled. The DSW plots were established the same day by sowing into a field that had been recently irrigated to field capacity. The same plant density was used for the latter two treatments.

Data were recorded on time from sowing / transplanting to flowering and to grain maturity, maximum plant height, and dry weight of grain, cob, and other non-ear aboveground plant parts. Dry matter per ha was computed by adding all above-ground components of dry weight (stover, grain and cob) and dividing by harvested plot area. Water use efficiency (WUE) was calculated as follows:

Rainfall data were taken each year for Chapingo (1981-1992) and Montecillo (1993-1995), with particular attention to the April-October period when plants were in the field.

Results

Time to flowering and grain maturity

The transplanted treatments reached flowering in 67 d, compared with 88 d for the DSW and 109 d for the DSD (Table 1). Similarly, transplanted maize required only 134 d to produce mature grain, compared with 151 d for DSW and 180 d for DSD.

Biomass yield

The grain and cob yield of transplanted plants was substantially more than that of plants from DSW and DSD (Table 2). The differences were not as large for other aboveground plant material, and there were significant differences only between transplanted plants (6.85 t / ha) and those from the DSD treatment (3.95 t / ha).

Plant height

This was determined once anthesis commenced. Data were not taken in all years, and differences among the treatments were not significant (Table 3).

Table 1. Time (days from sowing or transplanting) required by maize cultivar H-30 to begin flowering and to reach the mature grain stage.

	Flowering			Mature grain		
Year	T	DSW	DSD	T	DSW	DSD
1983	42	76	—	111	122	—
1984	69	87	120	142	146	193
1985	72	72	134	142	142	173
1986	85	98	116	141	156	203
1987	70	99	124	133	152	188
1988	68	76	120	142	153	191
1989	71	89	134	131	138	197
1990	72	87	91	128	148	158
1991	44	57	57	120	159	135
1992	50	141	81	140	169	173
1994	72	77	123	140	161	187
1995	90	104	97	139	167	185
Average	67±4 a	89±6 b	109±8 b	134±3 a	151±4 b	180±6 c

T = transplanting; DSW = direct sowing in wet soil; DSD = direct sowing in dry soil.
Treatment means followed by different letters are statistically different by Tukey's means separation test ($P \leq 0.05$).

Water use efficiency

The transplanted plants used available water most efficiently (Table 4). Transplanted plants yielded 5.31 kg / ha / mm of rain, followed by DSW and DSD with yields of 3.32 and 2.51 kg / ha / mm, respectively. Means for DSW and DSD were not statistically different.

Rainfall

Rainfall was the most important environmental variable, and varied across both locations and years (Fig. 1). Data from El Batán were included to show how much rainfall can vary over a short distance, as this CIMMYT research station is only a few kilometers from the experimental site at Chapingo. It is also noted that the largest monthly totals of rainfall can occur in any month from May to September, and that months with relatively low rainfall can occur at any point during the rainy season. The popular literature mentions periods of decreased rainfall in August and September, resulting in a so-called ‘canicula’ or ‘intraestival’ drought. No abrupt halts were observed, but rather periods of diminished rainfall. Another variable limiting the maize growing season is frost. The first frost normally occurs during early October in the study area, but frost did not affect the results of this study.

Discussion

Maize plants transplanted into the field at the beginning of the rainy season utilize rainfall for continued growth and development. Maize plants from seed sown in dry soil before the onset of rains or in wet soil shortly thereafter use the first rains for germination. This is likely to be a less efficient use of rainwater, since a greater proportion will be lost to atmospheric evaporation from the soil surface. The results of this research can be considered only in the context of weather conditions at Chapingo and Montecillo. Despite its proximity to Chapingo (8 km away), the weather at El Batán is quite different. For example, 920 mm of

Table 2. Biomass (t/ha) for maize cultivar H-30 obtained under rainfed conditions, Chapingo and Montecillo, Mexico.

	Grain			Cob			Other aboveground plant material		
Year	T	DSW	DSD	T	DSW	DSD	T	DSW	DSD
1981	5.52	4.15	—	—	—	—	9.10	7.81	—
1983	0.85	0.54	*	0.33	0.38	*	8.58	11.64	*
1984	3.33	2.54	2.11	5.54	0.59	0.60	5.54	9.30	7.11
1985	3.97	2.19	3.80	0.80	0.64	0.76	11.68	7.99	10.26
1986	1.68	1.55	0.37	0.32	0.30	0.08	5.19	3.68	2.07
1987	4.04	1.58	0.634	0.77	0.49	0.16	13.69	12.34	2.66
1988	1.23	0.53	0.20	0.29	0.17	0.12	6.44	2.57	2.91
1989	1.77	0.34	1.88	0.38	0.15	0.37	2.37	1.96	3.99
1990	2.27	1.94	1.94	0.42	0.33	0.31	3.34	1.93	2.08
1991	1.92	0.55	0.55	0.33	0.23	0.16	6.65	6.94	5.74
1992	1.75	1.04	1.04	0.31	0.10	0.27	5.80	0.92	2.12
1994	2.68	1.78	2.27	0.53	0.51	0.53	6.51	9.32	5.13
1995	1.30	0.87	0.58	0.36	0.47	0.27	4.24	6.06	3.40
Average	2.49 a	1.51 b	1.28 b	0.86 a	0.36 b	0.30 b	6.86 a	6.34 a	3.96 b
	(0.39)	(0.31)	(0.34)	(0.45)	(0.05)	(0.07)	(0.93)	(1.11)	(0.83)

T = transplanting, DSW = direct sowing in wet, DSD = direct sowing in dry.
* = loss by depredation.
( ) Standard error of the mean.
Treatment means followed by different letters are statistically different by Tukey’s mans separation test (P≤0.05).

Table 3. Plant height (m) attained by maize plants of cultivar H-30 under three planting treatments.

Year	Trans-planting	Direct sowing in wet soil	Direct sowing in dry soil
1983	1.69	1.96	—
1984	2.13	2.15	—
1986	2.08	1.98	2.06
1988	1.97	1.64	1.47
1991	1.63	1.73	1.59
1992	1.63	1.73	1.59
1994	2.34	2.58	2.23
1995	1.98	1.95	1.67
Average	1.93 ± 0.10 a	1.96 ± 0.11 a	1.76 ± 0.13 a

Treatments means followed by different letters are statistically different by Tukey’s means separation test (P≤0.05).

Table 4. Water use efficiency (kg ha^{-1} dry weight mm^{-1} rain) for maize cultivar H-30 under three planting treatments, Montecillo, Mexico.

Year	Trans-planting	Direct sowing in wet soil	Direct sowing in dry soil
1981	10.11	7.60	—
1983	2.18	1.30	—
1984	6.68	5.10	3.47
1985	7.69	4.23	6.07
1986	5.00	4.61	0.83
1987	9.03	3.53	1.25
1988	2.82	1.31	0.44
1989	4.11	1.10	4.48
1990	3.63	3.16	2.48
1991	4.31	1.23	0.91
1992	3.76	2.23	1.68
1994	6.12	4.06	4.41
1995	3.58	2.39	1.60
Average	5.31 ± 0.71 a	3.16 ± 0.55 b	2.51 ± 0.58 b

Treatments means followed by different letters are statistically different by Tukey’s means separation test (P≤0.05).

rain were reported for El Batán from April to October 1994, while only 515 mm of rain were measured at Montecillo.

Plants in the field are subject to depredation, diseases, high and low temperatures, drought, etc., during their life cycle. The flowering and grain filling stages are essential for large yields and good grain quality. There must be enough water available at flowering for fertilization. In part, the success of transplanting may be explained by the increased probability of transplanted maize completing flowering before the onset of drought. Diminished rainfall can occur in this zone during August and September, but transplanted plants began flowering during the last days of July, thus escaping periods of decreased precipitation. Moreover, these plants produced mature seed by the end of September, well in advance of the expected first frost, and before the onset of cool temperatures that would impair grain filling.

The beginning of the rainy season can vary between years, so in some years the rains would not coincide with a planned transplanting date. Consequently, two additional experiments were grown in 1994 and 1995. These experiments considered the effect of transplanting seedlings that were allowed to develop beyond 15 d (the normal age for transplanting), to simulate a circumstance in which transplanting was delayed to coincide with the beginning of rains. Seedlings of five different ages were transplanted into the field (data not presented). The results demonstrated that plants transplanted 25 d after emergence yielded about the same as those transplanted at 15 d of age.

Additional benefits of transplanting were also discovered during the course of these experiments. Transplanted plots required only one weeding — the maize plants developed in advance of the weeds so they easily suppressed weed growth, suggesting that transplanting would reduce the need for herbicides or hand labor to control weeds.

Undoubtedly, there will be years with good weather when equally good yields may result from direct sown maize. However, data from these experiments suggest that transplanting should have an advantage over direct sowing in most years.

In economic terms, little information is currently available on the feasibility of transplanting maize on a medium or large scale. Studies by Houg and Quac (1988) in southern Vietnam indicate that 80 men per day were required to transplant one hectare of maize. In contrast, our own studies have demonstrated the effectiveness of using a vegetable transplanting machine, which required few personnel, on a maize plot of one hectare.

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Triazole Priming of Maize Seed to Enhance Drought Tolerance During Field Establishment

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Abstract

Lowland tropical maize environments are often characterized by unreliable rainfall distribution at planting time. Triazoles are plant growth regulators which moderate the effects of drought and high temperatures. We evaluated the triazole 'Paclobutrazol' as a seed primer on two maize cultivars in 1994 and on five maize cultivars in 1995 in field trials conducted at Tlaltizapán, Morelos and at Cocula, Guerrero, and in greenhouse studies at the University of Guelph. In 1994, seeds of hybrids 'P 3288' and 'NK TB 8101' were primed with Paclobutrazol 50 alone and in combination with Ancymidol 25 and grown under severe and moderate drought stress in the dry winter season. Compared with the non-primed check at Tlaltizapán, the triazole treatments delayed seedling emergence by 2.4-3.2 days, reduced plant height by 4%, delayed anthesis by 1.4-2.0 days and reduced grain yield by 11-17% across both drought treatments. At Cocula results were similar, though yield differences were non-significant due to a high coefficient of variation. In 1995, five cultivars ('CML8 x CML9', 'CML19 x CML27', 'La Posta Sequía C_3', 'SIWA' and 'SIBA') (the last three from CIMMYT's drought breeding program), were seed treated with Paclobutrazol 80 imbibed, Paclobutrazol 20 seed coated, and in combination. The two field trials at Tlaltizapán involved a seedling survival trial with a gradation in levels of irrigation during the establishment phase and a mid-season drought stress trial. The seed coated treatment showed no significant response in either trial; the imbibing treatment reduced surviving seedling counts by 15-21% under severe water stress, slowed the rate of emergence, and resulted in non-significant reductions in biomass and grain yield. In greenhouse experiments at Guelph on the same genotypes and seed treatments, the Paclobutrazol imbibing treatment delayed emergence and reduced seedling height and fresh weight by 30% and 25% respectively, and gave inconclusive results under heat and drought stress. No differences were noted between the seed coated treatment and the check. We conclude that Paclobutrazol cannot be recommended at this stage as an imbibed seed treatment for tropical field maize.

Lowland tropical maize production is often restricted from reaching its full potential because of unreliable rainfall distribution at planting time, resulting in low stand establishment. One approach to field stress management, cited by Fletcher and Kraus (1995), is to shift the endogenous balance of plant hormones through the use of triazole plant growth regulators (PGR's), which lead to morphological and biochemical changes in the plants. Triazoles may function as plant 'multi-protectants', moderating the effect of environmental stresses such as drought and high temperature. The present study sought to determine if triazoles offer protection against seedling and flowering drought stress and therefore improve maize productivity under water deficits. We examined plants at several growth stages under harsh drought conditions in the field and for seedlings grown under controlled conditions.

Materials and Methods

1994 field trials

1994 field trials were conducted at Tlaltizapán, Morelos (940 masl) and Cocula, Guerrero (600 masl), Mexico, in the dry winter season. In both trials controlled irrigation was used to establish drought stress. The cultivar and triazole seed priming treatments were similar at both sites, but the drought stress methodology and plot layout differed. The cultivars used at both locations were 1) Pioneer 3288 hybrid from Westlaco, Texas, and 2) Northrup-King TB 8101 hybrid from Guadalajara, Mexico. TS6C$_2$, a drought tolerant open-pollinated variety, was also used at Tlaltizapán and the open-pollinated synthetic VS535 at Cocula. The following seed priming treatments were used:

1. Paclobutrazol 50 mg / l, seed imbibed for 18 h at 24°C or 2 h at 40°C.
2. Paclobutrazol 50 mg / l plus Ancymidol 25 mg / l, and seed imbibed as above.
3. Check, no imbibition.

At Tlaltizapán the treatments were 1) well-watered, where irrigation was applied every 10-14 d, and 2) severe stress, with three irrigations subsequent to establishment, whereas at Cocula the treaments were 1) normal, with seven irrigations subsequent to establishment and moderate stress, meaning six irrigations subsequent to establishment. At Tlaltizapán a RCBD (split-plot) with three replications was used, where cultivars comprised the main plot and seed priming treatments the sub plot. Each water regime constituted a separate trial. At Cocula a RCBD (split-split-plot) with three replications was also used, but irrigation regimes formed the main plot, cultivars the sub-plot, and seed priming treatments the sub-sub plot. At both sites the sub- or sub-sub-plot size was four rows 5 m long, with an established plant density of one plant every 0.25 m in rows 0.75 m apart. Data collected at Tlaltizapán included time to emergence, plant height at maturity, anthesis and silking dates, grain yield and aboveground biomass (from a 3 m^2 bordered plot area). Observations of percent green leaf area were made every second day, starting 35 d after flowering and estimates of the date of 75% foliar senescence were made by regressing these estimates on time for each plot. At Cocula emergence, anthesis date and grain yield from bordered plots were recorded.

1995 field trials

Trials in 1995 were conducted only at Tlaltizapán, Mexico, during the dry season. Controlled irrigation was used for modulating water stress in a seedling survival trial and a mid-season drought stress trial. The following five culivars were used: 1) La Posta Sequía C$_3$; 2) DTP1 SIWA C$_1$; 3) DTP1 SIBA C$_1$; 4) CML8 x CML9; and 5) CML19 x CML27. La Posta Sequía C$_3$ has a history of selection for tolerance to mid-flowering drought stress but no previous selection against seedling stress. DTP1 SIWA C$_1$ and DTP1 SIBA C$_1$ were derived from the Drought Tolerant Population-1 (assembled from diverse drought-tolerant sources) which had been divergently selected for ability to survive under seedling drought. SIBA was the best surviving fraction, and SIWA the worst surviving fraction. La Posta Sequía C$_3$, DTP1 SIWA C$_1$ and DTP1 SIBA C$_1$ were all open-pollinated varieties. CML8 x CML9 and CML19 x CML27 were single-cross hybrids with no history of selection under managed drought stress. All cultivars were adapted to the lowland tropics. The following seed priming treatments were applied:

1. IMB: Paclobutrazol 80 mg / l; seed imbibed for 18 h at 24°C or 2 h at 40°C
2. CT: Paclobutrazol 20 mg / l, slow release seed coated
3. IMB / CT: Combination of treatments 1 and 2
4. Check: untreated

Two separate trials were conducted:

1. Seedling survival. A line of sprinklers was placed at right angles to the 12 m long seeded rows, with a sprinkler at the head of each row. Two days after planting, approximately 45 mm of irrigation water was applied from the line source irrigation system. Irrigation took place in the early morning and under still air conditions. Catch cans showed that 45 mm of water was applied to the 6 m of row nearest the line source, dropping linearly with distance to 15 mm at 12 m from the line source. No further irrigation was applied, but 39 d after sowing (DAS) an unexpected fall of 39 mm of rain was received at the site.
2. Mid-season drought stress. Water was applied manually to the sown seeds at planting to ensure even establishment, and by gravity irrigation on 15 DAS (80 mm) and 29 DAS (50 mm). At 41 DAS 39 mm of rainfall fell. No further irrigation was applied. Premature death of all plots occurred around 115 DAS.

In the seedling survival trial, treated seeds were sown at a rate of one seed every 10 cm in 12 m rows. Rows were 30 cm apart, and the design was a 5 x 4 factorial with three replications. In the mid-season drought stress trial, main plots were cultivars and subplots were seed treatments. Plot size was two 2.5 m rows, spaced 0.75 m apart with 0.25 m between plants within the row. The design was an RCBD (split-plot) with three replications.

Data collected in the seedling survival trial included aboveground dry weight per plant of seedlings from the regions 3-6 m (alternate plants harvested) and 7-8 m from the line source 35 DAS when stress was quite severe; from regions 7-8 m from the line 53 DAS; and 5-6 m from the line 77 DAS, as all plants in the experiment were dying. Counts of living seedlings were made on nine occasions (17, 28, 35, 54, 74, 80, 87, 94 and 100 DAS) in the regions 3-6, 6-7, 7-8, 8-9 and 9-12 m from the line source. Counts over dates were combined and analyzed in a single analysis. In the mid-season drought stress trial measurements included counts of emerged seedlings versus time, scores of leaf rolling and leaf senescence, times from sowing to 50% anthesis and silking, and the proportion of plants which produced silks. When the crop was dead a bordered area of 3 m^2 from each plot was harvested for total biomass. Plants were cut at ground level, ears were removed, counted and dried, and the remainder of the plant chopped and dried to a constant weight at 80ºC. Dried ears were shelled, and the grain and biomass weighed. All weights are expressed on an oven-dry basis (80°C).

Greenhouse studies

These were conducted at the University of Guelph in 1994-95 using the same five genetic populations and four seed treatments that were field tested in 1995 at Tlaltizapán, Mexico. The seeds were sown in standard greenhouse flats (53 x 28 x 6 cm) with a peat-based synthetic medium (Promix , Premier Brands Inc., Yonkers, N.Y., 10740). The greenhouse was maintained at 22°C day / 16°C night and the flats were watered regularly. Emergence counts from 4 to 9 DAS were recorded daily, and seedling height and fresh weights were recorded at the terminal harvest at 56 DAS. Water deficit was imposed by withholding watering prior to harvest, and seedlings were visually rated for wilting. The experiments were replicated four times and run twice, in December, 1994 and January, 1995.

Results and Discussion

1994 field trials

There were very few significant effects from seed treatment in the Tlaltizapán field trials. The triazole treatments delayed seedling emergence by 2.4 to 3.2 d, reduced plant height to flag leaf insertion by 4%, delayed anthesis by 1.4 to 2.0 d, and reduced grain yield by 11 to 17% ($P < 0.10$) across both drought treatments. Triazole treatments caused the seedlings to be short and stocky, with unusually broad first and second leaves. Ears per plant and harvest index were depressed slightly under moderate stress. Treatment interactions were seldom significant (Table 1). At Cocula, the triazole treatments significantly reduced stand count at 60 DAS by 11 to 22.5% and delayed anthesis by 0.8 to 2.4 d when compared to the non-primed check, but yield differences were non-significant (Table 2).

1995 field trials

In the seedling survival trial at Tlaltizapán, live seedling counts were slightly reduced by the seed treatment IMB / CT in locations close to the irrigation line (Table 3). This reduction became highly significant at locations greater than 7 m from the line where water stress was severe in the first 38 DAS, presumably during the time when the seed treatment was most effective. In the driest zone, seedling survival of untreated seed was 44% greater than that of the IMB / CT treatment. It is possible that Paclobutrazol, acting as an anti-gibberellin, reduced rooting depth as well as top growth, and that this was the reason for reduced survival of IMB / CT treated seedlings under very dry conditions. There were also consistent and significant cultivar differences caused by a lower survival rate of the two hybrids near the line source, probably associated with their smaller seed weights at sowing. In the drier zones (7-12 m from the line), SIBA had a significantly higher seedling survival than SIWA (22% larger in the driest zone), suggesting that selection had improved the capacity of this

Table 1. Effect of maize cultivar and triazole (Paclobutrazol, Pac; Ancymidol, Anc.) seed treatment on various measures of crop morphology and performance under well-watered and severe levels of drought, Tlaltizapán, Mexico, 1994.

Treatment	Days to emergence (d)	Plant height (cm)	Days to anthesis (d)	Anthesis silking interval (d)	Grain yield (t ha^{-1})	Ears per plant	Biomass (t ha^{-1})	Harvest index	Days to 75% sen.
Drought									
Severe	9.4	153	77.6	18.8	0.41	0.32	6.95	0.08	117
Well-watered	9.1	205	79.1	4.3	2.43	0.80	11.11	0.24	129
P (drt)	**	***	NS	***	***	***	*	**	+
Hybrids									
P3288	9.2	171	76.9	8.4	1.62	0.66	9.00	0.19	118
NK8101	9.3	186	79.8	14.7	1.22	0.46	9.06	0.14	128
P (hybr)	*NS*	**	***	+	*NS*	*	*NS*	+	**
Seed Treatment									
Untreated	7.4	181	77.2	13.1	1.56	0.59	9.39	0.16	121
Paclobutrazol	9.8	182	78.6	10.9	1.30	0.53	8.77	0.16	124
Pac + Anc	10.6	174	79.2	10.7	1.39	0.56	8.92	0.16	124
P (strt)	***	*NS*	**	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Interactions (probabilities of significance)									
Drt x hybr.	*NS*	+	*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Drt x strt	*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
Hybr x Strt	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
D x H x ST	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*

+, *, **, *** and *NS* indicate differences that are significant at P <0.10, P<0.05, P<0.01, P <0.001 and P>0.10, respectively.

Table 2. Effect of maize cultivar and triazole seed treatment on mean squares of measures of crop morphology and performance under well-watered and moderate levels of drought stress, Cocula, Mexico, 1994.

Treatments	Emergence (%)	Anthesis (d)	Harvest stand count (% seeded)	Yield (g/m^2)
Drought	4.6 *NS*	6.4 *NS*	5.5 *NS*	502**
Hybrids	29**	22**	27**	8.6**
Seed treatment	24**	9.9**	26**	0.8 *NS*
CV (%)	2.1	2.2	10	32

+, *, **, *** and *NS* indicate differences that are significant at P <0.10, P<0.05, P<0.01, P<0.001 and P>0.10, respectively.

Table 3. Seedling survival trial: effects of cultivars and seed treatment on counts of live plants in zones differing in moisture availability because of differing distances from a line source irrigation system. Data are means of counts taken on 4-9 occasions from 17-100 DAS, Tlaltizapán, Mexico 1995.

Zone # Counts	3-6 m 1-9	5-6 m 1-4	6-7 m 1-4	7-8 m 1-9	9-12 m 1-9
Cultivars					
1. La Posta Sequia C_3	13.76	5.41	6.60	5.89	6.64
2. DTP1 SIWA C_1	13.30	5.06	6.50	5.81	5.56
3. DTP1 SIBA C_1	13.27	5.29	6.63	6.62	6.77
4. CML8 x CML9	12.45	4.63	5.71	5.73	5.84
5. CML19 x CML27	13.76	4.63	6.63	6.23	6.18
Seed Treatments					
1. IMB/CT[§]	12.83	5.03	6.28	5.42	4.90
2. IMB	13.39	4.73	6.20	5.68	5.99
3. CT	13.46	5.05	6.67	6.63	6.85
Untreated	13.56	5.20	6.50	6.52	7.04
Mean	13.31	5.00	6.41	6.06	6.20
P (cultivars)	***	*	*	***	***
P (treatments)	**	*NS*	*NS*	***	***
P (cult x trt)	*	*NS*	*NS*	***	***

[§] IMB and CT refer to Paclobutrazol 80 imbibed and Paclobutrazol 20 seed coated.

*, **, *** and *NS* indicate differences that are significant at P<0.05, P<0.01, P<0.001 and P>0.10, respectively.

population to survive this type of stress. SIBA was also less susceptible to the reduction in survival from IMB/CT, giving rise to a significant cultivar x treatment interaction that became greater as stress intensified. There were few effects of cultivar and treatment on seedling above-ground dry weight. In general IMB/CT and IMB alone reduced weight per seedling, but usually this reduction was not significant. The CT treatment had little or no effect on seedling dry weight or on seedling survival.

In the mid-season drought stress trial at Tlaltizapán, the application of Paclobutrazol, especially as the IMB form, slowed the rate of emergence significantly (Table 4), though final plant counts by 15 DAS showed no effect of treatment. Flowering dates, anthesis-silking interval (ASI), the proportion of plants with silks three weeks after anthesis, and scores of leaf rolling and senescence were all unaffected by seed treatment, indicating that its effect had worn off by about 50 DAS. There were important differences among cultivars in time to flowering. SIWA and SIBA were earlier flowering than other cultivars and therefore experienced less stress at flowering. This showed in their lower level of barrenness, the larger proportion of plants with silks, and their shorter ASI. Hybrid CML8 x CML9 was very susceptible to drought, as shown by its very large ASI and high leaf rolling score. Leaves of Population SIWA also rolled more than those of SIBA, and the two hybrids had slower leaf senescence under drought than La Posta Sequia C_3 (similar flowering date) or SIBA and SIWA (earlier flowering dates). Seed treatment had no effect on grain yield, ears per plant, total biomass or harvest index (Table 4). Cultivars differed significantly in productivity and partitioning, mainly because differences in flowering date led to escape from drought at silking. Hybrid CML8 x CML9 again showed a high degree of drought susceptibility.

Greenhouse experiments

Under favorable environmental conditions, the Paclobutrazol imbibition treatment delayed seedling emergence when rated at 6 DAS, but was equal to the check at 8 DAS. Seedling height and fresh weight were also reduced by 30% and 25%, respectively, under this treatment. No differences were noted between the seed coated treatment and the check (Table 5). In heat and drought stress tests in controlled environments, the responses to the Paclobutrazol imbibition treatment were inconclusive (data not shown).

Conclusion

Based on results obtained from four field experiments conducted in Mexico under harsh conditions of

Table 4. Mid-season drought stress trial: effects of cultivars and seed treatment on crop morphology and performance, Tlaltizapán, Mexico, 1995.

	Emerged seedlings 8 DAS (No.)	Sowing to anthesis (d)	Anthesis -silking interval (d)	Leaf rolling score[a]	Percent dead leaf area[b]	Grain yield ($t\ ha^{-1}$)	Total Ears per plant	Harvest biomass ($t\ ha^{-1}$)	index (%)
Cultivars									
1. La Posta Sequia C_3	28.8	84	3.25	1.36	51.9	0.24	0.39	5.11	4.5
2. DTP1 SIWA C_1	25.3	77	2.17	2.56	55.8	0.66	0.63	5.05	13.0
3. DTP1 SIBA C_1	26.0	75	2.58	1.86	57.3	0.73	0.65	5.41	13.2
4. CML8 x CML9	24.2	86	24.00	3.42	44.0	0.00	0.01	4.53	0.0
5. CML19 x CML27	29.8	84	8.83	1.56	46.5	0.15	0.25	4.97	2.9
Seed Treatments									
1. IMB/CT[§]	14.0	81	8.27	2.09	50.8	0.34	0.37	4.87	6.7
2. IMB	17.5	81	8.27	2.18	49.3	0.37	0.36	4.85	7.1
3. CT	38.0	81	8.20	2.13	53.0	0.35	0.39	5.20	6.3
Untreated	37.8	81	7.33	2.20	51.2	0.37	0.43	5.12	6.9
Mean	26.8	81	8.17	2.15	51.1	0.36	0.39	5.01	6.7
P (cultivars)	**	**	***	***	**	***	***	**	***
P (treatments)	***	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*
P (cult x trt)	**	*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*	*NS*

[a] Score is from 1 (no rolling) to 5 (completely rolled).

[b] Estimated percentage of total leaf area that is dead.

[§] IMB and CT refer to Paclobutrazol 80 imbibed and Paclobutrazol 20 seed coated.

*, **, *** and *NS* indicate differences that are significant at $P<0.05$, $P<0.01$, $P<0.001$ and $P>0.10$, respectively.

soil and atmospheric drought, Paclobutrazol as an imbibed seed treatment in tropical field maize is not recommended as a method to improve seedling survival.

Acknowledgments

Zeneca Agro, Canada, assisted with supplies of Paclobutrazol and in expediting the seed coating treatments. Northrup-King of London, Ontario arranged for the supply of maize seeds TB8101 through Guadalajara, Mexico. Pioneer Hi-Bred, Westlaco, Texas supplied the Pioneer 3288 maize seed. R.A. Fletcher was ever willing to discuss the triazole issue with us. We thank field staff from CIMMYT and CSAEG for their assistance in managing the field trials and in recording data.

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Table 5. Greenhouse experiments: seedling emergence and growth data of cultivars treated with Paclobutrazol seed treatments. Guelph 1995. Means in the vertical columns are separated using Duncan's New Multiple Range Tests, $P < 0.05$; DAS signifies days after sowing.

	DTP1 SIWA C_1		DTP1 SIBA C_1		CML8 x CML9		CML19 x CML27		La Posta Sequia C_3F_2	
Emergence (%)	6 DAS	8 DAS	6 DAS	8 DAS	6 DAS	8 DAS	6 DAS	8 DAS	6 DAS	8 DAS
Expt. I										
Untreated	96^{a}	100^{a}	96^{a}	100^{a}	58^{a}	100^{a}	29^{a}	96^{a}	71^{a}	100^{a}
CT	96^{a}	96^{a}	100^{a}	100^{a}	38^{ab}	100^{a}	29^{a}	100^{a}	63^{a}	100^{a}
IMB	63^{a}	88^{ab}	67^{b}	96^{a}	21^{b}	92^{ab}	21^{ab}	100^{a}	38^{a}	100^{a}
IMB/CT	38^{c}	71^{b}	58^{b}	100^{a}	21^{b}	79^{b}	4^{b}	96^{a}	50^{a}	96^{a}
Expt. II										
Untreated	29^{ab}	100^{a}	88^{a}	100^{a}	54^{a}	100^{a}	17^{ab}	100^{a}	79^{a}	100^{a}
CT	50^{a}	100^{a}	92^{a}	100^{a}	42^{a}	100^{a}	25^{a}	100^{a}	58^{an}	100^{a}
IMB	4^{bc}	71^{b}	8^{b}	100^{a}	0^{b}	92^{a}	13^{ab}	96^{a}	42^{n}	96^{a}
IMB/CT	0^{c}	67^{b}	13^{b}	96^{b}	8^{b}	92^{a}	0^{b}	92^{a}	38^{b}	96^{a}
Seedling height (cms)										
	Expt. I	Expt. II	Expt. I	Expt. II	Expt. I	Expt. II	Expt. I	Expt. II	Expt. I	Expt. II
Untreated	39.3^{a}	26.3^{a}	43.0^{a}	31.3^{a}	41.0^{a}	35.6^{b}	34.8^{a}	29.3^{a}	36.3^{a}	31.5^{ab}
CT	38.5^{a}	26.7^{a}	41.0^{a}	32.3^{a}	34.7^{a}	31.0^{ab}	34.2^{a}	26.5^{a}	32.0^{a}	34.7^{a}
IMB	26.2^{b}	21.4^{b}	34.0^{b}	23.3^{b}	36.8^{b}	28.5^{b}	32.7^{a}	25.0^{a}	29.3^{a}	26.7^{bc}
IMB/CT	27.8^{b}	23.3^{ab}	26.8^{c}	24.8^{b}	33.5^{c}	28.2^{b}	33.3^{a}	28.2^{a}	30.5^{a}	25.4^{c}
Shoot fresh weight (g)										
	Expt. I	Expt. II	Expt. I	Expt. II	Expt. I	Expt. II	Expt. I	Expt. II	Expt. I	Expt. II
Untreated	3.88^{a}	2.04^{a}	4.03^{a}	2.63^{a}	4.42^{a}	3.68^{a}	3.18^{a}	2.78^{a}	4.12^{a}	2.82^{a}
CT	3.87^{ab}	2.10^{a}	3.68^{ab}	2.60^{a}	3.85^{ab}	2.40^{b}	2.83^{a}	2.51^{ab}	3.33^{a}	3.38^{a}
IMB	2.58^{c}	1.80^{a}	3.02^{bc}	2.10^{a}	3.95^{ab}	2.79^{ab}	3.00^{a}	1.79^{b}	3.38^{a}	3.21^{a}
IMB/CT	2.68^{bc}	2.31^{a}	2.43^{c}	2.35^{a}	3.53^{a}	3.35^{ab}	2.73^{a}	2.38^{ab}	3.93^{a}	2.63^{a}

Genotypic Variation for Transpiration Efficiency in a Lowland Tropical Maize Population

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Abstract

Genotypic variation in transpiration efficiency (TE, biomass production per unit of transpiration) and the relationship between TE and transpiration were examined in 15 S_1 *lines of a lowland tropical maize population. Six plants per line were grown on stored soil water in 2 m-high, 30 cm diameter pots sealed at the top to prevent evaporation and entry of rain. Transpiration was calculated using time domain reflectometry (TDR) measurements taken from six depths at planting and at final harvest. Final harvest of biomass was made shortly after flowering when plants showed severe symptoms of drought stress. TE averaged 7.6 g* kg^{-1}*. Genotypic differences were highly significant. Values ranged from 5.8 to 11.0 g* kg^{-1}*. TE increased with decreasing transpiration (r = -0.72**). In some field trials, lines with high TE showed more severe leaf rolling (r = 0.57*) and less osmotic adjustment (r = 0.46,* $P < 0.10$*). They also tended to produce more biomass and grain and have delayed senescence under drought (*$P < 0.15$*). The results indicate considerable genotypic variation for TE in maize, but confirm as well that the adaptive value of a higher TE under drought may be offset by the negative relationship between TE and transpiration.*

Introduction

Most studies examining genotypic variation in transpiration efficiency (TE, biomass production per unit water consumption) have been conducted with C_3 species and genotypic variation in TE has usually been found. Results on the adaptive value of a higher TE under drought, however, are contradictory. Transpiration efficiency was often found to be negatively correlated with grain yield under drought (Ehdaie et al., 1991; Acevedo, 1993). The interdependence of water uptake and TE may explain part of this relationship. Genotypes of C_3 species which have a lower transpiration (or water uptake) are more likely to have a higher TE, because stomatal closure increases resistance to water vapor transfer relatively more than resistance to CO_2 transfer (Cowan and Troughton, 1971). Thus, the value of a higher TE under drought might be offset by a lower water uptake.

In species such as maize which employ C_4 photosynthesis, there may be a closer correlation between drought tolerance and TE. Theoretical and experimental evidence suggest that the TE of field-grown C_4 species decreases when stomatal resistance increases, because CO_2 transfer in C_4 species is relatively more affected by stomatal closure than by water vapor transfer (Cowan and Troughton, 1971; Sinclair et al., 1975; Garrity et al., 1982). Thus C_4 genotypes with a higher water uptake should exhibit a higher TE and very likely a higher grain yield. This hypothesis was examined in the present study. Genotypic variation in TE in a lowland tropical maize population was examined, and TE was related to water uptake and field performance.

Materials and Methods

Fifteen S_1 lines from the lowland tropical maize population ‘DTP1’ were used. This population was formed from a diverse array of source materials which have demonstrated some degree of drought tolerance (Bänziger et al., 1995).

Measurement of transpiration efficiency (TE)

Six plants per S_1 line were grown on stored soil water in 2 m-high, 30 cm-diameter pots sealed at the top with plastic foil to prevent evaporation and entry of rain. The trial design was a randomized complete block design in four replications. Each pot contained six pairs of time domain reflectometry (TDR) probes, inserted horizontally at depths of 15, 35, 65, 95, 125, and 155 cm. Volumetric soil water content was determined weekly using the Trase System 6050XI TDR (Soil Moisture Equipment Corporation, Santa Barbara, CA), and water content of the pots (PWC) was calculated. Plants were harvested about two weeks after flowering when they showed severe symptoms of drought stress and aboveground biomass (DM) was determined. Transpiration efficiency was calculated as

$$TE = DM/(PWC_{planting} - PWC_{harvest})$$

Field experiments

The 15 S_1 lines were also grown in replicated field trials during the dry winter season at CIMMYT's experiment station in Tlaltizapán, México. In each case the lines were replicated twice in an alpha(0,1) lattice design. One trial was grown under managed seedling drought stress, two trials were grown under managed mid-season drought stress, and two trials were grown under non-stressed conditions. Survival, plant biomass, and leaf rolling were measured in the trial under seedling drought stress. Anthesis date, grain yield, biomass, leaf rolling, and osmotic adjustment (Wescor Vapor Pressure Osmometer Model 5100B, Wescor, Logan, UT) were measured from bordered plants grown in single row plots in the other trials.

Results and Discussion

Genotypic variation in TE

Genotypic differences in TE were significant at $P < 0.01$ (Fig. 1). Values of TE ranged from 6.8 to 12.7 g kg^{-1}, which indicates considerable variation in tropical maize for this trait.

TE and water uptake

In the pot experiment, transpiration efficiency increased with decreasing water uptake of genotypes (Fig. 2). These results were confirmed by field experiments (Table 1). In two of the three experiments, the S_1 lines with higher TE showed more severe leaf rolling and smaller osmotic adjustment, indicating that they were experiencing more severe drought stress.

TE and field performance

Lines with higher TE were taller, produced more biomass, and yielded more than lines with low TE in some field experiments (Table 1). However, some of the correlations between field and pot performance were significant at only $P < 0.10$, and were not consistent over experiments. Seedling survival under drought stress was not correlated with TE.

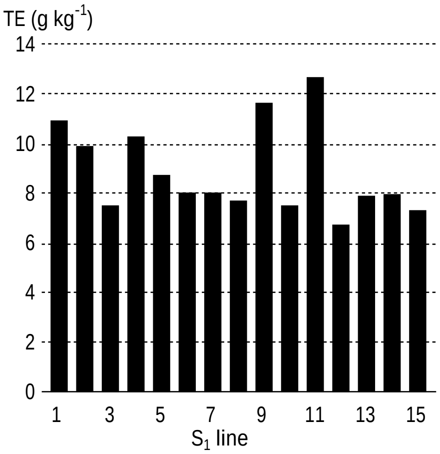

Figure 1. Transpiration efficiency of 15 S_1 lines from a lowland tropical maize population grown in 2 m high, 30 cm diameter pots at Tlaltizapán, México, 1993.

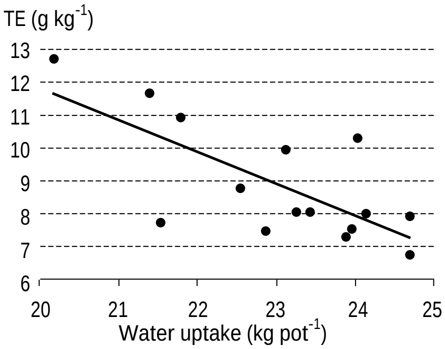

Figure 2. Relationship between transpiration efficiency and water uptake of 15 S_1 lines from a lowland tropical maize population when grown in 2 m-high, 30 cm-diameter pots at Tlaltizapán, México, 1993.

Table 1. Correlations between the transpiration efficiencies of 15 S_1 maize lines grown in 2 m-high, 30 cm-diameter pots and various traits measured on the same lines in field experiments at Tlaltizapán, México, 1992 to 1994.

	Seedling drought	Mid-season drought		Non-stressed	
	Expt. 1	Expt. 1	Expt. 2	Expt. 1	Expt.2
Anthesis date	NA	-0.16	-0.21	-0.16	-0.20
Survival	0.12	NA	NA	NA	NA
Leaf rolling	0.59*	0.55*	0.04	NA	NA
Osmotic adjustment	NA	NA	-0.46+	NA	NA
Plant height	NA	NA	0.44+	0.48+	0.52*
Grain yield	NA	0.27	0.43	0.18	0.45+
Biomass production	0.27	NA	0.42	NA	0.44+

+, *, ** indicates significance at $P < 0.10$, $P < 0.05$ and $P < 0.01$, respectively.
NA indicates that data were not taken.

Conclusion

The results indicate considerable genotypic variation for TE in maize. In spite of theoretical considerations, a negative correlation between total water transpired and TE was found, consistent with findings for C_3 plants. This indicated that the adaptive value of a higher TE under drought was partly offset by a lower water uptake. However, this unexpected correlation does not necessarily mean that the lower water uptake of certain genotypes was responsible for increasing TE with these genotypes, since high TE was generally associated with superior yields in water deficient field conditions.

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Studies on the Root and Shoot Water Relations of an Unusual Mexican Maize and a Typical Corn Belt Hybrid

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Abstract

In the semiarid region of northern Mexico, a significant amount of maize is grown in an unusual system referred to as "maíz de humedad"*, under which seeds are germinated in March with stored soil moisture, and plants usually survive more than 100 d without additional water until the rainy season begins in late June. In a series of experiments we sought to characterize the system and to compare the root-shoot growth and plant water relations of maize genotypes grown under this system and of a Corn Belt hybrid. The most important results from this study can be summarized as follows:*

1. *The* maíz de humedad *system is capable of producing three times more grain yield than the conventional system because the deep rooting system of humidity maize absorbs just enough water to maintain a small amount of transpiring leaf area during long dry periods prior to flowering.*
2. *Expanded leaves had higher turgor potentials than expanding leaves, due to a combination of lower leaf water potential and higher osmotic potential.*
3. *Root osmotic potential decreased in root tips growing under the water stress, the net result being that full root turgor potential was maintained even at root water potential differences between irrigated and water stressed plants of 1.0 MPa.*
4. *We expected the most important genotypic differences in this study to relate to the putative ability of* maíz de humedad *maize to grow and survive longer than a typical Corn Belt hybrid under water stress. Although some statistical differences between genotypes were observed in leaf turgor potential (y_p) at high levels of water stress, such differences in y_p were never larger than 0.3 MPa. In addition, more osmotic content per cm^2 of leaf was measured in* maíz de humedad *maize than in the hybrid. No conclusive adaptive advantages can be attributed to the small differences measured.*

In the semiarid region of northern Mexico a significant amount of maize is grown in an unusual system referred to as *maíz de humedad*. Under this system, seeds are germinated in March with stored soil moisture, and plants usually survive more than 100 d without additional water until the rainy season begins in late June. By trial and error farmers over many generations have selected genotypes and cultural practices that have resulted in higher yields relative to conventional maize production systems. The characteristics of the *maíz de humedad* system in northern Mexico have, however, been poorly documented.

Characteristics of *maíz de humedad* maize

The crop is planted in early March at 25,000 plants ha^{-1}, up to 20 cm deep in soil which has usually received no rainfall since the previous December or January (Fig. 1). Approximately 15,000 plants ha^{-1} remain alive when the rains commence in late June.

However at final harvest, grain yields under the *maíz de humedad* system are two or three times higher than under the conventional system, in which maize is planted in early July at 8 to 10 cm depth and densities of 35,000 plants ha^{-1} (Osuna, 1981). The risk of plant death due to the long period of water stress is high (ca. 50%) under the *maíz de humedad* system, though total or partial replanting with conventional maize is still possible once the rainy season begins. The success of the system depends on several factors, including soil structure (deep, volcanically-derived vertisols, seemingly easily penetrated by roots, and high in water holding capacity), which may permit plant survival on stored soil water until the rains begin some 3 months after planting. In addition, *maíz de humedad* genotypes, subjected to many generations of selection under extreme drought, are late in maturity (ca. 230 d from planting to maturity at this elevation of around 2000 masl), which enables them to escape drought stress during the critical flowering period (ca. 140 d after planting). At harvest, prolificacy and larger ears are apparent in this maize, in comparison with a high proportion of barrenness and smaller ears in the conventional genotypes.

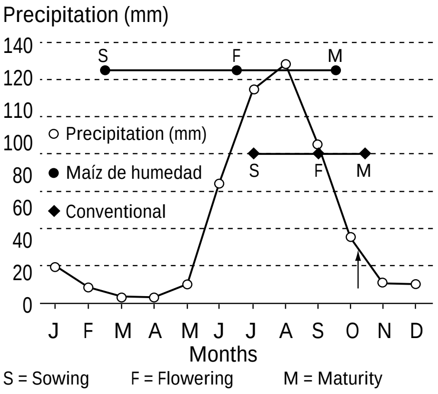

Figure 1. Typical pattern of precipitation in semi-arid northern Mexico, contrasted with the development pattern of *maíz de humedad* and conventional maize genotypes.

Plant water relations

Consistent and biologically useful results have been reported when the simplified equation, $\Psi = \Psi_s + \Psi_p$ (where Ψ is leaf water potential, Ψ_s is solute potential, and Ψ_p is turgor potential) is used in studies on plant water relations. The accumulation of solutes in the cells of the leaves of plants is now widely accepted as an adaptive mechanism in response to water deficits (Hsiao et al., 1976; Turner and Jones, 1980). Osmotic adjustment is generally in the range of -0.5 to -1.5 Mpa. Full turgor maintenance can be achieved via osmotic adjustment (Turner and Jones, 1980), and stomatal opening occurs at lower water potential in osmotically adjusted versus well watered plants grown under water stress (Jones, 1980; Turner and Jones, 1980). In contrast, Wenkert (1981) working in maize, and Wilson and Ludlow (1983) working with different crops, concluded that changes in solute content probably play a very limited role as an adaptive response to dry conditions. Studies in maize by Boyer (1974) showed that full turgor maintenance under water stress occurs only in the basal 2 cm of the leaf, yet leaf growth was significantly depressed at low water potentials despite high turgor potentials in the expansion zone. They concluded that other unknown factors caused this slow rate of growth under dry conditions. Thus, controversy exists regarding the value of osmotic adjustment in enhancing plant performance under drought.

Root adaptation to drought

The growth of roots in drying soils is important if the rate of water uptake is to be maintained. Although most reports on shoot-root growth under dry conditions suggest that the ratio is maintained, increased root growth in maize under stress has also been reported (Hsiao et al., 1976; Sharp and Davies, 1979). Passioura (1983) has proposed that coordination of the timing of exploration of different soil layers by roots may be more crucial than root penetration *per se* in maximizing yield under semiarid conditions. Considerable controversy exists about the ability of plant roots to grow in dry soils when other parts of the root system are in wet soil. Portas and Taylor (1976) measured substantial root elongation in soil layers at water potentials as low as -4.0 MPa. Theoretical considerations of root efficiency (water absorbed / root density / unit of time) in drying soils (Jordan and Miller, 1980) predict that in order to maintain a high water status plants must increase their root length density more than their shoot growth, and osmotic adjustment may well allow the maintenance of root growth.

Root osmotic adjustment

Sharp and Davies (1979) measured root water relations in maize. Measurements of root turgor potential were made at different distances from the root tip. These authors suggested that osmotic adjustment allows growing root tips to maintain high values of turgor potential during a drying cycle, thus allowing increased exploration of the soil by roots.

Several questions related to water relations in *maíz de humedad* maize remain unanswered:

1. Does osmotic adjustment play an important role in the turgor maintenance of growing maize leaves?
2. Do large differences exist among different plant parts in terms of turgor maintenance? If so, these may help explain the importance of turgor potential in growing tissues in comparison with tissues which already are fully expanded.
3. How different are genotypes grown under the *maíz de humedad* system from a typical Corn Belt hybrid with respect to plant water relationships? This maize has been selected over many generations for adaptive mechanisms to cope with drought stress, while Corn Belt hybrids suffer water stress only occasionally.

It was hypothesized in our case that *maíz de humedad* maize maintains its turgor at a higher level and for longer periods than other genotypes because of osmotic adjustment in shoots and roots. This osmotic effect may be identified directly by estimating the turgor potential of expanding tissues versus expanded tissues in both roots and shoots, or indirectly, using the close relationship between turgor and growth (Hsiao et al., 1976). During 1983 and 1984, a series of experiments on root-shoot growth and plant water relations involving maize from the *maíz de humedad* system and a Corn Belt hybrid were carried out under controlled environmental conditions at the University of Guelph.

Materials and Methods

The research was conducted under growth room conditions at the University of Guelph. The experimental units consisted of maize plants grown in 24 mini-rhizotrons (wooden boxes) each 1.20 m deep by 0.60 m wide, by 0.09 m in thickness, with a clear plexiglass front for observing roots. The plexiglass could be removed to obtain root and soil samples. Two plants per box were grown in a medium of loam plus sand in a 4 to 1 ratio. Attempts were made to maintain a uniform dry soil bulk density (1.20 kg dm^{-3}) when filling the boxes. Fertilizer was applied at rates of 6 g each of N, P_2O_5, and K_2O per box as 0-20-20, supplemented with NH_4NO_3. Three quarters of the fertilizer was mixed uniformly with the soil before filling the boxes, and the remainder was concentrated at 0.13 m below the top of the soil profile.

The experimental design was a completely randomized factorial with four replications. Treatments were two irrigation regimes by two genotypes, the genotypes being *maíz de humedad* maize (an open-pollinated variety, seed obtained from Adalberto Garcia, Pino Suarez, Durango, Mexico) and XL72AA (pedigree B73xMo17) provided by DeKalb Canada Ltd., Chatham, Ont. The latter is a representative hybrid from the Corn Belt. The irrigation regimes were irrigated or water-stressed.

The boxes were set up in a random arrangement, suspended at an angle of 22° from the vertical below a growth bench so that most roots grew along the plexiglass face and light did not illuminate the roots directly. The conditions of the room were: photosynthetically active radiation (PAR) at planting time was 380 mmol m^{-2} s^{-1} at the soil surface, 1.20 m below the lamps (fluorescent lights, Sylvania, Gro-lux WS). When plant height averaged 1.80 m, photosynthetic active radiation was 1200, 560, 330 and 220 mmol m^{-2} s^{-1} at 0.5, 1.0, 1.5 and 2.0 m beneath the lamps, respectively. The day / night temperature was 26 / 20 ± 2°C; day / night, relative humidity was 60 / 90 ± 5%, and day / night photoperiod was 16 / 8 h. At the start of the experiment the soil in the boxes was near field capacity (ca. 20% SWC). The irrigated plants received 4 dm^3 tap water every 4 d. In the water stressed treatments two drying cycles were imposed, but in this paper only the results from the first are presented. This began at planting and continued until about 6 d after, when measurements indicated that shoot and root growth had ceased in the stressed treatments; i.e., at 75 d after planting (DAP). At 76 DAP recovery from stress was evaluated by comparing the changes in ψ, ψ_s, ψ_p, beginning 14 h after water was applied to saturation in the lower third of the mini-rhizotron (bottom-wet treatment), and repeated again at 62 h after rewatering. Thus three water regimes were compared: water stressed, recovering after the bottom-wet treatment was imposed, and irrigated plants.

Leaf water relations

Water potentials of different plant parts change in a cyclic manner each day. Extreme values normally occur at dawn, when plants normally reach their highest values of water potential, and early in the afternoon when lowest values are observed. To determine whether this general pattern occurred here, diurnal water potential changes were followed. Differences between dawn and noon values under different levels of water stress were measured to estimate the osmotic adjustment and turgor maintenance in leaves of plants subjected to water stress. The water potential of leaves (LWP) was measured using a pressure bomb (Scholander et al., 1965) following the methodology described by Dow (1981).

Bulk osmotic potentials were measured for the same leaf strips as those used to measure leaf water potential. Immediately after reading LWP, each leaf strip was hermetically enclosed in a small plastic bag and placed in a refrigerator at 5 to 7^{o}C. Within 48 h a pestle was used to squeeze sap from the leaf sample and 8 ml of this was placed in an osmometer (Model 5100 Vapor Pressure Osmometer, Wescor, Logan, Utah) operating in the hygrometer mode, and the osmotic potential of the leaf sap solution determined. The osmometer had been previously calibrated using standard solutions of NaCl of known osmotic potential. Although the reliability of leaf sap osmotic potential estimates may have been reduced because of dilution by apoplastic water, it was not considered practical to quantify or correct for this dilution factor, which is thought to be about 15% in non-stressed plants (Wenkert, 1981). Conversions of osmometer readings to leaf osmotic potential were made using the equation: ψ_s=RTC$_n$; where: C$_n$= osmotic concentration; R = gas constant; and T = ambient temperature in °K. Turgor potentials were calculated as the difference between osmotic potential and leaf water potential: $\psi_p = \psi - \psi_s$.

Root water potential (RWP)

The equilibration method described by Slavik (1974) was used for estimations of RWP. With this procedure a series of solutions of known osmotic potential were prepared using PEG 6000 polyethylene glycol. The solutions were prepared using the following equation (Michel, 1983) which predicts the osmotic potential (ψ_s) of a given PEG concentration at a given temperature: y_s= 1.29[PEG]^{2}T - 140[PEG]^2 - 4.0[PEG]; where: PEG = the molar concentration of PEG and T = ambient temperature in °C.

Root osmotic potential (ROP)

Water stressed boxes were re-irrigated from the bottom by standing them in a plastic bag of water 15 cm deep. Three layers of soil were established: dry-top; middle-wet; and bottom-saturated. Roots segment samples were collected from each of the three layers generated by the irrigation regimes after removing the plexiglass from the boxes. To verify the existence of root osmotic potential gradients, two segments of the roots (ca. 1 cm) were measured separately: 0 to1 cm and 3 to 4 cm. After a preliminary cleaning of the root with paper toweling, a small brush was used to separate remnant soil particles. These roots were immediately sealed hermetically in a small plastic bag and stored in a refrigerator at 5 to 7 ^{o}C. For each osmometer reading six root segments were squeezed to obtain root sap in a procedure similar to that described for leaves. The difference between ROP and RWP was used to estimate root turgor potential (RTP).

Percent of soil water content (SWC) was estimated by gravimetric means (at 110°C for 72 hr) from soil cores taken from top, middle and bottom soil layers. Data were analyzed using the analysis of variance (ANOVA) procedure (SAS Institute Inc. Cary, North Carolina).

Results

Three water regimes were compared following a drying cycle imposed from 1 to 75 d after planting (DAP): water stressed, recovering, and irrigated plants. In Figures. 2, 3 and 4, changes in ψ, ψ_s and ψ_p, respectively, are presented for each water regime. At 75 DAP, just before sub-irrigation, y values of water stressed plants were recorded in the range -1.4 to -2.0 MPa. Under irrigation y values were in the range -0.3 to -0.7 MPa (similar to readings made under field conditions of the *maíz de humedad* maize in a previous experiment). At 74 DAP, one day before sub-irrigation, four readings were made at 5:00 (dawn), 7:00, 9:00 and 13:00 h to confirm that extreme differences between dawn (one hour before the lights were turned on) and afternoon exist in leaf water relations. In general, significant changes occurred during the first 2 h after the lights were turned on, but thereafter changes were small. For this reason only dawn versus afternoon results will be presented.

Leaf water potential (ψ)

Because no significant interactions among measured factors occurred for ψ, its components will be presented separately (Fig. 2). In all cases, irrespective of time of day or leaf position, *maíz de humedad* maize had higher values of y than XL72AA. Highly significant differences ($P<0.05$) among irrigation means were detected in ψ for water stressed (-1.7 MPa), recovering (-1.1 MPa), and irrigated plants (-0.5 MPa) (Fig. 2a). Expanded leaves had higher (0.1 or 0.2 MPa less negative) ψ values than expanding leaves, irrespective of genotype or irrigation regime (Fig. 3a).

Leaf osmotic potential (ψ_s)

Significantly lower ψ_s values were measured in water stressed plants (-1.7 MPa) than under irrigation (-1.0 MPa)(Fig. 2b). During the recovery period (14 h), values of ψ_s in recovering plants were only about 0.2 MPa greater than those under water stress, suggesting that plants may require more time than 14 h to decrease the solute concentration in their cells. Differences in ψ_s values taken at dawn versus afternoon were never larger than 0.2 MPa, perhaps because radiation loading in growth chambers is not as great as in the field. Small or no genotypic differences were measured in ψ_s. Expanding leaves had larger ψ_s values than expanded leaves (Fig. 3b).

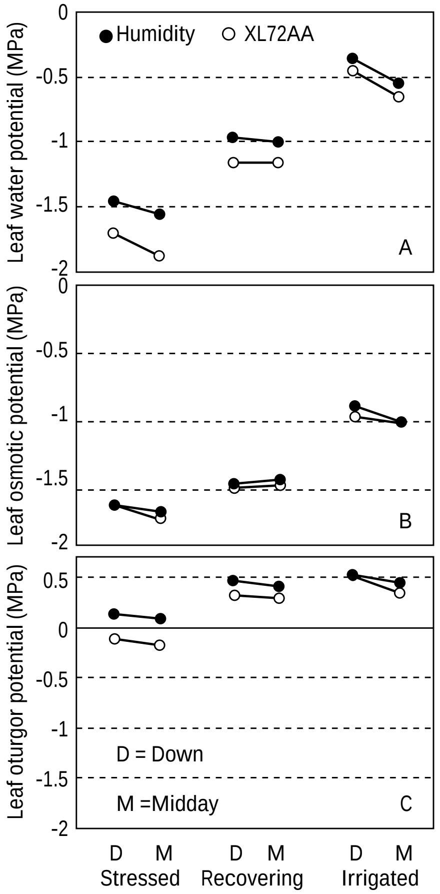

Figure 2. Leaf water relations of *maíz de humedad* maize and a Corn Belt hybrid when grown under two water regimes in controlled environment conditions.

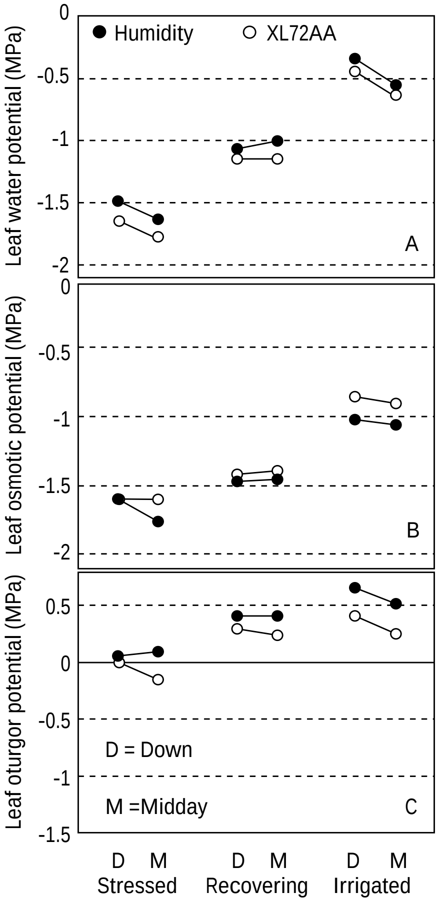

Figure 3. Leaf water relations of expanded versus expanding parts of leaves. Data are averages of two maize genotypes grown under three water regimes in controlled environmental conditions.

Leaf turgor potential (ψ_p)

The differences in ψ_p between genotypes ranged between zero and 0.3 MPa for irrigated and water stressed plants respectively (Fig. 3c). Larger (i.e., more positive) ψ_p values were observed in *maíz de humedad* maize than in XL72AA. Some negative ψ_p values were recorded, apparently because dilution effects by apoplastic water on the squeezed cell sap led to an overestimation of ψ_p. Under water stress ψ_p values were at their lowest, but during the recovery period similar ψ_p values to those of irrigated plants were observed (Fig. 2c). Expanded leaves had larger ψ_p values than expanding leaves on the same plant, irrespective of genotype, irrigation regime or time of day (Fig. 3c).

Root water potential (RWP)

In the irrigated boxes at field capacity (SWC approx. 19%; SWP = -0.3 MPa), RWP values at the top and bottom were practically the same (Table 1). At 75 DAP in the water stressed boxes (SWC 7%, SWP -4.0 MPa), no differences were detected between RWP values of root tips grown at the top versus the bottom of the boxes. However, RWP differences of -1.0 MPa were measured between irrigated and water stressed plants.

During the recovery period, 14 h after sub-irrigation, RWP in the irrigated bottom layer reached values of -0.1 MPa. In contrast, roots in the upper dry layer were at RWP of -1.1 MPa. After 62 h of recovery, RWP in the dry upper layer was -0.9 MPa, indicating that the process of rehydration was continuing, while in the sub-irrigated bottom layer RWP remained unchanged from the previous reading.

Root osmotic potential (ROP)

A full set of ROP and SWP measurements were obtained from samples collected simultaneously at 72 DAP prior to sub-irrigation on day 75. Recovering plants were sampled at 81 DAP. ROP, SWC and SWP values for three water regimes in three soil layers are presented in Figure 4 and Table 1. Root tips (1.0 cm) were compared with root segments from the more mature zone 3 to 4 cm from the tip. No genotypic effects were detected. Under water stress SWPs were less than -3.0 MPa, and corresponding ROP values were about -2.3 MPa (1 rep of data only). In recovering plants the SWP of the top, middle and bottom soil layers were -3.0, -0.3 and -0.01 MPa, respectively, and corresponding tip ROP values were -2.8, -1.6 and -1.1 MPa. Meanwhile, in non-water stressed boxes ROP values showed trends similar to those in water stressed plants. More negative values were obtained from roots growing in the driest layers, and it was here that a relationship between ROP and SWP could be observed.

Root tips of irrigated plants had ROP values about -0.3 MPa less than their adjacent root segments in all three soil layers. Similarly, smaller ROP values were measured in water stressed plants, but the drier the soil, the larger the difference between root tips and their adjacent root segments. These results may indicate that ROP gradients exist along the roots and that osmotica is accumulated in the root tip to increase the root turgor potential so that root growth is maintained even in very dry soils.

Root turgor potential (RTP)

Roots under irrigation and under water stress gave similar values of RTP, in spite of RWP and ROP differences of 1.0 MPa between the two irrigation regimes. Almost parallel decreases in both RWP and ROP occurred during the drying process. In the recovery period roots growing in very dry soil were at similar RTP than those before irrigation. The RTP values observed during the recovery period indicate that changes in osmotica are favored by a sudden increase of available water in the soil; e.g., higher RTPs were measured after 14 h of sub-irrigation at the bottom-wet layer of the boxes than under irrigation. At 62 h after irrigation, when the RTPs of roots at the bottom-wet layer were similar to those under irrigation, higher values of RTP were estimated at the top-dry layer. This increase in RTP may explain the observed growth of secondary roots in these dry soil layers.

Table 1. Root tip and shoot water relations of maize plants grown under irrigation and water stress in controlled indoor environments, Canada.

Water regime	Soil water layer	Soil water content (%)	Soil water pot.[†]	Root water pot.	Root osmotic pot.	Root turgor pot.	Leaf water pot.[‡]	Leaf osmotic pot.[‡]	Leaf turgor pot.[‡]
						MPa)			
Stressed	Top-dry	7	-4.0	-1.3	-1.8	0.5	-1.4	-1.4	0.0
Stressed	Bottom-dry	7	-4.0	-1.2	-1.9	0.7			
Recovery 1*	Top-dry	10	-0.45	-1.1	-1.7	0.6	-1.2	-1.4	0.2
Recovery 1	Bottom-wet	24	0.0	<-0.1	-1.1	1.0			
Recovery 2*	Top-dry	6	-4.0	-0.9	-1.9	1.0	-1.0	-1.2	0.2
Recovery 2	Bottom-wet	21	-0.0	<-0.1	-0.9	0.8			
Irrigated	Top-wet	19	-0.03	-0.3	-0.8	0.5	-0.6	-0.8	0.2
Irrigated	Bottom-wet	18	-0.03	-0.2	-0.9	0.7			

* Recovery I and 2 readings were made on the same water stressed plants at 14 h and 62 h after rewatering, respectively.

[†] Soil water potential values lower than -1.5 MPa estimated from water release curves of soils of similar textures and bulk densities.

[‡] Measurements of leaf water status from expanded leaves taken at noon.

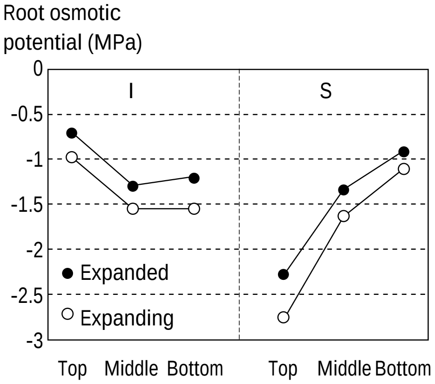

Figure 4. Root osmotic potential of expanding and expanded root sections in three parts of the root profile when grown under two water regimes. Data are averages of two maize genotypes grown under controlled environmental conditions.

Discussion

In the present study high levels of osmotic adjustment (about 1.0 MPa) were observed, values which are more than twice the maximum values reported by Bolaños and Edmeades (1991) in more mature tropical maize plants in the field. In the few cases where osmotic adjustment did not occur, this was perhaps because the level of stress or the rate at which stress developed did not allow accumulation of solutes in the cells.

Expanded leaves had equal or larger ψ_p values than expanding leaves. In most of the plants measured this was due to a combination of lower ψ values and equal or higher values of ψ_s. This conflicts with results from expanded versus expanding leaves in wheat (Munns et al., 1979) where fully expanded tissues were reported to be less turgid than expanding tissues. These authors argued that growing cells require a greater turgor potential than expanded cells. In maize Boyer (1974) also observed that expanding tissue had lower ψ_p values than expanded tissues. Boyer suggested that cell walls are less rigid in growing tissues and therefore ψ_p values are maintained at a lower level than in fully expanded tissues. Results in this study generally support this interpretation. More rapid net influxes of water can be achieved in expanding tissues if greater gradients in osmotic potential between the transpirational stream and the cytoplasm are established, although in only a few cases could this general observation be supported by data on LWC and osmotic content.

Decreases in root osmotic potential in root tips growing under water stress occurred in this experiment, confirming results from Sharp and Davis (1979). The net result is that full RTP was maintained even when RWP differences of 1.0 MPa between irrigated and water stressed plants existed. Irrigation of the lower soil layer of the water stressed boxes caused disproportional increases in RWP relative to increases in ROP, resulting in an actual increase in ψ_p values in both the irrigated and non-irrigated portions of roots. These changes have implications for root growth under dry soils. Under water stress some secondary root growth was observed in the upper dry layer. After rewatering the bottom root layer, most growth occurred in that layer, but secondary root growth was accelerated in the top dry layer as well. This enhanced lateral root growth in a dry layer of soil may be due to higher ψ_p values produced by a sudden imbalance caused by a rapid increase in RWP but a slower increase in ROP. Similar root growth in very dry soils was reported in maize by Portas and Taylor (1976).

The most important genotypic difference sought in this study was evidence of the ability of *maíz de humedad* maize to grow and survive longer than XL72AA under stress. Although some statistical differences in y_p under water stress (as a result of higher ψ and lower ψ_s) were measured in the experiment (when high levels of water stress were reached), genotypic differences in ψ_p were never larger than 0.3 MPa. Bolaños and Edmeades (1991) reported a range in leaf osmotic concentration of only 0.4 MPa in a wide array of tropical maize genotypes growing under water stress. Larger genotypic differences in osmotic adjustment have been recently reported in maize, and have been correlated with field performance (Chimenti et al., 1997). In the present study no substantial genotypic differences in growth and other visual signals of water stress were observed. Some doubt therefore exists concerning the adaptive advantages of the small genotypic differences observed in osmotic adjustment and turgor maintenance. Similar conclusions were drawn by Wilson and Ludlow (1983) when they compared the adaptation of several grasses to water deficits.

In conclusion, the capacity of *maíz de humedad* maize to provide superior production under these very dry conditions probably reflects its ability to germinate and establish from depths as great as 20 cm and its comparative lateness, which ensures that elongation does not begin till the rains arrive and the sensitive flowering period does not occur until the probability of water deficits is low. The relatively small differences in plant water relations observed in this study should certainly increase the ability of *maíz de humedad* maize to survive, recover from stress, and grow more roots under stress, but they are unlikely to be the main reasons for its superior adaptation to this extreme environment.

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Osmotic Adjustment in Maize: Genetic Variation and Association with Water Uptake

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Abstract

This paper reports on a study of osmotic adjustment in maize, an attribute linked to tolerance to water stress in some species. The hypotheses tested were: A) genotypes differ in their capacity for osmotic adjustment; and B) osmotic adjustment measured in the pre-flowering stage is associated with performance of plants exposed to water stress in the field. Twenty inbred lines were exposed to water stress under semi-controlled conditions during the 4 wk before flowering; stress was initiated at the sixth visible-leaf stage and was followed by a period of gradual drying out of the soil. Changes in water status of the plants were defined in terms of leaf relative water content (RWC) and osmotic potential (Ψ_o). Degree of osmotic adjustment (OA) was expressed as the estimated value of RWC for a defined value of Ψ_o (taken here as -2 MPa), referred to as RWCe. Thus, a high RWCe indicates a high degree of OA. All genotypes showed some deg2ree of OA. The range of RWCe obtained varied with genotype from 87% to 58%, and significant differences ($P<0.05$) in RWCe existed among genotypes. In a second experiment in the field, a subset of the inbred line collection was exposed to water stress 20 d before flowering. Water deficits reduced soil water extraction, dry matter, and yield. Variations in relative changes in these variables across genotypes were associated with variations in the degree of OA exhibited by the genotypes. We conclude that there is a substantial degree of intraspecific variation for OA in maize and that OA may explain some differences in yield observed in the field during water stress. These results suggest that OA estimates could be used to identify drought tolerant genotypes.

Breeding improved genotypes for drought-prone environments by selecting for grain yield is difficult because of year-to-year variability in the amount and temporal distribution of available soil moisture. Plant physiologists believe better adapted genotypes could be bred more efficiently if attributes that confer yield maintenance under water limited conditions could be identified and used as selection criteria (Ludlow and Muchow, 1990).

Osmotic adjustment results from the accumulation of solutes within the cell which lower osmotic potential and maintain turgor during periods of water stress. This allows turgor-driven processes which affect performance and yield to be maintained and the effects of drought to be minimized (Turner, 1986). Osmotic adjustment has been shown to be directly related to survival and yield in several crop species exposed to water stress (rice, sorghum, maize and wheat; Morgan et al., 1986; Sobrado, 1986; Turner et al., 1986; Santamaria et al., 1990), and implies that this attribute could be used directly in breeding programs for drought resistance.

In maize, it has been reported that osmotic adjustment occurs under water deficit in both field studies (Acevedo et al., 1979) and under controlled conditions in pots (Westgate and Boyer, 1985). However, there are contrasts in the magnitude of osmotic adjustment reported (Bolaños and Edmeades, 1991). The objective of this work was to determine the degree of intraspecific variability for osmotic adjustment in maize and to establish the degree of association between osmotic adjustment measured at the pre-flowering stage and the performance of plants exposed to water stress in the field. The results shown here were part of a project to study the use of osmotic adjustment as a selection criterion for drought tolerance.

Materials and Methods

Two types of experiments were carried out. The first, under semi-controlled conditions at the Facultad de Agronomía, evaluated genotypes for their osmotic adjustment capacity. The second, under field conditions at the INTA experimental station at Pergamino, studied the behavior of some of these genotypes under water stress.

Osmotic adjustment

Two sets of 20 inbred lines were evaluated for their capacity for osmotic adjustment, one set during 1993/94 and a different set in 1994/95. Within the two sets the subset comprising L 199, L 2846, L P125R, L P465, L Mo17, L RR#BK-1-18 and L 299-2 was repeated in both years. In the first experiment, plants were grown in 50 l pots in a 2:1 mixture of soil and sand (v:v), and well supplied with water and nutrients. There were 15 replicates of each genotype and one plant per pot. The pots were separated by at least 0.3 m between centers and arranged in a completely randomized design. For field grown plants, the watering regime was modified at the 6 visible-leaf stage, so that daily irrigation of the water stress treatment was reduced to 25% of evapotranspiration of the control plants. The objective was to avoid a rapid drying out of the soil that can affect the degree to which osmotic adjustment is manifested (Jones and Rawson, 1979). To avoid the effects of rain on plant water balance, pots were covered with a polyethylene film that also reduced incident short-wave radiation by 18%. During the 25 d of water stress, the daily mean temperature was 24 °C and the short-wave radiation 18.0 MJ m^{-2} day^{-1}. The mean evapotranspiration of the unstressed plants was 770 ml pot^{-1} day^{-1}. These conditions were similar in both years.

Estimates of capacity for osmotic adjustment of the inbred lines were derived from water status measurements made on leaves of plants exposed to water stress. During exposure to water stress the changes in water status were defined in terms of leaf relative content (RWC) and leaf osmotic potential (Ψo), using techniques described in Chimenti and Hall (1993). Every other day while stress was being imposed measurements were made of osmotic potential (Ψo) and relative water content (RWC) of the lamina of the uppermost fully expanded leaf. Before daybreak discs were cut from a single leaf from each of three plants per genotype, frozen in liquid nitrogen, and later thawed and measured for osmotic potential using psychrometric chambers (Wescor, model C-52, Wescor Inc., Logan, Utah, USA).

Estimates of osmotic adjustment were derived from ln RWC/ln Ψo relationships. The ln RWC/ln Ψo technique has the advantage, in the context of genotype comparison for OA, of using data obtained across a range of RWC values (Chimenti and Hall, 1993). Osmotic adjustment was judged to have occurred when the slope of the observed relationship deviated from that of an ideal osometer (i.e., a slope of 1 originating at the value for an RWC of 100%).

The degree of osmotic adjustment of each genotype was expressed as the value of RWC (derived from the functions fitted to the ln RWC/ln Ψo data) corresponding to a fixed value of Ψo (RWCe) (Chimenti and Hall, 1993; Morgan, 1983). RWCe summarizes the effect of variation between cultivars, taking into account differences in the value of parameters in the relationship. The Ψo value used in these experiments to estimated RWCe was fixed at -2.0 MPa, just greater than the value of Ψo at which the most sensitive genotype reached its lethal RWC. Higher values of RWCe indicated higher OA.

Field experiment

This was conducted during 1993/94. Plants of nine genotypes (L199, LP125R, L662, LP465, LRR#BK-1-18, L123, L299-2, L2846 and Lmo17) were arranged in a completely randomized design, using three replicated plots. Each plot consisted of three rows for each genotype, 0.7 m apart and 6.0 m long. There were two treatments: waters stressed and control. Twenty days before flowering, soil of the stressed plots was covered with a polyethylene film to avoid the effects of rain. Control treatments were irrigated. The stress period had a duration of approximately 50 d. Each week soil water was measured, either gravimetrically (between 0 and 30 cm depth) or by means of a neutron probe (Troxler 103 A, Troxler

Electronic Lab., North Carolina) (between 30 and 180 cm depth, at 20 cm intervals). The probe was calibrated with gravimetric soil samples. One aluminum access tube was installed to a depth of 2 m in the central row of each plot. Total available water for the entire profile was taken as the sum of available water in all soil layers. After maturity, two plant samples were taken from each plot for the determination of final dry matter production and grain yield.

Results

Linear regression models (Netter and Wasserman, 1984) were used to define the association between variables. The ln RWC / ln Ψo relationships were defined by 10 to 12 points in each set, and r values (usually exceeding 0.90) of the fitted functions were always significant ($P \leq 0.05$) in both years (data not shown). The RWCe values for the genotypes differed significantly ($P \leq 0.05$), confirming the existence of intraspecific variability for OA (Table 1). The range of values and ranks of lines were similar in both years.

Table 1. Mean values for RWCe (relative water content for a Ψo of -2.0 MPa) of maize inbred lines exposed to a water stress for 20 d during the preflowering period, 1994/95. Different letters following each mean indicate significant differences between those means at $P \leq 0.05$.

Genotype	RWCe (%)	
L 199	87.5	a
L 2846	81.8	ab
L P125R	80.3	ab
L P465	77.1	bc
L 1510	76.8	bcd
L P578	69.2	cde
L B-73	69.2	cde
L Mo17	66.8	def
L 3561	66.6	def
L P123	64.9	ef
L 662	63.2	ef
L 3579	61.8	ef
L 6015	59.7	f
L 229-2	59.4	f
L RR#BK-1-18	58.2	f

In the field experiment differences were observed among genotypes. For clarity, genotypes were separated into two groups according to their degree of OA; the high osmotic-adjusting group comprised L 199, L P125R and L P465, and the low-adjusting group comprised L Mo17, L RR#BK-1-18 and L 299-2. Differences ($P \leq 0.05$) between the control and the stress treatments were found in the amount of water uptake during the water stress period. When we compared the two groups, no differences were found between control treatments of each group (225 ± 12 and 220 ± 9 mm, respectively), but the results showed that genotypes with a higher OA took up 10% more soil water ($P < 0.10$) than those with low OA (Table 2). There were two patterns of soil water extraction among genotypes (e.g., Fig. 1), with major differences evident below 80 cm.

Water stress reduced grain yield and dry matter to a lesser degree ($P < 0.10$) in the high OA group (Table 2). Grain yield of the high OA group under stress was 89% of the yield of the same group under non-stress control conditions, while for the low OA group stress reduced yield to 73% of the control. Similar results were found for aboveground total dry matter production.

Table 2. Relative water uptake, yield and total aboveground dry matter production of genotype groups with high and low osmotic adjustment levels. Values represent the performance under water stress as a percent of their performance under well-watered control conditions. For each trait, groups differed at $P \leq 0.10$.

Osmotic adjustment level	Water uptake (%)	Yield (%)	Aboveground dry matter production (%)
High	76	89	91
Low	66	73	74

Discussion

These results, obtained in an experiment repeated over two years and confirmed by a field evaluation, allow maize to be added to the list of species for which intraspecific variability in osmotic adjustment has been shown to exist. The variation in RWCe values among lines was large, ranging from 58.2 to 87.5% (Table 1). This suggests that selection for high osmotic adjustment may prove to be relatively easy in maize.

The issue of stability of genotype rank for any attribute is a critical one, particularly when selection for this attribute is an objective. In comparing the two years of inbred line evaluations, crossovers in rank between groups were not detected and high OA lines remained within the high group and low lines within the low group. Some crossovers in rank, however, were found within groups. Kendall's Concordance Coefficient (Siegel, 1980) was used to check stability of rank. Significant ($P \leq 0.05$) concordance was found across the two years, indicating that the ranking for osmotic adjustment appears to be stable across years, at least in pot evaluations of the trait.

Inbred lines which are capable of adjusting osmotically under water deficit may have achieved this through two mechanisms. They may have produced greater root length, thus allowing soil water extraction in deeper layers, or they may simply have had a greater capacity to extract water from dry soil at this depth (Fig. 1). The end result being turgor maintenance at low soil water potential. Genotypes with this ability are capable of maintaining physiological processes at low leaf water status, thus minimizing the effects of water stress on grain yield and dry matter production.

In summary, our results demonstrate that there is a substantial degree of intraspecific variability for osmotic adjustment in maize, and that it is possible to screen material for this trait under semi-controlled conditions. Full evaluation of the potential usefulness of this trait in a maize drought tolerance breeding program must await determination of heritability of the trait, and the demonstration of an association between yield maintenance under water stress and OA in material of an otherwise similar genetic background. A study of the heritability of osmotic adjustment in maize is currently underway.

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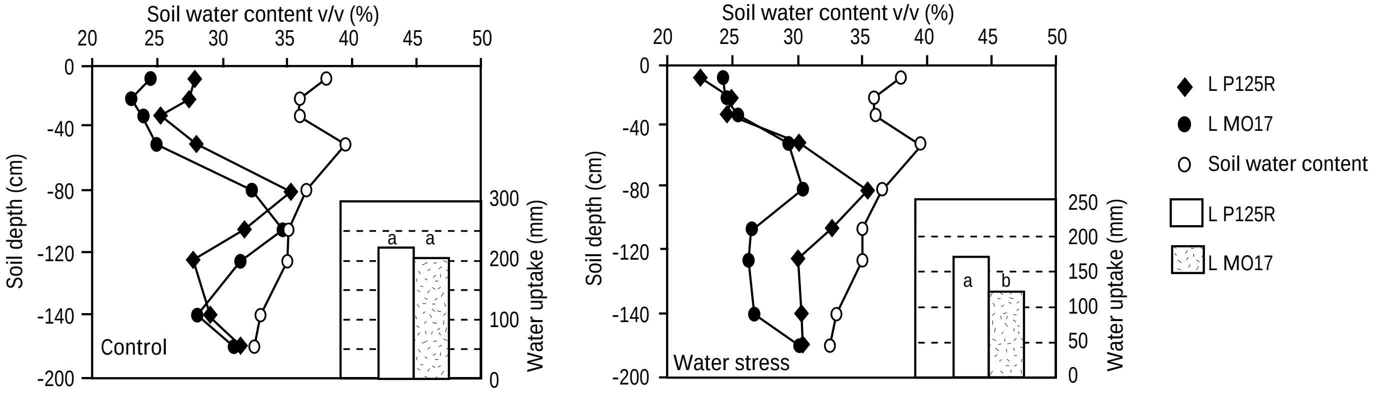

Figure 1. Examples of the pattern of soil water extraction for genotypes with high (L P125R, ●) and low (L MO17, ♦) capacity for osmotic adjustment. The upper figure corresponds to controls, and the lower to a water-stressed treatment. (°) indicates the soil water content at initial and (●, ♦) at the end of the stress period. Inserts at the bottom right of each figure show water uptake by each genotype (LP125R, LMO17).

Patrones Electroforéticos de las Proteínas de Dos Cultivares de Maíz Bajo Déficit Hídrico

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Abstract

The present work analyzes the effect of drought stress on the electrophoretic patterns of the root, stalk and leaf proteins from the maize cultivars Criollo Cajete and Michoacán 21 composite 1-104, grown in the field and in the greenhouse. Drought stress inhibited and promoted the synthesis of only a few proteins; the electrophoretic patterns differed between treatments, although they were similar for the leaves of both cultivars in the greenhouse. In addition, both cultivars grown in the greenhouse showed a greater number of protein bands than those grown in the field. The protein bands observed in this study may be related to those of a similar molecular weight observed by researchers in other studies.

En el presente trabajo se analizó el efecto del déficit hídrico en los patrones electroforéticos de las proteínas de la raíz, tallo y hojas de los cultivares de maíz Criollo Cajete y Michoacán 21 Compuesto 1-104 cultivadas en campo e invernadero. El déficit hídrico inhibió y promovió la síntesis sólo de algunas proteínas y los patrones electroforéticos fueron diferentes entre tratamientos; aunque, los de la hoja de ambos cultivares desarrollados en el invernadero fueron semejantes. Además, ambos cultivares desarrollados en el invernadero mostraron mayor número de bandas proteicas respecto a los del campo. Es posible que las bandas de proteínas observadas en este estudio con un peso molecular semejante a las documentadas previamente por otros autores guarden alguna relación.

Uno de los factores ambientales que afecta el crecimiento y rendimiento de maíz bajo condiciones de campo es la sequía, el cual causa un déficit hídrico en la planta. Entre los procesos bioquímicos afectado por este déficit está la síntesis de proteínas (Hsiao, 1973; Dhindsa y Cleland, 1975). Sin embargo, se desconoce los mecanismos por los que el déficit ejerce su efecto (Dhindsa y Cleland, 1975). La aplicación de choques calóricos a los tejidos induce la síntesis de varias proteínas (hsp); en contraste, en estudios realizados en el laboratorio se ha documentado la síntesis de unas cuantas proteínas por efecto del déficit hídrico. El presente trabajo tuvo como objetivo analizar los patrones electroforéticos de las proteínas de la raíz, tallo y hoja de dos cultivares de maíz bajo déficit hídrico.

Materiales y Métodos

Los cultivares de maíz usados en este estudio fueron el Criollo Cajete y Michoacán 21 Compuesto 1-104. El primero se cultiva en la región de la Mixteca Alta Oaxaqueña y el segundo fue colectado en el estado de Michoacán.

Experimento en invernadero

Se estableció en el invernadero del área de resistencia a sequía del Colegio de Postgraduados en Montecillo, México. Se utilizó un suelo de textura franco arenoso, cuyas constantes de humedad fueron capacidad de campo (CC) 11.6% y punto de marchitez permanente (PMP) 5.1%. La siembra se realizó el 10 de junio de 1992 y las plantas se desarrollaron con riego normal (RN) y sequía. Esta última, consistió en suspender el riego a los 40 d después de la siembra hasta que las plantas llegaron a marchitez permanente (MP), aplicándose un riego de recuperación (RR) 1 d después.

Experimento de campo

Se estableció en terrenos del Campo Experimental Forestal y Agropecuario Mixteca Oaxaqueña (CEFAMOAX), del Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP), ubicado en el municipio de Santo Domingo Yanhuitlán, Oaxaca. El clima del sitio experimental es templado subhúmedo con lluvias en verano. El suelo es de textura arcillosa y sus constantes de humedad son: capacidad de campo (CC) 33% y punto de marchitez permanente (PMP) 18.7%. La siembra se realizó el 20 de marzo de 1993 bajo los agrosistemas: riego, sequía y cajete. Para la condición de sequía, el riego se suspendió a los 23 d después de la siembra (DDS), durante 56 d, hasta los 80 DDS, momento en el que se aplicó el riego de recuperación (RR). Después de este riego el suelo se mantuvo con humedad cercana a CC. En el agrosistema de cajete, las plantas crecieron durante los primeros 80 DDS únicamente con la humedad residual del suelo y después, con las lluvias, la humedad del suelo se mantuvo cercana a CC.

Toma de muestras

Cuando las plantas del invernadero llegaron a MP y las plantas en campo llegaron a MT y en ambas después del RR, se tomaron muestras representativas de raíz, tallo y hoja de cinco plantas por variedad. Estas muestras se introdujeron en nitrógeno líquido (-196 °C) y posteriormente se leofilizaron. Las cinco muestras de cada órgano por variedad se juntaron y se molieron para después tomar una muestra para extraer la proteína y realizar la electroforesis.

Extracción de proteínas

Se mezclaron 40 mg de cada muestra con 1 ml de solución amortiguadora de extracción según lo señalado por Pérez et al. (1990). La mezcla se molió en un mortero durante 15 min (para romper a las células y liberar a las proteínas). Se centrifugó a 10 000 rpm durante 10 min. Finalmente, se separó el sobrenadante de cada muestra y se mantuvo en congelación a -20 °C hasta su análisis por electroforésis.

Electroforésis

La electroforésis se realizó en geles unidimensionales de poliacrilamida bajo condiciones desnaturalizantes, de acuerdo con lo propuesto por Laemmli (1970) y la separación se efectuó a 180 V.

Tinción y revelado de los geles

Para la tinción el gel se mantuvo en agitación en una solución fijadora (30 ml de etanol, 10 ml de ácido acético y 60 ml de agua desionizada) durante 60 min o más, se introdujo dos veces en etanol al 30%, se lavó tres veces con agua desionizada y se incubó en una solución de $AgNO_3$ 0.2% durante 30 min. Después de lavar el gel con agua desionizada se reveló con una solución de Na_2CO_3 2.5% más 55 ml de formaldehído. Cuando se observaron las bandas de proteínas se transfirió el gel a una solución de CH_3COOH 1%. Finalmente, cada gel se fotografió con una película polaroid 667 ASA 3000 y apertura f 8, 1/125 seg. En estas fotografías se calculó el Rf y el peso molecular en kilodaltones (kDa) de cada banda proteica por comparación con los marcadores de peso molecular incluidos en los geles.

Resultados

Se observaron diferencias en los patrones electroforéticos entre los agrosistemas, cultivares y órganos vegetativos, de las plantas desarrolladas en el campo y en el invernadero. Tanto en campo como en invernadero el déficit hídrico modificó, inhibió (disminuyó o eliminó) o activó (incrementó o indujo) la síntesis de algunas proteínas en la raíz, tallo y hoja (Cuadros 1 al 4). En las hojas del cv. Criollo Cajete desarrollado en el campo se observó un mayor número

Cuadro 1. Peso molecular de algunas bandas proteicas del cv. Criollo Cajete cultivado con riego, sequía y cajete en Yanhuitlán, Oax., durante 1995.

Organo vegetativo	Peso molecular (kDa)	Condición hídrica en la que se presentó
Raíz	68	Riego y sequía
	49	Unicamente con sequía
	41.5	Riego e incrementa ligeramente con sequía
	37.5 y 35	Unicamente con riego
Tallo	92 y 75	Riego y sequía
	86, 68, 55.5, 49, 37.5 y 34	Unicamente en cajete
Hoja	165, 155, 147.5, 106, 92, 70 y 39	Unicamente con sequía
	86, 68, 61.5 y 50.5	Con riego y sequía

de bandas proteicas en comparación con la raíz y el tallo, mientras que en Michoacán 21 el tallo contenía más bandas (Cuadros 1 y 2). Ambos cultivares desarrollados en el invernadero mostraron más bandas en la raíz respecto al tallo, y no se observaron diferencias entre los patrones electroforéticos de las hojas.

Discusión

Algunas respuestas de la planta a los diferentes tipos de estrés están relacionadas con la alteración de la expresión de genes y la síntesis de polipéptidos. Es probable que estas proteínas inducidas por el estrés permitan a la planta hacer ajustes bioquímicos y estructurales para tolerar el estrés. Existe poca información sobre el efecto del déficit hídrico en la síntesis de algunas proteínas; así, el presente trabajo aporta información nueva relacionada con los patrones electroforéticos de proteínas de dos cultivares de maíz que han mostrado cierta resistencia a la sequía. El análisis electroforético mostró que el déficit hídrico inhibió la síntesis de algunas proteínas y promovió la de otras, lo que concuerda con lo señalado por Dhindsa y Cleland (1975). Una razón por la que se afirma que la síntesis de proteínas disminuye como resultado del déficit hídrico es porque se inhibe la incorporación de aminoácidos en estos polímeros (Ben-Zioni et al., 1967). Por otro lado, la permanencia de algunas bandas proteicas en todas las condiciones hídricas (riego, sequía y cajete) tanto en campo como en invernadero indica que el déficit hídrico no alteró la síntesis de esas proteínas. Al respecto Bewley y Larsen (1980) señalan que la capacidad del tejido vegetal para conservar los poliribosomas bajo déficit hídrico está de alguna manera relacionada con su resistencia a la sequía, por lo que los tejidos o plantas más resistentes pueden continuar con la síntesis de proteínas aún con déficit hídrico. El número de bandas fue distinto entre los órganos y se modificó con las diferentes condiciones hídricas. La presencia de bandas equivalentes en MT, MP y aproximadamente 24 h después del RR, probablemente indica que este tiempo es muy corto para que la planta alcance su recuperación completa; estos resultados

Cuadro 2. Peso molecular de algunas bandas proteicas del cv. Michoacán 21 Compuesto 1-104 cultivado con riego, sequía y cajete en Yanhuitlán, Oax., durante 1995.

Organo vegetativo	Peso molecular (kDa)	Condición hídrica en la que se presentó
Raíz	167, 150, 137 y 120	Riego e incrementan notablemente con sequía
	110 y 97	Riego y cajete e incrementan notablemente con sequía
	49	Riego e incrementa notablemente en cajete
Tallo	147	Riego y se incrementa con sequía
	125 y 42	Unicamente con sequía
	107, 83 y 56	Cajete e incrementan notablemente con sequía
	35	Riego e incrementó notablemente con sequía
	30	Cajete e incrementó notablemente con sequía
Hoja	115	Riego, sequía y cajete

Cuadro 3. Peso molecular de algunas bandas proteicas del cv. Criollo Cajete cultivado en invernadero con riego y sequía en Montecillo, Méx., durante 1995.

Organo vegetativo	Peso molecular (kDa)	Condición hídrica en la que se presentó
Raíz	71	Riego y sequía
	48.5	Unicamente con sequía
	38 y 34	Riego y se incrementa ligeramente con sequía
	30 y 28	Unicamente con riego
Tallo	72	Riego, se intensifica en MP y se mantiene en RR
	62, 28.5, 22.5, y 20.3	Presente en MP y después del RR

MP: marchitez permanente, RR: riego de recuperación.

Cuadro 4. Peso molecular de algunas bandas proteicas del cv. Michoacán 21 Compuesto 1-104 cultivado en el invernadero con riego y sequía en Montecillo, Méx., durante 1995.

Organo vegetativo	Peso molecular (kDa)	Condición hídrica en la que se presentó
Raíz	80 y 74	Riego y RR y disminuyen con MP
	49	Unicamente con sequía
	37.5	Unicamente en MP
	27	MP y con RR
Tallo	72.5 y 22.5	Riego y RR
	30	MP y RR

MP: marchitez permanente, RR: riego de recuperación.

concuerdan con los obtenidos por Bewley et al. (1983) en mesocótilo de maíz bajo condiciones de laboratorio. Las proteínas con peso molecular de 27 y 70 kDa observadas en este estudio, podrían estar relacionadas con la familia de las hsp del mismo peso molecular identificadas en maíz (Czarnecka et al., 1984) y soya (Heikila et al., 1984) con déficit hídrico, ya que aparentemente, las proteínas hsp 70 son inducidas por diversos tipos de estrés (Van Breusegem et al., 1994). Por su parte Hershkovitz et al. (1991) indicaron que la sequía indujo la presencia de polipéptidos de 30 kDa localizados en las membranas de los tilacoides y de 45 kDa presentes en la membrana celular de Cianobacteria. En plántulas de *Spinacia oleraceae* una pequeña disminución del contenido de agua en el tejido indujo la acumulación de proteínas de 160 y 85 kDa (Guy et al., 1992). En el estudio con maíz realizado por Ristic et al. (1991) la línea de maíz ZPBL 1304 resistente al calor y a la sequía, sintetizó una banda de hsp de aproximadamente 45 kDa. Existe la probabilidad de que las bandas de proteína o proteínas observadas en el presente estudio de peso molecular semejante a las identificadas por otros autores estén relacionadas. La función de las proteínas sintetizadas bajo diferente tipo de estrés no se conoce; sin embargo, Vance et al. (1990) sugirieron que éstas pueden contribuir en la resistencia a la deshidratación de las plántulas de *Pinus ponderosa* tolerantes a la sequía.

En conclusión el déficit hídrico inhibió la síntesis sólo de algunas proteínas. Por la falta de información bibliográfica, este trabajo se considera que es un estudio iniciador, cuyas aportaciones pueden servir de base para el planteamiento de futuras investigaciones en el campo de la biología y genética molecular con miras al mejoramiento genético para la resistencia a la sequía de las plantas cultivadas.

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Efecto del Déficit Hídrico en la Longitud y Diámetro de los Entrenudos del Tallo de Cuatro Cultivares de Maíz

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Abstract

This study measured the effect of drought on the length and diameter of the stalk internodes of the maize varieties Cafime, Compuesto Temporal, Criollo Cajete, and Michoacán 21 composite 1-104 under normal irrigation, irrigation-drought (intermediate drought stress), and residual moisture or "cajete" (severe drought stress). Drought reduced the length and diameter of the internodes below the ears on the stalks of the four cultivars, a reduction that varied depending on the severity of the drought stress. The cultivars Criollo Cajete and Compuesto Temporal showed slight increases in the length and diameter of the internodes located above the ears. Under these circumstances, the greater length and diameter of internodes represents a moisture and assimilate sink for use in grain-filling, under reduced photosynthesis caused by drought. In addition, Criollo Cajete and Compuesto Temporal showed good grain yield under drought, making them likely candidates for use in a maize improvement program for the Oaxacan Mixteca region of Mexico.

Se cuantificó el efecto del déficit hídrico en la longitud y diámetro de los entrenudos del tallo de las variedades de maíz Cafime, Compuesto Temporal, Criollo Cajete y Michoacán 21 Compuesto 1-104 cultivadas en los agrosistemas de riego normal, riego-sequía (déficit hídrico intermedio) y humedad residual o "cajete" (déficit hídrico severo). El déficit redujo la longitud y diámetro de los entrenudos situados abajo de la mazorca en los tallos de los cuatro cultivares. Esa reducción fue dependiente de la severidad del déficit hídrico y el Criollo Cajete y el Compuesto Temporal mostraron longitud y diámetro de los entrenudos situados arriba de la mazorca ligeramente mayores. En esta condición, la mayor longitud y diámetro de los entrenudos representa un almacén de agua y de asimilados para ser utilizados en el llenado del grano, cuando la tasa fotosintética es disminuida por falta de agua. Además, el Criollo Cajete y el Compuesto Temporal mostraron mayor resistencia al déficit hídrico, ya que tuvieron buen rendimiento de grano (resultados no incluidos en este estudio), por lo que son buenos candidatos para ser incluidos en un programa de mejoramiento genético sobre resistencia a sequía en maíz para la región de la Mixteca Oaxaqueña.

El crecimiento de la planta resulta de la interacción de su genotipo con el ambiente que la rodea (Gardner et al., 1985) y es definido como un incremento irreversible de peso seco (Hess, 1975). En el caso de la planta de maíz, la altura total del tallo es el resultado de la suma de la longitud de cada entrenudo. Por otro lado, el diámetro de cada entrenudo está relacionado con el vigor del tallo y su resistencia al acame. Entre los factores que afectan el crecimiento, muchos autores involucran al agua. Su impacto negativo es más pronunciado en aquellos tejidos y órganos que se encuentran en crecimiento debido a su efecto directo sobre la división y alargamiento celular (Aspinall et al., 1964). En la presente investigación se cuantificó el efecto del déficit hídrico en la longitud y el diámetro de los entrenudos del tallo de la planta de cuatro cultivares de maíz.

Materiales y Métodos

Los cuatro cultivares de maíz usados en este estudio fueron Cafime, Compuesto Temporal, Criollo Cajete y Michoacán 21 Compuesto 1-104. El cv. Cafime se recomienda por el Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP) para sembrarse en la Mixteca Oaxaqueña bajo condiciones de temporal, ya que debido a su precocidad escapa a la sequía. El cv. Compuesto Temporal fue generado experimentalmente en el INIFAP con cultivares criollos que han mostrado cierta resistencia a la sequía. El Criollo Cajete es cultivado en la región de la Mixteca Alta en el agrosistema de humedad residual o “cajete” y ha mostrado una alta resistencia al bajo contenido de humedad en el suelo. El último, es un compuesto formado con líneas de la colección Michoacán 21 en la cual, Palacios de la Rosa en 1957 (Palacios et al., 1963-1964), descubrió un carácter que denominó “Latente”.

Las siembra se estableció el 20 de marzo de 1993 en los terrenos del Campo Experimental Forestal y Agropecuario Mixteca Oaxaqueña (CEFAMOAX), del INIFAP, ubicado en el municipio de Santo Domingo Yanhuitlán, Oaxaca. El clima del sitio experimental es templado subhúmedo con lluvias en verano. El suelo es de textura arcillosa y capacidad de campo (CC) y punto de marchitez permanente (PMP) de 33 y 18.7%, respectivamente. En los tres experimentos (tratamiento de humedad en el suelo) se utilizó un diseño experimental de bloques completos al azar con cinco repeticiones y cuatro cultivares, teniéndose un total de 20 unidades experimentales. Los tratamientos de humedad en el suelo o agrosistemas fueron: riego normal, riego-sequía y cajete.

El agrosistema de riego consistió en mantener la humedad del suelo próxima a CC, para lo cual se aplicaron riegos cada 8 o 10 d. En el agrosistema de sequía, el riego se suspendió a los 23 d después de la siembra (DDS), por un periodo de 56 d hasta los 80 DDS que fue cuando se aplicó el riego de recuperación (RR). Después de este riego el suelo se mantuvo con humedad cercana a CC. En el agrosistema de cajete, las plantas crecieron durante los primeros 80 DDS únicamente con la humedad residual del suelo, la cual fue cercana a PMP y después de este periodo se mantuvo cercana a CC, porque se estableció el periodo de lluvias. Cuando 50% de las plantas llegaron a antesis (Cafime, 81; Criollo Cajete, 105; Compuesto Temporal, 91; y Michoacán 21 Compuesto 1-104, 96 DDS), se seccionaron cinco plantas de cada cultivar y se cuantificó el número de entrenudos, la longitud y el diámetro de cada uno.

Resultados

En los resultados se incluyeron únicamente la longitud y diámetro del sexto entrenudo en adelante, contados a partir de la base de la planta, ya que los primeros cinco no fueron afectados por el déficit hídrico. Se observó que la longitud de los entrenudos del tallo de los cuatro cultivares fue menor en cajete, seguida por la de sequía y riego. La longitud de los entrenudos se fue incrementando de la base del tallo hacia la región superior, sobre la mazorca (Fig. 1). En el cv. Cafime el entrenudo 14 tuvo mayor longitud en cajete respecto al de la condición de sequía (Fig. 1A). En el Criollo Cajete las condiciones de sequía y cajete redujeron la longitud de los entrenudos a partir del 13, respecto a la condición de riego, pero la reducción fue mayor en sequía (Fig. 1B). Para el cv. Compuesto Temporal la mayor longitud se tuvo en condiciones de riego y con excepción del entrenudo 16, todos mostraron menor longitud en la condición de cajete, respecto al de sequía (déficit hídrico intermedio) (Fig. 1C). En el cv. Michoacán 21 Compuesto 1-104 todos los entrenudos mostraron fuerte reducción de su longitud con la sequía. Los entrenudos del 6 al 15 tuvieron menor longitud en sequía que en riego. Los entrenudos del 6 al 12 expresaron menor longitud en sequía y cajete respecto a riego. En cajete, los entrenudos 13 y 14 mostraron mayor longitud (Fig. 1D).

Con respecto al diámetro de los entrenudos los cultivares Cafime y Michoacán 21 mostraron tendencias similares en los tres agrosistemas (Figs. 2A y B) a excepción de los entrenudos 15 y 16 en Cafime. En Cafime y Michoacán 21 el diámetro de los entrenudos disminuyó más en el agrosistema de cajete (déficit hídrico severo) respecto al de sequía (déficit hídrico intermedio), pero en ambos la reducción fue menor que en la condición de riego. En los cultivares Criollo Cajete y Compuesto Temporal se observó que algunos entrenudos situados arriba de la mazorca tuvieron mayor diámetro cuando se sembraron en cajete respecto a los de sequía, inclusive los dos últimos entrenudos del cv. Criollo Cajete tuvieron mayor diámetro en aquella condición respecto a los de riego. Entre los cuatro cultivares el mayor diámetro de los entrenudos lo obtuvo el cv. Criollo Cajete, en las tres condiciones hídricas.

Discusión

Mediante estudios de crecimiento de la planta de maíz en condiciones normales de humedad en el suelo se ha observado que el patrón de alargamiento de los entrenudos es similar entre sí; pero la tasa de crecimiento de cada uno es diferente (Morrison et al., 1994). Cada entrenudo del tallo de la planta de maíz tiene diferente estructura y probablemente alguna función específica en la planta. Los entrenudos de la planta tienen dos funciones importantes: elevar a los órganos fotosintéticos para optimar la captura de la radiación fotosintéticamente activa y elevar a los órganos reproductores para asegurar la polinización y fecundación. Además, cada entrenudo tiene tejido vascular altamente lignificado que proporciona resistencia al tallo contra el acame. Los resultados del presente trabajo indican que los entrenudos de la base del tallo son más cortos que los superiores y que el déficit hídrico afectó la longitud y el diámetro de los entrenudos en desarrollo (Figs. 1 y 2) probablemente por inhibición del alargamiento por falta de turgencia de las células en crecimiento, según lo consignan Hsiao (1973), Boyer (1970), Michelena y Boyer (1982), y Sharp y Davies (1979). El grado de reducción de la longitud y el diámetro de los entrenudos estuvo relacionado con la severidad del déficit hídrico en los cuatro cultivares. Otros estudios han mostrado que la variación en el diámetro de los entrenudos del tallo puede estar relacionada con contenido de agua en la planta (Koslowski, 1983) o sea que están asociados positivamente. El diámetro de los entrenudos fue diferente para cada variedad, pero en general los de la parte media presentaron mayor diámetro; además, solo en cajete los cultivares Criollo Cajete y Compuesto Temporal mostraron mayor diámetro y longitud de sus entrenudos cercanos al sitio de localización de la mazorca. El mayor diámetro de los entrenudos está relacionado con una mayor capacidad del tallo para acumular agua y reservas, los cuales serán usados para el llenado del grano cuando la planta esté en déficit hídrico. Esta característica morfológica es uno de los mecanismos de resistencia a la sequía que permite al cv. Criollo Cajete adaptarse a la condición cajete cuya característica principal es un bajo contenido de agua en el suelo durante las primeras etapas de desarrollo de la planta. Los cultivares

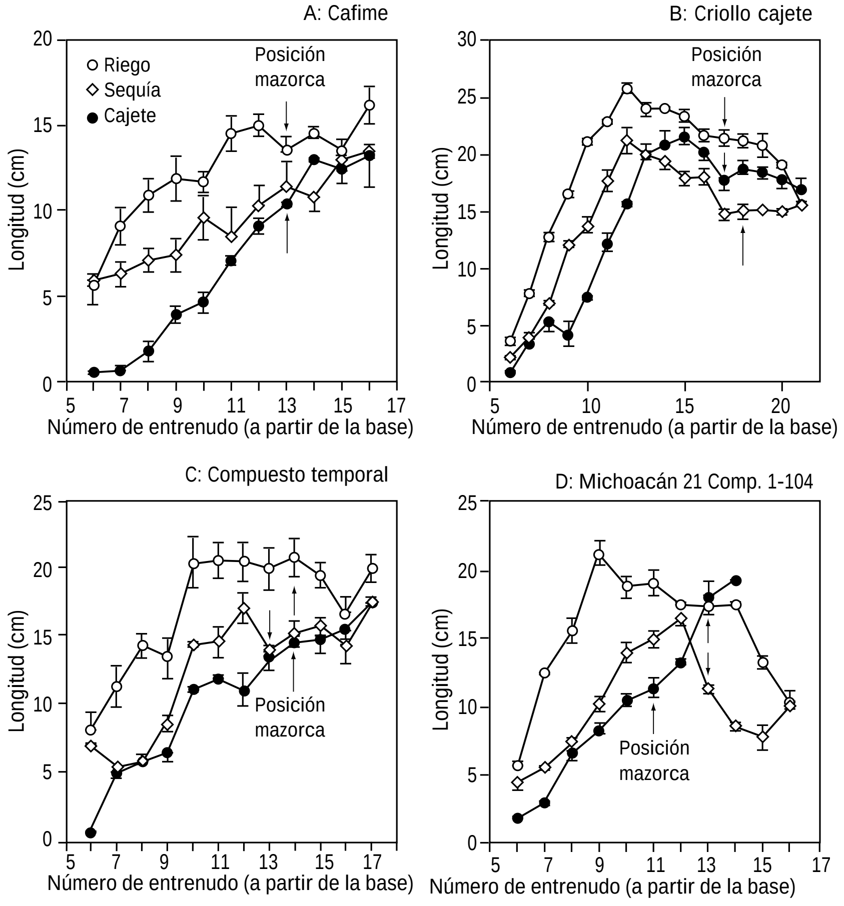

Figura 1. Longitud de los entrenudos del tallo de cuatro variedades de maíz, cultivadas en tres agrosistemas (riego, sequía y cajete). Yanhuitlán, Oax., 1995.

Criollo Cajete y Compuesto Temporal mostraron resistencia a la sequía, de acuerdo a los caracteres estudiados (y en rendimiento; Cuadro 1). Por lo tanto, deben considerarse como germoplasma para los programas de mejoramiento de maíz sobre resistencia a sequía para la región de la Mixteca Oaxaqueña, donde la sequía es el factor principal que limita la producción de este cultivo.

Cuadro1. Rendimiento de grano (g/planta) al 12% de humedad.

	Criollo cajete	Compuesto temporal
Riego	144	128
Sequía	149	77
Cajete	151	87

Rend = ^{g}/pl

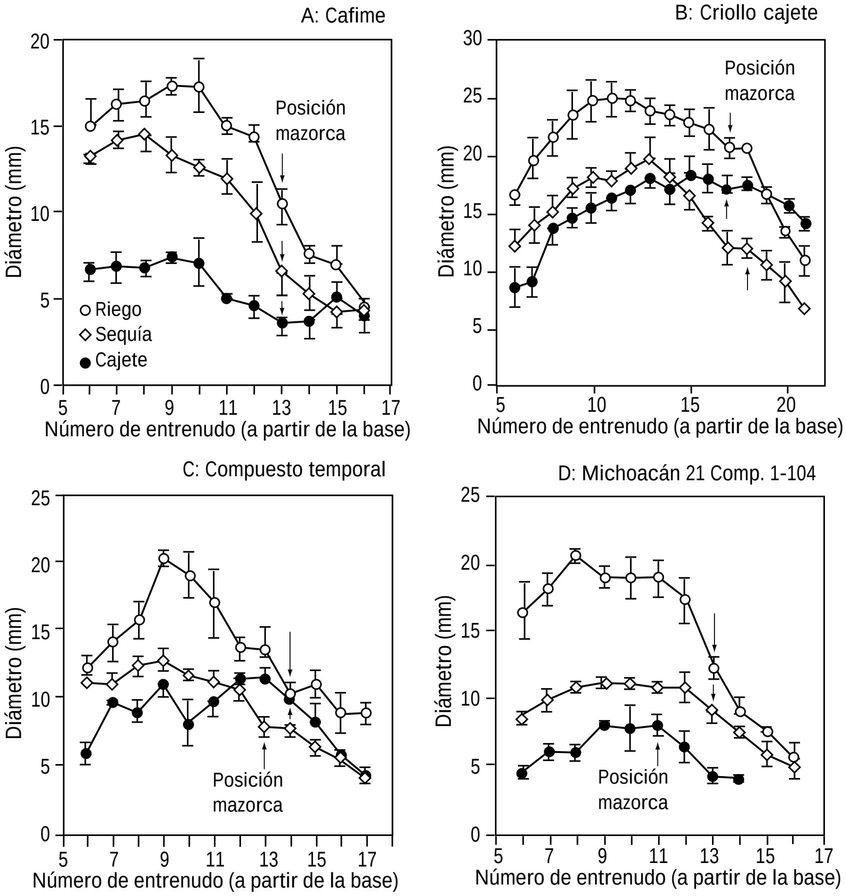

Figura 2. Diámetro de los entrenudos del tallo de cuatro variedades de maíz cultivadas en tres agrosistemas (riego, sequía y cajete). Yanhuitlán, Oax., 1995.

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Stomatal Conductance in Successive Selection Cycles of the Drought Tolerant Maize Population ‘Tuxpeño Sequía’

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Abstract

Three cycles (C_0, C_4 and C_8) of a Tuxpeño maize population selected for eight successive cycles under drought conditions by breeders from CIMMYT were studied to determine if selection changed stomatal conductance (g_s) and the capacity to accumulate abscisic acid (ABA). Four week-old greenhouse-grown seedlings were exposed to drought until their relative water contents averaged 60% (at a water potential = -1.7 MPa). ABA was measured by an enzyme immunoassay technique. There were no differences in ABA among selection cycles under drought or under well-watered conditions, indicating that indirect selection for ABA accumulation had not occurred during the breeding procedure and that ABA accumulation was not directly related to increased grain yield under drought. In the same experiment g_s was determined using the fourth leaf measured at midday under water-stressed and well-watered conditions. There were no differences in g_s among selection cycles under water deficit; however, under non-stress conditions significant differences were found. Seedlings of C_8 showed the greatest g_s (96.9 mmols m^{-2} s^{-1}), while C_0 and C_4 seedlings had lower values (71.2 and 64.6 mmols m^{-2} s^{-1}, respectively). The reduction in g_s with increasing water stress clearly resulted in reduced water loss from transpiration, but was not directly proportional to changes in ABA concentration.

Drought is the most important factor limiting crop productivity in many areas of the world, and there is evidence that it is becoming a more serious problem due to growing shortages of plant-available water (Conti et al., 1994). An estimated 80% of maize planted in lowland tropical environments suffers periodic yield reduction from water stress, with drought-related production losses ranging from 10 to 50% (Edmeades et al., 1989). Drought stress can greatly reduce grain yield if it coincides with flowering (Bolaños and Edmeades, 1993a), and sensitivity to drought stress is greatly increased at flowering (Shaw, 1988). Breeders are continually searching for lines tolerant to drought that can be used to enhance maize’s adaptation to water deficient environments, though most often selection is based only on grain yield. Yield selection in droughty environments is particularly difficult because of variation in the amount and distribution of rainfall, leading to an inability to control the timing and intensity of drought stress (Blum, 1988; Edmeades et al., 1989).

A Tuxpeño maize population, ‘Tuxpeño Sequía’, has been selected for eight cycles for drought tolerance by breeders at CIMMYT (Bolaños and Edmeades, 1993a). One component of their selection index was anthesis-silking interval (ASI), the number of days between 50% silking and 50% anthesis. Grain yield and its components, especially kernel number per plant, showed a strong association with ASI. Selection reduced the observed ASI from 34.2 d in the C_0 to 9.8 d in C_8. Their data suggest that selection for reduced ASI under carefully managed moisture stress imposed at flowering provides an effective and rapid route to higher and more stable grain yield in lowland tropical maize (Bolaños and Edmeades, 1993b). Changes in the accumulation of leaf ABA could be associated with these changes in ASI, and in turn could lead to changes in g_s under drought.

There has been an increasing emphasis among breeders over the past 15 years to select for stomatal behavior. This has arisen because of an increased understanding of the crucial role played by stomata in the control of water loss and CO_2 uptake, and because they provide a simple anatomical character that can be measured during selection (Jones, 1987). Nonetheless, leaf gas exchange is a complex, highly regulated process dependent upon interactions between mesophyll cells and stomata (Farquhar and Sharkey, 1982). Photosynthesis and transpiration respond differently to the same environmental factors, and stomata modulate the two processes to different degrees (Cowan and Farquhar, 1977).

Abscisic acid (ABA) is thought to play a vital role in the water economy of plants under water stress by reducing stomata aperture (among other metabolic responses), and thus reducing the rate of transpiration (Dörffling, 1980). Accumulation of ABA is rapidly induced in plant tissue as it loses turgor (Hartung et al., 1990) and ABA concentration has been suggested as an indicator of the degree of water stress experienced by tissue (Landi et al., 1995). An increase in the concentration of ABA in water-stressed leaves may increase drought tolerance by reducing g_s and consequently plant water loss (Landi et al., 1995). Variation among genotypes in ABA accumulation under drought conditions has been found in maize (Larqué-Saavedra and Wain, 1974, 1976; Pekic and Quarrie, 1988; Tuberosa et al., 1992; Landi et al., 1995).

The objective of this study was to determine if leaf ABA concentrations and g_s in C_0, C_4 and C_8 of Tuxpeño Sequía under drought had been affected by selection, and if these changes bore any relationship to those observed for grain yield and ASI in other studies.

Materials and Methods

Seedlings of C_0, C_4 and C_8 of Tuxpeño Sequía were grown under greenhouse conditions in pots filled with soil. When the seedlings were four weeks old, water supply was suspended and water deficits allowed to develop until the relative water contents (RWC) of the seedlings averaged 60% (water potential of -1.7 MPa). All leaf samples were collected at 0700 h in all experiments. Water potential (Ψw) was determined on the third leaf (fully expanded) with a pressure chamber. The determinations of osmotic potential (Ψs) and RWC were made on the fourth leaf, according to methods described by Larqué-Saavedra and Trejo (1990). One portion of the sampled leaf tissue was used for osmotic potential determinations, while the other portion was used for RWC estimates.

An enzyme immunoassay test (Sigma Company) was used to determine the leaf ABA concentration on samples of the third leaf. Samples had been stored at -20°C following collection. The main vein of the leaf was removed and the central portion of the lamina was lyophilized and ground with 80% methanol, with 10 mg l^{-1} of BTH (butylated hydroxy-toluene) added as antioxidant. Samples were incubated at -4°C for 24 h to extract the ABA. The leaf sample was then centrifuged and the solvent collected and filtered through a reverse phase cartridge to remove lipids and chlorophyll, the cartridge having previously been equilibrated with 5 ml of absolute methanol. Finally, 0.95 ml of tris-buffer saline pH 7.5 (25 mM) and 50 ml of absolute methanol were added and ABA assayed.

Measurements of g_s were made with a portable steady-state porometer (LICOR Model LI-1600). All measurements were on recently expanded leaves near the top of the canopy, with the leaves in full sunlight (ª 1400 mmoles m^{-2} s^{-1} of photosynthetic active radiation). Measurements were repeated each day for 3 d near noon, when conductance was near its maximum. Every day six plants from each replicate of each selection cycle were randomly selected, under drought and under well-watered conditions.

Results and Discussion

RWC of seedlings under drought averaged 60%, while seedlings kept under well-watered conditions had RWCs that averaged about 96% (Table 1). Values for shoot Ψw and Ψs under both treatments are shown in Table 1, and indicate that turgor was almost zero in stressed plants.

Leaf ABA accumulation

Plants with short ASI (C_8) were expected to have a higher leaf ABA accumulation than plants with long ASI’s, because of their tolerance to drought and the suspected association of tolerance with higher concentrations of leaf ABA (Larqué-Saavedra and Wain, 1976; Pekic and Quarrie, 1988; Landi et al., 1995). The cycles of selection however, did not differ in their capacity to accumulate ABA under either well-watered or water-stressed conditions (Table 1). These results suggest that leaf ABA accumulation is independent of ASI.

Stomatal conductance

Increased g_s should maximize productivity, and hence yield, by increasing CO_2 partial pressures within the leaf and hence assimilation rates (Jones, 1987). When leaf ABA concentration increases, stomatal conductance decreases in maize (Beardsell and Cohen, 1975; Ackerson, 1983).

In the present study, g_s under drought conditions did not differ significantly between selection cycles (Table 1). This is consistent with the ABA results, given ABA's role in stomatal control. Conversely, significant differences ($P<0.05$) were found under well-watered conditions (Table 1), suggesting that selection improved g_s under well-watered conditions. Greater g_s in C_8 may lead to lower leaf temperatures (a trait that was directly selected for from C_4 through C_8; Bolaños et al., 1993), and this may have resulted in higher grain yield. Similar results were reported for Pima cotton (*Gossypium barbadense* L.) lines selected to withstand heat (Cornish et al., 1991). The value of g_s was three times higher in a recent line (Pima 70) as compared to a line (Pima 32) released in 1949. Negative associations between canopy temperature and grain yield in wheat under well-watered conditions have also been reported by Sayre (1996).

Table 1. Relative water content, water and osmotic potential, leaf abscisic acid (ABA) accumulation and stomatal conductance (g_s) for C_0, C_4 and C_8 of the maize population Tuxpeño Sequía, observed in greenhouse-grown seedlings.

	Water stress conditions			Well-watered conditions		
	C_0	C_4	C_8	C_0	C_4	C_8
Relative water content (%)	61 ± 0.9	59 ± 2.1	59 ± 1.2	97 ± 0.9	97 ± 0.9	96 ± 0.6
Water potential Ψw (MPa)	-1.7 ± 0.01	-1.7 ± 0.08	-1.7 ± 0.03	-0.39 ± 0.03	-0.38 ± 0.04	-0.37 ± 0.05
Osmotic potential Ψs (MPa)	-1.7 ± 0.05	-1.6 ± 0.02	-1.7 ± 0.03	-0.93 ± 0.02	-1.01 ± 0.02	-0.94 ± 0.04
ABA (ng g^{-1} dry weight)	289.1 ± 23.1	282.3 ± 25.3	289.1 ± 27.7	51.4 ± 10.6	54.3 ± 9.6	56.7 ± 8.1
g_s (mmols m^{-2} s^{-1})	14.9 ± 2.7	15.1 ± 2.2	14.8 ± 2.9	71.2 ± 5.6	64.6 ± 5.0	96.1 ± 6.5

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Selection for Drought Tolerance in a Tropical Maize Population Increases Capacity of Photosynthetic Mechanism to Withstand Drought Stress

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Abstract

An efficient breeding program for drought tolerance is difficult to implement by using the sole criterion of yield performance under stress, therefore, physiological and phenological components of drought tolerance should also be considered during selection. The aim of this study was to investigate the effect of drought stress on leaf net photosynthetic rates in two contrasting selection cycles, C_0 *and* C_8*, of a tropical lowland maize population, 'Tuxpeño Sequía', that had been selected for tolerance to drought in the field. A split-plot design with five replications was used. Time of sampling was taken as main-plots and genotypes as sub-plots. Plants were grown in the greenhouse in gutters using a nutrient film technique. The two genotypes were water-stressed for three months, during which genotypic differences in photosynthesis were monitored. The photosynthetic capacity for the drought-sensitive genotype (*C_0*) was more affected than that of the drought tolerant one (*C_8*), as shown by differences in the* CO_2 *assimilation rate and the inter-cellular* CO_2 *concentration. It was further observed that increasing light intensity under drought stress resulted in a greater increase in the carbon exchange rate (CER) of the drought tolerant population. The authors conclude that CER appears to be one possible parameter that could be used in the identification of drought tolerant maize genotypes.*

An efficient breeding program for drought tolerance is difficult to implement using the sole criterion of yield performance under stress. Breeding for higher yield in drought-prone environments by selecting only for grain yield is difficult because the heritability for yield is low under these conditions and opportunities for the expression of plant characters that influence performance differ from one year to another (Ludlow and Muchow, 1990). Trait-based crop improvement, using physiological and phenological components is an alternative approach for breeding high yielding, drought-adapted genotypes.

Decreases in leaf water potential produce a reduction in the rate of photosynthetic CO_2 assimilation. Although stomatal closure occurs when higher plants are desiccated, chloroplast activity is also modified and, in some instances, may be more limiting to photosynthesis than the reduced CO_2 supply associated with increased stomatal resistance (Cornic et al., 1983). Photosynthesis may be impaired even when stomata remain open (Slavik, 1963), and water stress from increased concentrations of non-penetrating solutes, such as sorbitol, severely inhibits photosynthetic activities of leaf slices in the absence of stomatal control (Kaiser et al., 1981; Kaiser, 1984). It appears that stomatal closure may account for most of the decline in photosynthetic rate in short-term water-stress experiments, whereas non-stomatal inhibition is a major factor in plants gradually subjected to water stress for long periods in the field (e.g., Ackerson et al., 1977; Radin and Ackerson, 1981). Drought stress generally limits net photosynthetic rate, mainly as a result of a reduction in three coupled processes:

1. CO_2 diffusion into the leaves (Fereres et al.,1978; Catsky and Ticha, 1982; Krampitz et al., 1984).

2. Conversion of radiant energy into reduction energy (in the light reactions of PSII and PSI) (Lawlor, 1976; Bjorkman and Powles, 1984; Havaux, et al., 1988).
3. Reduction potential of CO_2 conversion into carbohydrates (taking place in the Calvin-Benson cycle) (Kumar and Gupta, 1986).

Drought tolerant species or varieties distinguish themselves from sensitive ones by their higher photosynthetic rates and, hence, by the maintenance of higher efficiencies among these three sub-processes (Skingh and Tsunoda, 1978). The limitation of CO_2 assimilation in plants, which is indicative of the photosynthetic rate, is attributed largely to internal resistance to CO_2 transfer. This means that, in terms of CO_2 diffusion, resistant plants are characterized by higher stomatal conductance and/or by a faster response of stomatal dynamics to the stress factor which, in turn, is certainly correlated with abscisic acid (ABA) accumulation in the leaf (Davies and Zhang, 1991). Maintenance of photosynthesis may be due to the capacity of genotypes to conserve a good leaf water status and/or to tolerate low leaf water potentials.

Genetic factors also play a part. Planchon (1987) observed a heterosis effect in maize in which photosynthetic rate was better in the hybrid than in parental lines for the same soil water potential under drought conditions. In a separate study eight cycles of full-sib recurrent selection were carried out in the lowland tropical maize population, ‘Tuxpeño Sequía’, under controlled moisture stress in the field, with the stress timed to coincide either with flowering or grain-filling using, among other selection criteria, physiological and morphological traits with presumed adaptive value under drought stress (Bolaños and Edmeades, 1993a). They reported gains in grain yield of around 100 kg ha^{-1} $cycle^{-1}$ from such procedures, but did not evaluate critically the concomitant changes in photosynthetic rate under stress. The objective of this study was to determine if selection for field drought tolerance in maize affected leaf net photosynthetic rate under a water stress induced by a high osmotic concentration of an inert material (polyethylene glycol, PEG) in solution culture. This study was carried out in two contrasting selection cycles, C_0 and C_8, of Tuxpeño Sequía. It was hoped that net photosynthetic rate might prove to be a useful criterion for evaluating drought tolerance.

Materials and Methods

Genetic material

Two elite maize populations from CIMMYT (Tuxpeño Sequía C_0 and C_8) were used. These two maize populations were chosen on the basis of putative differences in yield under drought conditions and response to water stress. Tuxpeño Sequía is a renamed version of ‘Tuxpeño Crema I’ C_{11}, a popular lowland tropical population with high and stable yield, and was chosen in 1975 for a methodological study of selection for improved drought tolerance (Fischer et al., 1983). Previous to this study it had not undergone any improvement specifically for tolerance to water deficits. Tuxpeño Sequía subsequently underwent eight cycles of recurrent full-sib selection for drought tolerance in the virtually rain-free winter crop season at Tlaltizapán (19 °N, 940 masl), Mexico, where timing and intensity of stress can be managed by irrigation.

Experimental design

The experiment was conducted in a split-plot design with the whole plots arranged in randomized complete blocks with five replications. Whole plots were time of sampling (morning and afternoon) and sub-plots were the two genotypes (Tuxpeño C_0 and Tuxpeño C_8).

Growing conditions and water stress treatments

The study was conducted at the State University of Gent in a greenhouse under controlled conditions. Plants were grown in polyethylene pots of 0.2 m diameter, which were filled with vermiculite, an inert rooting medium. The pots were placed in shelved gutters in which a nutrient solution was pumped continuously. A total of 32 plants were grown and received a treatment of polyethylene glycol (PEG) 10000, inducing -0.9 MPa of drought stress. Water stress was induced progressively at a rate of -0.1 MPa d^{-1}. The seeds were sown on 1 August, 1994, and the plants emerged on the 5th of August. Drought induction started when plants were 20 d old, and this is when the first phenological data were collected. A drought stress level of -0.9 MPa was reached after 15 d and measurements were taken.

The temperature during the growing period was kept between 21 and 32 °C, while relative humidity ranged from 50 to 70%. The plants were grown under a 14 h photoperiod with an average of 500 mmol m^{-2} s^{-1} photon irradiance. The nutrient solution pH was maintained between 6 and 6.5. The plants were disease-free and no pesticide was applied. The macronutrient composition of the growth solution was 41.1 g KNO_3, 13.7 g KN_2PO_4, 54.8 g $MgSO_4.7H_2O$, 13.7 g $(NH_4)SO_4$, 35.9 g $Ca(NO_3)_2.4H_2O$ and 4.1 g EDTA. The microelement composition was 0.3 g HBO_3, 0.27 g KCl, 0.17 g $MnSO_4.H_2O$, 0.027 g $ZnSO_4.H_2O$, 0.027 g (NH_4) $6Mo7O_{24}.4H_2O$ and 0.013 g $CuSO_4.5H_2O$. Electrical conductivity (EC) was kept below 2 mS cm^{-1}.

Measurements

Carbon exchange rate (CER) was measured on a fully expanded leaf near the center of the canopy with a portable photosynthesis system (Compact CO_2 / H_20 Porometer CQP-130, HEINZ WALZ) with part of the leaf placed in a cuvette. The photosynthetic system was connected to an infrared gas analyzer (IRGA) which measured CO_2 assimilation rate. CER was measured on a middle-aged, fully expanded leaf of all plant samples in order to assure that measurements were made on tissue of similar physiological age. Other photosynthetic parameters were also determined by the same machine. Net photosynthetic rates were determined at six different photosynthetically active radiation (PAR) photon flux densities, namely 600 (or greater); 250, 125, 50, 25 and 0 mmol m^{-2} s^{-1}. Only results from the water-stressed plants (-0.9 Mpa) are reported here. Data recorded were the transpiration rate per unit leaf area (mmol m^{-2} s^{-1}), CER per unit leaf area (mmol CO_2 m^{-2} s^{-1}), leaf conductance for CO_2 and H_2O per unit leaf area (mmol m^{-2} s^{-1}), and the internal leaf CO_2 concentration (C_i; ppm).

Results

Carbon exchange rate (CER)

Generally, differences ($P \leq 0.05$) were observed between the two lowland tropical maize genotypes and among PAR intensities. In Figure 1, CER is plotted against light intensity for a drought stress of -0.9 MPa to see whether light intensity influences photosynthesis under severe water stress in the two populations. In general, the CO_2 assimilation rate decreased ($P \leq 0.05$) with decreasing light intensity, and was always lower in the drought sensitive Tuxpeño C_0 (Table 1).

It was also observed that plants of the drought sensitive genotype further reduced the photosynthetic rate later in the day (Table 1). This reduction in photosynthetic rate could be attributed either to non-stomatal inhibition of photosynthesis or to a corresponding reduction in stomatal conductance as light intensity was decreased, or to both. Conversely, the photosynthetic rate of the drought tolerant genotype (C_8) was significantly increased in the afternoon, implying that the drought tolerant genotype was still able to translocate its assimilates to various parts of the plant. Under drought stress an increase in irradiance (Fig. 1) would benefit a drought tolerant genotype in terms of its ability to

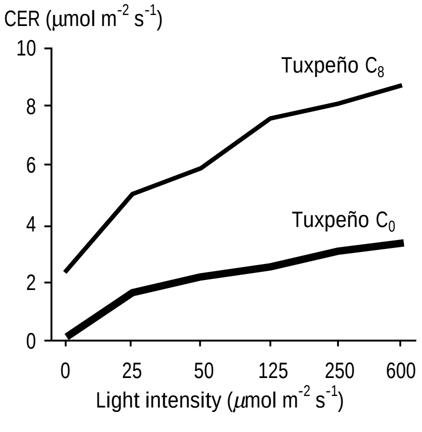

Figure 1. The effects of PAR intensity on CER in two populations of maize differing in drought intensity when grown in a nutrient solution containing PEG 1000 at a ψ = -0.9 MPa.

Table 1. Changes in CER per unit leaf area (μmol CO_2 m^{-2} s^{-1}) in two populations of maize differing in drought tolerance, observed at two times of the day under varying light intensities when grown in a nutrient solution containing PEG 1000 at a ψ = -0.9 MPa.

PAR intensity (μmol m^{-2} s^{-1})	C_0			C_8		
	Morning	Afternoon	Mean	Morning	Afternoon	Mean
600	3.54	3.21	3.36	8.47	9.15	8.81
250	3.55	2.60	3.08	7.27	9.01	8.14
125	3.10	1.95	2.52	7.06	8.17	7.61
50	2.98	1.39	2.18	4.62	7.12	5.87
25	1.96	1.34	1.65	4.02	5.98	5.00
0	0.04	0.21	0.26	0.07	4.66	2.37
Mean	2.53	1.78	2.16	5.25	7.52	6.39

$LSD_{0.05}$: Genotypes = 0.93
CV (%): Genotypes = 23.96

$LSD_{0.05}$: Time of sampling = 0.91
CV (%): Time of sampling = 14.36

maintain a reasonable photosynthesis rate. However, this observation may not apply to other cultivars whose physiological adaptations to drought stress are governed by other mechanisms.

In the field, water stress often occurs simultaneously with high irradiance and heat, which predisposes plants to photoinhibition and leads to a decrease in mesophyll photosynthesis. It is not clear whether photoinhibition is the basic cause of that decrease in C_0, or whether alterations in the primary photochemistry processes represent an adjustment to a previous impairment of carbon metabolism (Chaves, 1991).

Intercellular CO_2 concentration (C_i)

There were non-significant differences in C_i between the two genotypes at $\psi = -0.9$ MPa, though significant differences were observed between sampling times and among light intensities (Table 2). The C_i for both genotypes decreased with decreasing photon flux density when determined both in the morning and afternoon. However, this decline was more in the drought sensitive genotype than in the tolerant one. It was further observed that when light was completely withheld, the C_i for both genotypes increased. It can therefore be stated that the increase in C_i is a result of increased stomatal conductance which can be enhanced by increasing light intensity. It is normally assumed that an increase in intercellular CO_2 is associated with an increase in CER. There was, however, a significant negative correlation ($r=-0.76$, $P \leq 0.05$) between C_i and CER for C_8, though not for C_0.

Leaf CO_2 conductance

Differences ($P \leq 0.05$) were observed for CO_2 conductance between genotypes, sampling time, and among PAR intensities (Table 3) at y = -0.9 Mpa. Higher values of leaf CO_2 conductance were observed in the drought tolerant Tuxpeño C_8 than in the drought sensitive Tuxpeño C_0. The effect of light intensity on leaf CO_2 conductance was shown by varying light intensity, and a decrease in leaf CO_2 conductance was observed as light intensity decreased. This also shows that increased light intensity enhances photosynthesis under drought stress conditions by increased CO_2 uptake resulting from increased stomatal aperture, though in the presence of higher temperatures this may not be the case. Both CO_2 and H_2O conductance decreased with decreasing irradiance, thus confirming the role that increased light intensity plays in enhancing photosynthesis under drought stress conditions coupled with non-severe temperatures. There was a close linear relationship ($P < 0.05$) between CER (mmol m^{-2} s^{-1}) and leaf CO_2 conductance (mmol m^{-2} s^{-1}) (for C_8: CER = 0.095 + 0.255 (conductance); r = 0.99; and for C_0: CER = -0.077 + 0.245 (conductance), r= 0.98).

Discussion

The results obtained by Bolaños and Edmeades (1993a, b) suggest that responses to selection in grain yield, ASI and harvest index were not consequences of improved water relations, but rather were due to

Table 2. Changes in internal CO_2 concentration (C_i) (ppm) in two populations of maize differing in drought tolerance, observed at two times of the day under varying light intensities when grown in a nutrient solution containing PEG 10000 at $\psi = -0.9$ MPa.

PAR intensity	C_0			C_8		
(μmol m^{-2} s^{-1})	Morning	Afternoon	Mean	Morning	Afternoon	Mean
600	216	262	239	99	54	86
250	131	189	160	167	26	96
125	101	54	78	161	16	88
50	88	28	58	154	10	82
25	43	13	28	146	4	75
0	323	147	235	343	99	221
Mean	150	115	133	194	35	115

$LSD_{0.05}$: Genotypes = 42.60 CV (%): Genotypes = 37.8

$LSD_{0.05}$: Time of sampling = 63.24 CV (%): Time of sampling = 34.4

Table 3. Changes in CO_2 conductance (μmol m^{-2} s^{-1}) of two populations of maize differing in drought tolerance, observed at two times of the day when grown in a nutrient solution containing PEG 1000 at a $\psi = -0.9$ MPa.

PAR intensity	C_0			C_8		
(μmol m^{-2} s^{-1})	Morning	Afternoon	Mean	Morning	Afternoon	Mean
600	14.7	15.3	15.0	33.7	30.9	32.3
250	13.6	8.6	11.1	39.7	27.8	33.8
125	14.3	6.6	10.4	36.0	23.1	29.6
50	13.5	6.8	10.2	26.1	18.4	22.2
25	10.1	3.2	6.6	21.3	15.1	18.2
0	1.7	1.0	1.4	9.3	10.4	9.8
Mean	11.3	6.9	9.1	27.7	20.9	24.3

$LSD_{0.05}$: Genotypes = 3.61 CV (%): Genotypes = 23.73

$LSD_{0.05}$: Time of sampling = 4.40 CV (%): Time of sampling = 17.76

improved partitioning of biomass toward the female inflorescence at flowering. These findings are consistent with the present study, where differences in the plant's water status between C_0 and C_8 were not detected (data not shown). The biochemistry of photosynthesis was affected by drought in both genotypes, but more so in the drought sensitive genotype. The photosynthetic activity is probably limited by a reduction of CO_2 allocation to chloroplasts, as can be seen from rates of CO_2 assimilation, especially, of the drought sensitive cultivar (Table 1).

Our results further show that the effects of irradiance level and water status on the photosynthetic apparatus interact strongly, and suggest that water-stress effects are in part attributable to photoinhibition. It was shown that increasing light intensity under drought stress increased the photosynthetic rate of the drought tolerant genotype, but the photosynthetic machinery of the drought sensitive genotype was probably damaged by the prolonged drought intensity of -0.9 MPa. Net photosynthesis for these two genotypes was decreased, more so in the drought sensitive one, via partial stomatal closure. At $\psi = -0.9$ MPa stomata were partially closed (data for unstressed controls not presented) and there was a concomitant increase in C_i (Table 3), indicating a decrease in carboxylation efficiency. Non-stomatal effects on photosynthesis under drought are therefore important. If stomatal closure were the sole cause of a decrease in photosynthesis, a decrease in the ratio of internal to external CO_2 concentration would be expected, with a concomitant increase in transpiration efficiency (Farquhar and Richards, 1984).

The difference in performance between C_0 and C_8 under water stress was largely due to the ability of the drought tolerant genotype to partition more assimilates towards the ear (Bolaños and Edmeades, 1993b). However, selection for drought tolerance in this population did not change the water status of the crop, but instead it increased the capacity of the photosynthetic mechanism to withstand drought stress. Thus the CER observed under a level of drought stress that was the same for all genotypes appears to be one possible parameter that could be used in the development of drought tolerant maize cultivars in the future.

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Value of Secondary Traits in Selecting for Drought Tolerance in Tropical Maize

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Abstract

The use of adaptive traits which are secondary to the primary trait, grain yield, when improving drought tolerance is often advocated, even though their relationships to yield and their contribution to increased yield under water deficits are poorly quantified. Secondary traits should be (i) genetically variable and genetically associated with grain yield in the target environment; (ii) highly heritable; (iii) easy to measure; (iv) observed at or before flowering; and (v) provide an estimate of yield potential well before final harvest. The value of secondary traits can be established by correlation analysis, by comparison of near-isogenic lines, or by divergent selection for the trait of interest. Secondary traits examined thus far at CIMMYT include anthesis-silking interval (ASI), leaf and stem elongation rate under drought versus well-watered conditions (RLE), canopy temperature (CT), leaf rolling and erectness scores (LRS; LES), leaf chlorophyll concentration (CHL), staygreen score (LDS), tassel size (TS), leaf osmotic concentration (OSM) and lodging (LOD). Relationships between yield and yield components (weight kernel^{-1}, kernels ear^{-1}, ears plant^{-1} (WPK, KPE, EPP)) have also been determined. Correlations between some of these traits and grain yield under drought are: large (0.5-0.9) for EPP, KPE, PH, TS, and ASI; low (0.1-0.4) for WPK, CT, LDS, CHL and OSM; and <0.1 for LOD, LRS, RLE, LES and TBN. Divergent selection (4% selection intensity in each direction) showed that realized heritability and adaptive value of ASI and EPP were high (not higher than yield alone, however), while those for LDS and CT were low. LES, TS and OSM had little effect on yield, though LES and TS were highly heritable and OSM moderately so. Results suggest that selecting for a combination of these traits in addition to yield should result in faster improvements in yield and yield stability under drought compared with selection for yield alone, and possibly at no cost to yield under well-watered conditions.

Introduction

The use of secondary traits (the primary trait is usually grain yield) as selection criteria in crop breeding has often been suggested, yet the contribution of these traits to increased grain yield under stress has generally been poorly quantified. Many secondary traits have been proposed, all putatively related to improved survival or improved production in water-stressed environments, or to both (Edmeades et al., 1987; Ludlow and Muchow, 1990; Richards et al., 1993; Fukai and Cooper, 1995). For analysis it is useful to consider grain yield under drought stress as the product of [amount of water transpired * water-use efficiency (WUE) * harvest index] (Passioura, 1977), and to classify secondary traits according to which of these components they affect (Ludlow and Muchow, 1990).

Traits can be generally classified as those contributing to escape or tolerance. Earliness, for example, allows the crop to avoid terminal drought, and may also allow the crop to avoid coincidence between flowering and a mid-season dry spell such as the *canicula* that often affects maize production in Central America. The matching of crop development to the pattern of rainfall is perhaps the single most important breeding goal for rainfed environments (Bidinger et al., 1987; Muchow et al., 1994). Since earliness can be easily modified through conventional breeding techniques, we have concentrated on traits which allow the plant to *tolerate* drought; i.e., the ability to produce relatively high grain yields despite showing symptoms of water deficit.

Putative secondary traits associated with drought tolerance

Traits which have been suggested as contributing to drought tolerance are those which focus on :

1. Modified timing of supply and / or increased quantity of water available to the plant for transpiration through stomates. Because of the close relationship between water transpired and biomass produced (Tanner and Sinclair, 1983), increased water supply under drought enhances the general supply of assimilates to the plant. Examples of traits indicative of water availability at specific growth times under a given set of environmental conditions are rooting depth, intensity and root health (O'Toole and Bland, 1987); root pulling resistance as an indicator of root depth; ABA concentration (as it affects rooting behavior), degree of leaf area loss under drought; degree of leaf rolling; osmotic adjustment (Bolaños and Edmeades, 1991); low canopy temperature indicating continued transpiration (Fischer et al., 1983); predawn water potential (as a measure of root depth); increased hypocotyl extension that permits deep seeding on residual water supplies (Collins, 1914); and the plant's modification of the water flux through changes in hydraulic conductivity, leaf area, stomatal or cuticular conductance. The quantity of water transpired is also affected by traits which affect survival; e.g., improved seedling germination and survival under drought; low lethal water content, ABA concentration (Larqué-Saavedra and Wain, 1976; Pekic and Quarrie, 1987), and reduced photo-oxidation.
2. Increased water use efficiency: WUE is inversely proportional to the vapor pressure deficit, and is large when the proportion of fixed C used as respiration is low, or when the ratio of intercellular and atmospheric partial pressures (p_i / p_a) of CO_2 is high (Tanner and Sinclair, 1983). Thus WUE is highest in cool growing conditions, and varies within and among species (Condon and Richards, 1992; Richards et al., 1993). WUE is affected by traits such as those affecting tolerance of stress-induced injuries; e.g., high ratio of variable fluorescence (Fv) to maximal fluorescence (Fm) (Selmani and Wassom, 1993; Keeling and Greaves, 1990), high temperature tolerance, and the increase in osmolytes and heat shock proteins which may protect enzyme and membrane function under stress. WUE is directly affected by photosynthetic efficiency (Krieg and Hutmacher, 1982) and erect (vs. lax) leaves.
3. Increased harvest index: traits such as those which indicate a greater partitioning of assimilate supply to the growing ear at flowering; e.g., short anthesis-silking interval, rapid ear growth rate (Dow et al., 1984; Edmeades et al., 1993), reduced plant height (Fischer et al., 1983) and smaller tassels (Bruce at al., 1966) which compete less with ear growth at flowering, barrenness (measured as ears per plant (EPP) < 1.0) (Bolaños and Edmeades, 1993a), and traits which contribute to enhanced grain filling under terminal stress, such as the ability to mobilize preanthesis assimilate to grain (Nicolas and Turner, 1993) and delayed leaf senescence (Wolfe et al., 1988).

Clearly these classifications overlap strongly; for example, osmotic adjustment might be expected to increase assimilate supply during grain filling *and* delay leaf senescence. Traits may be measured directly, but for reasons of cost and convenience are often measured indirectly, as in the use of canopy temperature as a surrogate for enhanced water capture by the plant, or kernel weight as an integrator of factors contributing to enhanced grain filling. As noted by Ludlow and Muchow (1990), the selection of traits by a breeder will depend on the environment the plant faces. If terminal drought dominates the target environment, then traits affecting grain filling will be more important. If stress occurs mainly at establishment, then traits which affect seedling survival will have priority. The likelihood of stress at flowering will mean that traits which affect ear formation and barrenness will need greater emphasis.

In maize, drought at or around flowering arguably reduces productivity more than drought occurring at other times in the crop cycle. Losses to drought during establishment, for instance, can be offset by replanting, but stress at flowering, if severe, can eliminate grain yield completely (Denmead and Shaw, 1960), and the season is usually too far advanced at that stage to consider replanting or sowing an alternative crop of shorter duration.

Criteria for usefulness of secondary traits

Secondary traits should be:

1. Genetically variable and genetically associated with grain yield in the target environment, though if the correlation between the trait and yield is near 1.0 then it is usually simpler and cheaper to measure yield alone.
2. Highly heritable. If the product of square root of heritability of the secondary trait and the genetic correlation between the secondary trait and grain yield exceeds the square root of the heritability of grain yield, then faster progress for grain yield can be made by selecting for the secondary trait alone (Falconer, 1981).
3. Cheaper or faster to measure than grain yield.
4. Observed at or before flowering, since this allows the breeder to eliminate drought-susceptible lines from his crossing nursery and shorten the time to complete a selection cycle.
5. Able to provide an estimate of yield potential before final harvest. If, for example, grain yield under drought is strongly related to barrenness, and anthesis-silking interval (ASI) is a good indicator of barrenness (Bolaños and Edmeades, 1993b), then ASI may be a better measure of yield potential under drought than yield itself, if yield is affected by disease, lodging, cold, etc., during grain filling.

Most breeding programs use a combination of secondary traits and grain yield to develop a selection index used to identify superior genotypes (e.g., Bolaños and Edmeades, 1993a). It is important to note that no secondary trait will increase the efficiency of selection for drought tolerance unless its genetic variation is exposed by the environment under which the crop is growing (Bolaños and Edmeades, 1996).

Determination of the value of secondary traits

The value of secondary traits used in selection can be established by:

1. Correlation (phenotypic, r_P and genotypic, r_G) analysis, though outlying values can strongly affect the correlation. Data should be examined graphically to identify and perhaps discard outliers. Genetic correlations are the correlation of the additive genetic components of the two traits (Falconer, 1981), freed from the environmental correlations that are included in phenotypic correlations. Continued selection for secondary traits may result in a change in the underlying genetic correlation between traits (Falconer, 1981; McMillan et al., 1995), so these relationships require re-evaluation over time.
2. Utilizing the theory of selection indices (Falconer, 1981), where combinations of secondary traits and genetic correlations are used to optimize weights placed on each trait to maximize overall gain in grain yield and to determine potential gains obtained from selecting for an index of secondary traits plus grain yield versus selection for grain yield alone — see, for example, Bänziger et al. (1997), for an examination of secondary traits used in selecting for improved performance under low N. This approach is computationally demanding but theoretically rigorous.
3. Comparison of near-isogenic lines differing for the trait of interest. Developing such lines is time-consuming and expensive, and they are often not sufficiently isogenic to provide conclusive evidence about the value of a trait.
4. Divergent selection (DS) within a population for a trait of interest. This approach is well-suited to recurrent selection schemes in maize populations, which in CIMMYT's case are usually structured as 170-240 S_1 or full-sib families. A small fraction (usually 10 families with the largest values for the trait of interest but values for other traits, such as flowering date, similar to population means) is identified and the selected families intercrossed and advanced to F_2. The process is repeated for a similar sized fraction with the smallest values for the trait, and a bulk is made from all families representing the population itself and advanced to F_2. These three subpopulations

represent the two extremes of the population and the population mean for the trait of interest. These are then re-evaluated under drought, and the secondary trait and grain yield observed. This approach provides information on the adaptive value and the realized heritability of the trait. It suffers, however, from "noise" arising from differences in specific combining ability among the families used in each fraction, and can result in a distorted measure of the value of the trait; the yields of the two extreme subpopulations may both be less than that of the population bulk, for example. When repeated over many selection cycles and populations, however, this method provides a relatively consistent measure of adaptive value and realized heritability at a lower cost than developing near-isogenic lines.

In the discussion presented in the remainder of this paper, approaches 1 and 4 will be described for a group of traits measured among S_1 or full-sib maize progenies under two or more levels of drought stress.

Methods and Materials

Correlation analysis

This is described in detail elsewhere (Bolaños and Edmeades, 1996). In brief, genetic correlations were computed from 20 sets of a total of 3,509 inbred progenies adapted to the lowland tropics, grown in 50 trials under two or three water regimes at Tlaltizapán, Mexico, in the dry winter season. Three water regimes were established: a) well-watered (WW); b) intermediate or grain filling stress (IS), where irrigation was suspended permanently about 12 d prior to anthesis; and c) severe stress (SS), where irrigation was suspended about 25 d prior to anthesis until mid-grain filling, when one additional application was made.

Measurements - Stem-leaf extension rate (RLE) was measured in 13 trials in the SS and WW treatments, beginning about 15 d prior to flowering. The youngest visible leaf in the whorl of 4 plants per plot was marked by cutting 5 cm off the leaf tip. The height from ground to cut tip was measured, and one week later the measurement repeated on the same leaf. The absolute increment in height under drought was divided by that under well-watered conditions for the same family and the replicate to give RLE. Dates of 50% anthesis (AD) and 50% silking and the anthesis-silking interval (ASI) were recorded in all trials. Where plots failed to reach 50% silking approximately 20 d after 50% anthesis, they were declared missing values. Canopy-to-air temperature differentials (CT) were determined by taking 2-3 readings of sunlit leaves near the center of each plot in four trials, using a hand-held infrared thermometer between 1200-1500 h on mainly hot, clear, still days. Chlorophyll concentrations (mg cm^{-2}) of fully-exposed upper leaves were measured using a portable chlorophyll photometer on 1-3 occasions during the latter half of grain filling. Measurements were taken from near the center of one leaf (avoiding the central midrib) from each of 6 plants per plot. Visual scores of leaf rolling were recorded from each plot under drought in 20 trials on 1-2 occasions before anthesis, when differences in leaf rolling were obvious. Scores of leaf senescence of lower leaves were taken in each plot of 35 trials on 2-3 occasions about 7 d apart, towards the end of grain filling. In WW plots of 21 trials leaf erectness scores were recorded at one time immediately prior to anthesis. All scores were on a scale of 1 (unrolled, green or erect) to 5 (rolled, dead, or lax). Three weeks after anthesis plant height (from ground to point of flag leaf insertion) was measured in 19 trials and the number of primary tassel branches counted on 4 plants per plot in the WW treatment of 13 trials. At maturity, lodged plants and ear number were counted, and EPP and grain yield calculated in all 50 trials. The oven-dry weight of 100 grains was used to determine weight kernel^{-1} and kernels plant^{-1} in 42 trials, and kernels ear^{-1} in 40 trials.

Genetic correlations (r_g) among traits were computed for each trial and averaged. In order to show the effects of increasing water stress on r_g separated from the effects of heterosis, r_g values from 11 sets of S_1 progenies (2489 in total) were averaged by water regime. Phenotypic correlations (r_p) between grain yield under severe stress and secondary traits were computed by bulking all data from these same 11 sets of progenies.

Divergent selection

This was undertaken within the S_1 families making up several cycles of selection in a number of populations for traits or groups of traits.

Evaluations of progenies and measurements of variables were as described above. The total number of progenies evaluated in any single trial ranged from 166 to 250. Osmotic concentration was measured at pre-dawn in plants from three populations, and pre-dawn leaf water potential in one population. At the time of measurement plants were showing signs of leaf rolling at midday and were near 50% anthesis (Bolaños and Edmeades, 1991). Disks 5 cm in diameter were punched from 1-2 upper leaves on 6-10 plants per family, bulked, wrapped immediately in a plastic bag, frozen, and within a few days, thawed, the sap mechanically extracted and its osmolality determined using a Wescor 5100 vapor pressure osmometer. Predawn leaf water potential was measured in four of the uppermost fully-expanded and exposed leaves per plot. In the early morning (0500-0700 hours) leaves were cut and wrapped in moist cheesecloth, and within 2 minutes the balancing pressure required to express xylem sap was determined on the central mid-rib using a pressure chamber accurate to 0.05 Mpa.

Selection for the best and worst fraction for a specific trait or group of traits was carried out using Selection Assistant software (see Barreto et al., 1997). The "best for all traits" selection was based on the selection index or ideotype used to identify superior families for recombination during recurrent selection (Bolaños and Edmeades, 1993a). Grain yield, ears per plant, ASI and anthesis date were the traits weighted most heavily in this ideotype. Every attempt was made to select 10 families with the largest or 10 with the least values for the trait of interest, yet which had mean flowering dates and plant heights that were within 1.5 d or 0.15 m of the mean of the population. The 10 S_1 families selected were sown from remnant seed in a single 5 m-long row (21-26 plants / family), and the families intercrossed in all possible combinations and balanced so each family contributed roughly the same number of crosses. In forming the cycle, we bulked three remnant seed samples from each S_1 family, sowed the bulk as 250-300 plants, and intercrossed plants. In all synthetics, selected ears were bulked to form the F_1, 250 F_1 individuals were planted out and intercrossed, and 150-200 ears were then bulked to form the F_2 seed used in evaluation trials.

Evaluation of synthetics selected divergently for traits normally occurred under the three water regimes (WW, IS and SS) described above, over one or two seasons at Tlaltizapán, Mexico. Typically trials were sown in plots of 2-3 rows 5 m in length at a density of 5.3-6.6 plants m^{-2} in alpha (0,1) lattice or randomized complete block designs with 3 replications per water regime. In the case of osmotic concentration and pre-dawn leaf water potential, evaluation took place under a line-source irrigation scheme. The water gradient from the irrigation line was divided into 4 hydric regions differing in water availability (Bolaños and Edmeades, 1991). Yield data indicated the adaptive value of each trait or group of traits, while the observed value of the trait in the synthetics, relative to that expected from the progenies that formed those synthetics, provided an estimate of realized heritability. In one case (osmotic concentration) realized heritability was formally computed by dividing the percent gain over the mean of all synthetics in the evaluation trial by the percent gain of the progenies over their population mean (Bolaños and Edmeades, 1991). Evaluations reported here are of divergently selected synthetics from C_0 of Pool 26 Sequía, Pool 18 Sequía and TS6; a group of synthetics selected for high and low osmotic content in Pool 16 Sequía C_1, Pool 18 Sequía C_1 and TS6 C_0; high and low predawn leaf water potential in Pool 26 Sequía C_1;and synthetics from successive cycles of selection of La Posta Sequía, C_0, C_1, C_2 and C_3.

Results and Discussion

Correlation analysis

Grain yield under drought stress showed a strong genetic association with EPP, kernels per plant, kernels per ear, AD and ASI; a moderate degree of association with leaf senescence score, leaf chlorophyll concentration, plant height and CT; virtually no consistent association with lodging, leaf rolling score, leaf erectness, RLE and tassel branch number (Table 1). Phenotypic correlations were broadly similar in magnitude and sign to genetic correlations. As stress levels increased, grain yield became increasingly dependent on EPP, kernels per plant, AD and ASI, and less on weight per kernel and leaf chlorophyll concentration.

The negative association between AD and grain yield is characteristic of the winter cropping season, where later flowering families encounter hotter conditions during grain filling than those which flower earlier. Additionally, when water is withdrawn in the IS and SS treatments, early flowering families encounter less stress during flowering than those which flower later. Since the flowering period is the growth stage of maize at which it is most sensitive to drought, early flowering families generally yield better than those which flower later. This emphasizes the need to monitor the flowering dates of progenies under selection for improved drought tolerance in order to avoid selecting a fraction which simply escapes drought because it is earlier flowering (Bidinger et al., 1987). Similarly, leaf senescence scores are also affected by maturity and should be adjusted for AD accordingly. When selection is based on grain yield alone under these conditions, our experience suggests that populations can become up to 2 d earlier to flower per selection cycle. In a different selection environment (such as a dry summer), these associations between grain yield and maturity are expected to be less strong. The genetic association observed between leaf senescence score and grain yield was low but negative under well-watered conditions (slow senescence favored high yield), and became low but positive under drought stress, suggesting that N released by more rapid leaf senescence may contribute to increased grain yield in these dry soils where N movement to roots is limited (Wolfe et al., 1988).

Table 1. Effects of water regime on genetic correlations (r_g) of grain yield with several secondary traits for 3509 inbred (S_1 - S_n) maize progenies from up to 50 trials, and separately for 2489 S_1 progenies from 32 trials. Water regimes were well-watered (WW); drought during grain filling (IS); drought during flowering and grain fill (SS). Progeny trials were grown at Tlaltizapán, Mexico, between 1986 and 1990. Standard deviations of r_g estimates are computed from mean values obtained from each trial. Phenotypic correlations (r_p) were computed for grain yield under the SS regime and secondary traits for a single group comprising all S_1 progenies grown in 11 trials (adapted from Bolaños and Edmeades, 1996).

Trait	Mean of all genetic correlations	r_g, S_1 progenies			r_p, S_1 progenies yield, SS^{e}
		WW	IS	SS	
Ears plant^{-1}	0.73±0.19	0.58	0.82	0.90	0.77
Kernels ear^{-1}	0.75±0.13	0.71	0.78	0.71	0.50
Kernels plant^{-1}	0.84±0.13	0.79	0.88	0.86	0.90
Weight kernel^{-1}	0.22±0.16	0.23	0.20	0.14	0.46
Days to anthesis	-0.47±0.18	-0.32	-0.56	-0.58	-0.40
Anthesis-silking interval	-0.48±0.21	-0.42	-0.64	-0.60	-0.53
Lodging percentage	0.04±0.22	0.10	0.16	-0.03	-^{a}
Leaf rolling score	-0.08±0.18	-^{b}	-0.10	-0.03	-0.18
Leaf senescence score	0.07±0.18	-0.09	0.15	0.14	-0.11
Leaf erectness score	0.02±0.17	0.07	-^{c}	0.00^{d}	-0.18
Leaf-stem extension rate	-0.11±0.29	-0.10	0.42^{d}	-0.08	0.10
Canopy-air temperature diff.	-0.22±0.11	0.26^{d}	-^{b}	-0.20	-0.27
Tassel branch number	-0.02±0.24	-0.14	-^{c}	-^{c}	-0.16
Leaf chlorophyll conc.	0.15±0.16	0.19	0.21^{d}	0.11	0.17
Plant height	0.29±0.21	0.24	-^{c}	-^{c}	NS

[a] Missing value
[b] Trait only measured under SS or IS water regimes
[c] Trait only measured under well-watered regime, or a single value obtained for two regimes
[d] Data available only from one trial
[e] Degrees of freedom range from 905 to 2449; all correlations significant at $P < 0.01$

There is a clear dependency of grain yield on kernels per plant and this is mediated through EPP and less through kernels per ear. Drought induces barrenness, and a symptom of impending barrenness is an increase in ASI (Dow et al., 1984; Bolaños and Edmeades, 1993b; Edmeades et al., 1993). Thus we see a strong dependence of grain yield under stress on ASI. Around 25-35% of the variation in grain yield under stress is associated with variation in ASI, leaving 65-75% of the variation in grain yield to be explained by other causes.

The weak association of grain yield with traits such as leaf erectness, leaf senescence score, RLE, lodging, leaf rolling score, and canopy-air temperature differential is consistent with the lack of progress for these traits in the population Tuxpeño Sequía when it was subject to eight cycles of recurrent selection for improved performance under drought (Bolaños et al., 1993). That study, however, observed a small but significant correlated reduction in tassel size even though this trait had not been subject to selection (Bolaños and Edmeades, 1993b). Smaller tassels may, therefore, have adaptive value under drought, despite the lack of association between tassel size and grain yield observed in this study.

Divergent selection

The realized heritability of several traits was estimated in a study of synthetics developed from a single selection cycle in three populations (Table 2). It was expected that the best synthetics would have: higher RLE, lower air-canopy temperature differentials (CT); more upright leaves; a slower rate of senescence; a higher leaf chlorophyll concentration; a shorter ASI; and smaller tassels, when compared with the cycle bulk or with the worst selection. This was not true for RLE, CT and leaf chlorophyll concentration, but was consistently true for the traits leaf erectness; tassel branch number; ASI and leaf senescence score. We conclude that these latter four traits, which are mainly related to partitioning and morphological differences, are highly heritable, and should show consistent responses to selection. Data presented by Bolaños and Edmeades (1993a, b) and Fischer et al. (1987) confirm the heritablity of tassel size and ASI. The complex interaction of leaf senescence with N nutrition under drought apparently has masked changes in staygreen with selection, though they are apparent when selection cycles are evaluated under different levels of N availability (see Lafitte et al., 1997).

Heritability of a trait does not imply that it is of adaptive value under drought. Bolaños and Edmeades (1991) demonstrated that it was possible to select for increased levels of osmotic concentration in three populations (Table 3). This trait had a realized heritability of 0.58 for reduced levels of osmotica and 0.34 for increased levels of osmotica. Synthetics differing in level of osmotic potential did not, however, show differing grain yields under a drought stress imposed by a line source irrigation system. Under severe stress there was a tendency for the cycle bulk to outyield both of the divergent synthetics, suggesting that both represented abnormal conditions. Osmotic adjustment results in a decrease (i.e., more negative) in osmotic potential under stress, but does not appear to have an adaptive value for maize under Tlaltizapán conditions (but see Chimenti et al., 1997 for contrasting results), and genotypes exhibiting high levels of osmotica may simply be those whose growth under drought has slowed more than others.

Table 2. Responses of experimental synthetics and the cycle bulk when evaluated under appropriate levels of water stress during the dry winter season at Tlaltizapán, Mexico, in 1990. Synthetics were formed following divergent selection among S_1 families of three lowland tropical maize populations for several physiological or morphological traits. Based on the value of the traits observed in best and worst fractions, compared with the cycle bulk, the trait was classified for realized heritability.

Trait	Cycle bulk	Best selection	Worst selection	Heritable?
Pool 26 Sequía C_0				
RLE[a]	0.58	0.54	0.61	No
Canopy temp. diff. (°C)	0.86	0.52	0.22	No
Leaf erectness score[b]	3.00	2.56	3.33	Yes
Leaf senescence score[c]	4.25	3.69	4.98	Yes
Pool 18 Sequía C_0				
RLE[a]	0.62	0.65	0.75	No
Canopy temp. diff. (°C)	-0.98	-1.78	-1.78	No
Leaf senescence score[c]	3.84	3.70	4.03	Yes
Chlorophyll conc. (µg cm^{-2})	52.6	49.3	47.8	No
Anthesis-silking interval (d)	5.5	3.0	11.5	Yes
Tassel branch number (no)	18.8	12.9	22.9	Yes
TS6 C_0				
Stem and leaf extension[d] (cm)	32.3	33.4	36.9	No
Leaf erectness score[b]	3.63	2.75	3.88	Yes
Leaf senescence score[c]	3.29	2.61	3.81	Yes
Chlorophyll conc. (µg cm^{-2})	63.0	60.7	64.4	No
Anthesis-silking interval (d)	7.9	0.4	15.9	Yes

[a] Extension [stem + leaf] under drought relative to well-watered control. Large values are best.

[b] Scores: 1 is upright; 5 is lax

[c] Scores: 1 is completely green; 5 is completely senesced

[d] Extension [stem + leaf] under drought. Large values are considered best.

The adaptive value of traits was explored in divergent synthetics developed in Pool 26 Sequía C_{0-1} and in La Posta Sequía C_{0-3} (Tables 4, 5). In the first of these studies the “best for all traits” was clearly superior to the worst under all yield levels (Table 4). Selection for improved grain yield alone under stress resulted in a non-significant yield loss under well watered conditions, but the reverse was also true. Erect leaves, cool canopy temperatures, and short ASI were all superior to their lax, warm or long ASI counterparts, but did not give yields under stress that were greater than

Table 3. Solute potentials (ψ_s) and grain yields of synthetics formed from 10 S_1 progenies having either the greatest or the least solute potential, when evaluated under drought stress at Tlaltizapán in 1990. Divergent selections for ψ_s were made in three lowland tropical populations under drought stress in 1989 (adapted from Bolaños and Edmeades, 1991).

A: Osmotic potentials (ψ_s)

Population	Selection differential		Response differential		Realized heritability
	Mpa	% of mean	MPa	% of mean	
For low ψ_s					
Pool 16 Sequía C_1	0.18	13.1	0.10	7.1	0.54
Pool 18 Sequía C_1	0.17	12.7	0.13	8.9	0.70
TS6 C_0	0.22	15.2	0.10	7.4	0.49
Mean for low y_s					0.58
For high ψ_s					
Pool 16 Sequía C_1	0.16	11.3	0.04	2.5	0.22
Pool 18 Sequía C_1	0.16	12.4	0.07	5.2	0.42
TS6 C_0	0.17	11.7	0.06	4.5	0.39
Mean for high ψ_s					0.34
Mean realized heritability					0.46

B: Grain yields when evaluated in four hydric (H) regions of a line source irrigation system

	H1	H2	H3	H4	Mean
			t ha^{-1}		
High ψ_s selection	1.55	1.97	2.92	4.19	2.66
Low ψ_s selection	1.55	1.71	2.55	4.01	2.46
Cycle bulk	1.83	2.06	2.52	4.08	2.62
S_d	0.43	0.37	0.50	0.48	0.22
Mean	1.64	1.91	2.66	4.09	2.58

Table 4. Grain yield, grain yield relative to Pool 26 Sequía C_0 (/C_0), and anthesis-silking interval (ASI) of synthetics of Pool 26 Sequía C_0 derived from the 10 best and worst S_1 families for a specific trait or group of traits. Trials of progenies were conducted under well-watered (WW) conditions and under a severe moisture stress (SS) that coincided with flowering and grain filling at Tlaltizapán in 1986; the synthetics were evaluated under similar conditions in 1988 (adapted from Edmeades et al., 1989).

Synthetic	Grain yield				ASI$_{SS}$ (d)
	WW (t ha^{-1})	WW/C_0	SS (t ha^{-1})	SS/C_0	
Pool 26 Sequía C_0	4.93	100	1.58	100	2.0
Best for all traits	5.19	105	2.37	150	4.0
Worst for all traits	3.72	75	0.60	38	8.0
Best yield under stress	4.59	93	2.00	127	2.0
Best yield under irrigation	5.14	104	1.07	68	8.0
Shortest ASI	4.67	95	1.59	101	4.0
Longest ASI	3.50	71	0.86	54	8.0
Coolest canopy temperature	4.20	85	1.46	92	3.7
Warmest canopy temperature	3.95	80	1.09	69	6.0
Erect leaves	4.42	90	1.58	100	2.0
Lax leaves	3.70	75	1.13	72	4.0
LSD (0.05)	1.07		1.12		5.5
Significance	$P<0.05$		NS		$P<0.05$

the cycle bulk. This illustrates a point which has become increasingly apparent during this type of divergent selection: gains are almost always asymmetric, being greater in the “worse” direction than in the “best” direction. The “best for all traits”, however, was non-significantly better (by 50%) under stress than the cycle bulk, 19% better than the selection based on yield under drought alone, and 13% better under irrigation than the selection based on well-watered yield alone. These data suggest that traits other than yield may contribute around 15-20% improvement in gain during recurrent selection, a figure similar to that reported by Bänziger and Lafitte (1997) under low N.

The absence of association between canopy-air temperature differential and grain yield is disappointing, and relates to the low genetic correlation between these traits (-0.2) and the low heritability of canopy temperatures (0.3) (Bolaños and Edmeades, 1996). Canopy temperatures are difficult to measure accurately with an instrument with a narrow angle of acceptance (ours was 2.5°). The low LAI of inbred progenies (often <1.5) means that soil and background plants often affect the readings. Evaluation of pre-dawn leaf water potential by divergent selection showed that the trait was not heritable, nor was it correlated significantly with yield under severe stress (data not shown). The mean value for predawn leaf water potential in progenies was around -0.5MPa, with individual plots falling as low as -0.9 Mpa. Pre-dawn water potential may, therefore, be reflecting variation in soil water content rather than genetic variation.

The second data set presented is more comprehensive (Table 5). Synthetics from four selection cycles of La Posta Sequía were compared under five water regimes. Of these, two (93SS; 93IS) can be considered to be severely stressed with a mean yield of 0.77 t ha^{-1}; one (94IS) is moderately stressed (5.31 t ha^{-1}), and the other two are well-watered environments (mean yield 7.77 t ha^{-1}). A defect in this study is that the performance of all synthetics was related to that of the cycle bulk (entered twice in each replicate here), and if this was abnormally high or low all comparisons involving it were affected. We attempted to summarize the comparisons under the two severe stress environments for each synthetic by expressing its yield relative to that of the cycle bulk. Since not all synthetics were

Table 5. Analysis of La Posta Sequía (LAP) synthetics derived from divergent selection in various cycles of selection, and evaluated over two years (five environments differing in water availability) at Tlaltizapán, Mexico.

	Grain yield (t ha^{1})					Ears plant^{-1}		ASI (d)		Anth. (d)
Genotype name	93SS	93IS	94IS	94WW	93WW	93SS	93IS	93SS	93IS	93WW
La Posta Seq. C$_0$, F$_2$[a]	0.31	0.74	5.35	6.71	8.74	0.38	0.49	18.6	16.6	84.2
LAP C$_0$ Best ASI	0.74	0.72	5.68	6.57	8.89	0.63	0.40	5.5	15.5	81.3
LAP C$_0$ Worst ASI	0.21	0.23	5.00	7.31	8.82	0.20	0.15	20.1	25.3	84.8
LAP C$_0$ Best, green leaves	0.70	0.78	5.53	7.18	9.49	0.59	0.45	7.3	17.8	84.7
LAP C$_0$ Worst, green leaves	0.72	0.63	4.89	6.79	8.29	0.59	0.41	8.1	17.5	82.4
LAP C$_0$ Low canopy temp.	0.66	0.37	5.65	7.05	8.55	0.57	0.31	8.4	22.0	81.9
LAP C$_0$ High canopy temp.	0.29	0.37	5.39	6.60	8.58	0.34	0.30	15.6	22.8	82.7
LAP C$_0$ Erect leaves	0.40	0.75	5.19	6.46	7.56	0.41	0.46	11.5	12.7	82.9
LAP C$_0$ Lax leaves	0.48	0.43	5.10	6.90	7.80	0.45	0.28	12.7	27.0	81.7
LAP C$_0$ Best all	0.68	1.09	5.47	7.62	8.46	0.60	0.62	11.2	10.7	84.3
LAP C$_1$, F$_2$[a]	0.70	0.61	5.79	7.78	7.78	0.59	0.47	7.7	24.9	84.1
LAP C$_1$ Best ASI	0.45	0.87	4.77	7.11	8.29	0.52	0.52	9.3	11.5	85.1
LAP C$_1$ Best, green leaves	0.59	0.36	5.71	7.22	8.17	0.44	0.24	10.6	23.4	85.8
LAP C$_1$ Most leaf rolling	0.50	0.37	5.30	8.03	9.36	0.51	0.24	12.0	41.6	85.0
LAP C$_1$ Least leaf rolling	0.77	0.83	5.42	7.37	8.29	0.56	0.41	13.0	21.7	86.4
LAP C$_1$ Best all	1.25	1.22	4.98	6.39	8.39	0.84	0.76	4.6	8.6	81.3
LAP C$_1$ Worst all	0.18	0.11	4.79	6.95	8.59	0.28	0.21	15.2	31.1	87.4
LAP C$_2$, F$_2$[a]	0.88	0.65	5.24	7.36	8.35	0.65	0.50	4.6	13.4	81.2
LAP C$_2$ Best ASI	0.74	1.45	5.49	6.73	8.74	0.74	0.76	4.0	5.9	84.7
LAP C$_2$ Worst ASI	0.50	0.50	4.47	7.20	7.63	0.38	0.41	14.0	22.9	87.5
LAP C$_2$ Best, green leaves	0.50	1.04	5.19	7.63	8.39	0.59	0.61	7.4	10.8	84.7
LAP C$_2$ Worst, green leaves	0.85	0.79	5.55	7.77	8.82	0.74	0.54	6.1	15.0	83.1
LAP C$_2$ Small tassels	0.65	0.98	5.47	6.73	8.24	0.62	0.61	7.5	10.7	85.0
LAP C$_2$ Large tassels	0.87	0.93	5.04	7.57	9.49	0.70	0.53	5.9	11.9	84.1
LAP C$_2$ Erect leaves	0.63	1.38	4.99	6.20	8.34	0.63	0.66	8.6	8.4	85.0
LAP C$_2$ Lax leaves	0.59	1.06	5.60	5.98	9.98	0.64	0.56	6.3	9.4	83.7
LAP C$_3$, F$_1$[a]	0.77	1.35	5.87	7.85	9.07	0.67	0.70	6.9	8.3	84.3
LAP C$_3$ Best ASI, F$_1$	0.87	1.04	6.02	8.07	8.82	0.72	0.38	3.0	12.3	84.5
LAP C$_3$ Best, green leaves, F$_1$	1.00	1.63	6.95	7.82	9.75	0.86	0.67	6.1	9.5	84.5
LAP C$_3$ Small tassels, F$_1$	0.93	1.74	6.05	7.97	10.02	0.76	0.78	6.9	5.2	82.5
LAP C$_3$ Best all, F$_1$	0.65	1.86	6.19	7.93	9.21	0.56	0.76	5.6	7.0	85.2
Pop. 43 C$_6$ [b]	0.46	0.52	4.71	6.65	8.25	0.44	0.40	13.6	16.6	82.3
Pop. 43 C$_9$ [b]	0.18	0.57	4.71	6.67	9.35	0.33	0.42	12.9	16.6	85.6
Mean	0.65	0.88	5.31	6.80	8.74	0.57	0.50	9.1	15.6	84.0
LSD (0.05)	0.46	0.63	0.75	0.87	1.16	0.21	0.27	5.6	12.0	1.6
CV (%)	41	40	8	8	8	22	31	35	45	1
Significance	**	**	**	**	**	**	**	**	**	**

[a] Cycle bulks of La Posta Sequía, selected specifically for drought tolerance.

[b] Bulks of Population 43 (La Posta), selected for general performance through international progeny test

created in each selection cycle, relative yields were averaged over each synthetic comparison for that trait (Table 6). Values greater than 1.0 indicate that the synthetic yielded more than the cycle bulk, and where the anthesis dates of the synthetic is not more than 1-2 d less than the cycle bulk, it can be assumed that a genuine increase has occurred. Data again suggest asymmetric progress. Gains over the cycle bulk were recorded for ASI, delayed foliar senescence, erect leaves, unrolled leaves and for small tassels. However, gains were also recorded for accelerated leaf senescence and large tassel size, so we conclude these two traits are of little adaptive value. Selection for cool vs. warm canopies did not result in increased yield over the cycle bulk. The remaining traits (short ASI, unrolled leaves, and to a lesser extent erect leaves) showed an adaptive advantage in this study.

Conclusion

In an attempt to summarize the information presented here, each trait was scored using the five criteria used to identify secondary traits. Of these, association with yield under drought was considered the most important (40 points), heritability next (20 points), followed by cost (10 points) and scores relating to genetic variability, the growth stage at which the trait was observed, and the feasibility of using the trait to make crossing decisions in the same crop season (5 points each). We assumed that the observation of male flowering dates would be mandatory so that shifts in maturity would not take place during selection. Using these rather subjective measures, traits fall into three broad groups. The group receiving the highest scores was associated directly with yield components, especially those which are affected by barrenness under drought (ears per plant; kernels per plant and ASI). Where resources are scarce, these traits can substitute one for the other. A minimum data set might be: shelled grain yield, ears per plant and male flowering date. With slightly more resources, the observation of silking date (hence ASI) under stress seems warranted, since ASI can provide information at flowering to direct crosses and gives a reasonable estimate of yield potential well before harvest. Evidence suggests that focusing on traits which are indicative of partitioning in the plant at flowering (ears per plant and ASI) will result in increases in harvest index and grain yield in all water regimes (Bolaños and Edmeades, 1996).

A second group of lower utility is formed by morphological traits which have high heritability, are cheaply measured, but are not strongly associated with grain yield under stress. These are leaf erectness, tassel branch number, plant height and leaf rolling. The traits of seedling survival and leaf senescence also fall into this group. If resources permit, a breeding program may wish to measure these; we favor staygreen, seedling survival and leaf rolling scores from among this group.

A final group appear to be of low general utility in selecting for improved performance under drought stress. Some of these are estimators of plant water status and are expensive and somewhat difficult to measure. Our data suggest that it would not be worthwhile for a

Table 6. Grain yield and anthesis date of divergent selections for putative drought-adaptive traits relative to the yield of the cycle bulk, when grown in two severely drought stressed environments (grain yields 10% of well-watered plots). Data are derived from Table 5 for 1993 IS and SS water regimes, using days to anthesis reported under well-watered conditions.

	Number of comparisons	Yield relative to cycle bulk, severe stress	Anthesis date relative to cycle (d)	Relative importance under severe stress
Best for all drought-adaptive traits	3	1.58	-0.6	****
Worst for all drought-adaptive traits	1	0.21	+3.3	
Shortest anthesis-silking interval	4	1.18	+0.5	**
Longest anthesis-silking interval	2	0.54	+3.5	
Best for delayed foliar senescence	4	1.10	+1.5	*?
Accelerated leaf senescence	2	1.17	+0.1	
Low canopy temperature	1	1.00	-2.3	*?
High canopy temperature	1	0.62	-1.5	
Erect leaves	2	1.19	+1.3	**
Lax leaves	2	0.98	0.0	
Unrolled leaves under stress	1	1.21	+0.9	**
Rolled leaves under stress	1	0.67	+2.3	
Small tassel branch number	2	1.16	+1.0	*
Large tassel branch number	1	1.17	+2.9	

national maize breeding program to invest in measuring these traits, if its goal is to improve grain yield under drought. There may be reasons, associated with performance in target environments other than severe drought for observing certain of them (e.g., lodging; weight per kernel) during selection.

There are many secondary traits which have not been examined in CIMMYT's drought breeding program. Among the most promising candidates are those related to root size (root capacitance; root pulling resistance), synchrony of kernel development within the ear, recovery of the photosynthetic apparatus from stress (fluorescence; lethal water content; photo-oxidation), and capacity to remobilize stem reserves. It is important to recall that variation in traits such as ASI, with a correlation with grain yield of -0.5 to -0.6, accounts for only 25-35% of the variation observed in grain yield under drought. The challenge remains to identify traits which explain a significant proportion of this residual variation in yield. No secondary trait can be useful in selection if water stress is not managed in such a way as to reveal the genetic variability for the trait. Stress management during selection for drought tolerance in programs where resources prohibit a massive scale of multilocation testing will be an essential component of their success.

Corollary: The drought-tolerant maize ideotype

This is a plant which germinates and establishes under dry soil, has a high root/shoot ratio when young, can actively accumulate solutes in its cells, and has a waxy cuticle on upright dark green leaves which do not normally roll under stress. When drought-stressed, the leaves maintain their essential functions at low water potentials, and recover quickly when the stress is lifted. This plant is characterized by rapid ear growth at flowering, so it has a short ASI under stress, small tassels and is relatively short in stature. Signals sent from drying soil are relatively low in intensity and its stomates are not unduly sensitive to ABA. It will be prolific under well-watered

Table 7. Summary of secondary traits examined in maize, scored by six criteria used to determine the utility of such traits. The recording of anthesis date is considered a mandatory requirement to avoid shifts in maturity during selection.

Trait Range of score	Assoc. with yield under drought 1-40	Heritable? 1-20	Cost 1-10	Obs. at or before flowering?[b] 1-5	Yield pot. estimate prior to harvest?[c] 1-5	Total score
Ears plant^{-1}	35	14	9	3	2	63
Kernels plant^{-1}	33	12	6	1	1	53
Anthesis-silking interval	25	12	6	4	4	51
Kernels ear^{-1}	28	9	6	1	1	45
Leaf erectness score	6	15	8	4	4	37
Tassel branch number	5	17	7	3	2	34
Plant height	5	15	8	3	3	34
Seedling survival	10	6	4	5	5	30
Leaf senescence score	10	10	7	1	2	30
Leaf rolling score	6	10	7	4	3	30
Canopy-air temperature diff.	10	5	2	4	4	25
Lodging percentage	6	10	7	0	1	24
ABA concentration	4	10	1	3	4	23
Weight kernel^{-1}	8	8	6	0	0	22
Leaf chlorophyll concentration	8	2	2	4	4	20
Pre-dawn leaf water potential	6	5	2	3	3	19
Leaf osmotic concentration	1	9	1	3	3	16
Leaf-stem extension rate	2	2	4	4	3	15

[a] Assumes low labor cost and a difficulty of obtaining currency for equipment purchases

[b] Score reflects possibility of selecting and crossing desirable lines within the same cropping season. Traits measured well after flowering get a low score.

[c] Reflects the stage of crop development at which the trait can be measured; traits measured near harvest get a low score

conditions but single-eared and not barren under stress. It will not lodge even under severe drought stress. Its leaves have a long functional life, resulting in a high weight per kernel under drought. It has a high grain yield under well-watered conditions, and a stable and high grain yield under stress. The maturity of the crop is such that in an average year it exhausts all available soil moisture by the time it reaches physiological maturity.

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Growth and Productivity of Maize Under Nitrogen Stress

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Abstract

While it is well established that nitrogen (N) supply affects the reproductive development and yield of maize, the mechanisms involved are not fully understood. This presentation will summarize some of my laboratory's recent research on the role of N in maize productivity. Data obtained under controlled conditions using in vitro culture will be presented along with results of field trials to assess the impact of N supply on reproductive development. Except at the lowest levels of N supply, yield increases from N fertilizer additions in the field were mostly the result of more filled kernels due to less kernel abortion. Decreased N accumulation after flowering appeared to be most closely associated with N-induced kernel abortion. In general, N deficiency decreased the proportion of N partitioned to stalks and leaf sheaths, increased the proportion in reproductive fractions, and accelerated N remobilization from the leaves. Omission of N from the culture media of in vitro grown kernels markedly decreased endosperm dry weight, even though high levels of sugars were available. The effect of N availability was greatest during the period (first 12 days) of endosperm cell division. Subsequent decreases were attributed to lower activities of starch synthesis enzymes. These data show that N supply plays important roles in maximizing kernel initiation and set, and in the establishment and filling of the kernel sink.

Despite the known importance of N supply to the productivity of maize, relatively little is known regarding how N affects factors associated with reproductive development. Contributing to this lack of understanding, the initiation and development of reproductive structures occur in distinct phases, each of which can be affected by N. The number of potential kernel ovules is established early in plant development, with the kernel row number being set by the five leaf stage and the number of kernels per row by twelve leaves (Kiesselbach, 1949). The number of potential ovules that ultimately develop into mature kernels is further affected by the degree of pollination and by the extent of kernel abortion. Finally, the weight of individual kernels is a function of the kernel number and the assimilate supply during grain fill. While an increase in kernel number is usually responsible for N-induced yield enhancement of maize, increases in individual kernel weights have also been reported (Lemcoff and Loomis, 1986; Thiraporn et al., 1987; Jacobs and Pearson, 1992).

Although it is not known how N supply regulates this increase in final kernel number, it is clear that lack of N enhances kernel abortion (Pearson and Jacobs, 1987; Mozafar, 1990; Uhart and Andrade, 1995b). Complicating this understanding, kernel survival can be the direct result of how much N is supplied to the ear or the indirect result of an N-induced limitation in photosynthesis. The N supplied to developing ears can also come from two distinct sources: the current assimilation of soil N and the remobilization of N from the vegetation. When adequate levels of N are available, current assimilation is the major source for early kernel growth. However, when the supply of soil N is low, remobilization can become a major source of N for ear development. Unfortunately, the plant's ability to supply the ear with N from remobilization is limited, as too much N loss from the leaves could impair photosynthesis and decrease the supply of assimilates to the ear. Alternatively, if the initial remobilization of N were from stalks, the N supply to the ear could be maintained under low N conditions without a drastic impact on leaf photosynthesis. Although some studies have reported an earlier remobilization of N from the stalks than the leaves (Ta and Weiland, 1992), others have shown the opposite effect (Swank et al., 1982). Understanding how N supply regulates reproductive development and yield is further complicated by numerous reports of genotypic variation in the efficiency of N use (Tsai et al, 1984; Smiciklas and Below, 1990; Eghball and Maranville, 1991; Sabata and Mason, 1992).

The mechanisms involved in N regulation of kernel growth are difficult to study at the whole plant level because of the inability to manipulate stringently the supply of N from the plant to the kernel. The *in vitro* kernel culture technique circumvents this problem by allowing for growth of individual kernels under defined conditions of N supply (Cully et al., 1984; Singletary and Below, 1989). Similarly, because this technique controls most environmental factors and removes the influence of the mother plant, it is also well suited to evaluate genotypic variation in growth response to N supply (Czyzewicz and Below, 1994). My laboratory routinely uses *in vitro* kernel culture and field fertilizer applications to alter the supply of N to developing maize plants, and some of that work is summarized here. Our overall goal is to better understand how N governs maize growth and yield, with the hope that this information will help to improve the efficiency and environmental friendliness of N fertilizer use.

Materials and Methods

Two field experiments were conducted at the University of Illinois at Champaign-Urbana to examine how N supply affects ear formation and kernel development in maize. For each experiment, two genetically different maize hybrids (B73 x LH51 and LHE136 x LH82) were evaluated in the field over a three-year period (1990-92) with varying levels of N. The soil type was a Drummer silty clay loam (3.1% organic matter) that had previously been shown to be responsive to N fertilizer. Nitrogen fertilizer was hand applied at the V3 growth stage in granular form and immediately incorporated into the soil with cultivation followed by 2.5 cm of irrigation water.

One experiment consisted of the two hybrids grown with either a deficient (0 kg N ha^{-1}) or sufficient (269 kg N ha^{-1}) supply of N. Treatments were arranged in a randomized complete block design with three replications. Just prior to flowering (V18) and until the late milk stage (R3), four plants from each plot were harvested biweekly and separated into leaves, leaf sheaths, stalk, earshoot, and a non-grain reproductive fraction that consisted of husk, shank, and tassel. Dry weight of all fractions was determined and the tissue analyzed for reduced N. Kernel ovule potential was determined by counting the kernel ovules in a representative row and multiplying by the number of kernel rows, and kernel abortion by determining the number of kernels that failed to proceed past the previous growth stage. The time course of kernel abortion is expressed as the percentage of the potential kernel ovules which continue to develop. The data presented is averaged over the two hybrids and expressed on a thermal time basis using cumulative modified growing degree days in °C (Gilmore and Rogers, 1958).

In the other experiment, the two hybrids were grown with five rates of N fertilizer (0, 67, 134, 202, and 269 kg N ha^{-1}) supplied as urea. Treatments were arranged in a split-plot design with N level as the main plot and hybrid as the sub-plot. Four replications were used in 1990 and three replications in 1991. Four representative plants were sampled from each plot at the R2 growth stage to determine kernel ovule potential, and at physiological maturity (R6) for yield and yield components.

In addition to field trials, other experiments were conducted under controlled conditions using *in vitro* kernal culture. To provide material for *in vitro* culture, plants were grown in the field and / or greenhouse with moderate levels of N to preclude masking the growth response of the kernels to N supply in culture. Immature ears were harvested from these plants 3 days after self-or-sib pollination and aseptically dissected into explants (a six ovule cob section with one kernel ovule) as previously described (Singletary and Below, 1989). Each flask constituted an experimental unit, with four to eight replicates of each treatment. All treatments within a replicate originated from the same ear. Explants were taken from the middle portion of the ear (those between positions 18 to 35 from the base), and in some cases from the apex (those above position 36). These explants (five per flask) were placed on supports in 250 ml Erlenmeyer flasks containing 100 ml of a modified MS liquid medium and incubated in the dark at a constant 25 °C.

One experiment evaluated hybrid differences, while another examined the effects of time of N availability. For the hybrid study, treatments consisted of the different maize genotypes grown to maturity on media containing various (i.e. 0 to 50 mM) levels of N, supplied as an amino acid mixture. Explants for all treatments were transferred to fresh medium of the same composition midway through the experiment to ensure that growth was a function of N concentration and not the absolute amount of N in the flask. Mature kernels were oven dried and weighed, and then analyzed for reduced N.

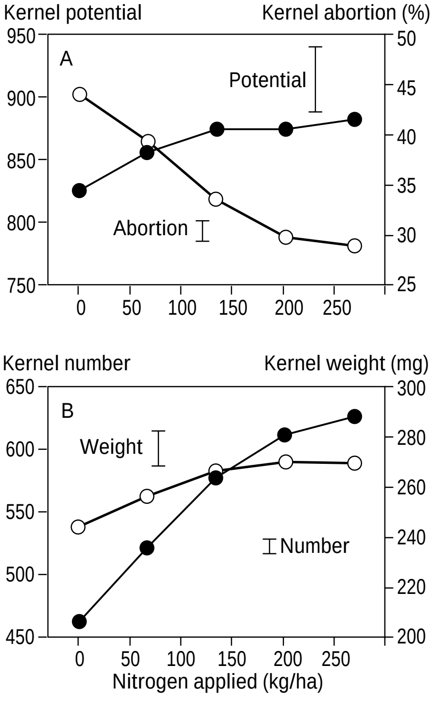

Figure 1. Effect of varying rates of soil applied N on components of maize reproductive development (A) and final yield (B). Values are the mean of two hybrids over two years. Bars indicate the LSD at the 5% probability level for comparison of N rates.

For the N timing work, treatments consisted of continuous adequate N, no N, or N addition after 4, 8, 12, 16, or 20 days in culture. Subsets of the kernels were harvested after 14 days to determine endosperm cell number and after 28 days for ADPG-PPase activity. Other explants were harvested throughout development to follow endosperm growth.

Results

Although the hybrids used in the field experiment differed in their potential number of reproductive ovules and in how they partitioned grain yield between kernel weight and kernel number (data not shown), the effect of N supply on these components was similar. Both hybrids also exhibited similar changes in the accumulation, partitioning, and remobilization of N during the initiation and course of N-induced kernel abortion; and these effects were remarkably similar over years. Therefore, for ease of presentation, the data is averaged over the two hybrids, and where possible, over years.

Increasing the N supply had a relatively minor impact on individual kernel weight, but a large effect on kernel number (Fig. 1 B). The addition of N fertilizer increased kernel weight by only 10%, and this increase was obtained with the first increment (67 kg N ha^{-1}) of N. Conversely, all increments of N resulted in a greater number of kernels, in a pattern very similar to the response of grain yield to N supply (data not shown). N-induced increases in kernel number were almost entirely the result of less kernel abortion, as N fertilization increased the number of potential kernel ovules by only 8% (Fig. 1 A).

In all cases, continued kernel development was strongly affected by N supply (Fig. 2 A). When adequately fertilized (high N plants), the percentage of filled kernels either increased or remained constant during initial kernel development. In

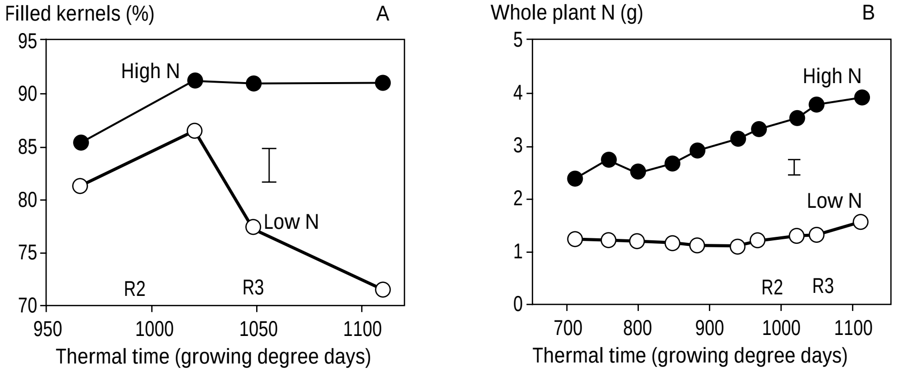

Figure 2. Time course of kernel development (A) and whole plant N accumulation (B) for maize plants grown with either an adequate (high N - 269 kg N ha^{-1}) or inadequate (low N - no applied N) supplies of N. Values are the average of two hybrids. Specific reproductive growth stages are designated on the x axis. The bars indicate the LSD at the 5% probability level for comparison of N levels within a sampling time, or sampling time within an N level.

contrast, plants grown with inadequate N (low N) showed an abrupt decrease in the percentage of filled kernels (i.e., an increase in kernel abortion) just prior to the onset of linear grain fill. In all three years and for both hybrids, this decrease occurred after plants accumulated between 1025 and 1050 growing degree days. A representation of this response is presented for plants grown in 1990 (Fig. 2 A).

The decrease in developing kernels of N-limited plants was preceded by a quiescence in N accumulation by the whole shoot (Fig. 2 B). Between 800 and 1050 growing degree days, adequately fertilized plants accumulated an average of 1.1 grams of N per plant compared with only 0.2 grams for unfertilized plants. The N content in leaves and stalks of adequately fertilized plants remained constant during this period, while N was remobilized from these organs in low N plants (Fig 3 A, B). This remobilization of N was greater (0.27 versus 0.05 g plant^{-1}; average of 37 versus 10%) for leaves than for stalks. Although the percentage of N partitioned to leaves and stalks decreased over time for both high and low N plants, N deficient plants distributed less N to the stalk and more to the leaves and reproductive fractions; especially in the period just before kernel abortion (Fig. 3 C, D).

For all hybrids, the dry weight of *in vitro* grown kernels increased markedly as the level of media N was raised from 0 to 10 mM (Fig. 4). Further increases in dry weight were less distinct, with the overall response to N rate being curvilinear. Variation was observed among the hybrids for the level of N needed to maximize kernel dry weight. The dry weight of B73 x LH105 was maximized at 15 mM N, whereas B73 x LO876 and B73 x Va35 kernels required 25 mM N, and B73 x LH51 kernels between 25 and 50 mM N to attain maximum kernel weight.

In contrast to dry weight, the pattern of kernel N accumulation in response to N supply was relatively similar for all hybrids (data not shown). This similarity occurred despite the differences observed in kernel dry weight, suggesting that kernels differ in their utilization of N. Plots of kernel dry weight versus kernel N concentration further demonstrate the differences in N use among these hybrids (Fig. 5). A given concentration of tissue N resulted in a hybrid-specific accumulation of dry weight by the kernel. Although the hybrids exhibited slightly different response patterns, an increase in kernel N concentration generally corresponded with an increase in kernel dry weight (Fig. 5).

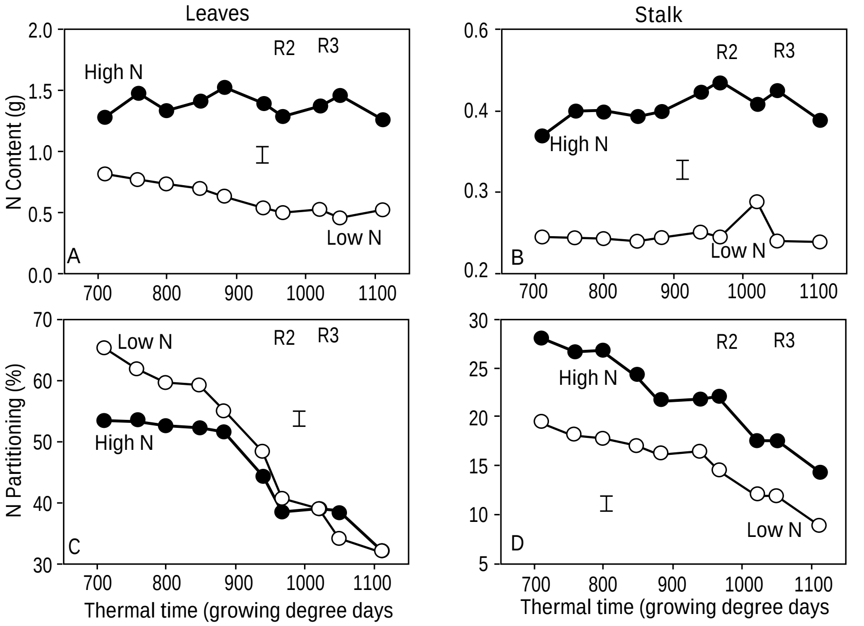

Figure 3. Changes in N content (A,B) and N partitioning (C,D) in leaves and stalks of maize plants grown with either an adequate (high N - 269 kg N ha^{-1}) or inadequate (low N - no applied N) supplies of N. Values are the average of two hybrids. Specific reproductive growth stages are designated on the x axis. The bars indicate the LSD at the 5% probability level for comparison of N levels within a sampling time, or sampling time within an N level.

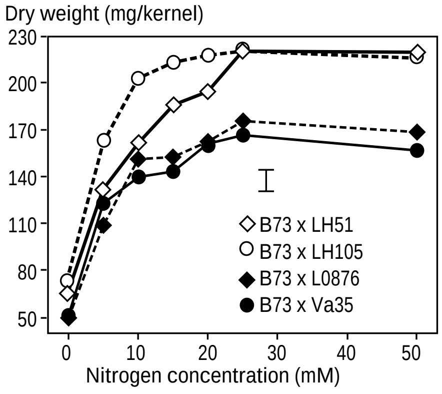

Figure 4. Effect of N concentration in the culture medium on the dry weight of kernels of different maize hybrids grown to maturity *in vitro*. The bar indicates the LSD at the 5% probability level for comparison of N concentrations within each genotype and genotypes at a given N concentration.

Delaying N availability decreased endosperm dry weight of *in vitro* grown kernels, with the effect being greatest when N was withheld the longest (Fig. 6). When N was limiting for even 4 days, a 22% decrease in final endosperm dry weight was observed. Withholding N for 8 days after culturing decreased endosperm dry weight by 46%, and even larger decreases were noted when N was withheld for 12 days or longer (Fig. 6). Kernels that received no N attained only 8% of the dry weight observed when kernels were continuously supplied with N. Some of the decrease in kernel weight is associated with a decrease in kernel sink capacity (see inset Fig. 6), while the remainder appears to be related to lower activities of the starch synthesis enzyme ADPG-PPase (Table 1).

Discussion

Nitrogen supply has a large effect on the grain yield of maize primarily by altering kernel number (Fig. 1 B). Although hybrid variation in kernel number was often associated with differences in the number of potential kernel ovules (data not shown), N supply affected kernel number primarily by altering kernel abortion (Fig. 1 A). Incremental increases in N supply resulted in successive decreases in kernel abortion, with only small effects on the number of potential kernel ovules.

Continued kernel development was closely associated with N supply as N deficiency resulted in an abrupt decrease in filled kernels (i.e., an increase in kernel abortion) just prior to linear grain fill (Fig. 2). This decrease was most closely associated with a lack of post-flowering N accumulation by whole plants. In contrast, plants supplied with adequate N continued to increase in N, and the percentage of filled kernels either increased or remained constant during this period.

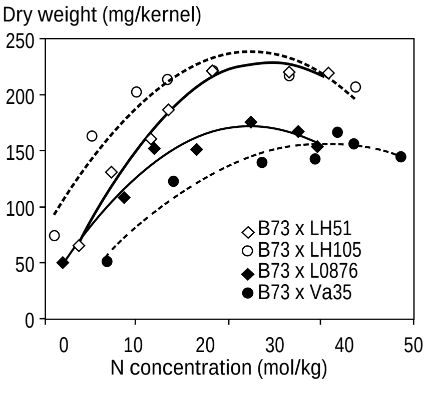

Figure 5. The relationship between dry weight and N concentration of kernels of different maize hybrids grown to maturity *in vitro*. Lines were fitted to data points of each genotype by second order polynomial equations, and in all cases the R^2 values were ≥0.93.

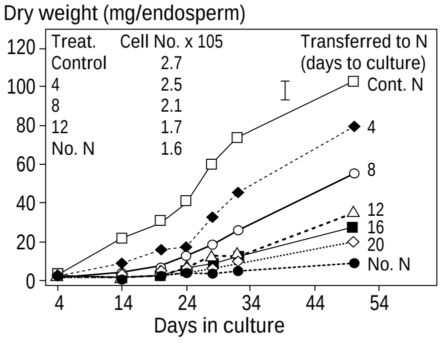

Figure 6. Effect of time of N availability on dry weight accumulation in endosperm of maize kernels (B73 x LH51) cultured *in vitro*. Treatments consisted of continuous N, no N, or the addition of N after 4, 8, 12, 16, or 20 days in culture. The bar indicates the LSD at the 5% probability level for comparison of N treatments with a sampling time. The effect of varying N availability treatments on the number of endosperm cells present after 14 days is shown in the insert.

Plants grown with inadequate N remobilized N from other plant parts in an attempt to supply the N needs of the developing ear (Fig. 3). Remobilization was most notable from the leaves, which lost about a third of their N between flowering and the onset of linear grain fill. A loss of N of this magnitude would be expected to have a correspondingly negative effect on canopy photosynthesis which could result in greater kernel abortion (Uhart and Andrade, 1995a). As opposed to other reports (Ta, 1991; Ta and Weiland, 1992), the stalk was not a major source of remobilized N in our study. Plants grown under N-deficient conditions attempted to maximize their use of N by allocating a large portion of plant N to the leaves (Fig 3C). However, the leaves are also the main source of remobilized N to the ear when the supply of N is limiting. This loss of leaf N would likely decrease the assimilate supply to the ear, contributing to enhanced kernel abortion.

Similar to other studies (Singletary and Below, 1989 and 1990), omission of N from the culture media of *in*

Table 1. The effect of time of N addition on activity of ADPG-PPase at 25 days in culture for maize kernels grown *in vitro*.

Time in culture (days)	ADPG-PPase activity (nmol m^{-1} endo^{-1})
Continuous N	914
4	975
8	715
12	401
16	113
20	92
No N	49
LSD (0.05)	60

vitro grown kernels markedly decreased endosperm dry weight, even though high levels of sugars were available (Fig. 4). We also found distinct differences between hybrids in kernel dry matter accumulation in response to N supply *in vitro* (Fig. 4). Among the hybrids tested, the media N level needed for maximum kernel dry weight ranged from 15 to 50 mM. These differences in the N level needed to achieve maximum kernel weight *in vitro* supports the idea that maize genotypes have differential requirements for fertilizer N in the field. Because *in vitro* cultured kernels of all genotypes exhibited relatively similar patterns of N accumulation in response to N supply, the differences in growth response to N in culture may be due to genetic differences in the efficiency with which these kernels use N to synthesize starch.

Deprivation of N for any period during kernel development decreased endosperm dry weight of *in vitro* kernels, with the largest effect occurring during the first 12 days (Fig. 6). Because this is the period of endosperm cell division, which determines the endosperm's potential size, our data shows an obligatory requirement for N to maximize sink capacity. After 12 days, N supply still influenced endosperm weight, likely due to an effect on the enzymes of starch synthesis (Table 1). Thus, based on this data, the availability of N is necessary throughout kernel growth for both the establishment and filling of the endosperm sink.

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Variation in Nitrogen Use Efficiency and Root System Size in Temperate Maize Genotypes

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Abstract

The potential for genetic improvement in nitrogen use efficiency (NUE) depends on the magnitude and nature of differences among varieties. The objective of this study was to evaluate NUE and its relationship to root system size in temperate maize genotypes. Twelve inbreds and ten hybrids were planted under two N levels (16 and 125 kg N ha^{-1}*) during 1993. Recognizing that root parameters may provide a partial explanation for differences in NUE, root system size was estimated using a portable capacitance meter. NUE differed significantly for inbreds and hybrids under both N treatments, with NUE under low N being roughly seven times greater than NUE under high N. In addition, there were wide differences in the genotypes' root system response to low N. No association was found between NUE and root system size as measured by capacitance. Thus, an increase in root system size would not appear to be an effective strategy for increased NUE.*

The heavy reliance of modern agricultural practices on chemical fertilizers poses two problems. First, high rates of nitrogen fertilization constitute an environmental hazard. Nitrogen has become a groundwater pollutant as an unintended consequence of modern farming practices. Second, the production of one kilogram of nitrogen fertilizer requires the energy input of about one and a half liters of oil (FAO, 1990). Dwindling oil reserves make it likely that fertilizer prices will rise in the future. Thus, a breeding program aimed at developing new varieties with higher nitrogen exploitation capabilities could alleviate environmental and economical problems associated with the use of inorganic fertilizers.

Nitrogen exploitation is influenced in part by the development and morphology of the root system. Or considered conversely, changed root systems are an indication of the ability of a particular genotype to respond to a stressful environment. Although few studies on roots have reported physiological changes in root systems as a response to changes in N, many studies have reported morphological changes in response to decreases in nitrogen availability. Thus, information on root parameters, such as root system size or distribution in the soil, is of importance when selecting N efficient genotypes. The objectives of this study were to compare nitrogen use efficiency (NUE) of temperate maize genotypes at two N levels, to assess differences in root system responses to N, and to determine the relationship of root system size to NUE.

Materials and Methods

Twelve inbreds spanning a developmental period from 1949-1983 were chosen based on their performance in hybrid combinations (Listed in Tables 1 and 2). The ten hybrids evaluated resulted from all possible crosses among five of the inbreds. To eliminate the effects of differences in vigor between inbreds and hybrids, inbreds were planted in a separate but adjacent trial. The experimental design was a split plot with nitrogen fertilization treatments as main plots and genotypes as subplots. Plot size consisted of a single row measuring 5.3 m in length and 0.75 m in width and having 24 plants row^{-1} spaced to give a plant density of approximately 60,000 plants ha^{-1}. Nitrogen treatments and genotypes were assigned at random within three reps. All plots were fertilized with 16 kg N ha^{-1}, banded at planting time. Two fertilization treatments were used: low (16 kg N ha^{-1}), and high (16 kg N ha^{-1} and 109 kg N ha^{-1} as a sidedress).

Root system size was estimated following the methods described by van Beem et al. (1996), in which the relationship between capacitance and root fresh weight was determined. Inbred and hybrid root capacitance under the two nitrogen levels was evaluated with a BK Precision 810A capacitance meter on four maize plants chosen at random within each plot. Yield (grams per plant) at 15.5% moisture was calculated using the equation: Yield = (plot dry weight (gm) / plants per plot) x (0.8 / 0.845), where 0.8 is the shelling percentage and 0.845 is the grain moisture correction factor. Nitrogen use efficiency was calculated following Moll et al. (1982) where NUE = Yield (grams grain plant^{-1}) / Available nitrogen (grams plant^{-1}).

Results

Variation in NUE

Analyses of variance showed significant differences ($p<0.01$) among genotypes for both N treatments (data not shown). Table 1 shows means and standard deviations of NUE for inbreds and hybrids planted under two N treatments. Under low N, inbred NUE ranged from 21.9 (Mo17) to 122.9 (RD4509). Similarly, hybrid NUE ranged from 230.5 (RD5529 x RD4509) to 329.1 (LH146 x RD5529). Although the interaction between genotype and N treatment was highly significant ($p<0.001$), there was a tendency for the genotypes with the highest NUE under low N to also be the genotypes with the highest NUE under high N. Two notable exceptions were the inbred RD4509 and the hybrid LH146 x Oh43 which showed the greatest genotype x N treatment interaction. Figure 1 shows the interaction between NUE of four selected genotypes and nitrogen fertilization. Overall, NUE under low N was roughly seven times greater than NUE under high N.

Differences in root system response to N levels

Table 2 shows mean capacitance for all genotypes under high and low nitrogen regimes and the respective probability for the difference of capacitance under the two regimes. The mean capacitance for high nitrogen was 32.2 nF, whereas the mean capacitance for low nitrogen was 27.7 nF. Overall, hybrids had a higher mean capacitance (33.6 nF) than inbreds (26.8 nF). Nitrogen treatment by root capacitance interactions were significant at $p<0.001$. The ratio of capacitance under high and low nitrogen treatments was used to analyze differences in the response of roots to nitrogen fertilization. Genotypes with ratios of approximately 1.0 either did not respond or had a minimal root response to increases in nitrogen; genotypes with ratios above 1.15 had a significant response to nitrogen (Table 2). Two hybrids, A639 x RD5529 with a significant response and Oh43 x RD5529 with a response approaching significance, responded to higher nitrogen levels by increasing root capacitance; the remaining eight hybrids did not have measurable responses. Of the twelve inbreds in this experiment, seven exhibited an increase in root capacitance under high nitrogen (LH146, RD5529, RD5501, A619, LH105, Oh43, and B14A), whereas the remaining five did not exhibit measurable changes.

Relationship between root capacitance and NUE

The correlation coefficient between root capacitance and NUE was 0.25 and 0.28 for inbreds and hybrids, respectively. Thus, no association was found between NUE and root system size. Genotypes, such as RD5529 and LH146 x RD5529 had high NUE and a high root capacitance. However, genotypes such as Mo17 and Oh43 x RD4509 were inefficient in their use of N and also had high capacitance readings.

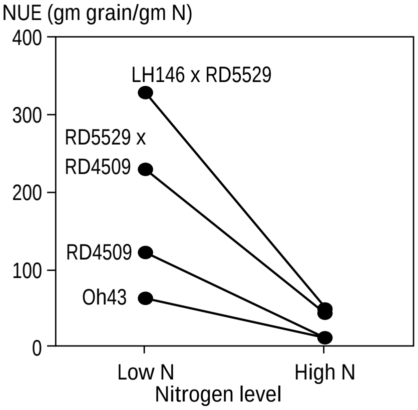

Figure 1. Interaction between NUE of four selected maize genotypes and nitrogen fertilization.

Discussion

Concerns associated with the overuse of nitrogen fertilizers continue to grow, and therefore development of nitrogen use efficient genotypes is being investigated. The first objective of this study was to compare the performance of temperate maize genotypes grown under different N fertility levels. Specifically, we were interested in determining differences in NUE and the magnitude of these differences. Most of the inbreds with high N efficiency under high nitrogen (LH146, RD5529, and RD5501) were also the inbreds with high N efficiency under low nitrogen. It seems that NUE among maize inbreds has improved over time, as demonstrated by the higher NUE values in more recently developed inbreds. Other inbreds of interest were RD4509 and A554, which had low NUE under high nitrogen but were among the best inbreds when planted under low nitrogen. Given the wide range of NUE values obtained from this set of genotypes, it would appear that the potential for developing high NUE genoypes exists.

An understanding of the effects of N treatments on root parameters and the association between root parameters and NUE may be important in determining appropriate selection criteria and breeding techniques for low-input conditions. Reports in the literature on the effects of nitrogen availability on root systems are conflicting. Bosemark (1954), Wiersum (1958), Brouwer et al. (1961), and Geisler and Krützfeldt (1983) reported that increases in N levels depressed root length and number. These results were in contrast with observations by Drew and Goss (1974), Tennant (1976), and Maizlish et al. (1980), who found increases in root system size with increased N levels. Anderson (1987) reported a decrease in the milligrams per millimeter of root with an increase in N, which allowed the root length to increase in response to N without altering the weight of roots. The present study found that one third of the genotypes responded to high N levels by increasing their root system size (as measured by capacitance). The

Table 1. Means and standard deviations (in parentheses) for NUE (in g grain g^{-1} N) for ten parents and their progenies of maize evaluated under two N levels, and year of release of the parents.

Genotype	Low N	High N	Release year
RD4509	122.9 (57.6)	10.4 (4.9)	1982
LH146	121.5 (44.2)	18.5 (8.8)	1984
RD5529	116.3 (46.9)	15.0 (6.8)	1983
RD5501	103.0 (46.3)	15.5 (7.4)	1981
A554	101.1 (37.0)	11.0 (3.2)	1963
A619	99.7 (23.6)	14.0 (3.4)	1961
LH105	94.2 (50.6)	12.1 (7.2)	1983
A639	73.2 (8.6)	11.9 (2.6)	1966
SD10	62.1 (28.1)	7.4 (3.7)	1965
Oh43	61.8 (35.5)	11.0 (6.6)	1949
B14A	50.2 (13.6)	8.0 (1.9)	1962
Mo17	21.9 (8.9)	4.4 (3.4)	1964
LH146 x RD5529	329.1 (31.2)	50.0 (9.9)	
Oh43 x RD5529	321.5 (49.6)	48.5 (8.8)	
LH146 x A639	319.6 (52.8)	51.1 (7.9)	
A639 x Oh43	310.9 (26.8)	47.0 (5.6)	
A639 x RD5529	307.8 (32.2)	56.3 (8.3)	
LH146 x RD4509	294.2 (32.6)	44.1 (1.8)	
LH146 x Oh43	287.2 (57.6)	51.4 (8.4)	
A639 x RD4509	276.5 (43.9)	47.2 (10.4)	
Oh43 x RD4509	238.3 (44.6)	36.8 (4.5)	
RD5529 x RD4509	230.5 (60.5)	44.6 (9.3)	

Table 2. Capacitance means[†] for maize inbred lines and hybrids under high and low nitrogen treatments.

	Capacitance means (nF)		
Entry	Low N	High N	Ratio of high N to low N
RD4509	22.4	21.6	0.96
LH146	20.0	30.3	1.52 **
RD5529	29.2	36.4	1.25 **
RD5501	25.7	31.6	1.23 **
A554	24.5	25.8	1.05
A619	24.8	37.4	1.51 **
LH105	22.2	33.5	1.51b **
A639	24.5	25.2	1.03
SD10	20.4	20.3	1.00
Oh43	22.4	32.5	1.45 **
B14A	21.2	36.4	1.72 **
Mo17	26.0	30.2	1.15
LH146 x RD5529	33.0	34.5	1.05
Oh43 x RD5529	31.7	36.5	1.15
LH146 x A639	32.0	33.2	1.04
A639 x Oh43	31.8	34.7	1.09
A639 x RD5529	30.0	36.5	1.22 **
LH146 x RD4509	32.8	33.9	1.03
LH146 x Oh43	35.0	32.8	0.94
A639 x RD4509	30.9	33.8	1.09
Oh43 x RD4509	36.3	37.0	1.02
RD5529 x RD4509	32.1	34.0	1.06

[†] Means are for 12 individual plant measurements.

** Significant differences at $P \leq 0.01$ for comparisons of capacitance between the low N and high N treatments.

remaining genotypes maintained root system size regardless of N availability. Thus, it appears that morphological responses to nitrogen availability vary among genotypes. One possible explanation for the discrepancy between these results and those of other investigators is the greater number of genotypes tested. In most studies, results of root responses were based on measurements obtained from less than ten genotypes, typically between one and four. We measured root responses of 22 genotypes and quantified genotypic differences in root responses that would have otherwise gone undetected in experiments with a more narrow set of genotypes.

To explain the differential N use efficiencies of genotypes, it was hypothesized that root parameters contributed to higher NUE values. However, no association was found between NUE and root capacitance. Thus, an increase in root system size would not appear to be an effective strategy for increasing NUE. A more likely explanation for high NUE might lie in a higher nitrogen absorption rate or in the more efficient use of nitrogen in the plant.

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Relationship Between Secondary Traits and Grain Yield of Maize in Low Nitrogen Soils in Malawi

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Abstract

Grain yield is an important criterion for selecting for tolerance to low nitrogen (N) in maize, but there are limitations to its use due to large genotype by environment interactions. There is need to identify alternative traits less prone to alterations by the environment, which breeders can use to select for tolerance to low N in maize. The objective was to identify traits that can be used to screen for tolerance to low N. Divergent selections for chlorophyll concentration were made in S_2 *lines from two maize populations grown at 0 and 80 kg N* ha^{-1}*. Chlorophyll measurements were made using a hand-held Minolta SPAD-502 chlorophyll meter. Plants with chlorophyll readings above and below the plot mean reading were selfed. Crosses were made between* S_3 *lines with large chlorophyll readings, small chlorophyll readings, and between lines with large and small chlorophyll levels, both within and between the two populations. Resulting hybrids were evaluated at 0, 40, and 80 kg N* ha^{-1}*. Chlorophyll readings of hybrids were not significantly different among N levels at the five-leaf stage, but differed significantly at flowering. Selections for high and low chlorophyll readings made under low N were not significantly different from selections made under high N when their hybrids were evaluated at different N levels. There were significant genotype-by-nitrogen interactions for chlorophyll at flowering, days to mid-silk, anthesis-silking interval, ear height and grain yield. Chlorophyll at flowering, days to mid-anthesis, days to mid-silk, test weight and number of kernels per ear were significantly correlated with grain yield at 0 kg N* ha^{-1}*.*

Most soils in Malawi are deficient in N. The cost of N fertilizer has increased beyond most peasant farmers' purchasing capacity. The result is low maize yields and household food deficits due to low application of N. Promoting genotypes which have high potential only in high N environments and perform poorly in low N environments will not help the peasant farmers who cultivate 80% of the arable land in Malawi.

Genetic variation in N demand and utilization among crop species has been reported by several workers. Nitrogen affects cell and tissue growth, thereby influencing leaf area and photosynthetic capacity (Brown, 1978; Novoa and Loomis, 1981; Pan et al., 1985; Wong, 1985). Bolton and Brown (1980), Wong et al. (1985), Sinclair and Horie (1989), and Muchow and Sinclair (1994) demonstrated a high correlation between light saturated leaf assimilation rate and N per unit area, and a reduction in photosynthetic rate of C_4 grasses when N supply decreased. Based on the hypothesis that chlorophyll level in the leaf affects photosynthetic rate and subsequently dry matter accumulation, varieties with high grain yield under low N may be identified by measuring leaf chlorophyll concentration, leaf N concentration or leaf dry matter content. Other traits such as maturity, plant height, ear height or yield components may also be indicative of performance under low N. This work sought to 1) identify morphological or physiological traits that allow easy and inexpensive screening for tolerance to low N in maize and 2) assess the heritability of such traits.

Materials and Methods

This work was done in the 1992-93 and 1993-94 seasons. Selection for chlorophyll level in eight S_2 lines of each of the two populations, ETO Blanco (Poza Rica 8432) and Chitedze Composite C ($CCCc_1$) was carried out at Chitedze Research Station (1150 masl) in Lilongwe, Malawi, on moderately acid ferric luvisols (pH 5.4-5.6). The 16 lines were grown in plots 12 m long on land where, in the previous two seasons, maize had been grown without applying chemical N. Planting was on ridges 90 cm apart and within-row plant spacing was 30 cm. Phosphorus (single superphosphate) was band applied at planting to rows at a rate of 40 kg ha^{-1} P_2O_5. Half the plot received N at a rate of 40 kg ha^{-1} which was split applied, half at planting and the second half six weeks after emergence. The other half of the plot received no N.

Selection for chlorophyll

Relative chlorophyll content was estimated first at V5 (five leaf stage) using a Minolta SPAD-502 chlorophyll meter (Minolta Camera Co., Ltd., 3-13, 2-Chome, Azuchi-Machi, Chuo-Ku, Osaka 541, Japan). Measurements were taken on ten competitive plants within each plot on the last fully expanded leaf and an average chlorophyll reading, expressed in SPAD units, was derived for each line within the two N regimes. Each plant was then measured and plants with 5 SPAD units higher than the average reading were tagged “high” (H) and those with 5 SPAD units lower than the average reading were tagged “low”(L). Some of these selected plants were selfed while others were crossed between the two populations and between the N regimes. Crosses made were:

1. H $CCCc_1$ lines x H Poza Rica 8432 lines in plus N soil (+N) - Six hybrids from eight lines were evaluated from this group.
2. H $CCCc_1$ lines x H Poza Rica 8432 lines in low N soil (-N) - Seven hybrids from ten lines were evaluated from this group.
3. L $CCCc_1$ lines x L Poza Rica 8432 lines in low N soil (-N) - Seven hybrids from ten lines were evaluated from this group.
4. L $CCCc_1$ lines x L Poza Rica 8432 lines in plus N soil (+N) - Two hybrids from two lines were evaluated from this group.
5. H $CCCc_1$ lines x L Poza Rica 8432 lines in low N soil (-N) - Three hybrids from six lines were evaluated from this group.
6. H $CCCc_1$ lines x L Poza Rica 8432 lines in plus N soil (+N) - No hybrids were evaluated due to inadequate seed production.

Lines from the selfed plants were grown under irrigation in the 1993 winter off season. The lines were crossed using the same scheme as before. To promote satisfactory seed set, 40 kg ha^{-1} P_2O_5 and 80 kg ha^{-1} N were applied in the proportion of 20:20:0, along with calcium ammonium sulfate at planting and V5 stage. In 1993-94, the crosses were evaluated at three locations: Chitedze and Kandiyani in Lilongwe and Chitala in Salima District. The experimental design was a split plot with 3 N levels as main plots (0, 40 and 80 kg ha^{-1} N), 32 genotypes as subplots and 4 replicates. Plots consisted of 5.1 m rows planted on ridges with a spacing of 0.9 m, and one plant per hill spaced 0.30 m apart within rows. Leaf chlorophyll was estimated at V5 as in 1993 and at flowering, where the leaf subtending the ear shoot was measured. Leaf tissue was sampled at V5 and at mid-flowering to determine the proportion of dry matter and total N. After harvesting, the leaves were oven dried at 40°C for 5 days and then weighed. The dry leaves were ground and sieved (2 mm mesh) before being sent to Chitedze Plant Laboratory for total N determination using the Kjeldahl methodology. Other measurements included days to 50% pollen shed and silking, plant and ear height, grain yield components from a sample of five ears, and total grain yield. At Chitedze, only measurement of leaf chlorophyll at V5 was possible, because the trial suffered from severe water-stress and had to be abandoned.

Results

Chlorophyll SPAD readings

Differences ($P \leq 0.01$) in ear leaf chlorophyll levels attributed to N levels and genotypes were observed at V5 and at flowering. Significant genotype x N level interactions were observed only at Chitala and only at flowering. Mean chlorophyll level (SPAD units) increased with increasing soil N fertility from 34.7 at 0 kg ha^{-1} N to 43.7 and 43.8 at 40 and 80 kg ha^{-1} N, respectively.

At Chitala, hybrids from parents selected for low or high chlorophyll readings in low and high N environments did not differ. At Kandiyani, hybrids from parents selected for high chlorophyll readings in high N environments had higher chlorophyll readings than hybrids from parents selected for high chlorophyll readings in low N environments, at V5 and at flowering. At Chitala, ear leaf chlorophyll level was negatively correlated with days to anthesis (r^2=-0.47**) and days to mid-silk (r^2=-0.48**), but was positively correlated with kernel number (r^2=0.58**) and grain yield (r^2=0.73) at 0 kg ha^{-1} N. These correlations were also observed at 40 kg ha^{-1} N, but not at 80 kg ha^{-1} N. At Kandiyani, chlorophyll level was significantly correlated with seed size (r^2=0.34*) and grain yield (r^2=0.41**) at 0 kg ha^{-1} N. At 40 and 80 kg ha^{-1} N, significant correlations were observed with the number of kernels per ear and with grain yield (r^2=0.44** and r^2=0.41, respectively, at 40 kg ha^{-1}; and r^2=0.41** and r^2=0.58**, respectively, at 80 kg ha^{-1} N).

Percent leaf dry matter

No significant differences in percent leaf dry matter attributed to N levels or genotype were observed at the V5 stage at Chitala, but differences were observed at the flowering stage. At Kandiyani, differences due to genotypes were observed both at V5 and flowering, but differences due to N levels were observed only at flowering. No significant genotype x N level interactions were observed. Percent leaf dry matter at flowering followed the same trend as leaf chlorophyll level at flowering. It increased from 36.1% at 0 kg ha^{-1} to 49.1% and 48.2% at 40 and 80 kg ha^{-1} N, respectively, at Chitala, and from 30.9% at 0 kg ha^{-1} to 44.2% and 46.2% at 40 and 80 kg ha^{-1}, respectively, at Kandiyani. At Chitala, percent leaf dry matter was correlated with number of kernels at 0 kg ha^{-1} (r^2=0.38*), days to anthesis (r^2=0.40*) at 40 kg ha^{-1} N and days to anthesis and mid-silk (r^2=0.40* and r^2=0.35*, respectively) at 80 kg ha^{-1} N. At Kandiyani, proportion of dry matter in the ear leaf was also correlated with kernel number per ear (r^2=0.35*) and grain yield (r^2=0.50**) at 0 kg ha^{-1} N. At 40 kg ha^{-1} N leaf dry matter was only correlated with seed size and no correlations among traits were observed at 80 kg ha^{-1} N.

Days to flower

Both N levels and genotypes influenced ($P \leq 0.01$) days to pollen shed and to silking at Chitala and at Kandiyani. A significant genotype x N level interaction effect ($P \leq 0.05$) for days to silking was observed at Chitala. Days to pollen shed in hybrids decreased from 58 to 54 at Chitala and from 68 to 66 at Kandiyani, when N level was increased from 0 to 40 kg ha^{-1} N, but remained unaffected when N level was raised further to 80 kg ha^{-1}. Days to mid-silking followed the same trend. Hybrids from parents selected for high chlorophyll under low N shed pollen earlier than hybrids from parents selected for high chlorophyll under high N, when evaluated at 0, 40 and 80 kg ha^{-1} N. Days to anthesis and to mid-silk were negatively correlated with grain yield at all fertility levels (r^2=-0.62*** and r^2=-0.63**, respectively, at 0 kg ha^{-1} N; r^2=-0.35* and r^2=-0.45**, respectively, at 40 kg ha^{-1} N; and r^2=-0.47** and r^2=-0.57***, at 80 kg ha^{-1} N) at Chitala. At Kandiyani similar correlations were observed, except no significant correlation with grain yield was observed at 80 kg ha^{-1} N.

Plant and ear height

Differences were observed due to both N levels and genotype for plant and ear heights at Chitala and at Kandiyani. Genotype x N level interaction effects were observed only for ear height at Chitala. Plant and ear height increased when N level was increased to 40 kg ha^{-1} N. Beyond 40 kg ha^{-1} N, increases in plant and ear height were minimal. At 0 kg ha^{-1} N, selection for high chlorophyll at low N showed higher average ear placement than for hybrids from parents selected at high N. No other effects were observed.

Reproductive yield components

Genotype effects and N level influenced kernel number per ear significantly. Number of kernels per ear increased with increasing N levels from 307 kernels at 0 kg ha^{-1} N to 356 kernels at 40 kg ha^{-1} N. Number declined to 346 kernels per ear at 80 kg ha^{-1} N, however, this decrease could well reflect a random change and is not considered to be important. Selections for high chlorophyll in a high N environment resulted in hybrids that had on average more kernels per ear than similar selections done in a low N environment. Average seed size was not affected by N level at Chitala, but was significantly affected by genotype effects. At Kandiyani, however, both N level and genotype influenced seed size. There was also a highly significant genotype x N level interaction.

Highly significant differences in grain yield attributed to N and to genotype were observed at Chitala and at Kandiyani. Significant genotype x N level interactions were also observed for yield at both locations. However, there were no significant differences in yield between hybrids whose parents were selected for high or low SPAD chlorophyll. Grain yields were significantly different between S_2 and S_3 hybrids, although, the S_3 hybrids were only higher than S_2 hybrids at 0 Kg ha^{-1}. Seed size was correlated with grain yield at 0 kg ha^{-1} N at Chitala (r^2=0.54***) and at Kandiyani (r^2=0.45**). Number of kernels per ear showed a significant correlation with grain yield at 0 kg ha^{-1} N, but only at Chitala (r^2=0.48**).

Broad-sense heritability

Days to mid-anthesis, days to mid-silking and ear height were highly heritable traits (broad sense; h^2=0.80, h^2=0.74, h^2=0.79, respectively). Chlorophyll levels at flowering, dry matter at mid-flowering, number of kernels, seed size and grain yield showed low heritability values (h^2=0.35, h^2=0.47, h^2=0.40, h^2=0.43, and h^2=0.41, respectively).

Conclusion

Days to mid-anthesis, days to mid-silking, plant and ear height, chlorophyll at flowering, number of kernels per ear, and seed size were traits which correlated positively with grain yield. These traits could therefore be used as selection criteria for high performance in low N environments. Chlorophyll level and dry matter levels at flowering, number of kernels, and seed size are good indicators of high performance in low N environments, but their heritabilities are low.

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Caracterización Fisiológica de Cultivares Tropicales de Maíz en Venezuela

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Abstract

Nitrogen is one of the factors that frequently limits maize production in tropical areas. As a result, large quantities of nitrogenous fertilizer must be applied as a basic input in order to achieve satisfactory yields in the region. Nevertheless, it is difficult to sustain this crop management system over the long run, given the high costs of fertilizers. A study was undertaken of 15 tropical cultivars derived from the CENIAP-FONAIAP-Venezuela Maize Program to characterize a range of morpho-physiological traits associated with optimal and zero N use, thus obtaining basic information about the genetic potential of elite germplasm from the Venezuelan national program. The following traits were evaluated: biomass accumulation; specific foliar area; chlorophyll content; nitrogen reductase activity (ANR); and N absorption. Significant differences were detected ($P \leq 0.05$) among the cultivars for ANR and chlorophyll content. Under conditions of low N, the variation was between 1.6 and 7.1 mmol h^{-1} g^{-1} and 0.55 and 1.29 mg g^{-1} of ANR and chlorophyll, respectively, whereas under conditions of high N the variations were between 3.3 and 16.8 mmol h^{-1} g^{-1} and 1.17 and 2.53 mg g^{-1}, respectively. The coefficient of correlation between ANR and biomass was $r=0.71$ ($P \leq 0.05$), and between ANR and N absorption was $r=0.8$ ($P \leq 0.05$). The results of this study can enhance the use of promising germplasm in a breeding program focused on developing maize that efficiently takes up and uses N.

Introducción

El rendimiento de los cereales está directamente relacionado con el uso del N (Hageman, 1979), y este nutrimento es el factor que con mayor frecuencia limita la productividad del maíz en las regiones tropicales y teóricamente puede solucionarse con la adición de fertilizantes nitrogenados. Sin embargo, con frecuencia el N no es aplicado en las cantidades necesarias debido al alto costo de los fertilizantes. Por lo anterior es necesario encontrar alternativas que conduzcan a la menor dependencia de los fertilizantes nitrogenados. Una estrategia potencial para alcanzar esta meta es el establecimiento de sistemas agrícolas, acordes con las condiciones ambientales y socioeconómicas en las regiones tropicales. La utilización de variedades mejoradas que posean elevadas tasas de absorción, asimilación y/o redistribución de N desde las estructuras vegetativas hacia las reproductivas puede ser un elemento tecnológico fundamental en estos sistemas agrícolas.

El desarrollo del grano depende del suministros de C y N, de hecho, el almidón y la proteína representan 90% del contenido de materia seca almacenada en el grano de maíz (Neyra y Hageman, 1978). Por otro lado, se han identificado las relaciones entre varios componentes del metabolismo del N con el rendimiento y contenido de proteína del grano (Below et al., 1981). Así, la actividad de la nitrato reductosa (ANR) está altamente correlacionada con ambos caracteres (Cregan y van Berkum, 1988; Deckard et al., 1973). Sin embargo, algunos autores sugieren que la ANR no refleja por si sola la asimilación in situ de NO_3 por los diversos cultivares. En maíz, entre 50 y 60% del N foliar está asociado con los cloroplastos y entre 90 y 95% del N removilizado desde las láminas foliares para la producción de grano proviene de los cloroplastos (Hageman, 1986). El incremento de la concentración de clorofila por unidad de área está altamente correlacionado con la concentración de N foliar (Wolfe et al., 1988). La variabilidad genética de los parámetros antes mencionados ha sido ampliamente documentada en maíz (Chevalier y Schrader, 1977; Eghball y Maranville, 1991; Hageman, 1986; Jackson et al., 1986; Muruli and Paulsen, 1981; Pollmer et al., 1979) y existe la posibilidad de realizar selecciones para obtener cultivares con propiedades ideales (Lafitte y Edmeades, 1994; Sherrard et al., 1984). Además de seleccionar los cultivares más eficientes, deben caracterizarse e identificarse las diferencias con los menos eficientes; así, podrían identificarse las variables responsables de la eficiencia del uso de los nutrimentos y con el desarrollo de métodos simples para evaluar esas variables podría cuantificarse la variabilidad genética; lo anterior permitiría realizar exitosamente la selección y el mejoramiento de cultivares con propiedades ideales.

La evaluación de las propiedades fisiológicas y bioquímicas directamente relacionadas con el metabolismo de C y el N y sus efectos en el rendimiento en colectas específicas es necesaria. Con ellas el fitomejorador podrá abordar con éxito un programa de selección de cultivares tolerantes a condiciones limitadas de N y/o eficiente en su uso. El objetivo del presente estudio fue obtener información básica preliminar del potencial genético en algunas propiedades fisiológicas vinculadas a la nutrición de N del germoplasma, elites del Programa de Maíz CENIAP-FONAIAP de Venezuela.

Materiales y Metodos

Los cultivares de maíz seleccionados para este estudio representan el germoplasma elite manejado por el Programa de Maíz del CENIAP-FONAIAP de Venezuela (Cuadro 1). El experimento se realizó en un invernadero del Instituto de Investigaciones en Recursos Agroecológicos-CENIAP, Maracay. Se seleccionó un suelo Typic Haplustult procedente de Pao, Cojedes. Las muestras de suelo fueron tomadas de los primeros 0.2 m del perfil, presentaron textura franco arenosa, pH 5.4, 1.13% de materia orgánica y 21, 42 y 288 ppm de P, K y Ca, respectivamente. El suelo fue secado al aire y tamizado con una malla con poro de 4 mm. El bajo pH del suelo se corrigió con 103 mg $CaCO_3$/kg de suelo seco (300 kg $CaCO_3$/ha), e incubación durante 21 días, hasta que se alcanzó pH 6.2 (López y Sánchez, 1990). Se utilizaron botes de plástico de 0.22 m de diámetro y 0.24 m de profundidad, para 5 kg de suelo. El suelo se mezcló con 39 mg de P_2O_5 (100 kg P_2O_5/ha), 130 mg $K_2$0 (90 kg K_2O/ha) y la mitad de las dosis de N y 342 mg (+ N para 200 kg N/ha), el resto de la dosis de N fue aplicada tres semanas después de la germinación. En cada bote se sembraron dos plantas. Los tratamientos se distribuyeron en un diseño de parcelas divididas, con cuatro repeticiones. Las plantas fueron regadas diariamente durante los 50 días del ensayo con agua desmineralizada. El invernadero fue enfriado con una cortina de agua, manteniendo una temperatura promedio de 29ºC durante el período experimental; la radiación y HR promedio fueron 575 (mmol m^{-2} seg^{-1} y 70%, respectivamente.

Cuadro 1. Germoplasma del programa de maíz, CENIAP-FONAIAP, Venezuela.

Cultivar	Procedencia
1. Beto 73	Venezuela (CENIAP)
2. La Máquina 8022	Guatemala (CIMMYT)
3. Tuxpeño Sequía C6	México (CIMMYT)
4. Compuesto Duro 77	Venezuela (CENIAP)
5. Ferke (1) 8223	México (CIMMYT)
6. Tuxpeño Crema PB C11	Venezuela (CENIAP)
7. Agua Blanca Portuguesa 88	Venezuela (CIAP)
8. Santa Rosa 91-A	Nicaragua
9. Suwan x La Posta AM	México (CIMMYT)
10. Amarillo 3 x Mezcla Amarilla	Venezuela (CENIAP)
11. CENIAP Amarillo 381	Venezuela (CENIAP)
12. Across 8149	México (CIMMYT)
13. Padre CENIAP 81*	Venezuela (CENIAP)
14. Madre CENIAP 81*	Venezuela (CENIAP)
15. CENIAP PB8**	Venezuela (CENIAP)

* Híbrido simple; ** híbrido doble.

ANR se evaluó por el método in vivo en la última hoja superior completamente expandida, de acuerdo con la técnica descrita por Farnden y Robertson (1980) y se expresó en (moles NO_2 h^{-1} mg^{-1} peso fresco. El nitrato es reducido a nitrito en oscuridad utilizando el NADH endogeno (tejido) como reductante, se determinó la generación de nitrito por el método espectrofotométrico. El contenido de clorofila fue cuantificado en la misma hoja por el método descrito por Bruinsma (1963). Se extrajo la clorofila con acetona al 90%, el material sólido de la planta se removió por centrifugación. El extracto de clorofila se midió con el espectrofotómetro. El ·rea foliar específica (AFE) se evaluó con 10 discos de la hoja, evitando tomar nervadura central, correspondientes a 0.343 cm^2. La biomasa aérea se obtuvo cosechando las plantas a los 50 días, y secando el material a 75ºC por lo menos durante 48 h. Este material fue molido y tamizado en una malla con poro de 2 mm y se utilizó para cuantificar el N total, con el método Kjeldahl (FAO-IAEA, 1987). Los datos fueron analizados utilizando un diseño de parcelas divididas, se obtuvo un análisis de varianza y correlación.

Resultados y Discusión

Se observaron diferencias estadísticamente significativas en la biomasa, ANR y clorofila ($P<0.05$) y altamente significativas en AFE ($P<0.01$) entre los cultivares; pero en la absorción de N no hubo diferencias. Además, todos los caracteres fueron diferenciados significativamente ($P<0.01$) por la dosis de N (Cuadro 2). La aplicación de N abatió 65% su propia absorción y 60% la ANR, ambos caracteres están vinculados directamente con la eficiencia de la absorción del N (Cuadro 3). Esta diferencia significativa en la absorción del N o en el contenido de N total ha sido considerada evidencia del control genético entre cultivares (Chavalier y Schrader, 1977; Moll et al., 1982).

La ANR fluctuó desde 1.6 hasta 7.1 mmol h^{-1} g^{-1} peso fresco, sin la aplicación de N (-N) entre los 15 cultivares (Fig. 1b); así , la variación fue más amplia que la observada por Feil et al. (1993) en plántulas de maíces tropicales. Con base en la biomasa aérea, ANR y absorción de N (Fig. 1a-c) se identificaron dos grupos, los de alta acumulación de N (Across 8149, Ceniap Amarillo 381, Amarillo 3 x Mezcla Amarilla, Tuxpeño Sequía y La Máquina 8022) y los de baja acumulación (los cultivares restantes).

Por otro lado, la biomasa aérea estuvo positivamente correlacionada con la absorción de N ($P\leq0.05$) y con la ANR ($P\leq0.01$) sólo cuando no se aplicó N (Fig. 2a, Cuadro 4). La absorción de N se correlacionó significativa y positivamente con la ANR en ambos tratamientos de N (Fig. 2b, Cuadro 4), lo cual es consistente con el papel dual del contenido de N (formas NO_3) como inductor y substrato de la enzima (Neyra y Hageman, 1978).

Los contenidos de clorofila presentaron correlación significativa y positiva con la biomasa aérea, absorción de N y ANR ($r = 0.64$; $r = 0.53$; y $r = 0.53$, respectivamente) en el tratamiento -N (Fig. 2c, 3a-b). Al respecto, Lafitte y Edmeades (1994) han indicado que la concentración de la clorofila puede estar íntimamente relacionada con la absorción de N y su asignación, especialmente durante el ciclo de crecimiento vegetativo. En contraste, el AFE no se correlacionó

Cuadro 2. Analisis varianza para biomasa (g $planta^{-1}$), Absorpcion N x 10^{-2} (g $planta^{-1}$), ANR (μmol h^{-1} g^{-1}) y AFE (cm^2 g^{-1}) en 15 cultivares tropicales de maíz, Venezuela.

	gl	Biomasa	Abs N	ANR	Clorofila	AFE
Repetición	3	5.7 ns	3.3 ns	2.6 ns	1.2 ns	3.12 ns
Nitrógeno (N)	1	96.1**	106.4 **	65.0**	16.0**	21.1 **
Genotipo (G)	14	1.9*	1.8 NS	2.5*	2.7*	2.9 **
N x G	14	1.0 ns	0.7 ns	1.2 ns	0.8 ns	1.93 *

*, ** significativo a P = 0.05 y 0.01, respectivamente

Cuadro 3. Promedio de algunos caracteres fisiológicos asociados con la eficiencia en la absorción de N de 15 cultivares tropicales de maíz evaluados sin (-N) y con aplicación (+N) de una dosis de 200 kg de N/ha cultivados en invernadero.

	-N			+N			
Carácter	Media	Amplitud	S_d[a]	Media	Amplitud	S_d	-N/+N[b]
Biomasa aérea (g $planta^{-1}$)	16.2	(12.9-19.6)	0.59	27.7	(23.2-34.9)	1.05	0.58
ANR (μmol NO_2 h^{-1} g^{-1})	4.0	(1.6- 7.1)	0.47	10.1	(3.3-16.8)	0.87	0.40
Clorofila (mg g^{-1})	0.98	(0.55-1.29)	0.05	1.58	(1.17-2.53)	0.09	0.62
Abs. N (mg $planta^{-1}$)	13.4	(7.4-19.3)	0.87	37.9	(31.2-47.9)	1.95	0.35
AFE (cm^2 g^{-1})	261	(235-312)	6.4	281	(243-347)	8.4	0.93

[a] Error estandard de la diferencia entre medias de 15 cultivares

[b] Relación de la media en la condición de -N y +N

significativamente con alguno de los otros caracteres evaluados, resultó altamente variable entre los cultivares (Fig. 1e) y se incrementó con la aplicación de N. Así, puede decirse que los cultivares respondieron diferencialmente al suministro de N. Esto muestra que la caracterización de los cultivares debe realizarse incluyendo el suministro de este nutrimento.

Conclusiones

En el estudio se demostró que existe a nivel de plántula una respuesta diferencial en varios caracteres morfo-fisiológicos dependiente del cultivar, vinculada con la absorción y el nivel de N. Así, se han identificado cultivares con mayor potencialidad de absorción de N, que podrían continuar utilizándose en el estudio de los caracteres primarios de productividad del cultivo (rendimiento y nivel de N en el grano).

Cuadro 4. Correlación entre caracteres relacionados con la eficiencia de absorción de nitrógeno de 15 genotipos de maíz evaluados sin (-N) y con (+N) aplicación de una dosis de 200 kg de N/ha evaluados en condiciones de invernadero.

	AFE	ANR	Clorofila	Biomasa
Absorción N				
- N	+ 0.42ns	+ 0.62*	+ 0.53*	+ 0.65*
+ N	+ 0.28ns	+ 0.68*	+ 0.15ns	+ 0.18ns
AFE				
- N		- 0.0	- 0.21ns	- 0.19n
+ N		- 0.03ns	+ 0.006ns	- 0.26ns
ANR				
- N			+ 0.53*	- 0.71**
+ N			+ 0.23ns	- 0.32ns
Clorofila				
- N				- 0.64*
+ N				- 0.30ns

*, ** significativo a nivel de $P \leq 0.05$ y $P \leq 0.01$

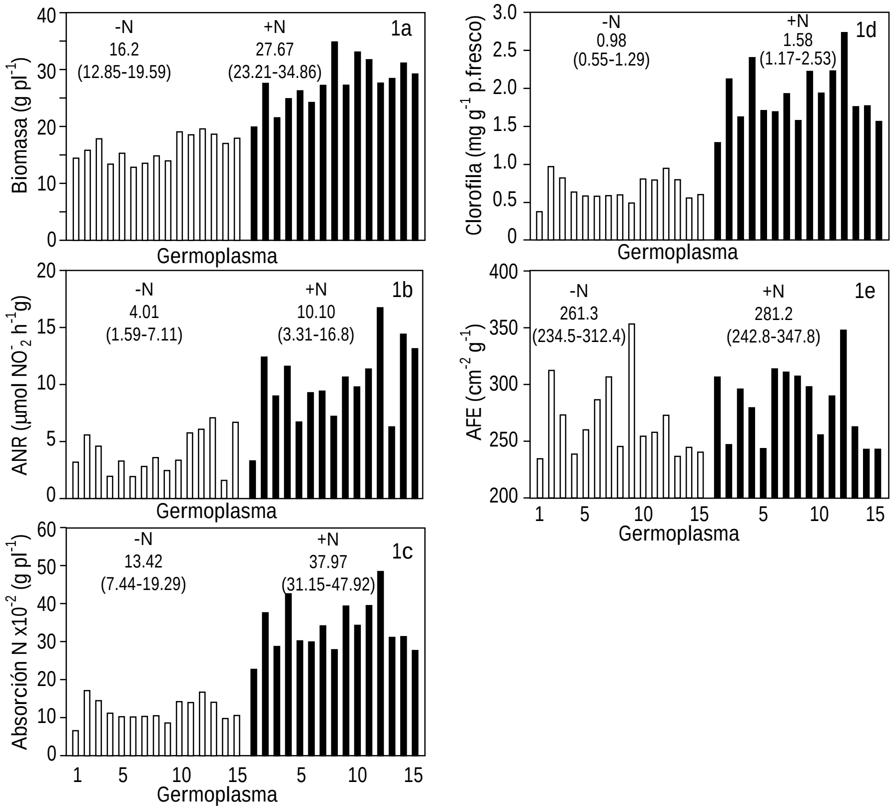

Figura 1. (a), actividad de la nitrato reductasa (ANR); (b), absorción de N; (c), contenido de clorofila; (d), área foliar específica (AFE); (e) de 15 cultivares de maíz tropical sin aplicación (-N) y con aplicación de 200 kg de N/ha (+N).

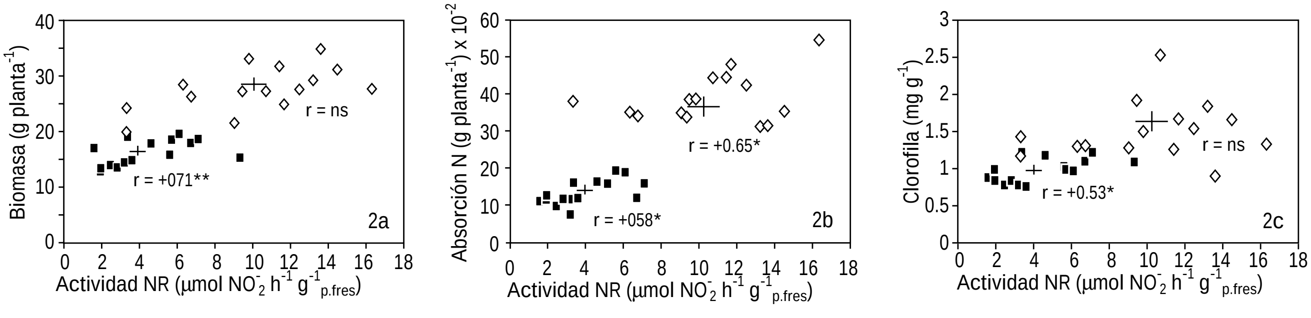

Figura 2. Relación de la actividad de la nitrato reductasa (ANR) y biomasa (a), absorción de N (b) y clorofila (c) en 15 cultivares de maíz tropical sin aplicación (-N) y con aplicación de 200 kg de N/ha (+N). Las cruces representan los errores estándar. *, ** con un nivel de probabilidad del 5 y 1%, respectivamente.

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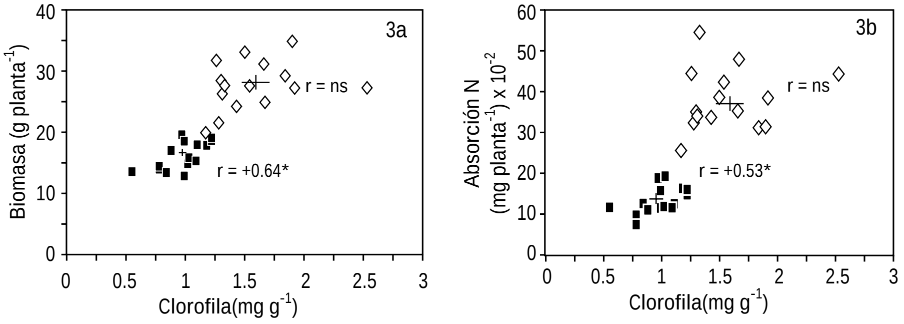

Figura 3. Relación de los contenidos de clorofila y biomasa (a) y absorción de N (b) en 15 cultivares de maíz tropical sin aplicación (-N) y con aplicación de N (+N). Las cruces representan los errores estándar, * significativo a un nivel de probabilidad del 5%.

Development and *per se* Performance of CIMMYT Maize Populations as Drought-Tolerant Sources

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Abstract

CIMMYT has been developing source populations for drought tolerance (DT) using two approaches. One involves recurrent selection of elite populations that has resulted in the production of lowland tropical sources of drought tolerance (Late-maturing: Tuxpeño Sequía C_8; TS6 C_3; La Posta Sequía C_5; Pool 26 Sequía C_3. Early-maturing: Pool 18 Sequía C_4; Pool 16 C_{20}). A second, slower approach has been to screen a wide range of improved and unimproved germplasm for unique sources of drought tolerance, and to combine these into a single gene pool which is then improved for agronomic performance. In 1986 22 sources were screened under drought for tolerance. The best 13 of these were crossed in a diallel, and the individual crosses evaluated under drought. The best 74 (out of 168 possible) crosses were recombined in a half-sib crossing block for four cycles (i.e., to C_4),and named Drought Tolerant Population-1 (DTP1). In C_5 and C_6 the breeding scheme shifted to recurrent S_1 selection, and the best 222 prescreened S_1 families were sib-increased and evaluated in multi-location international trials. In each cycle the best 40 S_1 families were recombined. At the same time, 160 landraces and 156 elite source materials were evaluated per se and in crosses with DTP1 under drought In 1990 the best 25 of these were introgressed into an elite fraction of DTP1 to form DTP2, using half-sib crossing blocks for three cycles to ensure recombination. Both DTP1 and DTP2 were of mixed color, intermediate in maturity, with adaptation approximately 60-65% lowland tropical, 15-20% subtropical and 20% temperate. Presently the best fractions of DTP1 and DTP2 are being merged by grain color, improved for disease reaction, husk cover and drought tolerance, and inbred lines are being extracted. In international trials both populations perform at 90-95% of the level of La Posta Sequía C_3, are superior under severe stress or in subtropical locations, and have shown a good level of stability across environments.

Introduction

Why develop source populations?

Breeders rely on germplasm sources of drought tolerance (DT) when they feel that their own germplasm does not have a sufficiently high frequency of DT-related genes, or even lacks variability for DT. How germplasm sources of DT are used by the breeder depends mainly on the adaptation of the germplasm source to the target environment. In rare cases the germplasm source is well-adapted and high-yielding when evaluated in the target environment and can be directly released. Usually, however, additional breeding effort is required. Breeders may use the source of DT in varietal or line crosses to produce a product with a moderate degree of DT for release as the F_1 to farmers, or when they wish to extract germplasm with a higher frequency of DT alleles. Broad adaptation of the source is preferred when it is used as one side of a population cross or hybrid in which the F_1 generation is the final product. When sources are used in this way, it is preferable that they carry a high level of tolerance to other stresses along with excellent agronomic characteristics, since there is no opportunity to eliminate poorly adapted genotypes from the finished product.

Instead of selecting for DT in an adapted population or, while extracting lines, breeders may also choose to improve the adaptation and yield of the source of DT through recurrent selection or to extract better adapted inbred lines from a source of DT (see Beck et al., 1997). Recent data indicate that the probability of obtaining DT hybrids is significantly greater when the source population from which the lines were extracted also has a high level of DT (Edmeades et al., 1997c). For example, the probability of obtaining a hybrid that yielded 40% greater than the trial mean under severe drought stress was four times greater if lines had been extracted from a population improved for DT rather than from the same base population that had been improved by conventional means. Data presented by Duvick (1995) also suggest that improved performance of inbred lines in the US over the past 60 years accounts for a larger proportion of the increase in yield of hybrids derived from those lines than does the increase in heterosis between those lines.

Finally, breeders may transfer DT to an adapted but otherwise susceptible material by backcrossing, using either conventional methods or marker-assisted selection. Since DT is a polygenic trait, conventional backcrossing is only an effective method in transferring DT provided the breeder is able to test widely for the presence of DT in successive backcrossing generations and provided the source population is at least moderately adapted to the target environment. The requirement to field-screen large numbers of backcross generation plants and the need to use an adapted source are much less important during marker-assisted selection, when only a small part of the genome is targeted for transfer to the recipient genotype. With these techniques the transfer can be accomplished in only 2-4 generations of backcrossing, and field facilities for screening are only needed to *confirm* the presence of that fraction of the genome that carries DT — and then only in perhaps 2-5% of the backcross families formed in any single generation (Ribaut et al., 1997). For marker-assisted selection to be cost-effective, however, the source needs to have a considerably higher level of DT than that found in the recipient germplasm, implying that poorly adapted sources with a high level of DT are of much greater value when this technique is used compared with conventional backcrossing.

Methods and Materials

Development of drought tolerant source populations at CIMMYT

For the last 15-20 years, CIMMYT has been developing source populations for drought tolerance following two main approaches. The first is based on the premise put forward by Blum (1983) that “ ......unidentified drought-adaptive alleles exist at relatively high frequencies in common breeding populations.....” Blum cited as supporting evidence the fact that conventional breeding programs continue to produce varieties with improved productivity under drought stress. CIMMYT therefore sought to identify DT families within elite high-yielding populations structured as full-sib, S_1 or S_2 families. The populations were chosen either because they were already relatively drought-tolerant (as with Tuxpeño Sequía; Fischer et al., 1983), or to improve DT in a wide range of elite, broadly-adapted germplasm (as in Pool 16 Sequía, Pool 18 Sequía, Pool 26 Sequía and La Posta Sequía). Today Tuxpeño Sequía, La Posta Sequía and Pool 16 Sequía are being used increasingly by national program cooperators. Pool 18 Sequía and Pool 26 Sequía, on the other hand, have not gained wide acceptance because of a lack of stability. All populations are of lowland tropical adaptation, have a semi-dent/dent grain texture, and represent a reasonable range of maturities and grain colors (Table 1). Selection schemes used in developing these populations have been described in detail elsewhere (Fischer et al., 1983; Fischer et al., 1989; Bolaños and Edmeades, 1993; Edmeades et al., 1995a, b, 1997a; Chapman and Edmeades, 1998). In brief, populations undergoing full-sib recurrent selection were improved by identifying 60 superior families for recombination out of 250 being tested under three levels of drought stress. During recombination the next set of full-sib families were created, and one improvement cycle required one year to complete. Populations undergoing improvement by S_1 recurrent selection were handled differently. A large number (500, but occasionally as many as 1500) of S_1 families was created in Poza Rica and screened under heat and drought; the best 200-250 of these were sown from remnant seed in Tlaltizapán under two to three levels of water stress, and the superior 50 of these were recombined. The new group of S_1 families was formed in the full-sibs that resulted from the recombination.

One cycle took two years to complete and provided the opportunity to develop inbred lines from superior S_1 families identified during testing. Note that the population designated as TS6 is actually Tuxpeño Sequía C_6 that was switched from full-sib recurrent selection to S_1 recurrent selection; cycle numbers of TS6 date from this change in selection methodology.

A second approach used at CIMMYT to develop source populations for DT was to screen sources of germplasm with superior performance under drought but which may lack yield potential and good agronomic characteristics in well-watered environments. It was expected that the agronomic performance of these sources might be inferior to that of elite germplasm under well-watered conditions. It is, however, important to recall that conventional elite maize populations began as such unimproved sources only 20-30 years ago, and we were therefore confident that yield, disease reaction and lodging resistance could be improved by conventional selection methods. It was considered unlikely that this source population would be released directly, but that breeders would use it crossed to elite adapted germplasm or after improving it for agronomic performance. The original intention of this approach was to screen many sources for the array of putative secondary drought-adaptive traits described in the literature (see, for example, Ludlow and Muchow, 1990), but this was beyond our resources. Screening therefore was undertaken in germplasm from many different backgrounds for yield and for the normal array of secondary traits that we record during our recurrent selection procedures.

Development and composition of DTP1

Thirteen of 22 potential source populations were identified as DT and intercrossed (Table 2). Adaptation of components was: lowland tropical (60%), subtropical (22%) and temperate (18%); 15% came from landrace collections, including sources of the *latente* syndrome for drought tolerance (Castleberry and Lerette, 1979). These 13 components were crossed in a diallel, and the individual crosses evaluated under drought. The best 74 (out of 168 possible) crosses were recombined in a half-sib crossing block, taking care not to eliminate any of the 13 original components as females. At the C_2 stage germplasm from three additional landraces was introgressed (about 20% total contribution) (Table 2) and half-sib selection under mild selection pressure continued for a further two cycles, using a population size of around 350 families. Two cycles of S_1 recurrent selection followed; around 200 progenies were tested at 10-12 international sites, and the best 40 recombined (Edmeades et al., 1991, 1995b). During the last cycle of international S_1 testing, 2-6 S_2 families were created in each selected S_1 family, screened under heat and drought, separated for color, and recombined to form a yellow (DTP1-Y C_7) and a white (DTP1-W C_7)

Table 1. Description of elite maize populations that have undergone recurrent selection for drought tolerance at Tlaltizapán, Mexico.

Population	Began as	Cycles of sel.	Breeding scheme	Color	Maturity	Grain type	Adaptation[b]	Special features	Lines extracted? (level)	Adapted to countries
Tuxpeño Sequía	Tuxpeño-1 C_{12}	8	FS	W	L	D	LT	Broadly adapted		W. Africa C. America
TS6	Tuxpeño Sequía C_6	3	S_1	W	L	D	LT	Broadly adapted	S_8	W. Africa C. America
La Posta Sequía	Pop. 43 C_6	5	S_1	W	L	D	LT	High yield Streak resistant	S_8	W. Africa C. America, Asia
Pool 26 Sequía	Pool 26 C_{12}	3	S_1	Y	L/I	D	LT		S_8	Andean zone
Pool 18 Sequía	Pool 18 C_{15}	4	S_1	Y	E	F/D	LT	Early	S_8	Asia
Pool 16 Sequía	Pool 16 C_{12}	5[a]	FS/S_1/S_2	W	E	D	LT	Early, broadly adapted	S_7	W. Africa

[a] Population was handled as full-sibs between Ivory Coast and Mexico, switched to S_1, then to S_2 recurrent selection. Latest version is Pool 16 C_{20}

[b] LT = lowland tropics (<1200 masl); ST = subtropics (2000 masl >sites >1000 masl)

population. The best S_2 lines were advanced to S_4. At present these populations are intermediate in maturity, mixed for color and texture, and susceptible to leaf and ear diseases. They have been superseded by the combined population formed by merging DTP1 and DTP2 (see below).

Development and composition of DTP2

While DTP1 was being improved, additional source materials were screened under well-watered conditions and under moderately severe mid-season drought stress. Selection was based on delayed foliar senescence, small (more negative) osmotic potential (when measured), high grain yield, a reduced level of barrenness under stress, a short anthesis-silking interval, and lodging resistance under stress. Sources evaluated in this manner came from:

1. Landrace collections (300) held by CIMMYT's Germplasm Bank from collection sites <1000 m elevation and with annual rainfall <600 mm.
2. Elite selections with reputed drought tolerance (104): from Mexico, southern Africa, Thailand, USA, and CIMMYT's conventional program.
3. Elite selections with known drought tolerance (52) from CIMMYT's drought breeding program

The population DTP2 was formed by the introgression of 25 new DT sources into DTP1 C_5 (Table 2). Adaptation of components of DTP2 is estimated as lowland tropical (65%), subtropical (15%) and temperate (20%), and 11% of its germplasm can be traced directly to landraces. The population is of intermediate maturity, mixed color and texture, and susceptible to foliar and ear diseases. Initially components were recombined during three cycles of half-sib recombination under mild selection pressure. This was followed by one cycle of S_1 recurrent selection under drought and heat. Recombination of the best 40 families was by grain color to form DTP2-Y C_5 and DTP2-W C_5. The best 200 S_1 families from each color fraction of DTP1 C_7 have been evaluated under two levels of drought stress in a combined trial with 200 DTP1 C7 S_1 families, and the superior 60 families in each color class have been recombined to form DTP-Y C_8 and DTP-W C_8.

Table 2. Contributions of selected sources to the composition of Drought Tolerant Populations 1 (DTP1) and 2 (DTP2).

DTP1		DTP2	
Source	Percent contribution	Source	Percent contribution
Cycle 0	Cycle 0		
Tuxpeño Sequía C_8	14.4	DTP1 (various cycles)[a]	58.0
Latente x Corn Belt	18.3	Pool 18 Sequía C_1, best all	1.8
Michoacan 21	14.2	Pool 16 Sequía C_1, best all	1.8
KSX 2301	7.3	Pool 26 Sequía C_1, best all	1.8
AN1 x AN2 (Tuxpeño)	7.4	La Posta Sequía C_1, best all	1.8
Obregon Sequía 8332	6.9	Sint. de S_3's, La Posta Seq., C_0	1.8
Obregon Sequía 8322	7.0	Sint. de S_3's, Pool 26 Sequía	1.8
Antig. x Rep. Dom. small tassel C_6	6.4	S_3's of Pool 18 Sequía C_0	1.5
Crosses among QPM Pops. 62, 64 and 66	18.1	Pioneer 3165, F_2	1.8
		TS6 C_1, best yield SS	1.8
Total	100.0	KSX 2301	1.8
		TL8421 x *Latente* (BF)	1.8
		Tabloncillo Sinaloa 31	1.8
		CG 4419	1.8
Later introgressions (C_2)	20.0	R201	1.8
Pepitilla Brazil 2482		Pool SPE C_4, best all	1.8
Sinaloa 31		Tamaulipas 25	0.9
Nuevo Leon Gpo 2		FRB73 x FRMo17	1.8
		KI14	0.9
		[(SD10 x H28)x K55]	0.9
		Experimental Corn Belt hybrid #5	2.3
		Experimental Corn Belt hybrid #6	1.3
		G4734	2.3
		H-430	1.3
		Ob. Seq. 8349 x Ob. Seq. 8332	2.3
		SPMAT C_4, best all	1.3
	Total		100.0

Results and Discussion

Evidence of performance

Drought-tolerant elite populations - Several studies have compared advanced selection cycles with original cycles of selection or their conventionally-selected counterparts: Tuxpeño Sequía C_8 with C_0 and with Pop. 21 C_6 (Bolaños and Edmeades, 1993; Byrne et al., 1995); La Posta

Sequía C_3 with C_0 and Pop. 43 C_9; Pool 26 Sequía C_3 with C_0 and Pool 26 C_{23} (Edmeades et al., 1995c); Pool 18 Sequía C_3 with C_0 and with Pop. 31 C_5 (unpublished data). In all cases populations following a similar number of cycles of improvement by conventional selection have not shown any improvement in tolerance to mid-season drought, while drought-tolerant selections have shown consistent improvements of around 100 kg ha^{-1} yr^{-1}. Advanced cycles of these elite drought-tolerant sources were tested in international drought network trials grown at 19 to 21 sites (Edmeades et al., 1997b). Among the early maturing group (Table 3) Pool 18 Sequia C_3 and Pool 16 C_{20} performed well in severely and moderately stressed environments. Pool 16 C_{20} had, in recent years, undergone several cycles of selection for drought tolerance interspersed with conventional selection. Both entries were more stable and higher yielding than the two conventionally-selected reference entries (RE) as defined by Lin and Binn's (1988) superiority index (Table 3). Among the late maturing group (Table 4), La Posta Sequía C_3 yielded the same across sites as the average of the best local check, with a mean yield of 3.6 t ha^{-1} and good stability. The performance of TS6 C_1 was disappointing, especially in low yielding sites, and was below average for stability. The earliest entry in the trial, Pool 26 Sequía C_3, was also unstable (using the superiority index as a measure) and low yielding. It was, however, the highest yielding entry in the lowest yielding sites (Table 4), perhaps because its early maturity allowed it to escape some of the consequences of low rainfall. Each of these three elite sources showed ear rot susceptibility, and more attention must be given to ear rot resistance, if these sources are to be used for direct release by national programs.

The CIMMYT Maize Program periodically conducts trials of open-pollinated source germplasm in Preliminary Evaluation Trials (PETs), in which germplasm currently under development in its breeding programs is stratified by maturity, color and adaptation, and compared in trials at 5-7 international locations. Results from the latest of these (Table 5) confirm the superiority of La Posta Sequía C_3 (first out of 25 entries) and the disappointing performances of TS6 C_1 (22nd out of 25) and Pool 26 Sequía C_3 (10th out of 14). Pool 16 C_{20} and Pool 18 Sequía C_3 ranked, respectively, 2nd and 11th out of 14. In general the drought source populations perform at average to above-average in these types of evaluations under well-watered conditions.

Additionally CIMMYT's Physiology Program conducts many evaluations in which elite drought tolerant selections are included as check entries. Thus, in an evaluation of PET 3 and PET 4 under drought at a single site in 1994, TS6 C_1, La Posta Sequía

Table 3. Across-site means of various characteristics observed in five early maturing drought tolerant maize genotypes, two reference genotypes (RE), and two local check genotypes. The trial had 12 entries in total. Superiority index (Lin and Binns, 1988) is smallest for entries that are the most stable across sites (adapted from Edmeades et al., 1997b).

	Grain yield at sites with stress level:									
	All sites (t ha^{-1})	Low (t ha^{-1})	Moderate (t ha^{-1})	Severe (t ha^{-1})	Superiority index	Anthesis date (d)	ASI (d)	Ears per plant	Rotted ears (%)	Senesc. score (1 to 5^a)
DTP1 C_5 Early Sel.	2.63	4.63	2.70	0.89	53.1	59.4	3.59	0.80	10.6	2.59
Pool 18 Sequía C_3	2.53	4.10	2.67	0.99	52.3	54.5	2.29	0.83	7.7	2.71
Local Check 1	2.50	4.18	2.38	0.94	69.9	58.3	3.56	0.76	6.6	2.80
Pool 16 C_{20} Syn. 1	2.47	4.05	2.58	1.03	57.5	54.2	2.64	0.83	8.5	2.65
TEYF Drt Tol. Syn. 2	2.31	3.65	2.59	0.86	91.7	53.7	2.49	0.82	8.9	2.80
Santa Rosa 8330 RE	2.29	4.18	1.90	1.00	94.2	58.7	3.45	0.78	7.8	2.49
TEWF Drt Tol. Syn. 2	2.27	3.89	2.37	0.79	84.0	55.2	2.78	0.80	9.0	2.71
Across 8331 RE	2.20	4.12	1.90	0.83	107.2	58.5	3.57	0.76	10.7	2.63
Local Check 2	2.17	4.09	1.82	0.69	129.7	58.3	3.89	0.70	8.9	2.81
Mean	2.38	4.11	2.36	0.87	79.5	56.8	3.06	0.79	8.8	2.69
Number of sites	21	6	7	7	21	21	21	21	15	9
Prob. F test	0.04	0.10	0.00	0.20		0.00	0.00	0.00	0.45	0.67
LSD (0.05)	0.28	0.51	0.48	0.40		1.8	1.25	0.07	3.6	0.40

[a] Score of 1 = green; 5 = dead

C_3 and Pool 26 Sequía C_3 showed consistently good performance versus the reference entries (Table 6A). It is of interest also to compare the performance of OPV source populations with that of hybrids. In an international test of late white hybrids, La Posta Sequía C_3 was included as an open-pollinated check entry. Sites were generally unstressed. Data from 27 sites indicate that CML254 x CML247, the top-yielding hybrid, averaged 6.9 t ha^{-1} and flowered in 64 d, compared with La Posta Sequía C_3 at 5.6 t ha^{-1} and 62 d. In this trial set the best and worst hybrid entries outyielded La Posta Sequía C_3 by 23% and 5% respectively. In another trial conducted under drought, heat, low N and well-watered conditions, yields of single cross hybrids, varietal hybrids and OPVs were averaged across environments, standardized

Table 4. Across sites means of various characteristics observed in seven late-maturing drought tolerant maize genotypes, two reference genotypes (RE), and three local check genotypes. The trial had 20 entries in total. Superiority index (Lin and Binns, 1988) is smallest for entries that are the most stable across sites (Adapted from Edmeades et al., 1997b).

	Grain yield at sites with stress level:									
	All sites (t ha^{-1})	Low (t ha^{-1})	Moderate (t ha^{-1})	Severe (t ha^{-1})	Superiority index	Anthesis date (d)	ASI (d)	Ears per plant	Rotted ears (%)	Senesc. score (1 to 5[a])
La Posta Sequía C_3	3.58	6.06	2.95	0.99	78.6	64.5	2.45	0.87	12.7	3.32
Local check #2	3.56	5.68	3.36	0.88	86.0	63.6	2.85	0.85	5.8	3.36
Across 8627 RE	3.42	5.53	2.91	1.17	82.3	62.8	2.34	0.92	8.4	3.11
Ngabu 89DTP1	3.36	5.48	2.86	1.08	71.4	61.6	2.58	0.84	13.7	3.25
DTP2 C_4	3.35	5.57	2.75	1.08	73.1	60.5	2.32	0.85	16.0	3.28
Local check #1	3.34	5.23	3.06	1.08	60.2	62.8	2.40	0.84	10.1	3.16
Sete Lagoas 89DTP1	3.34	5.56	2.70	1.13	73.4	61.4	2.16	0.85	13.6	3.22
TS6 C_1	3.31	5.57	2.99	0.58	117.9	64.2	2.24	0.80	13.0	3.12
Local check #3	3.25	5.36	2.80	0.92	102.2	62.4	2.83	0.80	9.4	3.40
Farako Ba 8625 RE	3.20	5.51	2.48	0.96	98.4	61.4	2.49	0.87	12.4	2.99
Harare 89DTP1	3.11	5.16	2.66	0.87	117.6	62.0	2.80	0.83	14.0	3.20
Pool 26 Sequía C_3	2.93	4.61	2.36	1.37	156.6	58.4	2.33	0.87	12.5	3.34
Mean	3.30	5.39	2.84	1.01	89.8	61.8	2.55	0.85	13.0	3.25
Number of sites	19	7	7	5	19	19	19	19	12	10
Prob. F test	0.06	0.02	0.22	0.22		0.00	0.62	0.01	0.00	0.32
LSD (0.05)	0.32	0.58	0.55	0.39		1.36	0.83	0.06	4.1	0.29

[a] Score of 1 = green; 5 = dead

Table 5. Performance of drought-tolerant source populations in the 1992 Preliminary Evaluation Trials (PET) (adapted from CIMMYT, 1995).

			Yield							
Entry	PET	No of sites	Mean (t ha^{-1})	Greatest (t ha^{-1})	Least (t ha^{-1})	Of entry (t ha^{-1})	No of entries[a]	Rank of entry	Anthesis of trial (d)	Anthesis of entry (d)
Pool 16 C_{20}	1	5	4.1	4.8	2.8	4.7	14	2	50	51
Pool 18 Sequía C_3						3.7		11		48
Santa Rosa 8330 RE[b]						3.6		12		53
DTP1 C_5 Across 89	2	5	4.8	5.6	4.0	5.0	16	6	56	56
Across 8331 RE[b]						4.5		14		53
La Posta Sequía C_3	3	5	3.5	4.6	2.5	4.6	25	1	61	59
TS6 C_1						3.0		22		61
Suwan 8222 RE[b]						4.1		3		61
Pool 26 Sequía C_3	4	5	5.0	5.9	3.7	4.7	14	10	59	56
Across 8627 RE[b]						4.8		9		59
DTP2 C_4	5	7	4.7	6.6	3.9	6.6	14	1	74	79
Tlaltizapán 9045						5.3		4		77

[a] Excludes local checks

[b] Long-standing CIMMYT reference entries

and adjusted for flowering date. Two commercial hybrids, DK 888 and P3264, significantly outyielded the leading elite OPV source (TS6 C_2), and two others (KTX 3101 and G5431) outyielded La Posta Sequía C_3 and Pool 26 Sequía C_3. These OPV sources in turn outyielded the hybrids PNR 473, B73 x Mo17 and SC 701 by substantial margins. Thus heterosis often provides superior performance under stress, but is not a panacea in all conditions. Inbred lines which have been developed from a number of elite source populations (Table 1), have undergone topcross testing and are available to national programs on request.

DTP1 and DTP2 - Comparisons involve the same trials as those for elite source germplasm. In international trials of early germplasm (Table 3), an early fraction of DTP1 C_5 was highest yielding across sites. Its superiority was most marked in well-watered locations, probably because it was also the latest maturing entry. Despite this, it ranked sixth out of 12 in severely stressed environments. In the trials of later maturing entries (Table 4), several site-specific selections formed by recombining the 10 best families at that site yielded about 6% less than La Posta Sequía C_3 across 19 environments but were more stable in performance (Edmeades et al., 1997b). Some also outyielded La Posta Sequía C_3 in low yielding environments by about 10%, mainly because they were 3-4 d earlier to flower. They performed significantly better than Pool 26 Sequía C_3 over sites, perhaps because they were on average 3-4 d later to flower. DTP2 C_4 was a population bulk rather than an elite fraction, yet it performed well in the same trial. A similar pattern emerges from the PET trials (Table 5). An elite fraction of DTP1 (Across 89 DTP1) ranked 6th of 16 entries in PET 2, while DTP2 C_4 outyielded all other (13) entries in PET 5. It repeated this performance

Table 6. Performance of drought-tolerant source populations: (A) In Preliminary Evaluation Trials (PET) when grown under drought at Tlaltizapán, Mexico, in 1994; and (B) In a trial comparing hybrids and open-pollinated varieties under well-watered and droughted conditions in Tlaltizapán; under heat and drought in Obregón; and under low N in Poza Rica, México.

			Yield							
Entry	Trial	No of sites	Mean (t ha^{-1})	Greatest (t ha^{-1})	Least (t ha^{-1})	Of entry (t ha^{-1})	No of entries[a]	Rank of entry	Anthesis of trial (d)	Anthesis of entry (d)
A: Drought										
TS6 C_1	PET 3	1	0.36	1.29	0.04	1.29	25	1	88.0	87.3
La Posta Sequía C_3						0.69		2		90.0
Suwan 8222 RE[a]						0.33		13		86.7
DTP2 C_4	PET 4	1	0.85	1.75	0.18	1.75	16	1	87.3	81.3
Pool 26 Sequía C_3						1.25		3		84.3
Across 8627 RE[a]	1.06	5	90.3							
B: Drought, well-watered and low N										
F_1 hybrids										
DK 888	OPV/hybrid	4	0.00	2.22	-0.99	2.22	88	1	77.4	77.7
P 3264						0.80		5		73.7
KTX 3101						0.45		11		75.8
G 5431						0.24		25		75.4
PNR 473						-0.70		82		76.5
FRB73 x FRMo17						-0.89		87		68.1
SC 701						-0.99		88		80.3
Open pollinated varieties										
TS6 C_2						0.62		7		76.5
DTP2 C_4						0.37		15		75.0
DTP1 C_6						0.17		32		73.1
La Posta Sequía C_3						0.02		37		78.2
Pool 26 Sequía C_3						0.00		38		73.7

[a] Long-standing CIMMYT reference entries

[b] Because of the large range of flowering dates grain yields were standardized (mean = 0) and linearly adjusted for days to anthesis, so that yields over all entries averaged zero.

under drought when included as a check in PET 4 (Table 6A), but only ranked 32 out of 88 on the comparison of OPVs and hybrids (Table 6B).

Thus, although a wide range of germplasm, including some landraces, was used to form DTP1 and DTP2, both have a surprisingly high yield potential, perhaps because they contain about 20% of elite Corn Belt germplasm. Stalks are above average in quality. DTP2 lodges less than DTP1, and both are around 1.75 m tall under moderate drought. Resistance levels for ear rots and foliar diseases are relatively low, and husk cover is unsatisfactory. The dominant heterotic response of these populations is not yet known, but early indications suggest they will fall mainly in the Tuxpeño group. White and yellow inbred lines have been extracted from both populations.

Conclusions

Data confirm Blum's (1983) assumption that drought-adaptive alleles are present in elite populations, and that their frequency can be increased by screening segregating populations under a stress managed to reveal the genetic variability for DT existing in the population.

Elite, drought-tolerant sources of germplasm spanning a reasonable range of maturities and grain color are available for lowland tropical environments. There is no evidence of a consistent loss in yield potential associated with improved DT. An increase in stability and yield level under all stress levels has been observed in Pool 18 Sequía, Pool 16 C_{20} and La Posta Sequía. A loss of stability across sites may have occurred in TS6 and in Pool 26 Sequía. Cycle bulks and inbred lines are available from each of these sources.

The longer-term strategy of developing drought tolerant populations from components with a high primary level of drought tolerance associated with diverse mechanisms for DT has resulted in two populations which perform surprisingly well under diverse water regimes but which are relatively susceptible to diseases common to the lowland tropics. Cycle bulks and inbred lines separated by color are now available from these populations.

Based on the level of DT in elite, locally-adapted germplasm, and the level of adaptation and performance of DT source germplasm, breeders will need to adopt various strategies to develop a high yielding adapted product with DT. In a program with limited resources it will be more efficient to focus on improving elite germplasm for DT by including some sites where stress can be carefully managed, rather than searching among sources with poor agronomic characteristics for unique drought-adaptive genes. The unreliable nature of drought dictates that cultivars must perform well in good and stressed environments. This condition will be most likely met if selection for drought tolerance takes place in elite adapted germplasm exposed periodically to carefully-managed conditions of stress during the selection process.

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From Stress-Tolerant Populations to Hybrids:
The Role of Source Germplasm

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Abstract

The performance of populations experiencing water deficits at flowering and during grain filling or low N stress can be improved by recurrent selection, and the challenge now is to determine if those benefits carry over to hybrids which are derived from these populations. To test whether the frequency of stress-tolerant hybrids was increased by selecting inbred lines from stress-tolerant source populations versus conventional populations, we developed random inbred lines from four pairs of populations. Each member of the pair traced to a common population but differed in history of selection for stress tolerance. Drought tolerance was examined by comparing: TS6 C_2 with Tuxpeño Sequía C_0 and with Pop. 21 MRRS C_2; La Posta Sequía C_3 with Pop. 43 C_9; and Pool 26 Sequía C_3 with Pool 26 C_{23}. The effect of selection for low N tolerance was studied by comparing Across 8328 BN C_5 with Across 8928. Each pair was sown in neighboring plots, managed identically, and selected in the same manner. For each population approximately 100 S_2 families were selected. Inbred lines were each crossed to two conventionally selected inbred line testers, and topcrosses (TCs) were grown in 2-4 environments varying in the level of target stress. Under drought stress TCs derived from drought tolerant populations significantly outyielded those from conventional populations by an average of 22% (310 kg ha^{-1}) at 1.56 t ha^{-1}, nonsignificantly by 1% (43 kg ha^{-1})at 5.29 t ha^{-1}, and yielded 2% less than the conventional TCs (-130 kg ha^{-1}) under well-watered conditions (6.08 t ha^{-1}). The probability of obtaining a hybrid that yielded 40% greater than the trial mean under severe stress was 4-fold greater when lines were extracted from a drought-tolerant source population than from its conventional counterpart. Topcrosses from Across 8328BN outyielded conventionally-derived lines under low N by a significant 11.1% (200 kg ha^{-1}) at 1.90 t ha^{-1}, and by a similar amount under high N (3%, or 200 kg ha^{-1}) at 6.0 t ha^{-1}. We conclude that drought- or N-tolerant elite source populations provide a greater proportion of drought- or N-tolerant inbred lines and hybrids. This suggests that investment by CIMMYT and national programs in increasing the stress-tolerance of source and F_2 populations formed during line recycling is fully justified.

Progress in plant breeding depends on being able to identify alleles related to improved performance and to either fix them in a specific genotype or cultivar, or to increase their frequency within a population so that the performance of the population *per se* is improved (Falconer, 1981). The choice of source population, therefore, plays a critical role in any breeding program, since it determines the frequency of desirable alleles at the onset of the selection process (Hallauer, 1991). If that frequency is very low, few or no fixed lines will carry the alleles of interest, and progress from recurrent selection for traits controlled by those alleles will be very slow. Fortunately, there is evidence that there is a reasonably high frequency of drought-adaptive alleles present in many common breeding populations. Such variation is of special value because it exists in elite backgrounds and its use is less likely to be hampered by linked deleterious genes than when identified in landraces (Hallauer, 1991). Supporting this contention Blum (1983) cites as evidence the fact that many empirical breeding programs have produced varieties with improved performance and yield stability under stress, when compared with the parent population. For some adaptive traits, however (e.g., osmotic adjustment; Bolaños and Edmeades, 1991), maize seems to lack variability. For other traits, such as anthesis-silking interval (ASI), variation remains quite large, because there may not have been heavy natural selection pressure for a short ASI during crop evolution (Bolaños and Edmeades, 1993b). Since it seems likely that maize evolved under relatively infertile conditions, crop evolution may have exploited some of the genetic variability for improved performance under low N. However, inasmuch as improved partitioning to the ear relates to improved performance under low N (Bänziger et al., 1998), alleles for improved grain yield under low N may still exist at reasonable frequencies in source populations.

Desirable alleles are normally fixed through inbreeding and hybridization in maize. Random inbreeding within a population will provide a group of lines from a population whose performance in test crosses should be normally distributed with a mean yield approximately the same as that obtained from a cross between the tester and the population itself. A survey of F_1 varietal cross data suggested that such crosses show around 20% mid-parent and 8% high-parent heterosis (Hallauer and Miranda, 1981, p. 342), and this is probably the degree of heterosis one should also expect from random sets of inbred lines crossed to testers. Elimination of inbred lines with low GCA based on early generation topcross tests will, naturally, increase the mean level of high-parent heterosis expected in topcrosses of advanced lines.

What are the effects of selection in the base population on the mean performance of hybrids derived from that population? There is a general expectation that reciprocal recurrent selection (RRS) between two populations will give rise to high yielding hybrids, though this is a result of improved performance by the base populations themselves and an increased level of heterosis between lines derived from the two populations (Hallauer and Miranda, 1981). Studies by Moll and coworkers (1977) demonstrated that six cycles of RRS between two populations, Jarvis and Indian Chief, improved the chances of obtaining superior single crosses, and approximately 86% of single crosses produced from randomly-derived lines of C_0 fell below the mean performance level of the crosses derived from C_6. Thus the probability of obtaining a hybrid that yielded equal to the mean of all hybrids in C_6 was about 3.6 times greater in C_6 than in C_0. Betrán and Hallauer (1996) compared single-cross hybrids from S_7 lines derived from BSSS and BSCB1, two populations being improved by RRS. The crosses between lines from C_0 averaged 4.88 t ha^{-1} versus 7.54 t ha^{-1} for crosses between lines derived from C_9, and there was virtually no overlap between the distributions of grain yields from the two sets of hybrids. A similar result was obtained from crosses of S_3 lines among these same populations (Russell, 1991). These studies suggest that through selection it is possible to improve the level of heterosis between populations in well-favored environments, implying that selection of specific testers could also magnify through heterosis the effects of genes which provide adaptation to specific environments. A study of commercial lines and hybrids developed over the past 70 years, based mainly on the Reid-Lancaster heterotic pattern, shows, however, that the main reason for better performance of modern hybrids has been an improvement in the *per se* performance of the lines and less to an increase in heterosis between lines (Duvick, 1995), suggesting that RRS may have improved the *per se* performance of lines derived from these populations. No similar studies of performance in environments experiencing abiotic stress have been published.

As resource allocations within CIMMYT move from developing source populations and open-pollinated varieties towards the development of inbred and hybrid products, the question remains of how best to utilize elite populations, especially those carrying high allele frequencies for a single trait. There is convincing evidence that the performance of populations experiencing water deficits at flowering and during grain filling can be improved by recurrent selection at no cost to performance in well-watered conditions (Edmeades et al., 1997; Bolaños and Edmeades, 1993a). Similar evidence of improved performance under low N by recurrent selection is provided by the studies of Lafitte and Edmeades (1994).

The objective of the present study was to determine if improvements observed in tolerance to drought and low N through recurrent selection in elite source populations carry over to hybrids which are derived from these populations. To test whether the frequency of stress-tolerant hybrids was increased by selecting inbred lines from stress-tolerant source populations versus conventional populations, random inbred lines were developed from pairs of populations. Each member of the pair traced to a common population but differed in its history of selection for stress tolerance.

Methods and Materials

Choice of germplasm

Four groups of populations were chosen for this study (Table 1). Three groups consisted of pairs of contrasting populations, while a fourth, Tuxpeño, included also the original population, Tuxpeño Sequía C_0, in the study. Each member of the pair or group differed in history of selection for stress tolerance, and in general each had a similar number of cycles of selection for stress tolerance or for improved performance under conventional selection conditions from a point where the populations had been identical. The exception was Across 8328 BN C_5, which had completed five cycles of selection for improved performance under low and high N at Poza Rica since 1983, while its conventional counterpart, Across 8928, had completed only three cycles of selection since that date. The effect of selection for drought tolerance was examined by comparing: TS6 C_2 with Tuxpeño Sequía C_0 and with Pop. 21 MRRS C_2; La Posta Sequía C_3 with Pop. 43 C_9; and Pool 26 Sequía C_3 with Pool 26 C_{23}. The effect of selection for low N tolerance was studied by comparing Across 8328 BN C_5 with Across 8928.

The scheme for improving these populations for drought or low N tolerance has been described in detail elsewhere (Bolaños and Edmeades, 1993a; Edmeades et al., 1997; Lafitte and Edmeades, 1994; Lafitte et al., 1997). Briefly, conventionally-selected populations were improved for tolerance to drought or low N by growing progenies under drought and/or heat stress (in Tlaltizapán and Obregón) or under low N stress (in Poza Rica). Selection was based on an index of primary (yield) and secondary traits thought to impart increased tolerance to mid-season drought or to N-deficiency throughout the growing season, while maintaining or increasing grain yield under non-stressed conditions. Selection schemes were full-sib alone (Across 8328 BN), full-sib and S_1 (TS6) or S_1 recurrent selection alone (La Posta Sequía and Pool 26 Sequía), using a selection intensity of around 20-35% for full-sibs, and 10% for S_1 selection schemes. Recombination of selected families and formation of progenies took place under disease pressure at Poza Rica. Evaluations have demonstrated yield gains of around 100 kg ha^{-1} yr^{-1} under the relevant stresses in these populations (Edmeades et al., 1997; Lafitte et al., 1997).

Table 1. Versions of four populations from which random inbred lines were extracted, topcrossed and tested under various stresses. All populations are adapted to the lowland tropics.

	Improved for[a]:	Cycles of selection[b]	Level of inbreeding	Tester (no. top-crosses)	Tester (no. top-crosses)	Evaluated (N,WW,IS, SS, heat)[c]
Tuxpeño, Population 21						
(late white dent)				CML247	CML254	
Tuxpeño Sequía C_0	Original	-	S_2	80	89	(IS,SS WW,heat)
TS6 C_2	Drought	8	S_2	100	95	
Pop. 21 MRRS C_2	Convent.	8	S_2	94	91	
La Posta, Population 43						
(late white dent)				CML247	CML254	
La Posta Sequía C_3	Drought	3	S_2	89	96	(IS,SS, WW,heat)
Pop. 43 C_9	Convent.	3	S_2	89	98	
Pool 26						
(intermediate yellow dent)				CML287	CL00331	
Pool 26 Sequía C_3	Drought	3	S_2	100	67	(IS,SS, WW)
Pool 26 C_{23}	Convent.	3	S_2	92	90	
Amarillo Dentado, Population 28						
(late yellow dent)				CML287	CL00331	
Across 8328 BN C_5	Low N	5	S_2	99	86	(+N, -N, 2 seasons)
Across 8928	Convent.	3	S_2	90	91	

[a] Main selection criterion; Covent. refers to conventional selection under well-favored conditions

[b] Number of selection cycles completed since the populations being compared diverged from a common base.

[c] WW, IS and SS refer to stress imposed at Tlaltizapán: WW = well-watered; IS = water-stressed mainly during grain filling; SS = severely water-stressed during flowering and grain filling; heat = exposed to high temperature and drought in Obregón; N is either +N (unstressed) or -N (exposed to low N stress) at Poza Rica.

Conventionally-selected populations were improved using either the international progeny-testing scheme (for Across 8928 and Pop. 43 C_9) described by Pandey et al. (1986), or by a half-sib or S_1 recurrent selection scheme at Poza Rica station, as described by Pandey and Gardner (1992) (for Pool 26). In the case of Pop. 21 MRRS C_2, from the point of divergence of this population from Tuxpeño Sequía C_0 in 1975, it has undergone six cycles of selection through the international progeny testing scheme (Pandey et al., 1986), followed by two cycles of selection in an RRS scheme at Poza Rica, using ETO Blanco as the opposing heterotic population (Vasal et al., 1997). In all cases selection was based on progeny performance under well-watered or high N conditions, with the possible exception of trials conducted at international sites where moderate levels of drought and N stress may have been encountered.

Creation of random inbred lines and topcrosses

All line formation was conducted at Poza Rica station. Each member of the group of populations was sown in neighboring plots on the same day, managed identically, and selected in the same manner. Initially a bulk of each population comprising 500 plants was sown and individual plants were selfed. At harvest rotted ears were rejected, small or partially filled ears discarded, and 100 S_1 ears were selected from each population using identical selection criteria in each population comprising the group. Each of these S_1 ears was sown ear-to-row in rows 2.5 m in length at a density of 5.3 plants m^{-2}, and 3-6 plants per family were again selfed. At harvest some S_1 families were rejected (<10%) and 100 S_2 ears selected as described previously.

Topcrosses (TCs) were created by sowing the 100 S_2 lines from each population in an isolated crossing block with two testers and detasseling the inbred lines. Testers were used as males and sown on two dates, separated by 2-3 rows of female S_2 lines. Coincidence of flowering was not complete between the testers and the lines. Between 1% and 15% of TCs were eliminated from the study because their seed supply was inadequate for further testing (see Table 1 for final TC numbers). Testers selected were those currently being used in CIMMYT's Lowland Tropical Breeding Program to separate advanced inbred lines into two groups. Broadly speaking, these testers have been chosen for their capacity to separate lines grown under well-favored conditions into Tuxpeño and non-Tuxpeño groups, though there are many exceptions. They have not been used to separate progenies under stressed conditions. For late white populations CML254 was the Tuxpeño tester and CML247 the non-Tuxpeño tester. For late yellow populations the Tuxpeño tester was CML287 and the non-Tuxpeño tester was CL00331.

Evaluation of topcrosses

Drought - TCs of Tuxpeño, La Posta and Pool 26 were grown in three environments differing mainly in the level of drought stress. A well-watered control provided an expression of yield potential, though the yield level obtained varied according to the season (summer vs. winter), and the field used. Water-stressed environments were created in the dry winter season by withdrawing irrigation at specific times during the crop cycle. An intermediate level of stress occurred when preflowering water supply consisted of three full irrigations (one sprinkler and two gravity). A severe stress consisted of preflowering applications of 2.5 full irrigations (a half irrigation is considered to be gravity application to alternate rows). The objective of the intermediate stress was to provide moderate water deficits (some degree of leaf rolling) about 5 d prior to 50% silking, and then to apply no further water to the crop. The severe stress environment was one in which leaf rolling was quite noticeable 15 d prior to 50% silking and stress was severe during flowering. This was usually followed by a final full irrigation when 90% of female flowering data was complete to fill the rather small amount of grain that had been set. Timing of irrigation was altered according to symptoms. Experimental designs were alpha (0,1) lattices with two replications per environment and an incomplete block size of 10 plots. Plot size was 1 row 2.5 m in length, and established plant density, obtained by overplanting and thinning, was 5.3 plants m^{-2}. Row width was 0.75 m. Each plot was bordered at the back by other plots, but at the front faced an open alley 0.5 to 1.5 m in width.

Measurements taken on each plot included plant height and ear height (distance from ground to ligule of flag leaf or point of insertion of uppermost ear), days to 50% anthesis and silking, and scores of leaf rolling (1 = unrolled; 5 = fully rolled). During grain filling, when differences among plots became apparent, leaf senescence was scored on a 0 - 10 scale, where each unit represented 10% of total plant leaf area which was senesced. At harvest the one border plant next to the alley was removed, lodged plants recorded, and remaining plants counted and harvested. Ear number was recorded. An ear was counted if it had one or more grains present. Ears were dried, shelled and grain yields expressed at constant oven dry weight after drying grain samples at 80°C.

Heat + drought - In Obregón, TCs of La Posta and Tuxpeño were sown in mid-April so that flowering and grain filling coincided with daily maximum temperatures which frequently exceeded 38 °C. Plot size was 1 row 3m in length, with an established plant density of 4.0 plants m^{-2} in rows 0.75 m wide. Plots were unbordered at both ends. Water stress was imposed on the crop by lengthening the period between water applications from the normal 14 d to 21-28 d. Infestation by red spider mite further lowered yields. Measurements were as described above except that the whole plot was harvested, intact ears were weighed in the field, a shelling percentage for the whole trial was determined by shelling a subsample of ears, and grain moisture was determined on a single shelled subsample of grain from the whole trial taken within an hour of harvest.

Nitrogen - Evaluation of TCs of Population 28 took place in Poza Rica in two adjacent blocks that differed in their level of available N (Lafitte and Edmeades, 1994) in both summer and winter seasons of 1995. The high N block received 200-18-0 kg ha^{-1} of N:P:K, with 125 kg of the N being applied broadcast prior to planting and the rest 25-35 d after planting as a sidedressing. The low N block was depleted of N initially by cutting and removing crop biomass. For the next 15 crop cycles no fertilizer N was applied, though crop residues were generally retained. During the current evaluation fertilizer applications were 0-18-0 kg ha^{-1} N:P:K. Plot size was 1 row 2.5 m in length, and established plant density was 5.3 plants m^{-2} in rows 0.75 m wide. Each plot was bordered at the back by other plots, but at the front faced an open alley approximately 0.5 to 1.5 m in width. Measurements taken were as described above, except that at harvest two border plants were removed next to the alley. In addition, measurements of ear leaf chlorophyll concentration were taken in the low N treatment using a SPAD 502 chlorophyll photometer (Minolta, Japan) at approximately two weeks after 50% silking on 5 plants per plot, using alternate, well-bordered plants in the row for this observation. Values were averaged for each plot.

Statistical procedures

Analyses of variance were performed within and across environments within each group of populations, and tests of significance for population and tester effects were conducted, using a fixed model (SAS, 1985). In most cases the distributions of grain yield for each tester within each group and population did not deviate significantly from a normal distribution. Means and standard deviations were obtained for each population-tester combination (SAS, 1985). Probabilities with which a given level of yield will be exceeded were computed. Frequency distributions of grain yield for the two testers were then added for each population within each group, and this was repeated for probabilities. The chance of selecting a topcross with a given yield level from the stress-tolerant population versus the conventionally-selected version was estimated by dividing the cumulative probability of the stress-tolerant population by that of the conventionally-selected population for that yield level, within each environment and population.

Results and Discussion

Drought

Under severe stress TCs derived from drought tolerant populations significantly outyielded those from conventional populations by an average of 21% (307 kg ha^{-1}) at a mean yield level of 1.62 t ha^{-1}, but yielded 1% (-30 kg ha^{-1}) less than the conventionally selected populations under intermediate stress at a yield level of 5.33 t ha^{-1}, and 4% less than the conventional TCs (-233 kg ha^{-1}) under well-watered conditions (6.13 t ha^{-1}) (Table 2). Thus although there was an improved performance of TCs derived from the drought-tolerant populations under drought, this became zero at yields of around 5 t ha^{-1} and negative at yield levels above 5.5 t ha^{-1}. Across all populations and water levels yields of TCs from the two groups of populations were almost identical. Results varied among the populations. Relative advantages of stress-tolerant source populations under the three water regimes for Tuxpeño were: 28%, -2% and -6%; for La Posta were 21%, 12% and 1%; for Pool 26 were 16%, -7% and -4%. The apparent loss of yield potential in TCs from drought-tolerant populations versus conventionally-selected populations is not unexpected, in that conventionally-selected populations have been improved for these types of environments, while the target environments for drought-tolerant germplasm has a much lower yield potential. It is, however, inconsistent with selection gains observed in drought-tolerant populations under well-watered conditions, which in several studies (Bolaños and Edmeades, 1993a; Byrne at al., 1995; Edmeades et al., 1995) have been shown to be similar or greater than those obtained in conventional selections. The choice of testers used in this study (see below) may offer some explanation for these results.

The comparison of TCs derived from an original population versus its drought tolerant equivalent (Tuxpeño Sequía C_0 vs. TS6 C_2) showed improvements due to selection at the three water levels of 35% (350 kg ha^{-1}), 6% (320 kg ha^{-1}), and 2.3% (160 kg ha^{-1}). Since tolerance to severe drought stress is mainly additive in nature (Betrán et al., 1997), gains due to selection are approximately halved when randomly-derived inbred lines from each population are crossed with testers that have no specific drought adaptation. Coors and Mardones (1989), reporting on the result of recurrent selection for prolificacy, observed that ear number per plant rose by 0.02 per cycle in the original population, while in testcrosses between three testers and the selection cycles this rate of increase fell to 0.01 per cycle. In the same study gains in yield per cycle in the population were four times those observed in the testcrosses. If we double gains in TCs then eight cycles of selection in Tuxpeño Sequía averaged about 550 kg ha^{-1} total gain across three water levels. This compares well with the 860 kg ha^{-1} reported by Bolaños and Edmeades (1993a) and 470 kg ha^{-1} reported for this population by Edmeades et al. (1995).

Table 2. Effect of selection for drought tolerance in four populations on the performance of topcrosses from each selection when evaluated under a range of drought stress levels or under heat. Populations were selected for drought tolerance or improved conventionally under well-favored conditions (see Table 1). Tuxpeño Sequía C_0 is the unselected population from which TS6 C_2 (drought-tolerant) and Pop. 21 MRRS C_2 (conventionally selected) were derived. Experiments were conducted in 1995-6 at Tlaltizapán and Obregón, Mexico. Means followed by different letters differ significantly.

	Anthesis date (d)	Plant height (cm)	Ear height (cm)	Grain yield			
				Heat	Severe stress (t ha^{-1})	Intermed. stress	Well-watered
Tuxpeño, Pop. 21							
Tuxpeño Sequía C_0	78.8 a	191 a	104 a	0.35 a	1.01 a	5.76 a	6.95 a
TS6 C_2	78.1 b	191 a	102 a	0.35 a	1.36 b	6.08 b	7.11 b
Pop. 21 MRRS C_2	78.9 a	198 b	109 b	0.38 a	1.06 a	6.20 b	7.58 c
	***	***	***	ns	***	***	***
La Posta, Pop. 43							
La Posta Sequía C_3	79.8	196	107	0.68	1.93	4.24	5.17
Pop. 43 C_9	80.3	196	108	0.59	1.59	3.79	5.13
	**	ns	ns	***	***	***	ns
Pool 26							
Pool 26 Sequía C_3	76.7	222	125	2.03	5.61	5.77	
Pool 26 C_{23}	74.8	230	132	1.75	6.03	6.04	
	***	***	***	***	***	**	

, *, ns designate differences among or between populations significant at $P<0.01$, $P<0.001$ or not significant.

Early flowering can provide a considerable yield advantage under drought that is imposed at flowering and which increases in intensity with time. The mean dates of male flowering, however, were not sufficiently different among versions of populations to account for the increased yields in TCs derived from drought-tolerant sources. In fact, across populations drought tolerant TCs had a mean anthesis date 0.2 d later than that of TCs from conventional populations (Table 2). The interval between anthesis and silking (ASI) was 1.23, 0.40 and 0.16 d less in the drought-tolerant selections versus conventional selections in the SS, IS and WW environments (Table 3). This was also reflected in the level of barrenness: ears per plant at the three corresponding water regimes were 0.91, 1.04 and 1.03 across populations for drought-tolerant selections, versus 0.83, 1.02 and 1.02

for conventional selections. That is, under severe drought stress, drought-tolerant selections formed 10% more ears, and this largely accounted for the increase in yields. This close relationship between ASI and ears per plant under drought has been observed in other studies (Bolaños and Edmeades, 1993b). Resistance to barrenness is thought to be related to more rapid ear growth at flowering, which is associated with a reduced ASI (Edmeades et al., 1993). Similar changes were observed between Tuxpeño Sequía C_0 and TS6 C_2. Here the ASI declined from 5.7 to 2.8 d, and ears per plant rose from 0.72 to 0.87 (Table 3).

Heat and drought

The trials conducted at Obregón suffered from extremely low yields, high levels of barrenness and long silk delays (Tables 2, 3). Additionally, yields were reduced by a severe red spider mite infestation during grain filling. Among the TCs from Tuxpeño versions there were no significant differences in grain yield, though TCs of La Posta Sequía C_3 outyielded those of Pop. 43 C_9 by a significant 15% and had a significant 12% more ears per plant. TS6 has been exposed to the heat and drought of the Obregón site only once in its eight selection cycles, whereas progenies of La Posta Sequía have been selected there in each of its three selection cycles. These data are consistent with those previously reported from Obregón showing little genetic gain in Tuxpeño Sequía but significant improvements in La Posta Sequía (Edmeades et al., 1995). Together they suggest that heat and drought tolerances may be controlled by separate genetic mechanisms.

Probability analysis for drought tolerance

The frequency distributions of grain yield by versions within populations for each environment are shown in Figure 1. The displacement of the drought-tolerant selection towards higher yield levels under severely stressed conditions is clear, though there was a major degree of overlap of distributions within each water stress level. There was no clear distinction between distributions under IS and WW environments. It would have been helpful to have had an environment with a mean yield level of 3-4 t ha^{-1} included in this study. The standard deviation of yields under drought was much smaller than that for yield under IS and WW conditions. Cumulative probability functions of yields under stress (Fig. 2) show that under drought the probabilities of obtaining topcross yields between 80% and 120% of the mean for that group were around 20-30% greater with the drought-tolerant versions of the populations than with their conventionally-selected counterparts. For each population we estimated the probabilities of obtaining topcrosses which exceeded 30% and 50% of the mean for the combined group of topcrosses for each population (Table 5). On average there was a 3.2:1 and a 4.7:1 chance of obtaining topcrosses that met these conditions under severe drought stress, when stress-tolerant versions of the population were used as the source of the inbred lines. This was not the case under unstressed conditions. Here the chances of obtaining topcrosses which exceeded the mean by 10% and 20% were 0.73:1 and 0.77:1, when

Table 3. Effect of selection for drought tolerance in four populations on anthesis-silking interval and number of ears per plant of topcrosses of inbred lines from each selection when evaluated under a range of drought stress levels or under heat. Populations were selected for drought tolerance or improved under well-favored conditions (see Table 1). Tuxpeño Sequía C_0 is the unselected population from which TS6 C_2 (drought-tolerant) and Pop. 21 MRRS C_2 (conventionally selected) were derived. Experiments were conducted in 1995-96 at Tlaltizapán and Obregón, Mexico. Means followed by different letters differ significantly.

	Anthesis-silking interval				Ears per plant			
	Heat	Severe stress	Intermed. stress	Well-watered	Heat	Severe stress	Intermed. stress	Well-watered
	d							
Tuxpeño, Pop. 21								
Tuxpeño Sequía C_0	6.2 a	5.7 a	1.5 a	0.0 a	0.47 a	0.72 a	1.00 a	1.02 a
TS6 C_2	5.4 b	2.8 b	1.1 b	-0.2 b	0.51 a	0.87 b	1.02 b	1.05 b
Pop. 21 MRRS C_2	6.6 a	5.1 a	1.9 c	0.1 a	0.47 a	0.75 c	1.02 b	1.04 ab
***	***	***	***	ns	***	***	*	
La Posta, Pop. 43								
La Posta Sequía C_3	4.2 a	2.6 a	0.7 a	0.5 a	0.66 a	0.93 a	1.04 a	1.01 a
Pop. 43 C_9	4.8 b	3.0 b	1.0 b	0.6 a	0.59 b	0.87 b	0.98 b	0.99 b
*	*	*	ns	***	***	***	*	
Pool 26								
Pool 26 Sequía C_3	2.5 a	0.1 a	0.3 a	0.93 a	1.05 a	1.03 a		
Pool 26 C_{23}	3.5 b	0.2 a	0.4 a	0.88 b	1.06 a	1.03 a		
***	ns	ns	***	ns	ns			

, *, ns designate differences among or between populations significant at $P<0.01$, $P<0.001$, or not significant.

stress-tolerant source populations were used.

Nitrogen

Topcrosses from Across 8328BN C$_5$ outyielded conventionally-derived lines under low N by a significant 11% (200 kg ha^{-1}) at a mean yield level of 1.90 t ha^{-1}, and by a similar amount under high N (3%, or 200 kg ha^{-1}) at a yield level of 6.0 t ha^{-1} (Table 4). Significant version effects were also observed for ASI and for leaf senescence. Topcrosses of Across 8328 BN C$_5$ had a shorter ASI and a greater delay in senescence under low and high N than did those from Across 8928. Lafitte and Edmeades (1994) reported a significant increase with selection in numbers of green leaves below the ear during grain filling when evaluating *per se* performance of Across 8328 BN. Yield comparisons were complicated by the different numbers of selection cycles that the two versions had undergone from their point of common parentage. If we assume a gain of 60 kg ha^{-1} cycle^{-1} from two additional cycles of international testing (Pandey

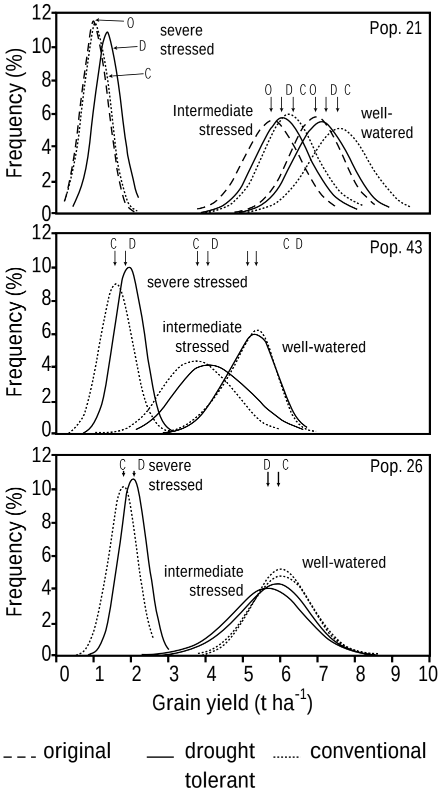

Figure 1. Frequency distributions of grain yield of topcrosses made from randomly selected inbred lines derived from populations selected by conventional means or for drought tolerance. Arrows indicate means for each group of topcrosses (O = original population; D = drought-tolerant selection; C = conventional selection). Data were collected under three water stress levels in Tlaltizapán in 1995. See Table 1 for details of populations and numbers.

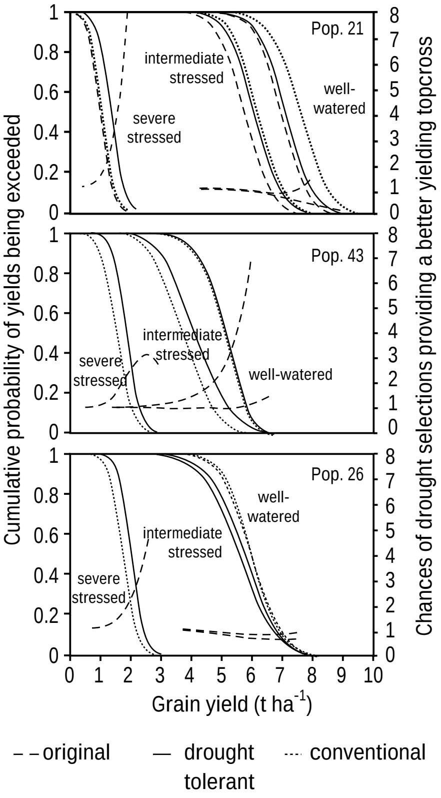

Figure 2. Cumulative probabilities that a given yield level will be exceeded by topcrosses made from randomly selected inbred lines derived from populations selected by conventional means or for drought tolerance. Also shown are the chances that a given yield level will be exceeded by using the drought-tolerant population as the source of inbred lines rather than the conventionally selected population (Chance = ratio of cumulative probabilities for topcrosses with different selection history).

Table 4. Effect of selection for improved performance under both low and high N conditions and under high N alone by conventional means on characteristics of topcrosses of inbred lines from each version of Amarillo Dentado, Pop. 28, when evaluated under two nitrogen levels in two cropping seasons at Poza Rica, Mexico, in 1995. For details see Table 1. Means followed by different letters differ significantly.

	Time to anthesis (d)	Anthesis-silking interval (d)	Plant height (cm)	Ear height (cm)	Chorophyll concentration (SPAD[b])	Leaf senescence score[a]	Grain yield (t ha^{-1})	Ears per plant	Lodging (%)
Low N									
Across 8328 BN C$_5$	69.5	2.7	148	69	26.0	4.7	2.0	0.93	25.3
Across 8928	70.1	3.3	149	70	25.3	4.8	1.8	0.92	24.9
High N									
Across 8328 BN C$_5$	65.2	-0.2	226	123	5.8	6.1	1.05	15.4	
Across 8928	65.4	0.0	227	124	6.1	5.9	1.03	13.9	
P (population)	*	**	ns	ns	ns	**	***	ns	ns
P (N level)	ns	***	***	***	ns	***	*	**	
P (population x N level)	ns	+	ns	ns	**	ns	ns	ns	

[a] Score: 0 = 0% total leaf area is dead; 10 = 100% of total leaf area is dead.

[b] Units read from the Minolta SPAD 502 chlorophyll photometer

et al., 1986), the TCs derived from the two populations may have yielded similarly under high N, though this seems unlikely to be the case at low N. If we assume that the two testers contributed nothing to improved performance of topcrosses at low N, then gains observed here are equivalent to 400 kg ha^{-1}, or 80 kg ha^{-1} cycle^{-1}, a value which agrees well with the 75 kg ha^{-1} cycle^{-1} gain under low N reported by Lafitte and Edmeades (1994). Frequency distributions and cumulative frequencies showed similar results to those observed under drought (Figs. 3, 4). There was virtually no overlap in the distributions of TC yields between the two N levels. Under both N levels the chances of obtaining TCs with yields of 30 and 50% more than the population mean was around twice as great in Across 8328 BN C_5 as in Across 8928, and these odds were similar for a 10% and 20% yield increase over the mean under high N (Table 5).

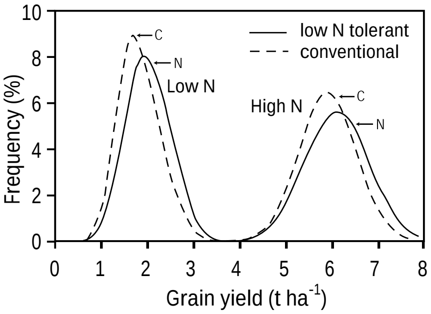

Figure 3. Frequency distributions of grain yield of topcrosses made from randomly selected inbred lines derived from Across 8328 BN C_5, selected for improved performance under low and high N, and Across 8928, selected by conventional means under high N alone. Arrows indicate means for each group of topcrosses (N = low N/high N selection; C = conventional selection). Data were collected under two nitrogen levels at Poza Rica in 1995.

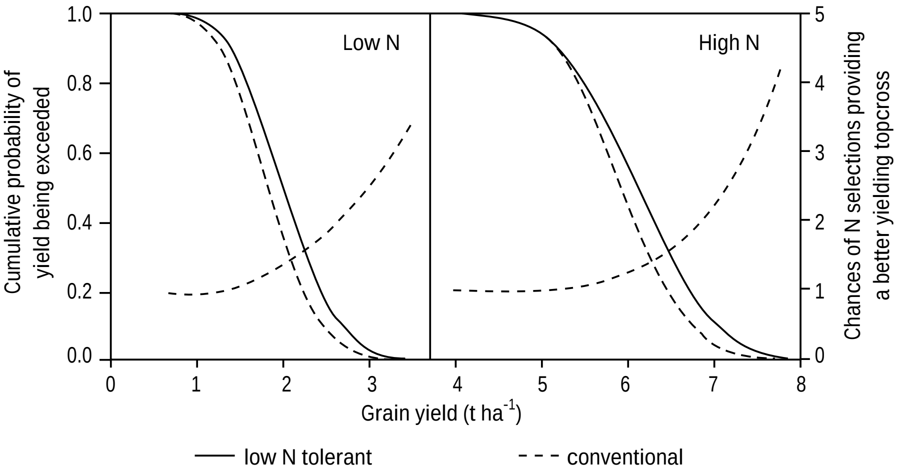

Figure 4. Cumulative probabilities that a given yield level will be exceeded by topcrosses made from randomly selected inbred lines derived from populations selected by conventional means (high N only) or for improved yield under low and high N. Also shown are the chances that a given yield level will be exceeded by using the low N-tolerant population as the source of inbred lines rather than the conventionally selected population (Chance = ratio of cumulative probabilities for topcrosses with a different selection history)

Table 5. Probability of yields exceeding given levels under two levels of stress in different versions of populations. *P* > 1.1, 1.2, 1.3, 1.5 refer to the probability with which topcrosses of randomly-derived lines will exceed a yield level which is 10%, 20%, 30% and 50% greater than the mean of all topcrosses for that environment, respectively; *C* > 1.1, 1.2, 1.3 and 1.5 refers to the chances of obtaining a topcross which yields 10%, 20%, 30% and 50% more than the mean of all topcrosses when the stress-tolerant version of the population is used to derive lines compared with the conventionally-selected version.

	Mean yield (t ha^{-1})	Severely stressed environment (SS, or -N)				Mean yield (t ha^{-1})	Relatively unstressed environment (WW, or +N)			
		P >1.3	*P* >1.5	*C* >1.3	*C* >1.5		*P* >1.1	*P* >1.2	*C* >1.1	*C* >1.2
A: Drought										
Tuxpeño, Population 21	1.14					7.21				
Tuxpeño Sequía C_0		0.08	0.02				0.09	<0.01	0.27	<0.01
TS6 C_2		0.37	0.18	3.4	5.9		0.14	0.02	0.42	0.22
Pop. 21 MRRS C_2		0.11	0.03				0.33	0.09		
La Posta, Population 43	1.76					5.15				
La Posta Sequía C_3		0.18	0.04	3.0	3.2		0.26	0.07	1.0	1.3
Pop. 43 C_9		0.06	0.01				0.26	0.06		
Pool 26	1.81					5.61				
Pool 26 Sequía C_3		0.21	0.04	3.3	5.0		0.36	0.16	0.78	0.80
Pool 26 C_{23}		0.06	0.01				0.46	0.20		
B. Nitrogen										
Amarillo Dentado, Pop. 28	1.90					6.00				
Across 8328 BN C_5		0.18	0.05	1.9	2.3		0.29	0.05	1.7	2.7
Across 8928		0.10	0.02				0.18	0.02		

Effects of choice of tester

Testers used in this study were those selected by the CIMMYT lowland tropical maize subprogram for their capacity to separate heterotic groups in generally well-favored conditions. They were probably selected because they were heterotic for genes which give rise to high yield under well-favored conditions, but these are not likely to be the same genetic systems that give rise to superior performance under severe drought or low N conditions. Choice of tester may therefore have influenced the outcome of this study. Had a tester been used that had been developed to reveal differences among lines under severe drought, or under low N, the difference between the mean TC performance from the two populations within each group may well have been greater under severe stress, and the point of crossover of yield of TCs from different versions of populations may have occurred at a higher yield level.

Conclusions

- The chances of obtaining a hybrid that yields 30-50% better than the average of a random set of hybrids under severe drought or low N-stress are increased by 2-6 times if source populations improved for tolerance for 5-8 years to the target stress are used in line development. Probability functions of grain yield developed during this study will help breeders place a value on stress-tolerant source populations and on selection schemes that systematically expose segregating progenies to these stresses, thus permitting the increase in frequency of stress-adaptive genes in the source populations at each recombination.

- Data presented here are consistent with the following: *“..... to increase the probability of obtaining better hybrids from a given population the most direct way is to improve the population itself, which can be done through some recurrent selection method.”* Hallauer and Miranda (1981).

- These results do not exclude the possibility of extracting and identifying stress-tolerant hybrids from conventionally selected populations, especially when other traits make those populations valuable. However, alleles that impart stress tolerance need to be present at a low frequency in these populations, and the breeding program needs to have resources to screen a large number of hybrids under stress if a significant number of stress-tolerant hybrids are to be identified in the short term. In the long term, recycling of stress-tolerant lines and screening F_{2-4} populations and topcrosses under conditions of managed abiotic stress will increase the frequency of stress-adaptive traits in working populations.

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Variation in Grain Yield Among Early Flowering Varieties in Mozambique

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Abstract

Maize is an important crop in Mozambique, grown by most small-scale farmers. These farmers require highly productive varieties that flower early. Early flowering allows plants to escape terminal water stress as well as providing food for families at times of scarcity. Consequently, one objective of the Mozambican Maize Breeding Program is to select high yielding early-flowering varieties. Evaluation of new varieties is complicated by large variety by environment interactions. A preliminary, retrospective analysis was conducted to determine the extent and nature of variety by environment interactions. Data from a group of 14 early flowering varieties grown across 11 environments were used for the analysis. Environments ranged from northern to southern Mozambique, including rainfed and irrigated environments, and fertilized and unfertilized environments. Environment and error variances were relatively large in comparison to the variety variance, and the variety by environment variance was twice that of the variety variance. Nevertheless, there were differences between varieties which related to phenology, with longer duration varieties performing better than shorter ones. There was also variation for yield within early and later flowering groups across environments, part of which was related to initial plant stand. Pattern analysis showed that rainfed environments in the north discriminated amongst varieties differently than southern irrigated environments. High and low input environments also discriminated differently among the varieties. Recommendations for the Mozambican maize breeding program are made.

Maize is the most important crop in Mozambique. It is grown across a wide range of agroecological zones, including upland and lowland locations. Most of the crop is cultivated under rainfed conditions with little fertilizer input. Hence, yields are low and there is considerable variation among locations and seasons, especially in the south, where rainfall is erratic and unreliable. Mean yields were reported to be 0.63 t/ha by the FAO (1994), which is one of the lowest averages in the southern African region. Maize is sown at the commencement of the rains between October and December, and is subject to drought at the season's end. Early flowering material is utilized to escape this terminal drought and as a source of food when other supplies are low. Farmers prefer maize with white flint-type seed. At present, open-pollinated varieties (OPVs) are preferred over hybrids, because farmers cannot afford to buy new seed every year.

One of the objectives of the Mozambican maize breeding program is to select for high-yielding early-flowering varieties which are suitable for small-scale farmers. Evaluation of new varieties is complicated by large variety by environment interactions, both across seasons and years. Bueno et al. (1989) found both location by variety interactions and variety by input level interactions at two locations in southern Mozambique. To date, the extent and nature of variety by environment interactions across all Mozambique has not been determined. In this paper, a preliminary investigation of these interactions is made using several trials conducted since 1992. This data set was utilized to gauge the extent of variation in variety performance across environments and from this, recommendations are made aimed at increasing the efficiency of the Mozambican maize breeding program.

Materials and Methods

The trials were originally designed to identify varieties with higher yields. A subset of 14 open-pollinated, white, mostly flint varieties were identified from these yield trials, combinations of which have been utilized across 11 different environments in Mozambique (Table 1). Commercial varieties Matuba, Manica and Umbeluzi have already been released within Mozambique. The other varieties were from organizations outside of Mozambique, including CIMMYT. The environments comprised a mixture of management levels, seasons, sowing dates and locations as shown in Table 2.

Table 1. Fourteen open-pollinated maize varieties grown in up to 11 environments in Mozambique.

Variety	Number of environments in which the variety was grown
Mayo 82	11
Ximatama	8
CW-1	11
Ikenne 83	6
Ikenne 84	8
Pop 10	11
EV 8725 SR	11
VL 11	9
EV 8430 SR	11
Pop 32 SR	11
Umbeluzi S1 C1	6
Matuba	11
Umbeluzi	11
Manica	11

A randomized complete block design with four replicates was utilized in each environment. Each plot comprised four 5 m rows spaced 0.80 m apart, and 0.25 m between plants within rows, with the exception of environments in Zambézia Province. At Gurúè and Chuabo Dembe in Zambézia Province, plots were four rows wide and either 5 or 8 m long, with 80 cm between rows and 50 cm between hills within rows, two plants per hill. Thus plant density was the same, but the arrangement of plants within plots differed. The influence of these different arrangements on relative variety performance was assumed to be small. Yield was determined from the central two rows of each plot. Grain moisture content was measured with an electronic moisture meter and used to adjust yield relative to 15% moisture. In each environment, grain yield and days to 50% flower were analyzed using standard analysis of variance procedures with the following model

$$p_{ij} = m + g_i + r_j + \in_{ij} \qquad (1)$$

where p_{ij} is the phenotypic observation on variety i in replicate j; $i=1,\ldots,n_g$ $j=1,\ldots,n_r$ where n_g and n_r are the number of varieties and replicates, respectively; m is the grand mean; g_i is the effect of variety i, $N(0, \sigma_g^2)$; r_j is the effect of replicate j, $N(0, \sigma_r^2)$ and $\in_{ij}$ is the interaction effect between variety i and replicate j, $N(0, \sigma_\in^2)$. The following model was utilized for the combined analysis

$$p_{ijk} = m + e_j + g_i + (ge)_{ij} + (r/e)_{jk} + \in_{ijk} \qquad (2)$$

where p_{ijk} is the phenotypic observation on variety i in replicate k at environment j; $i=1,\ldots,n_g$, $j=1,\ldots,n_e$, $k=1,\ldots,n_r$; where n_g, n_e, and n_r are the number of varieties, environments and replicates; m is the grand mean, g_i is the effect of variety i, $N(0,\sigma_e^2)$; e_j is the effect of environment j, $N(0,\sigma_e^2)$; $(r/e)_{jk}$ is the effect of replicate k within environment j, $N(0, \sigma_{r(e)}^2)$; $(ge)_{jk}$ is the interaction effect between variety and environment, $N(0, \sigma_{ge}^2)$; $\in_{ijk}$ is the interaction effect between variety and replicate within environment, $N(0, \sigma_\in^2)$.

Analyses were conducted using the residual maximum likelihood method (REML) (Patterson and Thompson, 1971, 1975; Harville, 1977), assuming all model effects were random. In

Table 2. Location name, sowing date and management level for the 11 environments used in the study.

Location abbreviation	Location	Province	Sowing date	Irrigation	Fertilizer
UMB9394	Umbeluzi	Maputo	24 Sept. 1993	+	+
UMB9495	Umbeluzi	Maputo	21 Nov. 1994	+	+
UMB9293 +	Umbeluzi	Maputo	14 Oct. 1992	+	+
UMB9293 -	Umbeluzi	Maputo	11 Nov. 1992	+	+
CHO9293 +	Chokwé	Gaza	13 Jan 1993	+	+
CHO9293 -	Chokwé	Gaza	13 Jan 1993	+	+
NAMIALO	Namialo	Nampula	10 Jan 1995	-	-
NAMPULA	Nampula	Nampula	3 Jan 1995	-	-
GUR9293	Gurúè	Zambézia	21 Dec. 1992	-	-
GUR9394	Gurúè	Zambézia	20 Dec. 1993	-	-
ChD9394	Chuabo Dembe	Zambézia	4 Jan 1994	-	-

accordance with the random model, REML was used to calculate best linear unbiased predictors (BLUPs) for each variety and environment. BLUPs are best described as predicted effects that are predictions of performance in future environments. Variance components for each environment and for the combined analysis were calculated by equating observed means squares with expected mean squares. Variety mean repeatability (heritability) was calculated using these variances as follows for a single environment:

$$h = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_\varepsilon^2}{n_r}} \qquad (3)$$

assuming that variance components are as described for equation 1, and n_r, the number of replicates, equals four. Variety mean repeatability for the combined analysis was calculated as

$$h = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{n_r} + \frac{\sigma_\varepsilon^2}{n_r \cdot ne}} \qquad (4)$$

where the components of the equation are described in Equation 2. Repeatability was calculated assuming the varieties were tested in randomized block experiments with four replicates at 11 locations, and hence $n_e = 11$.

We classified environments and varieties to assess the nature of the variety by environment interaction. Before classifying environments, grain yield data were standardized following Fox and Rosielle (1982) by subtracting the environment mean and dividing by the standard deviation for the environment. Before classifying varieties, the environmentally standardized data were weighted by the square root of the variety mean repeatability to reduce the contribution to the classification by environments with a lower repeatability (Burr, 1968; Fehr, 1987; Bull et al., 1992). The standardized and weighted grain yield data were then classified using squared Euclidean distance as a dissimilarity measure, and incremental sums of squares as a grouping strategy (Ward, 1963; Burr, 1968, 1970; Wishart, 1986). The classifications were truncated following the guidelines of DeLacy (1981).

Results

Significant differences ($P<0.05$) in yield were found among varieties in seven of the eleven environments. Variety mean repeatability ranged between 0.2 in Umbeluzi in 1992/93 without inputs (UMB9293-) to 0.79 in Umbeluzi in 1992/93 with inputs (UMB9293+) (Table 3). Low repeatability values also occurred in both Chokwé environments and in Nampula. Grain yields varied between 4.96 t/ha at UMB9293+ to 2.07 t/ha for the rainfed environment in Namialo (Table 3).

The estimated variance components for grain yield are shown in Table 4. Both the estimated error and environmental variances were considerably larger than the variety variance. In addition, the variety by environment variance was approximately two-fold greater than the variety variance. Nevertheless, variety mean repeatability was estimated to be moderately high at 0.76, indicating some overall variation in grain yield among varieties. For days to flower, the repeatability was very high. The relationship between BLUPs for grain yield and days to flower are shown in Figure 1. The correlation was significant ($P<0.05$), indicating that some of the overall variation in grain yield can be attributed to the duration between planting and

Table 3. Variance components and variety mean repeatability for grain yield (h^2), and grain yield (t/ha) for each location.

Environment	σ_g^2	σ_ϵ^2	h^2	Mean yield
UMB9394	0.508	0.678	0.75	3.14
UMB9495	0.470	0.553	0.77	3.68
UMB9293 +	0.559	0.583	0.79	4.96
UMB9293 -	0.037	0.585	0.20	3.88
CHO9293 +	0.198	0.930	0.46	3.81
CHO9293 -	0.145	0.867	0.41	3.07
NAMIALO	0.238	0.423	0.69	2.07
NAMPULA	0.090	0.704	0.34	2.41
GUR9293	0.400	0.787	0.67	2.55
GUR9394	0.577	0.706	0.67	2.24
ChD9394	0.351	1.689	0.58	3.06

Table 4. Variance component and variety mean repeatability estimates from the combined across-environments analyses (REML).

Source	Grain yield	Days to flowering
Environments	0.73 ±0.35	29.86 ±13.59
Replicates/Environments	0.05 ±0.03	0.19 ± 0.15
Variety	0.12 ±0.06	13.44 ± 5.52
Variety x Environment	0.21 ±0.06	4.55 ± 0.78
Error	0.75 ±0.06	4.95 ± 0.63
Variety mean repeatability	0.76	0.96

flowering. Longer duration varieties were generally higher yielding than shorter duration varieties, though the varieties EV 8430 SR, POP 10 and POP 32 SR were higher yielding than expected. Classification analysis of varieties was terminated at the seven-group level. At this truncation level, 70.4% of total variety by environment sum of squares was accounted for. The hierarchy tree and composition of groups is shown in Figure 2. The first truncation mostly divided the varieties into longer and shorter duration varieties. Exceptions were the earlier flowering varieties EV 8430 SR and POP 32 SR, which behaved similarly to later maturing varieties.

The performance of the seven variety groups across the 11 environments is shown in Figure 3. The earlier flowering groups, groups 17 and 20, performed relatively well in the rainfed environments in Nampula Province, Nampula and Namialo, but relatively poorly at other sites. The only exception was at Umbeluzi, 1993/94, where yields of Group 17 were relatively good whilst those of Group 20 were the worst. Grain yield and days to flowering were correlated (P<0.05) only at Umbeluzi with inputs (r^2=0.40) and Chokwé with inputs (r^2=0.55).

Although days to flowering explained some of the variety by environment interaction, it did not explain variation among later flowering and earlier flowering groups, nor the reasons for dissimilarity in relative performance between the varieties EV 8430 SR and POP 32 SR and the other early flowering varieties. There was a significant correlation (P<0.05) between initial plant stand and grain yield at three sites (Umbeluzi 1993/94, r^2=0.86; Namialo, r^2=0.83; and Chuabo Dembe, r^2=0.69) which likely contributed to the variety by environment interaction. For example, poor plant stands may explain the relatively low yield of CW-1 at these three environments.

The environmental classification indicated that the two rainfed environments in Nampula Province (Nampula and Namialo) discriminated differently among varieties when compared to the southern irrigated and rainfed environments in Zambézia Province (GUR9293, GUR9394 and ChD9394; Fig. 4). In addition, the two

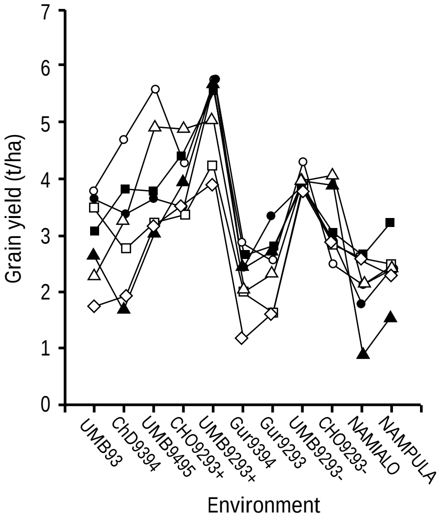

Figure 3. Mean grain yields of seven maize variety groups across 11 environments in Mozambique.

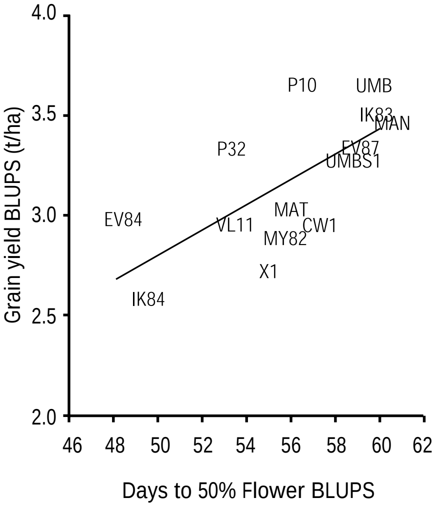

Figure 1. Best linear unbiased predictors (BLUPs) for grain yield plotted against those for days to 50% flowering for 14 maize varieties grown across 11 environments in Mozambique. The regression line is shown with Y = 0.06x - 0.33 (r^2=0.47, P<0.05).

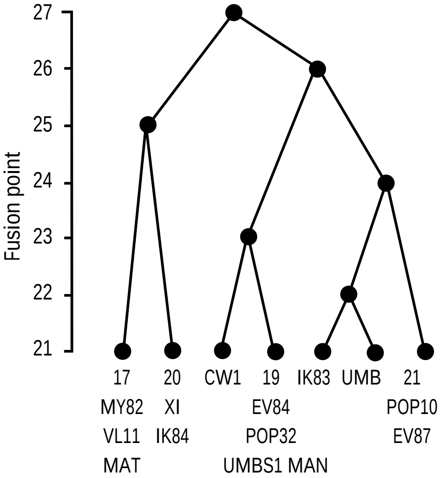

Figure 2. Dendogram to the seven group level for the classification of grain yield data for 14 maize varieties grown across 11 environments. If there was one variety in a group, that variety served as the group name; for groups with more than one variety, the variety names appear under a group number/name.

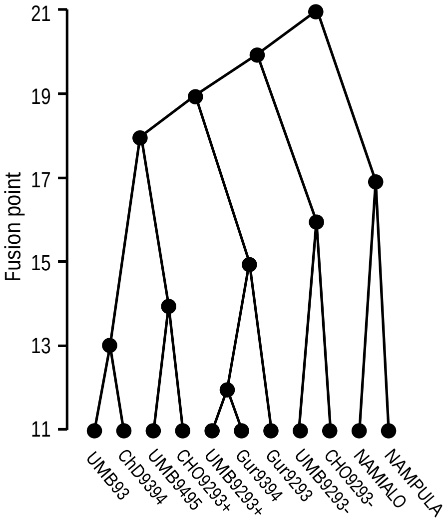

Figure 4. Dendogram for classification of 11 environments based on grain yields of 14 varieties of maize. The environments are described in Table 2.

unfertilized trials in Chokwé and Umbeluzi (CHO9293- and UMB9293-) discriminated differently when compared to the fertilized trials in the same region (CHO9293+, UMB9293+, UMB9394 and UMB9495). There were no other obvious relationships between seasons and/or locations except that the two Gurúè environments discriminated among varieties in a similar manner, which may be expected given that Gurúè is an upland site with relatively colder temperatures during the latter part of the growing season.

Discussion

Maize is grown by virtually 100% of farmers in Mozambique. The crop is produced for home consumption as well as for sale within the country. Earlier flowering material is known to be well suited to the growing conditions in much of Mozambique where terminal drought stress occurs. Hence, a large part of the research effort has concentrated on identifying higher yielding earlier flowering varieties. Our combined analysis of early maturing varieties showed considerable variation between environments, large variety by environment interactions and a large amount of error relative to variety variance. Nevertheless, there was a moderate to high variety mean repeatability, indicating that some varieties yielded better than others across environments. This overall variation between varieties was partly related to days to flower, with longer duration varieties generally yielding more than those with shorter duration. However, there were varieties that performed better than expected based on their phenology, including POP 10, EV 8430 SR and POP 32 SR. The variety POP 10 was of particular interest, since it was intermediate in duration (56 d to flower) but was one of the highest yielding entries.

Differences in initial plant stand and duration also contributed to variety by environment interaction. Groups of earlier flowering varieties performed relatively better when grown in the rainfed environments in Nampula Province. Presumably, they were able to escape the terminal drought stress that develops in this environment, but they were lower yielding in other environments.

The classification of environments indicated that the Mozambican breeding program may have to target environments which are rainfed and which have low inputs of fertilizer separately from those using both irrigation and fertilizer. Bueno et al. (1989) suggested that there was an interaction between variety and input level in two southern Mozambican environments. These results need to be verified to separate the effect of different levels of inputs from location and season effects. Our preliminary results indicate that for multi-environment trials, there may be large variety by location by season interactions, especially when sites in southern Maputo Province and those in Zambézia Province are used. If this finding is verified through more extensive multi-environment testing, then it will be necessary to test variety performance over several sites and years.

The experimental error for the variety trials was relatively high, which limits the breeder's ability to discriminate among varieties and/or select efficiently. For instance, breeders may have to use more replicates to better discriminate among varieties and this will be at the expense of the number of varieties that can be evaluated in each trial or season. To help address this problem, trend analysis or lattice designs could be used to partition and adjust for field variation, thus leading to smaller error variances. In addition, as staff gain more skills in management of research sites, experimental error values may be reduced.

Most environments used in these experiments were high input environments using irrigation and fertilizer, or they were in relatively less stressed upland regions, such a Gurúè. In addition, the level of incidence of stem borer, maize streak virus and downy mildew in these environments was very low, whereas researchers have suggested that losses from these pests and diseases are usually considerable in Mozambique (Berger, 1980; Bodke, 1981). Hence, the selection of superior varieties may be biased by better environments. Our results indicate that the rainfed low-input environments discriminate among varieties differently, in comparison to the higher-input environments. Thus, in order to select varieties that are suited to the needs of farmers in Mozambique, researchers must sample environments across seasons and locations, looking especially for locations with lower-input levels and higher levels of pests and diseases.

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Response of S_4 Maize Lines Evaluated Under Stress and Non-Stress Environments

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Abstract

Ninety-one S_4 maize lines were evaluated along with nine homozygous inbred lines in two sets of environments: a stress set, with four environments (severe drought, moderate drought, low nitrogen, and high density) and a non-stress set with five natural environments, each located in different ecological zones in Côte d'Ivoire. Wricke's (1962) ecovalence (W^2), Hühn's (1979) non-parametric S_3 statistic that combines yield and stability, and Eberhart and Russell's (1966) stability parameters, b_i and S^2, were used to identify stable lines across different environments. Canonical correlation analysis was used to predict the association between yield in the natural environments and yield in stress environments. Results indicate that the yield stability of the lines was associated with their stalk and root quality. A total of 54% and 17% of the lines had negative ASI under severe drought and high density, respectively. Yield under high density and low nitrogen was correlated with yield under the natural environment ($P<0.01$). Yield under severe drought was only correlated with the yield under moderate drought ($r = 0.52$; $P<0.01$). Yields under low nitrogen and under moderate drought stress were positively correlated. The superiority of genotypes under optimal conditions tended to be maintained under stress. Three lines performed reasonably well under low nitrogen, moderate and severe droughts.

Drought and low fertility are the largest causes of maize yield loss in the tropics (Edmeades et al., 1995). Breeding for high productivity under low levels of available nitrogen and moisture will enable cultivars to fit into environments instead of altering the environments by adding inputs (Coffman and Smith, 1991). Genetic variability for nitrogen use efficiency has been reported by many investigators (Allan and Darrah, 1978; Muruli and Paulsen, 1981; Balko and Russell, 1980; Short, 1991; Lafitte and Edmeades, 1994). A positive but non-significant correlation was observed between inbred parents and hybrid progenies for nitrogen use efficiency. The stability of yield performance of single cross hybrids seems to be partly a property of the inbred parent lines (Eberhart and Russell, 1966). Useable genetic variability for drought and gains from selection have been reported by several workers (Diallo and Rodriguez, 1987; Edmeades et al., 1987; Bolaños and Edmeades, 1993; Byrne et al., 1995). Selection gains observed under drought have also been observed under low N (Edmeades et al., 1995). Poor root and stalk quality are some of the most important factors limiting maize production in the savanna of West and Central Africa. Use of high population density in the breeding nursery allows the identification of lines with good stalk and root quality. Visual selection of lodging resistant inbred lines at higher plant densities should be effective for improving hybrid yield performance (Hallauer et al., 1988). Allan and Darrah (1978) reported a significantly ($P<0.01$) improved response to higher plant populations from cycle 0 to cycle 3 in maize populations adapted to the Kenyan highlands.

Development of synthetics is one way of concentrating specific traits in one cultivar. To develop lines with specific traits, we adopted the strategy of using managed stressed environments (drought stress, low nitrogen, and high population density) along with multilocation testing. The objectives of this study were to: (i) identify inbred lines which combine drought tolerance, good stalk and root quality, and nitrogen use efficiency; (ii) determine the correlation between inbred line yield under various stresses and natural environments; (iii) determine how performace under stresses due to severe drought, moderate drought, low nitrogen and high population density are associated; and (iv) determine if yield in natural environments can be predicted from yield under different stresses.

Materials and Methods

Ninety-one S_4 maize lines were evaluated along with nine homozygous inbred lines in two sets of environments: a stress set with four environments (severe drought, moderate drought, low nitrogen, and high density) and a non-stress set with five natural environments, each located in a different ecological zone in Côte d'Ivoire. The environments were as follows:

Stress environments

Drought stress - The trial was planted at Ferkessédougou (Côte d'Ivoire) during the 1995A dry season. Sprinkler irrigation was used when necessary. A lattice design (10x10) with three replications was used. One row plots, 2.5 m long, 0.75 m between rows and a final density of 53,300 plants/ha were established. Recommended doses of fertilizers (105 kg N, 72 kg P_20_5 and 72 K_20) were applied. After full plant establishment three weeks after planting, irrigation was stopped until plants remained wilted in the morning. At this stage irrigation was applied once and then plants were maintained under drought stress until harvest, during which time there was 20 mm of rain. Data recorded included days to silking and pollen shed, anthesis-silking interval (ASI), ear per plant and yield. Yield was calculated using the actual shelling percentage.

Moderate drought stress with heat - The trial described above was planted a second time at Ferkessédougou, on the same date. The only difference was that this trial was irrigated regularly. This trial was affected by heat in spite of the optimal moisture conditions.

Low nitrogen - During the 1995B major growing season, the same trial was planted again at Ferkessédougou, but this time under rainfed conditions. Plot layout was the same, but in this case six replicates were planted. No fertilizer was applied, to provide low N conditions, though phosphorus content in the soil was adequate. The same data as in the drought trials were recorded.

High density - The same trial was planted at Badikaha, about 100 km southeast of Ferkessédougou, using the same design but with a density of 106,000 plants/ha.

Non stress environments

These environments were represented by one site (Bouaké) in the transitional forest/savanna ecological zone, two sites (Touba, and Odienné) in the Northwestern Guinea savanna zone, one site (Badikaha) in the northern Guinea savanna zone and one site (Sinematiali) in the transitional Guinea savanna/Sudan savanna zone. The trials were evaluated under rainfed conditions, optimal density (53,000 plants/ha) and optimal doses of fertilizers (105 kg N, 72 kg P_20_5 and 72 K_20). The same design and the same number of replications as the stress set were used, but 5 m long row plots were established. The same measurements were taken as in the stressed trials, except that yield was calculated using a standard shelling percentage (80%).

Stability analyses

Stability analysis for yield included the following stability parameters:

a) Wricke's(1962) ecovalence (W^2): $W_i^2 = \Sigma(X_{ij} - \overline{X}_{i\cdot} - \overline{X}_{\cdot j} + \overline{X}_{..})^2$ where is the mean response of genotype $_i$ in environment $_j$, $\overline{X}_{i\cdot}$ is the mean response of genotype $_i$ across all environments, $\overline{X}_{\cdot j}$ the mean of environments $_j$ and $\overline{X}_{..}$ is the general mean. Stable genotype has a small W^2 value.

b) Hühn's (1979) non parametric S^3 statistic that combines yield and stability. The parameter is based on yield ranks of genotypes in each environment and is defined as: $S^3 = \Sigma(r_{ij} - r_{i\cdot})^2 / \overline{r_{i\cdot}}$ where r_{ij} is the rank of the i_{th} genotype in the j_{th} environment and $\overline{r_{i\cdot}}$ is the mean of ranks over all environments for the i_{th} genotype. Small S^3 values correspond to stable genotypes.

c) Eberhart and Russell's (1966) stability parameters b_i and S^2, where b_i is the regression coefficient of the i_{th} variety on the environmental index measured as the mean yield of all varieties in that environment minus the mean of all environments, S^2 is the deviation from regression of the i_{th} variety minus the average variance of a variety mean at the j_{th} location.

A stable genotype will be one with unit regression coefficient ($b_i = 1.0$) and a very small deviation from regression ($S^2 = 0$).

Stability index

For each variety, the estimates of stability parameters and average yield were ranked as low, medium and high with numerical scores of 1, 2, and 3 respectively. The assignment of the scores was done on the basis of confidence intervals. For yield, a score of 1 was given if the average yield was less than the lower value of the interval, a score of 2 if it was in the interval, and a score of 3 if it was bigger than the upper value of the interval. Scores of 3, 2, and 1 were given to estimates of the Eberhart regression coefficient if it was in a 95% confidence interval, in a 99% confidence interval but not in the 95% confidence interval, and outside the 99% confidence interval, respectively. Because low estimates of the remaining parameters are desirable for high stability, the scores of these parameters were assigned in reverse order. Stability of each genotype was assessed by computing its total score based on all parameters. The genotypes were ranked according to those scores. The most stable lines were those lines with the highest total scores.

Canonical correlation analysis

This was performed by dividing the environments into the two sets, stress and natural environments. The inter-set and intra-set correlations and canonical correlations were used to predict yields in the natural environments from yields in the stress environments.

Results

In the natural environments, rainfall was adequate except at Sinematiali, where the rains came late and the trial suffered from water logging and nitrogen leaching. In the stress environments, the nitrogen soil content in the nitrogen trial was not low enough to cause a large yield reduction. The correlations of yield in the stress and natural environments were used to study the relationships between yields in those environments (Table 1). Correlations between yield under high density and yields in the natural environments were higher than those between high density yield and yields under stress environments. Yield under low nitrogen was positively correlated with yield under moderate drought. High positive correlations were also found between yield under low nitrogen and the yields at Badikaha, Odienné, Sinematiali, and Touba. Yields under severe and moderate drought were positively correlated. The first canonical correlation (0.89, $P<0.007$) indicated that lines which performed well under all stress environments would also perform well under all natural environments. High yields at Sinématiali were associated with high yields under low nitrogen, as explained by the second pair of canonical variates and the parent variables.

Highly significant differences were obtained for yield, days to silking and number of ears per plant in all environments. The yield of genotypes in the different environments varied greatly and was correlated ($P<0.01$) with number of ears per plant at Sinematiali ($r = 0.56$) and under high density ($r = 0.56$), low N ($r = 0.56$) and severe drought ($r = 0.79$) (Fig 1). For yield, the GxE interaction was highly significant. Consequently, variety

Table 1. Phenotypic correlations[1] of grain yield among trials.

	Stress environments				Natural environments			
	Badikaha	Bouaké	Odienné	Touba	High density	Low nitrogen	Severe drought	Moderate drought
Badikaha								
Bouaké	0.69							
Odienné	0.80	0.61						
Sinématiali	0.68	0.41	0.62					
Touba	0.76	0.62	0.80	0.60				
High density	0.73	0.65	0.76	0.49	0.66			
Low Nitrogen	0.64	0.46	0.68	0.71	0.61	0.59		
Severe drought	0.38	0.31	0.41	0.37	0.30	0.25	0.40	
Moderate drought	0.52	0.51	0.60	0.55	0.49	0.43	0.50	0.52

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[1] All correlation coefficients are estimated on the basis of 100 data points and their observed significance levels are less than or equal to 0.012.

means were compared site by site, and genotypes were grouped by maturity for comparison. The mean yields varied from 0.45 t ha^{-1} (under severe drought) to 5.00 t ha^{-1} at Touba (natural environment) (Fig 1).

Yields, days to silking, and number of ears per plant of high yielding lines across stress environments are presented in Table 2. Under severe drought, yield varied from 1.72 t ha^{-1} to 0.45 t ha^{-1}, the earlier lines giving the highest yield under severe drought stress (data not shown). Nine lines performed well under severe drought (Table 2). Days to silking were delayed and ears/plant were reduced by drought. The yield under high density (6.79 to 1.71 t ha^{-1}) was quite high for S_4 lines. The highest yielding lines under high density were different from the highest yielding lines under severe drought (Table 2). The number of ears/plant was less affected than it was under severe drought (0.72 vs 0.45, respectively). Under low N,

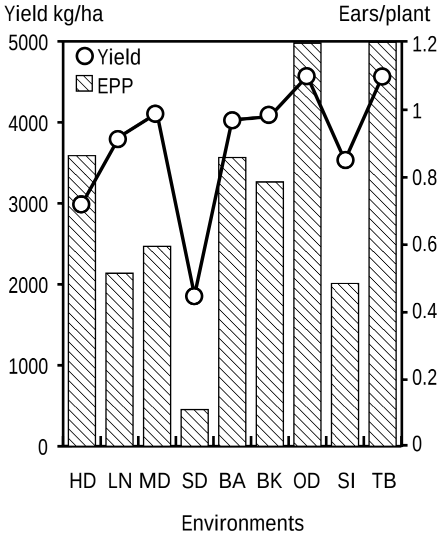

Figure 1. Yield and ears/plant (EPP) means across environments: high density (HD), low N, (LN), moderate drought (MD), severe drought (SD), Badikaha, Bouaké (BK, Odienné (OD), Sinématiali (SI), and Touba (TB).

Table 2. Yield, days to silk and number of ears/plant of lines with good performance under different stresses.

Entry no.	Pedigree	Yield (t ha^{-1})	Silk (days)	Ears/plant
Severe drought				
5	8721SRBC6-217-1-1sb-	1.05	68	0.68
8	P43SRC9FS100-1-2-1sb-#1	1.19	68	0.80
9	P43SRC9FS100-1-2-4sb-#1	1.41	68	0.73
13	P43SRC9FS43-1-2-2sb-#1	1.72	69	0.84
70	EV8729SR-95-2-2sb DR	1.44	66	0.91
72	EV29SR-93-1-1sbsb DS	0.93	68	0.65
73	EV29SR-93-1-2sbsb DS	1.21	68	1.00
74	EV8725SR-100-1-2sb DS	0.91	69	0.47
84	P43SRC9FS58-1-2-1sb-#1	0.87	68	0.83
	Mean	1.19	68	0.76
	Grand Mean	0.45	68	0.45
	CV	89	27	52.9
	LSD	0.45	20	0.26
Low nitrogen				
13	P43SRC9FS43-1-2-2sb-#1#1	3.78	67	1.11
38	TZLCOMP3-12-3-7-#1#1	3.77	64	1.06
42	TZLCOMP3-159-2-4-#1#1	4.14	63	1.02
44	TZLCOMP3-168-1-2-#1#1	3.54	63	1.13
64	P22SR-54-1-1sb-#1#1DRSTRSTR	3.54	66	0.96
69	EV8729SR-95-2-1sb-#1#1DR	3.50	62	0.90
71	P22SR-7-1-1sb-#1#1DS	2.98	62	0.97
74	EV8725SR-100-1-2sb-#1#1DS	2.69	63	0.90
84	P43SRC9FS58-1-2-1sb-#1#1	3.41	64	1.20
	Mean	3.48	64	1.03
	Grand Mean	2.20	66	0.92
	CV	32	10	16.5
	LSD	0.55	5	0.11
High density				
13	P43SRC9FS43-1-2-2sb-#1#1	4.01	63	0.76
31	EV87TZBSR-7-1-1-#1#1	5.61	63	0.85
42	TZLCOMP3-159-2-4-#1#1	6.79	61	0.93
58	8725SRG-43-5-2sb-#1#1	5.27	64	0.81
64	P22SR-54-1-1sb-#1#1DRSTRSTR	6.06	64	0.79
71	P22SR-7-1-1sb-#1#1DS	5.28	65	0.71
74	EV8725SR-100-1-2sb-#1#1DS	5.36	61	0.75
84	P43SRC9FS58-1-2-1sb-#1#1	5.21	61	0.88
96	(49*POR18043)-3-3-3-2-BBB-4-B-#-B-B#1	5.21	64	0.92
	Mean	5.50	63	0.82
	Grand Mean	3.76	63	0.72
	CV	26	14	15.76
	LSD	1.07	9	0.12
Moderate drought				
13	P43SRC9FS43-1-2-2sb-#1	4.57	69	1.03
39	TZLCOMP3-124-1-1-#	4.34	64	0.94
47	TZLCOMP3-178-2-4-#	4.92	62	0.87
61	EV87TZBSR-94-1-6-#	3.80	66	1.17
65	EV8725SR-72-1-sb DR	3.97	63	1.00
70	EV8729SR-95-2-2sb DR	4.20	64	1.40
71	P22SR-7-1-1sb	5.28	67	1.15
74	EV8725SR-100-1-2sb	3.77	68	1.04
84	P43SRC9FS58-1-2-1sb-#1	3.23	66	1.45
	Mean	4.23	65	1.12
	Grand Mean	2.54	70	0.99
	CV	36	3	21.19
	LSD	1.02	3	0.23

yield varying from 4.14 to 0.62 t ha^{-1} was recorded (complete data not shown). Entry 13, which ranked first under severe drought, ranked second in the low N trial. Entry 42 ranked first under both high density and low nitrogen, but ranked 74 in the severe drought trial. Under moderate drought (drought under normal irrigation but with high heat) yields ranged from 5.28 to 2.54 t h^{-1}. Four lines which did well under severe drought also did well under moderate drought (Table 2). Under the natural environments, the highest mean yield (5.00 t ha^{-1}) was recorded at Touba and the lowest (2.01 t. ha^{-1}) at Sinématiali (Fig 1). Three lines were identified that performed well across all environments, both stressed and natural (Table 2). The average yield across environments along with percent root and stalk lodging under high density, and a stability index for six stable and four unstable lines are presented in Table 3. The yield stability measured with this method seems to be associated to the root and stalk quality of the lines (Table 3).

Discussion

This method of selecting in a combination of stressed and non stressed environments is a multi-environment test that compares well with the multilocation testing of progenies used by the CIMMYT Maize Program. In our case the stresses were managed and S_4 lines were evaluated to identify lines with specific traits to be recombined to develop synthetics. A managed stress environment may not represent the true environment because in nature a wider range of stress conditions (e.g., diseases or insects) is likely to be encountered. This is one of the reasons why natural environments were included.

The yield of the genotypes in different environments varied greatly and was correlated with the number of ears per plant in three stress environments (high density, low nitrogen, and severe drought) and one natural environment (Sinematiali, where the plants suffered from water logging and nitrogen leaching). These results support the findings of Guei and Wassom (1992), Lafitte and Edmeades (1994), and Byrne et al. (1995).

Anthesis-silking interval (ASI) was negative in some cases, particularly under stress (data not shown). ASI had already been reduced by selection during the process of inbreeding, so some lines may have problems with pollen shed under stress. Consequently the silks emerged before anthesis. Because of these complications, it seems likely that ASI will not be an effective

Table 3. Average yield, mean root and stalk lodging and stability index for six stable and four unstable lines. Unstable lines are those with stability index < 10, and stable with a stability index > 10.

Entry no.	Pedigree	Environment BA	BK	OD	SI	TB	LN	HD	MDr	SDr	Mean	Silk mean	Ears/ plant mean	Lodging HD	Stab. index
		Mean yield t ha^{-1}										(days)		(%)	
5	8721SRBC6-217-1-1-sb	4.04	4.52	5.74	2.17	6.16	2.12	3.98	3.42	1.05	3.69	63	0.87	10	14
15	P43SRC9FS6-1-3-2sb-#	4.52	5.29	6.85	1.61	6.90	2.48	4.45	2.92	0.88	3.99	68	0.98	5	11
37	TZLCOMP3-12-3-6-#	4.59	4.17	5.16	3.34	5.55	2.69	3.84	2.72	0.67	3.64	61	0.92	13	14
46	TZLCOMP3-168-2-5-#	4.27	1.96	4.55	2.72	4.43	2.88	2.47	2.14	0.62	2.89	69	0.80	21	7
55	TZLCOMP3-67-2-1-#	3.79	5.13	6.49	2.32	5.16	2.67	3.51	3.67	0.46	3.69	64	0.91	19	15
57	TZLCOMP3-86-1-4-#	4.03	2.11	4.09	2.49	5.32	2.65	2.45	1.91	0.23	2.81	64	0.78	28	7
66	EV8725SR-100-1-1sb DR	4.15	3.44	7.40	3.14	6.15	2.72	4.44	3.55	0.93	3.98	62	0.88	15	15
68	EV8725SR-186-1-1sb DR	2.84	2.32	3.90	0.92	4.31	1.74	1.84	3.15	0.34	2.37	65	0.78	31	6
70	EV8729SR-95-2-2sb DR	4.65	4.78	5.57	3.57	4.66	2.54	4.77	4.20	1.44	4.02	61	1.04	10	15
77	P22SR-9-1-2sb## STRS	2.74	2.74	3.54	2.75	3.99	2.85	2.59	2.47	0.27	2.66	63	0.78	39	7
General mean		3.57	3.26	4.98	2.01	4.99	2.14	3.59	2.47						
SD		0.72	1.16	1.18	0.78	1.08	0.68	1.08	1.03						

BA = Badikaha SI = Sinématiali HD = High Density TB = Touba SDr = Severe drought
BK = Bouaké OD = Odienné LN = Low Nitrogen MDr = Moderate drought Stab. = Stability

selection criterion for stress tolerance among these inbred lines.

The highest correlations between yields under stress environments and natural environments were observed between high density and Odienné, and low nitrogen and Sinematiali. Odienné was one of the highest yielding sites and Sinematiali was the lowest yielding site. The highest correlations between yields under different stresses were observed between high density and low nitrogen, severe drought and moderate drought, and moderate drought and low nitrogen. The latter relationship was also reported by Edmeades et al. (1995). In spite of the highly significant and positive correlations obtained between yields under some stresses, very few lines performed well across all stresses. The early lines suffered less than the late lines under stress. Those genotypes were favored not only because their critical period of life might escape the stress, but because they need less moisture or N to accomplish their life cycle. Yield stability was weakly associated with the stalk and root quality. This might partially explain why the maize yield of cultivars with poor root and stalk quality is much more unstable from year to year in the Savanna of West and Central Africa.

In this study, stable lines were identified using several stability parameters. Entries 13, 74, and 84 in spite of their good performance across stress and natural environments, did not have large stability indices (9, 10, and 9 respectively). This is probably due to the fact that in all environments their average yields were far above the environmental average yields, and there were differences among their average yields across environments with higher values in high yielding environments. Consequently they had a regression coefficient greater than one and large values for ecovalence, which led to smaller indices than those of lines classified as stable in Table 3.

In general, lines which performed well under high density, low nitrogen, and moderate drought would also perform well under natural environments. Yield under moderate drought was closely related to yield under other stresses, including severe drought and natural environments. This study suggests that low nitrogen and moderate drought can be used to identify stable lines in the transitional and savanna zones of Côte d'Ivoire, if disease pressure is not intense. It is therefore recommended that selection under stress and multilocation testing should be combined as suggested by other researchers (Bolaños and Edmeades, 1993; Pandey et al., 1986). Severe drought does not seem to be effective for inbred line evaluation, and there is also concern about whether the performance *per se* under drought bears much relationship to hybrid performance. Evaluating inbred lines under high density will help to identify lines with good stalk and root quality.

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Estimación del Potencial de Rendimiento de Líneas Resistentes a Sequía del CIMMYT en Cruzamientos con Diferentes Probadores

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Abstract

Two experiments provided by CIMMYT were planted in the 1995 rainfed spring-summer season at the Ameca, Jalisco experiment station of the Biological and Agro-livestock Sciences Center, University of Guadalajara. The first experiment was a yield test of S_5 *topcrosses of Tuxpeño lines (TS6C1) and La Posta SeqC3 (UNG95B-5935D). The second included an isolated group of single-cross and three-way hybrids with Tuxpeño and La Posta lines (UNG95B-5934E), in both cases with drought resistance. Based on the results, one can conclude that: 1) the lines with La Posta germplasm yielded better when crossed than the lines with Tuxpeño germplasm, possibly because the testers in the first experiment (CML247 and CML254) are Tuxpeño-related materials; 2) there were no line x tester interactions, which indicates that either of the two testers (CML247 and CML 254) can be used to select for combining ability between the Tuxpeño and La Posta drought-tolerant lines, at least in this area; 3) the lines that showed the greatest tendency towards combining ability in the two experiments were La Posta SeqC3-H297-2-1-1-1-B and La Posta SeqC3-H297-2-1-1-2-B, and it is recommended that these be used immediately and intensively in hybridization programs to incorporate drought tolerance into commercial hybrids.*

Después de la fertilidad del suelo, la sequía es el factor abiótico que más afecta el rendimiento de grano de maíz en las aéreas tropicales y subtropicales de México y causa pérdidas significativas. Con frecuencia la sequía se presenta antes de la floración, lo que ocasiona un retraso en la floración femenina y un incremento del periodo entre la floración masculina y la femenina (ASI). Esta asincronía ha sido reconocida como el factor de mayor reducción del rendimiento del grano en maíz (Ribaut et al., 1995); así, la selección se hace en condiciones de sequía para ASI reducida y elevado número de mazorcas por planta, se mejora en forma paralela el rendimiento de grano y la tolerancia a sequía (Edmeades et al., 1995). Previamente, se han presentado resultados, principalmente de los trabajos desarrollados en CIMMYT, de los avances de la selección de poblaciones tolerantes al estrés de sequía (Bolaños y Edmeades, 1993a, 1993b; y Bolaños et al., 1993) obtenidas principalmente aprovechado la varianza aditiva de los caracteres en selección; esos resultados muestran el incremento del rendimiento en condiciones adversas, sin que se afecte el de las condiciones adecuadas de humedad. Así, falta saber si las líneas derivadas de las poblaciones tolerantes a sequía transmiten esta característica a los híbridos que se formen con ellas y si las líneas que ha desarrollado CIMMYT a partir de las poblaciones TS6C1 y LA POSTA SEQ C3 tienen potencial para ser utilizadas en la formación de híbridos comerciales con rendimientos competitivos cuando se desarrollen en temporal.

En relación con la transmisión de caracteres Edmeades et al. (1995) observaron que al derivar líneas de poblaciones tolerantes al estrés, incrementó la probabilidad de obtener híbridos también tolerantes, por lo que es importante tener dentro de un programa de mejoramiento de híbridos una parte dedicada al mejoramiento de poblaciones bajo condiciones de estrés. Con base en lo anterior, el objetivo del presente estudio es estimar el valor de la aptitud combinatoria de un grupo de líneas tolerantes a la sequía derivadas por CIMMYT cruzadas con diferentes probadores para proponer su uso en hibridación.

Materiales y Métodos

El CIMMYT proporcionó dos grupos de evaluación de mestizos clasificados como UNG95B–5934E y UNG95B–5935D, en el primero se evaluaron 16 líneas, 11 derivadas de LA POSTA SEQ C3 y 5 de TS6C1, con diferentes probadores: las líneas CML 249, CML 254, CML 269, CML 271, CML 274, CML 273, CML 277 y las cruzas: CML 24xCML 36, CML 24xCML 37, CML 264xCML 271 y CML 247xCML 254, no quedaron representados todos los probadores en todas las líneas y se tuvo un total de 83 mestizos más siete testigos; en el segundo experimento, se evaluaron los mestizos de nueve líneas derivadas de TS6C1 y 12 de LA POSTA SEQC3, algunas de ellas estuvieron incluidas en el primer experimento, con los probadores: CML 247 y CML 254, se tuvo un total de 42 mestizos y 8 testigos.

Los dos experimentos se realizaron durante el ciclo primavera-verano 95 con temporal en el Campo Experimental de Ameca Jal., del Centro Universitario de Ciencias Biológicas y Agropecuarias de la Universidad de Guadalajara, la preparación de suelos y paquete tecnológico fue el recomendado para la zona y no tuvo estrés de sequía ni de nutrimentos.

Resultados

Sin considerar a los probadores CML 247 y CML 254, los mestizos generados con líneas derivadas de las población La Posta Sequía C3 tuvieron significativamente mayor rendimiento respecto a los mestizos delas líneas del TS6C1, mientras que la diferencia en el rendimiento entre probadores y su interacción entre ellos no resultó estadísticamente significativa. El rendimiento medio de los mestizos de TS6C1 y el probador CML 254 fue menor que el de los testigos y el de los mestizos de La Posta Sequía C3, mientras que el mayor correspondió a los mestizos de las líneas de La Posta y los probadores CML 254 y CML 247 (Cuadro 1).

Los mejores mestizos e híbridos triliniales con mayor rendimiento medio de grano, estadísticamente iguales entre sí se presenta en los Cuadros 2 y 3; se observó que las líneas LPSC3–H297–2–1–1–1–B y la LPSC3–H297–2–1–1–2–B integraron ocho de los 20 mestizos con mayor rendimiento

Cuando se comparó el rendimiento medio de 16 líneas con diferentes probadores (Cuadro 4), se observó

Cuadro 1. Rendimiento medio de los mestizos de las líneas de La Posta Sequía C3 y TS6C1 con dos probadores y su interacción con el grupo UNG95B–5835D, evaluados en Ameca Jal., Méx., durante el ciclo primavera-verano de 1995.

Fuente de mestizos	Probador	Número	Rendimiento (t/ha)	S.D
TS6C1	CML 247	9	8.46	1.81
	CML 254	9	7.61	1.81
La Posta Seq C3	CML 247	12	9.59	1.49
	CML 254	12	9.65	2.48
Testigos		8	9.05	
D.M.S. (0.05) = 0.85				

Media de: mestizos TS6C1: 8.04N.S., mestizos La Posta Seq C3: 9.62 *, mestizos del probador CML 254: 8.63 N.S., mestizos del probador CML 247: 9.03 N.S., interacción probador*línea N.S., D.M.S. (0.05) = 0.86

Cuadro 2. Mestizos e híbridos trilineales con mayor rendimiento de grano, del grupo UNG95B–5835D, evaluados en Ameca Jal., Méx., durante el ciclo primavera-verano de 1995.

Mestizo	Rendimiento (t/ha)
LPSC3–H297–2–1–1–1–BxCML 254	11.82
LPSC3–H16–3–2–4–1–BxCML 254	11.47
TS6C1F98–2–3–4–2–BxCML 247	11.40
D 890	11.34
LPSC3–H20–4–1–2–2–BxCML 254	11.30
LPSC3–H17–1–2–3–2–BxCML 247	11.24
LPSC3–H44–1–1–2–2–BxCML 254	11.12
P3001W	10.95
LPSC3–H297–2–1–1–1–BxCML 247	10.86
A7520	10.65
LPSC3–H297–2–1–1–2–BxCML 247	10.50
TS6C1F62–2–1–3–1–BxCML 247	10.39
LPSC3–H17–1–2–3–2–BxCML 254	10.16
LPSC3–H16–3–2–3–2–BxCML 247	10.00

Media: 8.96 t/ha, D.M.S. (0.05) = 3.82, C.V. = 21.3%

Cuadro 3. Mestizos con mayor rendimiento de grano del grupo UNG95B–5934E, evaluados en Ameca Jal., Méx., durante el ciclo primavera-verano de 1995.

Mestizo	Rendimiento (t/ha)
CML 273/LPSC3–H297–2–1–1–1–B	11.97
CML 264xCML 271/LPSC3–H297–2–1–1–2–B	10.57
CML 273/LPSC3–H1–2–2–2–2–1	10.13
CML 247xCML 254/LPSC3–H297–2–1–1–1–B	10.00
CML 254/LPSC3–H44–1–1–2–2–B	9.94
CML 273/LPSC3–H297–2–1–1–2–B	9.83
CML 249/LPSC3–H297–2-1–1–1–B	9.52
CML 254/LPSC3–H44–1–1–3–2–1	9.21
CML 254/LPSC3–H20–4–1–1–2–B	9.10

Media: 7.48 t/ha, D.M.S. (0.05) = 2.96, C.V. = 19.9%

que las de mayor rendimiento o tendencia de aptitud combinatoria fueron: LPSC3– H297–2–1–1–1–B, LPSC3– H297–2–1–1–2–B y LPSC3–H44–1–1–2–2–B.

Discusión

La diferencia significativa del rendimiento medio de los mestizos indica que las líneas de La Posta tienen mayor habilidad para combinarse con los probadores CML 247 y CML 254 respecto a las líneas de la población TS6C1 y que las líneas probadoras están relacionadas genéticamente con las de TS6C1 de tal forma que no hay una heterosis significativa. El rendimiento medio de los probadores a través de los mestizos, resultó estadísticamente similar, aunque hubo una tendencia a incrementarse con el probador CML 247, pero no con el CML 254; algo semejante se observó en la interacción línea por probador, por lo que se puede decir que cualquiera de los dos probadores puede ser utilizado para seleccionar líneas derivadas de las poblaciones antes mencionadas; aunque, con base en las tendencias se recomienda utilizar el probador CML247 para las líneas de TS6C1 y el CML 254 para las de La Posta.

Cuadro 4. Rendimiento medio de grano de líneas TS6C1 y La Posta Seq C3 con diferentes probadores del grupo UNG95B–5934E, evaluadas en Ameca Jal., Méx., durante el ciclo primavera-verano de 1995.

Mestizo con línea	Número de probadores	Rendimiento (t/ha)
LPSC3–H297–2–1–1–1–B	6	9.17
LPSC3–H297–2–1–1–2–B	4	8.81
LPSC3–H44–1–1–2–2–B	6	8.25
LPSC3–H1–2–2–3–1–B	4	8.24
LPSC3–H1–2–2–3–2–1	4	7.97
TS6C1–F62–2–1–3–1–B	6	7.89
LPSC3–H1–2–2–1–2–1	6	7.81
LPSC3–H1–2–2–2–1–1	4	7.78
LPSC3–H1–2–2–2–2–1	4	7.66
LPSC3–H44–1–1–3–1–1	7	7.46
TS6C1–F165–2–1–1–1–B	5	7.42
LPSC3–H20–4–1–1–2–B	8	6.91
TS6C1–F217–3–3–3–1–B	2	6.72
TS6C1–F238–1–3–2–2–B	5	6.55
LPSC3–H44–1–1–3–2–1	6	6.30
TS6C1–F165–2–1–1–2–B	5	6.08

Media: 7.48 t/ha, D.M.S. (0.05) = 2.96, C.V. = 19.9%

La superioridad de las líneas de La Posta, se confirmó por su mayor contribución en la formación de los mejores mestizos (23 de 27 mestizos), particularmente las líneas que se presentaron con mayor frecuencia: LPSC3–H297–2–1–1–1–B y LPSC3–H297–2–1–1–2–B, por lo que estas líneas pueden tener un uso extensivo en los programas de hibridación con la ventaja de llevar la tolerancia al estrés de sequía.

Con base en lo anterior se concluye que:

1. Las líneas derivadas de La Posta tuvieron mayor rendimiento en los cruzamientos que las provenientes del Tuxpeño, posiblemente debido a que los probadores en el primer grupo (CML247 y CML254) están relacionados con el Tuxpeño.
2. La interacción entre líneas por probador no mostró significancia estadística, lo que indica que se pueden utilizar indistintamente ambas líneas probadoras (CML247 y CML254) para seleccionar alta aptitud combinatoria entre las líneas de Tuxpeño y La Posta resistentes a sequía, por lo menos en ésta localidad.
3. Las líneas que mostraron una tendencia de mayor aptitud combinatoria en los dos grupos, fueron: La posta SeqC3–H297–2–1–1–1–B y La posta SeqC3–H297–2–1–1–2–B.

Por lo que se sugiere que sean utilizadas intensivamente en los programas de hibridación para incorporar la tolerancia a la sequía a híbridos comerciales.

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Prueba de Cultivares Criollos de Maíz en la Cordillera del Tentzo, Puebla

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Resumen

The Tentzo Cordillera faces problems of drought, thin soils and a rough topography. Nevertheless, through an ongoing process of selection, farmers have obtained cultivars adapted to these marginal conditions. In earlier work to collect and test maize landraces, the following collections were found to be superior: 1394, 1439 and 1452 for favorable edaphic environments, and 1393, 1439 and 1449 for marginal environments (López et al., 1990). As a second step, in 1989 trials were established at two sites with the two groups of collections for the differing soil conditions, using H-28, H-220 and the farmers' landrace as checks. Although the hybrids showed better plant type than the landraces, the latter were earlier, had better ear aspect, higher grain percentage and higher grain yield per hectare. Collections 1393 and 1394 were the best performers. These results demonstrate the need to conduct genetic improvement in specific areas using the local landraces as the source material to increase yields and grain production in Mexico's rainfed areas.

Introducción

La generación de cultivares mejorados de maíz en México se ha desarrollado principalmente en los campos experimentales de los centros de investigación. En consecuencia se ha acumulado un efecto genético de especialización para las condiciones del campo experimental (Muñoz et al., 1976), condiciones frecuentemente diferentes a las prevalecientes en las áreas para las que se recomiendan los cultivares. Es por esta razón que con frecuencia los cultivares mejorados en condiciones de temporal son igualados o superados por los criollos en diversas características; así, han demostrado su superioridad en rendimiento de grano (Arellano, 1976; López, 1993; Mejía, 1976), en aspecto de planta y mazorca (Valadez, 1988), en porcentaje de grano (Gil y Muñoz, 1992; Vaca, 1990) y en resistencia a enfermedades (Gil y Muñoz, 1992).

Lo anterior evidencia la necesidad de desarrollar programas de mejoramiento en niveles más específicos, tomando como base el potencial genético y de adaptación que tienen los cultivares criollos en sus nichos ecológicos (Muñoz, 1991).

La región de la Cordillera del Tentzo se encuentra al sur del Valle de Puebla, presenta una altitud promedio de 2000 msnm, una precipitación media anual de 713 mm, distribuyéndose en los meses de abril a octubre, un clima templado subhúmedo, suelos delgados y relieve accidentado, lo cual conforma un ambiente restrictivo para el desarrollo de los cultivos.

Al inicio de 1987 se hizo una exploración etnofitogenética en esta región a fin de colectar cultivares criollos de las principales especies cultivadas. En 1987 y 1988 se evaluó el maíz y se seleccionó un grupo de seis cultivares (López et al., 1990).

El objetivo de esta investigación fue evaluar el comportamiento de los cultivares seleccionadas en una superficie superior a la considerada en las unidades experimentales utilizadas durante 1987 y 1988, en diferentes localidades de la región.

Materiales y Métodos

La investigación fue desarrollada en 1989 bajo condiciones de temporal y suelo favorable en la región de la Cordillera del Tentzo, Puebla, en las localidades de San Baltazar Torija y San Baltazar Tetela y en condiciones de suelo desfavorable en San Juan Tzicatlacoyan y San Martín de los Teteles. Las diferencias entre los suelos fueron la profundidad, pendiente y fertilidad.

Se evaluados las colecciones (Col) Col-1394, Col-1439 y Col-1452, en las localidades de suelo favorable, y Col-1393, Col 1439 y Col-1449, en las localidades de suelo desfavorable. Para todos los casos los testigos fueron el H-28, H-220 y el criollo del agricultor.

La siembra se realizó con el establecimiento del temporal, en San Juan Tzicatlacoyan fue el 12 de junio, en San Baltazar Tetela el 13 de junio, en San Baltazar Torija el 18 de junio y en San Martín de los Teteles el 20 de junio. La distancia entre surcos fue de 90 cm y entre matas 50 cm, y se mantuvieron dos plantas por mata. Las labores culturales se realizaron tomando en cuenta las recomendaciones del Plan Puebla, CEICADAR, Colegio de Postgraduados, Montecillo, México.

Por cada cultivar y en cada localidad se establecieron, en forma aleatoria, dos repeticiones de 500 m^2 constituyendo así un lote de 6000 m^2 por localidad, se delimitaron, al azar, siete parcelas de dos surcos de 5 m de largo para evaluar las siguientes variables: días a floración femenina, aspecto de planta y mazorca (escala: 1, mejor; 5 peor), porcentaje de grano y rendimiento.

Resultados

Evaluación de los cultivares en condiciones favorables de suelo.

Con base en los días a floración femenina (Cuadro 1), las colectas fueron las más precoces, las siguieron los testigos y los híbridos fueron más tardíos, de éstos, el H-28 fue el más tardío para la floración femenina.

Aunque con ligeras diferencias entre sí los cultivares mejorados presentaron mejor aspecto de la planta que los criollos y el H-220 fue el más sobresaliente (Cuadro 1). No obstante al mejor aspecto de la planta de los híbridos su mazorca fue la de peor aspecto, sobre todo en el H-28 (Cuadro 1).

El porcentaje de grano o coeficiente de desgrane fue más alto en las colectas Col-1394 y Col-1452 y el más bajo correspondió al H-28 (Cuadro 2).

Cuadro 1. Promedios de días a floración y aspecto de la planta y la mazorca de cinco genotipos de maíz crecidos en dos localidades de Puebla, Méx.

	DAFF		ASPPL		ASPMZ	
Genotipos	L1	L2	L1	L2	L1	L2
Col-1394	88	87	2.57	2.35	2.42	2.35
Col-1439	91	87	2.28	2.57	2.42	2.57
Col-1452	89	88	2.35	2.42	2.57	2.42
H-28	94	91	2.71	2.07	2.85	2.85
H-22	92	88	2.35	2.35	2.42	2.78
Criollo local	91	87	2.35	2.50	2.42	2.71

DAFF=Días a floración femenina, ASPPL=Aspecto de planta, ASPMZ=Aspecto de mazorca, L1=San Baltazar Tetela y L2= San Baltazar Torija.

En el rendimiento promedio de las dos localidades, los testigos fueron superados por las colectas. El cultivar criollo del agricultor fue el mejor testigo y el H-28 el peor (Cuadro 2).

Evaluación de los cultivares en condiciones desfavorable de suelo.

En la condición desfavorable los cultivares testigo fueron ligeramente más tardíos o similares a las colectas y de todos o los más tardíos fueron Col-1449 y H-28 (Cuadro 3); además, la Col-1393 sobresalió por su mejor aspecto, mientras que el H-28 fue el peor, especialmente por la mazorca (Cuadro 3) y el porcentaje de grano

Cuadro 2. Promedios de porcentaje de grano y rendimiento de cinco genotipos de maíz crecidos en dos localidades de Puebla, Méx.

	PORGR		RENDGRHA	
Genotipos	L1	L2	L1	L2
Col-1394	87.8	89.4	3515	2208
Col-1439	85.4	88.8	3872	1304
Col-1452	87.6	89.3	3910	1693
H-28	81.9	82.6	2053	909
H-22	75.6	80.3	2412	1031
Criollo local	84.9	87.6	3017	1589

PORGR=Porcentaje de grano, RENDGRHA=Rendimiento de grano kg/ha, L1=San Baltazar Tetela y L2=San Baltazar Torija.

Cuadro 3. Promedios de los días a floración, aspecto de planta y mazorca de cinco genotipos de maíz crecidos en dos localidades de Puebla, Méx.

	DAFF		ASPPL		ASPMZ	
Genotipos	L1	L2	L1	L2	L1	L2
Col-1393	96	98	1.71	2.28	2.57	2.57
Col-1439	94	98	1.92	2.35	3.14	2.78
Col-1449	98	100	1.92	2.78	2.78	2.85
H-28	101	102	2.00	2.85	3.14	3.42
H-22	98	98	1.71	2.42	3.00	2.92
Criollo local	95	98	2.00	2.50	2.92	2.78

DAFF=Días a floración femenina, ASPPL=Aspecto de planta, ASPMZ=Aspecto de mazorca, L1=San Juan Tzicatlacoyan y L2=San Martín de los Teteles.

fue menor sólo para la Col-1449 y el H-28 (Cuadro 4).

El rendimiento de grano fue superior en las colectas y de éstas, la de mayor rendimiento fue la Col-1393, además en esta condición desfavorable de suelo también el H-28 fue el testigo con menor rendimiento (Cuadro 4).

Discusión

Las diferencias en las características de los cultivares crecidos en ambas condiciones edáficas se atribuye principalmente a diferencias en la profundidad del suelo y por lo tanto en su capacidad para retener el agua, y al relieve, que causa diferencias en la fertilidad del suelo.

La mayor precocidad de los cultivares criollos es una característica favorable cuando el cultivo es de temporal. La importancia de la precocidad es la menor duración de las etapas fenológicas críticas, como la floración, que influyen en el rendimiento de grano.

Cuadro 4. Promedios de porcentaje de grano y rendimiento de cinco genotipos de maíz crecidos en dos localidades de Puebla, Méx.

Genotipos	PORGR		RENDGRHA	
	L1	L2	L1	L2
Col-1393	88.1	85.5	1442	1459
Col-1439	86.1	85.6	1003	1519
Col-1449	86.8	83.8	1018	824
H-28	83.7	78.5	799	511
H-220	77.3	75.3	818	857
Criollo local	83.8	81.9	939	1223

PORGR=Porcentaje de grano, RENDGRHA=Rendimiento de grano kg/ha, L1=San Juan Tzicatlacoyan y L2=San Martín de los Teteles

El tamaño del grano es una característica muy importante para los agricultores temporaleros, y para lograr un mayor tamaño y por lo tanto mayor rendimiento de grano, siempre seleccionan mazorca con olote delgado. Al respecto, en el presente trabajo los cultivares criollos presentaron mayor porcentaje de grano en comparación con los híbridos. En relación con el rendimiento conforme el ambiente es más restrictivo, el tamaño del grano debería ser más afectado que el del olote ya que este último se forma primero; en consecuencia, el porcentaje de grano disminuiría pero esto último no se obsrvó en la condición de suelo desfavorable (Cuadro 4).

El mayor rendimiento de los cultivares criollos, específicamente el de la Col-1393 y Col-1394, se asoció a su precocidad, a su mejor aspecto de planta y mazorca y a su mayor porcentaje de grano.

Los resultados de este trabajo evidencian la importancia de desarrollar el mejoramiento genético en áreas específicas tomando como base los cultivares criollos que ahí se cultiven; de esta forma se tendrá mayor posibilidad de incrementar los rendimientos y la producción de grano en las áreas de temporal de México.

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Formación y Prueba de Compuestos de Maíz en Nochixtlan, Oaxaca

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Abstract

The region of Nochixtlán is located in the northwest part of the state of Oaxaca, Mexico, in the area known as the *Mixteca Alta*. One hundred maize populations were collected and evaluated here, among which a pattern was detected in the number of days to female flowering. The populations were grouped into four categories (ultra-late, late, intermediate, and early); the best landrace cultivars were selected in each category and integrated into composites. These composites were tested at three sites during 1993 and 1995, using as checks the best commercial cultivars and the outstanding landraces in each maturity class. Yield potential differed between the test localities and was mainly limited by the availability of water. It was noted that, based on their yields, plant type, and ear, the composites *Mixteca Alta Precoz*, *Intermedio* and *Tardío* (early, intermediate and late) were outstanding at locations of low and medium yield potential. By contrast in the high-potential locality, the composites were surpassed by the commercial hybrids, but still outperformed the superior populations by category of earliness. The conclusion is that the composites Mixteca Alta Precoz, Intermedio and Tardío have outstanding potential for rainfed conditions in the Mixteca Alta region.

El área de Nochixtlán se localiza al noroeste del estado de Oaxaca, en la región conocida como Mixteca Alta. Es una zona básicamente de secano, donde los cultivos principales son el maíz, el frijol y el trigo. En 1986, cuando se realizó la recolecta y se evaluaron 100 variedades de maíz del municipio de Nochixtlán, Oaxaca se observó que el productor maneja un patrón de precocidad que ha formado a través del tiempo y en función de diversos factores ambientales, este patrón está constituido por cuatro categorías dependientes de los días a floración femenina: ultratardío o cajete, tardío, intermedio y precoz (Legaria et al., 1989). De cada categoría se definieron los cultivares criollos sobresalientes de acuerdo con modelo I de resistencia a sequía propuesto por Muñoz y Rodríguez (1988); así, se integraron en compuestos. En 1993 y 1995 se evaluaron esos compuestos en tres condiciones ambientales contrastantes, con la finalidad de conocer su potencial para ser incluidos en algún programa de mejoramiento genético de maíz de temporal. En esta evaluación se incluyeron como testigos los mejores criollos de cada categoría y los cultivares comerciales recomendados para la región de Nochixtlán.

Materiales y Métodos

Material genético

En 1993 se utilizaron los compuestos Cajete (CCAJ), Mixteca Alta Tardío (CMAT), Mixteca Alta Intermedio (CMAI) y Mixteca Alta Precoz (CMAP); los testigos fueron los híbridos comerciales H-135 y H-311; los híbridos generados por el Colegio de Postgraduados para el Valle de Puebla CPVH-1, CPVH-2 y CPVH-3, las colecciones sobresalientes de los precoces Col-519 y Col-568 (Ortiz y Muñoz, 1990), dos generaciones avanzadas del H-135 (GA135a y GA135b) y dos del H-311 (GA311a y GA311b). En 1995 no se utilizaron los híbridos generados por el Colegio de Postgraduados, las generaciones avanzadas ni el CCAJ, pero se incluyeron la colecta sobresaliente de tipo intermedio Col-448 y la de tipo tardío Col-554.

Localidades de evaluación

En 1993 se instalaron los experimentos en las comunidades de La Luz Etlatongo (Loc 1) y San Juan Sayultepec (Loc 2), el 12 y 10 de mayo, respectivamente. En 1995 el ensayo se efectuó en San Mateo Etlatongo (Loc 3) y la siembra se realizó el 19 de abril.

Labores culturales y riegos

En todas las localidades se barbechó y surcó antes de la siembra. Para combatir las arvenses se hizo una aplicación de Hierbamina y Gesaprim (1 L y 1.5 kg por ha) antes de la emergencia, se realizaron dos escardas, excepto en la Loc 2 donde no se efectuaron por el exceso de humedad. Los riegos se aplicaron siguiendo el criterio del productor cooperante; así, en la Loc 1 no se aplicó ninguno, por lo cual el cultivo se desarrolló con largos períodos de sequía, en la Loc 2 se aplicaron dos riegos en las primeras etapas del crecimiento, y en la Loc 3 se aplicaron cuatro riegos en diversas etapas del cultivo.

Fertilización

Se utilizó la fórmula 110-70-00 N:P:K, se aplicó la mitad del nitrógeno y todo el fósforo en la siembra y el resto del nitrógeno en la segunda labor.

Parcela y diseño experimental

Cada parcela estuvo constituida por dos surcos de cinco metros cada uno, la distancia entre surcos fue de 80 cm y de 50 cm entre matas, con dos plantas por mata. El diseño experimental fue el bloques completos al azar en ambos ensayos con cinco repeticiones en el de 1993 y tres en el de 1995.

Toma de datos

Las variables que se consideraron fueron: rendimiento (REN), días a floración media femenina (DFF), altura de la planta (AP) y calificación de sanidad (CASA), de mazorca (CAMA) y de planta (CAPA).

Análisis estadístico

La información generada se sometió aun análisis de varianza y comparación de medias de los tratamientos utilizando la DMS, al nivel de 5% de probabilidad.

Resultados

El análisis de varianza para las variables estudiadas en las tres localidades, mostró que con excepción de CASA en la Loc 3 todas las características presentaron diferencias altamente significativas en las tres localidades (Cuadro 1). En la Loc 1 los materiales con mayor rendimiento fueron: GA311b, H-135, CMAT, CMAP, Col-568, CMAT y GA135a. El material más tardío fue el CCAJ con 127 d a floración femenina y el más precoz la Col-519 con 100 d. En calificación de sanidad sobresalieron CMAI y CCAJ, debido a su adaptación a la zona. La mayor altura de planta la alcanzó CCAJ, superando al resto significativamente (Cuadro 2).

La adaptación de un cultivar a una zona se refleja en la calificación de la planta y la mazorca. Así, también en la Loc1 CMAI, CMAT, H-135 y GA311b sobresalieron estadísticamente en ambas características. En contraste, únicamente CMAP, Col-568 y GA135a fueron superiores en CAPA y H-311 en CAMA. Al sumar las características favorables se tiene que el único compuesto con mayor puntuación (4) fue CMAI y los que le siguieron con 3 fue CMAT, H-135 y GA311b (Cuadro 2).

Por otro lado, en la Loc 2 el grupo con producción estadísticamente superior estuvo formado por los compuestos CMAT, CMAP y CMAI, los híbridos H-311 y CPVH-3 y la colecta Col-519. El menor rendimiento correspondió a CCAJ, que también resultó el más tardío para florecer y el de la planta de

Cuadro 1. Grados de libertad (G.L.), cuadrados medios (C.M.), nivel de significancia y coeficiente de variación (C.V.) para los caracteres de maíz evaluados en tres localidades (Loc 1, 2 y 3) de la región de Nochixtlán, Oaxaca, Méx.

	Rend. (gr/pl) [SAQ6]	DFF	AP (cm)	CASA	CAMA	CAPA
G.L.	14	14	14	14	14	14
Loc 1						
C.M.	399.61**	225.88**	2635.07**	0.81**	0.68**	0.46**
C.V.	27.1	2.6	9.4	16.0	10.5	9.8
Loc 2						
C.C.	944.49**	572.07**	4282.58**	0.52**	0.73**	1.33**
C.V.	26.4	3.5	6.9	14.7	12.3	16.5
G. L.	8	8	8	8	8	8
Loc 3						
C.M.	4104.24**	103.45**	792.45**	0.14NS	0.36**	0.52**
C.V.	17.0	2.8	5.4	11.3	9.6	12.7

** Significancia al 1% de probabilidad, NS: no significativo, REN: rendimiento; DFF: días a floración femenina, AP: altura de la planta, CASA, CAMA y CAPA: calificación de sanidad, mazorca y planta, respectivamente.

mayor altura. Los híbridos H-135 y H-311 y sus generaciones avanzadas fueron tardíos, los híbridos CPVH-1, CPVH-2 y CPVH-3 presentaron ciclo intermedio y los compuestos CMAT, CMAI y CMAP, como se esperaba, resultaron tardío, intermedio y precoz, respectivamente (Cuadro 3).

Cuadro 2. Características de 15 cultivares de maíz evaluados en La Luz Etlatongo, Oaxaca, Méx., durante 1993.

Cultivar	Rend. (gr/pl)	DFF	AP (cm)	CASA	CAMA	CAPA	CF
GA311b	57.7 a	111 i	126	2.9	3.2 a	2.7 a	3
H-135	55.5 a	111 i	150	2.8	3.5 a	2.8 a	3
CMAI	55.5 a	110 i	158	2.2 a	3.3 a	2.8 a	4
CMAP	53.2 a	102 p	130	3.2	3.1 a	3.4	2
COL-568	48.8 a	102 p	141	3.1	3.4 a	3.5	2
CMAT	48.5 a	111 i	146	2.9	3.3 a	3.0 a	3
GA135a	46.7 a	116 t	115	2.9	3.8	2.7 a	2
H-311	39.8	113 t	103	3.0	3.5	3.3	1
C-519	39.8	100 p	137	3.4	3.5	3.5	1
GA311a	38.3	116 t	123	2.9	3.8	3.1	-
GA135b	36.9	115 t	121	3.3	3.9	3.3	-
CCAJ	36.2	126 ut	206a	2.1 a	3.8	2.8 a	1
CPVH-2	35.5	111 i	140	3.3	3.9	3.4	-
CPVH-3	33.0	108 i	140	3.5	4.3	3.4	-
CPVH-1	31.5	108 i	141	3.3	4.3	3.3	-
DMS	15.0	6.5	29.9	0.6	0.5	0.4	

a: Grupo estadísticamente superior, con una probabilidad del 5%, CF: Características favorables, p: precoz, i: intermedio, t: tardío, ut: ultratardío, REN: rendimiento; DFF: días a floración femenina, AP: altura de la planta, CASA, CAMA y CAPA: calificación de sanidad, mazorca y planta, respectivamente.

Cuadro 3. Características de 15 cultivares de maíz evaluados en San Juan Sayultepec, Oaxaca, Méx. durante 1993.

Cultivar	Rend. (gr/pl)	DFF	AP (cm)	CASA	CAMA	CAPA	CF
CMAT	93.8 a	99 i	230	2.2 a	2.5 a	2.1 a	4
CMAP	90.5 a	87 p	201	2.9	2.4 a	2.8	2
CMAI	88.2 a	95 i	218	2.3 a	2.5 a	1.7 a	4
CPVH-3	80.0 a	96 i	209	3.0	3.5	3.1	1
H-311	76.0 a	109 t	185	3.0	2.8 a	1.7 a	3
C-519	73.7 a	89 p	194	3.4	2.9 a	2.6	2
C-568	71.9 a	93 p	199	2.8	2.7 a	2.6	2
CPVH-1	71.4 a	95 i	211	3.1	3.3	2.7	1
H-135	69.7	110 t	209	2.9	3.2	2.1 a	1
CPVH-2	68.1	101 i	202	3.0	3.2	3.2	-
GA311a	66.9	110 t	180	3.1	3.0	1.9 a	1
GA135a	57.0	113 t	203	3.1	3.4	2.3	-
GA311b	55.3	111 t	164	2.9	3.2	2.3	-
GA135b	52.9	113 t	183	3.1	3.4	2.2 a	1
CCAJ	47.7	124 ut	293 a	2.5 a	3.5	3.3	1
DMS	23.7	4.6	31.6	0.5	0.5	0.5	

a: Grupo estadísticamente superior, con una probabilidad del 5%, CF: Características favorables, p: precoz, i: intermedio, t: tardío, ut: ultratardío, REN: rendimiento; DFF: días a floración femenina, AP: altura de la planta, CASA, CAMA y CAPA: calificación de sanidad, mazorca y planta, respectivamente.

En cuanto a la sanidad (CASA), la que refleja la adaptación de las variedades a la zona, en la Loc 2 los compuestos CMAT, CMAI y CCAJ tuvieron la mayor calificación. En contraste, respecto a la mazorca (CAMA) los mejores fueron CMAP, CMAI, CMAT, H-135, Col-519 y Col-568 (Cuadro 3). De acuerdo con lo anterior, en la Loc 2 los compuestos con mayor número de características favorables fueron CMAI y CMAT, seguidos por el híbrido H-311.

En la Loc 3 se observó que las variedades con rendimiento significativamente mayor fueron los híbridos H-135 y H-311, el segundo grupo lo formaron CMAT y CMAI, todos ellos superaron al criollo del productor y a los criollos sobresalientes de cada categoría del patrón de precocidad. Los híbridos comerciales y el criollo resultaron tardíos, las demás variedades mantuvieron la precocidad que originalmente se utilizó para su clasificaron. En este caso, si AP se toma como medida de vigor se observa que los materiales tardíos e intermedios superaron significativamente a los precoces (Cuadro 4). Finalmente, en esta Loc 3 los híbridos H-311 y H-135, la colecta CMAT, y el criollo sobresalieron en CAMA, así como en CAPA sobresalieron el H-311, H-135, CMAI, C-554 y el criollo.

Discusión

En las dos localidades donde se realizaron las evaluaciones durante 1993 las variedades que resultaron sobresalientes en REN, CAMA, CAPA, CASA y número de características favorables fueron los compuestos CMAT, CMAI, CMAP, ya que superaron o igualaron a los híbridos comerciales H-135 y H-311, y a los otros cultivares de polinización libre. Cabe destacar que en las dos localidades, pero especialmente en la Loc 1, hubo limitación de agua en los períodos críticos del cultivo. Lo anterior podría ayudar a explicar el bajo rendimiento de los híbridos y la adecuada respuesta de los compuestos, los que fueron formados con cultivares sobresaliente de cada región, éstos últimos tienen mejor adaptación y respuesta a las condiciones adversas que frecuentemente enfrenta el productor de maíz en la zona de Nochixtlán, Oax. En contraste, a pesar de que los híbridos CPVH-3, CPVH-2 y CPVH-1 fueron generados para cultivarse en condiciones ambientales parecidas a la de Nochixtlán, obtuvieron las peores calificaciones para mazorca, planta y sanidad lo que da idea de su pobre adaptación a la región.

Es probable que CCAJ haya presentado los menores rendimientos, el mayor tiempo a floración femenina y altura de planta debido a que al modificarse la fecha y forma de siembra se alteró el microambiente para el cual fue adaptado, ya que este tipo de maíz ultratardío se siembra en febrero y marzo, sólo con humedad residual con el sistema denominado «cajete».

Por otro lado en la Loc 3 se presentaron las mejores condiciones de producción, por ello los híbridos comerciales obtuvieron los mayores rendimientos. Además, CMAT y CMAI superaron a las criollos sobresalientes de cada una de las categorías de precocidad, por lo que son materiales adecuados para iniciar un programa de selección. Otro aspecto sobresaliente es que en la Loc 3 en donde hubo condiciones favorables, los cultivares tardíos destacaron, pero en la Loc 2, con menor potencial de producción, los intermedios fueron los de mayor rendimiento. Por último, en la Loc 1, con las peores condiciones de cultivo, los cultivares intermedios y precoces tuvieron mayor número de características favorables e igualaron o superaron a los comerciales. Lo anterior coincide con lo expuesto por Muñoz (1991), respecto a la existencia en México de una gran cantidad de nichos ecológicos en donde se adaptan solo algunos cultivares obtenidos para los grandes valles.

Cuadro 4. Características de nueve cultivares de maíz evaluados en San Mateo Etlatongo, Oaxaca, Méx., durante 1995.

Cultivar	Rend. (gr/pl)	DFF	AP (cm)	CASA	CAMA	CAPA	CF
H-311	188.1 a	96 t	220 a	2.2	1.7 a	1.7 a	4
H-135	153.3 a	94 t	242 a	2.2	1.5 a	1.7 a	4
CMAT	115.6	94 t	231 a	2.2	2.0 a	2.5	2
CMAI	105.0	87 i	223 a	2.2	2.2	2.3 a	2
CR	90.6	93 t	250 a	2.3	2.0 a	2.0	3
CMAP	87.6	80 p	200	2.5	2.3	2.7	-
C-519	86.5	82 i	205	2.7	2.2	2.8	-
C-554	83.0	94 t	225 a	2.7	2.5	2.2 a	2
C-448	82.5	90 t	236 a	2.5	2.5	2.5	1
DSH	54.5	7.4	35.3	0.8	0.6	0.8	

a: Grupo estadísticamente superior, con una probabilidad del 5%, CF: Características favorables, p: precoz, i: intermedio, t: tardío, ut: ultratardío, REN: rendimiento; DFF: días a floración femenina, AP: altura de la planta, CASA, CAMA y CAPA: calificación de sanidad, mazorca y planta, respectivamente.

Conclusiones

Los compuestos CMAT, CMAI y CMAP formados con las poblaciones sobresalientes de cada una de las categorías del patrón de precocidad en Nochixtlán, Oaxaca, son una buena opción para iniciar un proceso de mejoramiento de maíz para temporal el la zona. Para generar variedades mejoradas para temporal se debe considerar el patrón de precocidad y las diferentes condiciones en las cuales el agricultor produce maíz.

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Maize Germplasm Conservation Within Rainfed Agriculture: A Proposal

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Abstract

Plant breeding programs in water stressed and nutrient-limited environments generally have scarce resources for seed storage and germplasm conservation. This study was carried out to evaluate some locations and containers that could allow satisfactory germplasm conservation without great investment. Seeds of two maize landraces (Chapingo accessions 448 and 519) were packed in paper bags, metal cans, plastic bottles and laminated aluminum foil packets. They were stored at Huetamo, Mich. (427 masl), Chapingo, Mex. (2250 masl), Tecámac, Mex. (2298 masl) and San Juan Tetla, Pue. (3300 masl). A refrigerated room (-1 to 5 °C and 36% R.H.) was used as a reference environment. Locations were more suitable for seed storage as altitude increased. Paper bags were the least suitable container. The landraces differed for seed germination. Storage in the warm climate of Huetamo in paper bags was the worst combination for preserving seed viability.

Modern agriculture is associated with a trend towards the disappearance of landraces. However, the genetic resources that remain may have important unutilized characteristics of tolerance to environmental stresses, resistance to diseases and nutritional quality. In terms of production, some landraces are sometimes more important than the available improved varieties (Muñoz, 1991). Consequently, an economical system to preserve seed of collected germplasm by using low cost facilities capable of being used at the village level is a high priority. IBPGR (1985) stated that it is possible to take advantage of natural facilities such as natural caves, mines and high altitude sites, in order to diminish the need for refrigeration during seed storage. The Nordic genebank in Svalbard, Norway, is an example of the use of natural facilities. There, seed is stored in glass ampoules arranged in a steel container that is introduced into the gallery of a depleted coal mine, where temperature ranges between -3 and 4 °C. Another example is the facility operated by the Qinghai Academy of Agricultural Sciences Xining in Qinghai, P.R. China. In this case, seed is stored at ambient temperature at 2295 masl at a latitude of 37°N. After drying, the seed is packed and sealed in steel boxes. Under this system, germination of pea and broad bean seeds was not reduced appreciably after 11 and 15 years, and germination of wheat was shown to still be 66% after 16 years in storage. Moisture-resistant containers help maintain seed viability and vigor (Ching and Abu-Shakra, 1965). If seed is kept in containers made of porous material it soon absorbs humidity and viability declines (Bass et al., 1961). This study was carried out in order to identify inexpensive storage environments and container types that allow germplasm preservation.

Materials and Methods

Seed of two maize landraces, Chapingo accessions 448 and 519, from the Mixteca region, Oaxaca, Méx., were evaluated. Seed of both accessions was harvested at Montecillo, México, in November 1990. From harvest until August 1992, when the experiment began, the seed remained under normal room conditions (ambient temperature and humidity) at Chapingo. Samples of this seed were then moved to four locations in Mexico, differing in altitude and hence mean temperature, and stored under normal room conditions at each location (Table 1). The cold room of the Universidad Autónoma de Chapingo's genebank was used as a reference environment, where temperatures ranged from -1 °C to 5 °C, with 36% relative humidity.

Four types of containers were tested: mono-layer paper bags (like those used for controlled maize pollination and made of 0.13 mm thick paper), 1.5 l plastic bottles with screw caps (made of PET, polyethylen tereptalate, and impermeable to water and carbon dioxide), 1.5 l metal containers (closed by means of pressure applied to the lid), and laminated aluminum foil packets made of an outer polyester layer, a middle laminated aluminum layer, and an inner polyethylene layer (the polyethylene layer is sealed by heat and prevents entry of moisture, the aluminum layer provides a further barrier against moisture and radiation, and the polyester layer protects the aluminum layer against injury and oxidation) (Cromarty et al., 1985). One kilogram of seed was stored in each container. The design used was a RCBD factorial (two seed sources x four containers) design, with four replications at each site.

In August 1992 the initial status of the seed was evaluated, and this was repeated after 7 and 12 months of storage. Germination tests were performed in a controlled environment chamber at 25°C under fluorescent light. Samples of 25 seeds per experimental unit per replicate were placed on damp paper towels that were then rolled up and positioned vertically in plastic bags in the chamber for 7 d. Germination percentage was recorded as percent normal seedlings according to the International Seed Testing Association (1976) standards: normal seedlings are those that possess radicle, epicotyl and hypocotyl, all well developed and without injury; in addition, the primary leaf must be well developed and emerging from the coleoptile.

Table 1. Storage locations in Mexico and their characteristics.

Site	Latitude (N)	Longitude (W)	Altitude (masl)	Average temp. (°C)	Annual rainfall (mm)
Huetamo, Mich.	18° 37'	100° 54'	427	29.2	809
Chapingo, Méx.	19° 29'	98° 53'	2250	15.0	645
Tecámac, Méx.	19° 35'	98° 55'	2298	15.0	563
SJ Tetla, Pue.*	18° 10'	98° 39'	3300	8.4	1216

Source: García, 1981.

* This site is near the Iztaccíhuatl volcano.

Table 2. Percent seed germination of two maize landraces as affected by storage site and storage container.

	Months				
	0	7	12		
Germination %	88.5 a	83.0 b	81.7 b		
	Location				
	Genebank	SJ Tetla	Tecamac	Chapingo	Huetamo
Germination %	88.6 a	88.0 ab	87.2 ab	85.1 b	73.1 c
	Containers				
	Aluminum packets	Metal cans	Plastic bottles	Paper bags	
Germination %	86.7 a	87.1 a	87.0 a	76.8 b	

Means with the same letter within each treatment factor are not significantly different (Tukey's mean separator test, P≤0.05).

Results

An important decrease in germination took place between 0 and 7 months of storage (Table 2). Storage at the low elevation site, Huetamo, in paper bags caused the greatest loss in seed viability. The landraces showed significant differences in percent germination. At the start of the experiment accession 448 had 83% germination while that for accession 519 was 94% ($P < 0.05$). Seven months after the experiment began accession 448 had a germination rate of 79% while accession 519 had 90% germination.

Interactions with storage time

A marked reduction in germination was observed at Huetamo from 0 to 7 months (Fig. 1). At Chapingo germination was also significantly reduced during the period 0 to 12 months, but the decline was small compared with Huetamo. Germination of seed stored at the genebank, San Juan Tetla and Tecámac remained almost unchanged through the storage period. Seed stored in impermeable containers (i.e., aluminum packets, metal cans and plastic bottles) did not show a significant reduction in germination throughout the storage time. In contrast there was a large reduction in germination in the initial 7 months of seed stored in paper bags (Fig. 2).

Genotype x location and container interactions

The interactions of locations or containers with genotypes for germination percentage were not significant. When maize seed was stored in the high altitude locations of Chapingo, Tecámac and San Juan Tetla, differences among containers were not significant. At Huetamo moderately reduced germination was associated with storage in impermeable containers, while storage in paper bags was associated with large reductions, as germination fell to around 40% after 12 months of storage (Fig. 3). Storage in paper bags was a totally ineffective storage method in this environment.

Discussion

The higher the altitude and the cooler the environment, the better the conditions for germplasm storage (Table 2). Germination levels at the two highest locations, San Juan Tetla and Tecámac, were not significantly different from that observed at the genebank. The existence of sites that performed as well as the genebank indicates the feasibility and opportunity for storage offered by high altitude, cool sites.

Seed from the two landraces was produced in the same environment, thus differences in germination are likely to be the result of genetic causes. These differences in seed quality indicate that the genetic constitution, even within species, is an important determinant of their potential for conservation. Differences among varieties within species have been previously reported by James et al. (1967), Roos (1984) and Rincón (1989).

Impermeable containers seem to be the most economic way to preserve seed quality, especially when their use is contrasted with the cost of humidity control in a conventional genebank facility. Similar results were obtained by Mumford and Freire (1982), working with rice. The container that best maintained viability, after 21 months of storage, was a laminated aluminum foil packet (88%), whereas paper and cotton bags resulted in poor germination (55 and 53% respectively). Under cool and relatively dry storage conditions, the importance of the container is much reduced. Harrington (1972) stated that the beneficial effects of impermeable containers on the conservation of seed quality is enhanced under adverse storage conditions. This was also exemplified by Chang and Verena (1983), using rice seed stored under ambient temperature. They observed that viability expired in 9 months when seed was kept in paper bags, but was maintained beyond 36 months in laminated aluminum containers. Impermeable seed containers, preferably those such as screw-top bottles commonly available in villages, offer good possibilities for safe seed storage in most environments, providing the seed is well-dried prior to sealing in the container.

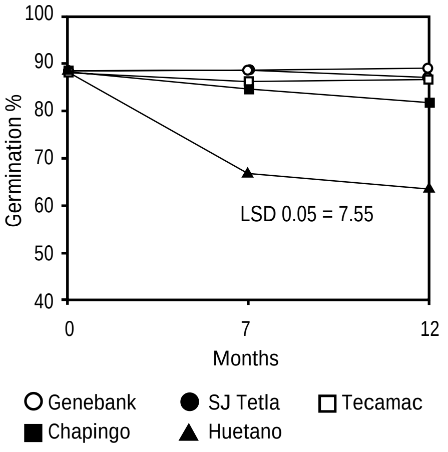

Figure 1. Germination of seed stored in different environments versus storage time.

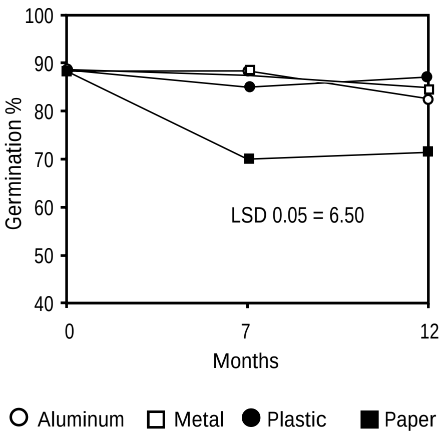

Figure 2. Germination of seed stored in different containers versus storage time.

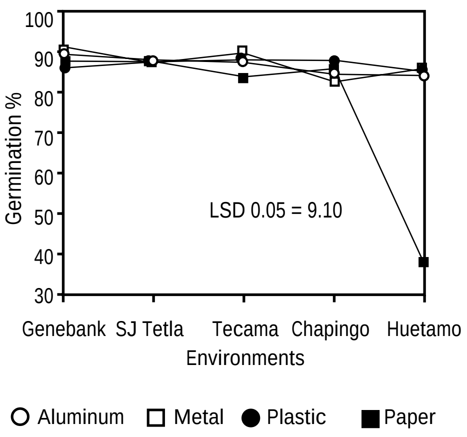

Figure 3. Germination of seed stored in different containers and different environments.

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Performance of Promising Tropical Late Yellow Inbred Lines Under Water Stress Conditions

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Abstract

Drought tolerance is an important and challenging breeding goal in the lowland tropics. CIMMYT's Lowland Tropical Maize Subprogram has developed a tremendous array of inbred lines with different attributes. A group of 121 promising late-yellow inbred lines was evaluated under drought at Tlaltizapán, México during the winter 1994/1995 season. They were developed from different CIMMYT populations by continuous selfing, using high plant densities and non-stressed water conditions during the inbreeding process. The objective was to assess genetic variation within this set of lines. In turn, selected lines could be used in developing source germplasm, new inbred lines through recycling, and developing specific hybrid combinations. Differences ($P \leq 0.01$) were detected among lines for all traits measured. Mean grain yield ranged from 4.7 to 0.2 t ha^{-1}. For anthesis-silking interval (ASI), the range was from 6.5 to -4.5 days. The highest number of ears plant^{-1} was 1.6, while the lowest was 0.3. Ear aspect rating ranged from 4.8 to 1.2 (1-5 score, 5 = excellent). Phenotypic correlations indicated that an increase in grain yield under drought stress is associated with a reduction in ASI and barrenness, and better ear aspect. More than 20 lines were identified that had superior performance under drought stress conditions

Drought is a limiting factor in most maize producing areas of the lowland tropics. Over the past decade, CIMMYT's Lowland Tropical Maize Subprogram has developed an array of inbred lines using different breeding procedures. At present, the germplasm available from the subprogram includes lines extracted from original source populations, inbreeding tolerant populations, and recycling elite lines within and between heterotic populations. These lines were developed by continuous selfing, using high plant densities and non-stressed water conditions during the inbreeding process. Many promising lines have undergone at least eight generations of selfing, are quite vigorous, and yield 3 to 5 t ha^{-1} under normal water regimes. The subprogram emphasizes the evaluation of advanced promising inbred lines for various relevant stresses such as drought, low N, soil acidity, disease and insect pressure.

The objectives of this particular study were to compare the performance of promising tropical late yellow inbred lines originating from different source germplasm under drought stress conditions, to understand the association of yield with secondary traits under drought stress conditions, and to identify superior lines for further use in the ongoing germplasm and hybrid development program.

Materials and Methods

Genetic materials

One hundred and twenty-one tropical late-yellow lines with varying inbreeding levels and derived from different source germplasm were used in this study (Table 1). These lines came from original source populations, inbreeding tolerant populations, and populations generated by recycling of elite lines within and between heterotic groups. The lines were developed by continuous selfing, using high plant densities and well-watered conditions during the evaluation and inbreeding.

Experimental procedures and data collection

The experiment was conducted during the rain-free winter season (December-March) of 1994/95 at the CIMMYT experimental station in Tlaltizapán, Mexico. Moisture stress was managed by irrigation withdrawal achieving an intermediate drought stress (water stress during late flowering and throughout grain filling). Plots consisted of one 2.5 m row, with a distance of 0.75 m between rows and 0.20 m between plants. Rows were overplanted and thinned after emergence to approximately 66,000 plants ha^{-1} .

Days from planting to anthesis (AD) and silking (SD) were calculated from the date on which 50% of the plants had begun shedding pollen or had silks emerged from the husk. Anthesis-silking interval (ASI) was obtained by subtracting AD from SD. Plant height (PH), measured from the base of the plant to the first tassel branch and ear height (EH), measured from the base of the plant to the insertion of top ear, were averaged for five competitive plants in each plot. EH/PH ratio was obtained by dividing EH by PH. Number of ears per plant (EPP) was determined by dividing the total number of harvested ears by the total number of plants. Grain yield, expressed at 155 g H_2O kg^{-1} was obtained from shelled grain. Ear aspect rating (EARASP) was determined by using a 1-5 scale, where 1= excellent and 5 = poor.

Design and statistical analysis

The trial contained 121 entries, and was arranged in a square lattice design with two replications. Analyses of variance were performed using the SAS MIXED procedure (SAS Institute, INC., 1992). Simple phenotypic and genotypic correlations were estimated using the SAS VARCOMP procedure.

Results and Discussion

Analyses of variance (Table 2) indicated highly significant ($P \leq 0.01$) effects due to genotypes for all traits. Mean ASI was 1.32 days (Table 2), suggesting that drought stress was not very severe at flowering stage. Mean grain yield ranged from 4.7 to 0.2 t ha^{-1}. For ASI, the range was from 6.5 to -4.5 days. The highest number of ears plant^{-1} was 1.6, while the lowest was 0.3. Ear aspect rating ranged from 4.8 to 1.2. Significant differences and a wide range of values indicate that there is useful variation among this group of promising tropical late yellow lines for yield and secondary traits under drought stress conditions.

Grain yield correlated negatively with ASI and EARASP, and positively with EPP (Table 3). ASI was associated negatively with EPP, and positively with EARASP. In other words, an increase in grain yield under drought stress is associated with a reduction in ASI and barrenness, and better ear aspect. These results confirm previous data where ASI and EPP have been reported as important secondary traits when selecting for drought

Table 1. Origin of late yellow lines included in this study.

Source†	Number of lines	Grain texture
Pop. 24	7	Semident
Pop. 24 STE	18	Semiflint/Flint
Line recycling, Pop. 24	6	Dent
Line recycling, Pop. 24 STE	6	Semident
Pop 27	11	Flint
Line recycling, Pop. 24 x Pop.27	7	Flint
Pop. 28 TSR	18	Semident/Flint
Pop. 28 DMR	4	Semident
Pop. 36	7	Dent
Sint. Am. TSR	33	Semident/flint
Line recycling, Pool 22	4	Semident/Semiflint
Pop. 79	1	Flint

† STE refers to a population selected for tolerance to inbreeding.

Table 2. Phenotypic and genotypic correlations† among traits measured on tropical late yellow inbred lines grown at Tlaltizapán, Mexico during 1995 under water stress.

	EH/PH	ASI	Yield	EPP	EARASP
EH/PH	1.00	0.08	-0.04	-0.11	0.05
ASI	0.19*	1.00	-0.36**	-0.31**	0.30**
Yield	0.02	-0.45**	1.00	0.65**	-0.74**
EPP	-0.21*	-0.50**	0.82**	1.00	-0.49**
EARASP	-0.01	0.36**	-0.78**	-0.71**	1.00

† Values above the diagonal refer to phenotypic and values above the diagonal to genotypic correlations, respectively.

*,** Significant at 0.05 and 0.01 levels of probability, respectively.

tolerance and yield potential in tropical maize (Bolaños et al., 1993; Edmeades et al., 1995).

The best performing 20% of the lines were selected using a combined index and eyeball selection criteria. This selected fraction has greater yield, less barrenness, shorter ASI, and better ear aspect than the overall mean (Table 3). For these superior 23 lines, grain yield averaged 3.4 t ha^{-1}. Outstanding inbred lines known as CIMMYT maize lines (CMLs), made available in recent years by CIMMYT to research partners, were among the superior lines; specifically, CMLs 20, 27, 29, 31, 52, 282, and 298. The other high yielding but unreleased lines were evaluated in testcrosses during 1995, and preliminary results indicate good combining ability for some of them (data not presented). Populations 24 and 27 appear to be good sources for extracting inbred lines with drought tolerance.

More than 20 lines (including seven CML's) were identified that have superior performance under drought stress conditions. These lines could be used in developing source germplasm, new inbred lines through recycling, and developing specific hybrid combinations to help alleviate drought problems in the lowland tropics.

Table 3. Mean for grain yield and other agronomic traits of top performing 23 late yellow tropical lines evaluated at Tlaltizapán, Mexico under water stress conditions.

Entry	Source	Yield (t/ha)	ASI (days)	EPP (ratio)	Ear asp. (1-5 score)	EH/PH (ratio)
CML52	Pob. 79	4.4	1.50	1.58	1.94	0.60
CML20	Pob. 24	4.7	0.00	0.96	1.54	0.57
112	Rec. Pool 22	4.4	0.00	0.96	1.32	0.54
18	Rec. Pob. 24 STE	4.0	0.00	1.04	1.21	0.51
117	Sint. Am.	4.1	2.00	1.15	1.69	0.52
7	Pob. 24 STE	3.4	-1.00	1.29	1.68	0.59
65	Pob. 36	4.0	0.00	1.20	2.08	0.60
CML27	Pob. 27	4.1	2.00	1.20	2.08	0.53
21	Pob. 24 STE	3.3	0.00	1.31	1.87	0.53
23	Pob. 24 STE	3.0	-2.50	0.96	1.33	0.53
CML31	Pob. 27	3.6	-0.50	1.05	2.07	0.52
79	Sint. Am.	3.0	0.50	0.92	1.81	0.46
CML29	Pob. 27	3.6	0.00	0.81	2.18	0.55
CML282	Rec. Pool 22	2.9	0.00	0.92	1.69	0.48
48	Pop. 28 TSR	2.8	0.50	1.05	1.71	0.53
10	Pob. 24	3.2	2.00	0.96	1.58	0.54
64	Pop. 36	2.9	0.50	0.98	2.17	0.52
40	Pob. 27	3.0	0.00	0.92	2.05	0.56
38	Pob. 27	2.8	-2.00	0.96	2.52	0.59
20	Pob. 24	3.0	2.00	1.04	1.70	0.57
28	Rec. Pob. 24 STE	2.5	0.00	0.92	1.77	0.52
113	Rec. Pool 22	2.8	0.00	0.96	2.79	0.48
CML298	Sint. Am.	2.7	0.00	0.96	2.48	0.52
Mean of 23 lines		3.4	0.22	1.05	1.88	0.54
Mean of 121 lines		2.1	0.89	2.70	1.32	0.55

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Comportamiento de Líneas S_1 de Maíz Bajo Condiciones de Humedad Restringida

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Abstract

This research was carried out during 1991 in two test environments under irrigation and rainfed conditions in the state of Coahuila, Mexico, to evaluate using two testers groups of S_1 lines from the "NEPO" population, known for its high grain lysine content, and to assess line performance under a system of irrigation-drought. A total of 133 test crosses were made and compared to six hybrids (five experimentals and one commercial), using a random block design and two replications per environment. The experimental units comprised rows 4.4 m long, with a distance of 0.8 meters between rows. Results showed that test crosses surpassed the best check by 7% and 11% for ear yield under irrigation and drought, respectively. Yields under the two conditions ranged from 7.70 to 0.84 t ha^{-1} and 7.06 to 1.49 t ha^{-1}, respectively. An outstanding group of S1 lines was identified for yield (4-5 t ha^{-1}), general combining ability and other agronomic traits in both environments. However, only four lines were selected based on having a drought index > 1, which indicates their adaptability for environments with low rainfall. We conclude that the irrigation-drought system was efficient for selecting S_1 lines and that Tester 1 (Compuesto Norteño C_2) was the best at discriminating among lines. With the selected genotypes, we are in a position to obtain better hybrids and better nutritional quality than with the commercial hybrid "AN-310," which is widely accepted in various rainfed zones in the country.

El maíz constituye la fuente principal de hidratos de carbono (energía) y, en menor medida, el complemento proteico de la dieta del mexicano. Sin embargo, la calidad de sus proteínas se altera con la modificación de la proporción de sus componentes, tales como la lisina y el triptofano, aminoácidos esenciales para el hombre y animales no-rumiantes. Considerando lo anterior y la gran cantidad de superficie de temporal dedicada a este cultivo, el Instituto Mexicano del Maíz (IMM) de la Universidad Autónoma Agraria Antonio Narro inició en 1978 un programa de mejoramiento integral, tendiente a obtener híbridos y variedades con alta calidad nutritiva del grano, alto potencial de rendimiento y tolerancia a la sequía en zonas de temporal. Estudios experimentales han demostrado que la incorporación del gen mutante opaco-2 incrementa significativamente el contenido de lisina y triptofano (Nelson et al., 1965; Beeson, 1966). En este contexto, el objetivo de este trabajo fue conocer la respuesta agronómica, de líneas S_1 de maíz evaluadas con riego y sequía utilizando dos probadores con adaptación a condiciones deficientes de humedad.

Materiales y Métodos

La presente investigación se realizó durante 1991 con líneas S_1 derivadas de la población NEPO (Norteño-enano-precoz-opaco). Tal población incluye colecciones de maíces criollos precoces, con adaptación a los estados de Coahuila, Durango, Nuevo León, San Luis Potosí y Zacatecas de la República Mexicana; la fuente de enanismo provino de la población Selección Super Enana del IMM, y la del gen opaco-2 de una población del CIMMYT. Posterior a un proceso sucesivo de recombinación y selección hacia la conjunción de precocidad, enanismo, espiga chica, hojas erectas y grano opaco modificado, se inició un proceso de mejoramiento cíclico de generación de líneas, con alto contenido de lisina en el endospermo; la evaluación de la lisina se realizó con el método microbiológico MCG-99 (Vega, 1984). Las líneas S_3 sobresalientes fueron agrupadas por tipo de madurez (en cuatro estratos: de mayor a menor precocidad) recombinando por dos ciclos, e iniciando la obtención de líneas S_1 que fueron cruzadas con dos probadores (P1 = Compuesto Norteño C2 - Sint - 2 y P2 = VS - 201 - 191 x VS - 201 - 8) generando un total de 133 cruzas de prueba. La evaluación de las cruzas incluyó seis híbridos como testigos. Los materiales se evaluaron en dos localidades, denominadas: General Cepeda y Parras de la Fuente, ambas en el estado de Coahuila, México; la primera localidad se caracteriza por una precipitación media de 500 mm y temperatura media anual de 18 ºC, y la segunda por una precipitación media de 357 mm y temperatura media anual de 16 ºC. Es conveniente indicar que en la localidad de General Cepeda se practicó la evaluación en condiciones de riego y en la de Parras en condiciones de temporal. El diseño experimental utilizado fue un bloques al azar con partición de efectos con dos repeticiones por ambiente. Cada parcela consistió de un surco de 4.6 m de largo con 21 plantas y 0.22 m de separación entre ellas, la distancia entre surcos fue 0.80 m; así, la densidad fue 57,000 plantas ha^{-1}. Los caracteres evaluados fueron: altura de planta y mazorca, acame de raíz y tallo, mazorcas podridas y rendimiento de mazorca con 15.5% de humedad. Para una mejor discriminación de las líneas S1 se evaluó la aptitud combinatoria general (ACG) y el índice de sequía (IS), siguiendo la metodología propuesta por Fischer et al. (1984).

Resultados

El análisis de varianza mostró que las cruzas de prueba, tanto en el ambiente de riego como en el de temporal, presentaron gran variabilidad genética dentro y entre los grupos de las líneas S_1 para el rendimiento de mazorca y altura de planta, y en otros datos no mostrados. Así, en promedio algunas cruzas de prueba fueron 7% y 11% superiores al mejor testigo en la producción de mazorca bajo riego y temporal, respectivamente. Los intervalos de rendimiento de mazorca en los ambientes señalados fueron de 7.7 a 0.8 t ha^{-1} y de 7.1 a 1.5 t ha^{-1}, respectivamente. Es conveniente indicar que algunas líneas S_1 en combinación con el probador 1 (ciclo mejorado del Compuesto Norteño) estuvieron entre las más productoras y homogéneas en ambos ambientes de prueba con rendimiento de mazorca superior a las 6 t ha^{-1}.

El rendimiento de mazorca en el ambiente de riego de la mayoría de las cruzas fue superior a la media de los testigos hasta en 9%. Mientras que para el ambiente de temporal sólo el grupo I, dentro de probador 1 (5.4 t ha^{-1}) excedió 26% la media de los testigos (4.3 t ha^{-1}) (Cuadro 1). Sobresale el hecho de que en promedio, el probador 1 (Compuesto Norteño) fue superior al probador 2 (VS-201-191 X VS-201-8) ya que el primero mostró mayor rendimiento de mazorca tanto con riego como en temporal. Lo anterior muestra la alta posibilidad de liberar en corto tiempo materiales que respondan adecuadamente en ambos ambientes, temporal y riego; en el primer caso, algunas cruzas de prueba mostraron gran superioridad, con rendimiento hasta 70% mayor que el híbrido AN-310 (utilizado como un testigos, con rendimiento promedio de 4.1 t ha^{-1}, en temporal y recomendado ampliamente para áreas temporaleras semiáridas de México).

El porcentaje de mazorcas podridas fue mayor en condiciones de temporal; sin embargo, la mayoría de las cruzas de prueba mostraron menores porcentajes respecto a la media de los testigos. En general, la altura de planta fue del orden de 1.5 m, valor deseable para maíces temporaleros; la heterogeneidad

Cuadro 1. Altura de la planta, porcentaje de mazorcas podridas y rendimiento de mazorca promedio de las líneas (L) S_1 de maíz en combinación con dos probadores (P) bajo riego y sequía.

		Altura de planta (cm)			Mazorcas podridas (%)			Rendimiento de mazorca (t ha^{-1})		
Fuente	Grupo	Riego	Sequía	Combinado	Riego	Sequía	Combinado	Riego	Sequía	Combinado
L/P1		166	157	160	29	35	31	4.97	4.41	4.65
	GI	162	170	152	23	29	34	4.96	5.37	4.23
	GII	160	138	149	37	39	34	5.08	3.62	4.16
	GIII	169	150	155	28	44	36	4.60	3.82	4.35
	GIV	174	158	150	26	34	44	4.85	3.69	4.78
L/P2		159	142	149	29	39	34	4.91	3.63	4.30
	GI	158	135	152	20	36	35	5.26	3.90	4.30
	GII	159	139	150	52	45	34	4.86	3.86	4.22
	GIII	164	147	155	20	39	39	4.39	3.62	4.70
	GIV	162	148	153	16	35	36	4.30	3.14	4.45
Cruzas		162	149	155	25	37	32	4.56	4.02	4.47
Testigos		164	141	152	28	47	39	4.79	4.27	4.59

exhibida por las cruzas bajo los dos ambientes de prueba permiten establecer que bajo temporal la altura media de las cruzas tendió a incrementar (1.4 a 1.5 m); bajo riego la situación fue inversa (1.62 m a 1.64 m).

Entre las líneas seleccionadas para riego sobresalió la línea (NP S3 GII)F2-6 por su rendimiento (6.2 t ha^{-1}) y ACG (1.23). Además, también las líneas (NPS3GII)F2-13 y (NPS3G11)F2-4 mostraron valores sobresalientes de rendimiento de mazorca y ACG. El resto de las líneas tuvieron valores de ACG inferiores a la unidad y sólo medianos rendimientos de mazorca. El promedio de mazorcas podridas, de este grupo de líneas fue 22%, aunque dos de ellas presentaron valores de solo 14%. Para reducir el número de mazorcas podridas, deberá dársele mayor atención a la cobertura de la mazorca, lo cual probablemente se traduciría en un mayor rendimiento y sanidad del grano. La mayoría de las líneas tuvieron valor bajo de acame de raíz (2% en promedio) en contraste con los valores de acame del tallo (10%) (Cuadro 2). Finalmente, puede decirse que la mayoría de las líneas tuvieron portes aceptables tanto para altura de planta como de mazorca.

Aunque los rendimientos de mazorca de las líneas S$_1$ bajo condiciones de temporal fueron ligeramente inferiores al producido con riego, podría considerarse aceptable, ya que todas tuvieron rendimiento de mazorca superior a las 5 t ha^{-1}, a pesar de que sólo una línea tuvo un valor de ACG mayor a la unidad. Sin embargo el porcentaje de mazorcas podridas resultó elevado en la mayoría de las líneas respecto al obtenido con riego, ya que bajo temporal la pudrición se elevó hasta 50% sobre la media de las líneas seleccionadas (Cuadro 3). Posiblemente, este fue un factor importante para la reducción del potencial de rendimiento de las líneas evaluadas.

En temporal el daño promedio por acame de raíz fue significativamente mayor al observado con riego (2 y 14%, respectivamente). Sin embargo, hubo líneas con valores aceptables que podría considerarse de valor por sus otros atributos. Las plantas y mazorca, resultaron de porte intermedio pero de menor estatura, respecto al de las que crecieron con riego, lo que indica que la humedad jugó un papel importante en la

Cuadro 2. Líneas seleccionadas para riego por su aptitud combinatoria (ACG) y sus caracteres agronómicos.

	Altura (cm)		Acame (%)		Mazpod	Rendmaz	
Líneas	Pta.	Maz.	Raiz	Tallo	(%)	(t ha^{-1})	ACG
(NP S3 GII)F2-6	154	81	0	18	23	6.23	1.23
(NP S3 GI) F2-13	164	76	0	15	22	6.21	1.22
(NP S3 GI) F2-4	167	77	7	5	22	6.20	1.20
(NP S3 GI) F2-32	165	87	4	17	14	5.86	0.86
(NP S3 GI) F2-17	171	79	1	21	19	5.82	0.82
(NP S3 GI) F2-18	153	71	3	2	25	5.79	0.79
(NP S3 GI) F2-56	166	80	0	8	19	5.69	0.69
(NP S3 GI) F2-10	173	88	3	1	14	5.66	0.66
(NP S3 GII) F2-60	140	74	0	9	37	5.52	0.52
(NP S3 GII) 64	165	88	1	6	25	5.51	0.52
Media	162	80	2	10	22	5.85	
Media General*	163	82	2	8	29	4.85	

Pta.: planta, Maz.: mazorca, Mazpod: mazorca podrida, Rend: rendimiento

* La media general en los cuadros 2-4 incluye 133 cruzas de prueba (61 líneas cruzadas con P1 y 72 con P2); el resto son 12 testigos expreimentales y comerciales, dando un total de 145 tratamientos.

Cuadro 3. Líneas seleccionadas para sequía por su aptitud combinatoria general (ACG) y caracteres agronómicos.

	Altura (cm)		Acame (%)		Mazpod	Rendmaz	
Líneas	Pta.	Maz.	Raiz	Tallo	(%)	(t ha^{-1})	ACG
(NP S3 GII)F2-70	171	91	23	11	40	5.66	1.02
(NP S3 GI)F2-4	140	67	8	6	22	5.53	0.89
(NP S3 GV)F2-24	152	72	6	15	26	5.51	0.87
(NP S3 GI)F2-26	147	78	18	7	34	5.49	0.85
(NP S3 GI)F2-10	164	82	16	5	26	5.46	0.82
(NP S3 GI)F2-39	158	82	13	14	35	5.29	0.65
(NP S3 GI)F2-6	147	76	16	6	31	5.23	0.59
(NP S3 GII)F2-64	154	77	22	12	35	5.16	0.52
(NP S3GII)F2-60	135	69	3	17	45	5.14	0.50
Media	152	77	14	10	33	5.39	
Media General	147	76	14	10	38	4.09	

Pta.: planta, Maz.: mazorca, Mazpod: mazorca podrida, Rend: rendimiento expresión de este carácter. Las cuatro líneas con comportamiento superior en los dos ambientes presentaron rendimientos de mazorca entre 5.9 y 5.3 t ha^{-1}, índice de sequía (IS) cercano a 1.0 y ACG entre 0.51 y 1.04, porcentaje de mazorcas podridas de 20 a 41%, lo cual puede ser un reflejo de la mala cobertura de la mazorca; el porcentaje de acame, tanto de raíz como de tallo, fue inferior a 13%; la altura de la planta y la mazorca fluctuaron entre 154 y 168 cm y 72 y 85 cm, respectivamente, por lo que podría considerarse de porte bajo (Cuadro 4).

Discusión

Los resultados de esta investigación mostraron que algunas cruzas de prueba son buenos candidatos para solucionar parcialmente, a corto plazo, algunos problemas de las áreas de temporal especialmente los que superan el rendimiento de mazorca de los testigos. Con lo anterior, se podría apoyar a las áreas agrícolas marginadas en donde se utiliza el maíz como parte importante de la alimentación, con híbridos o variedades de alto valor nutritivo. Lo anterior se basa en el hecho de que las líneas que se utilizaron en las cruzas de prueba, son resultado de un proceso de selección para incrementar el contenido de lisina, posterior a la introducción del gen opaco-2 en la población parental NEPO y su modificación por selección; resultados en este mismo sentido fueron documentados por Kovach et al. (1988).

Se seleccionaron dos grupos de líneas S_1 para cada uno de los ambientes de prueba; aunque los rendimientos más altos se obtuvieron con riego, hubo cuatro líneas S_1 con comportamiento semejante en ambos ambientes, y aunque su rendimiento de mazorca decreció ligeramente en temporal, todas rindieron más de 5 t ha^{-1}. Esto permite hipotetizar que la selección les ha permitido amortiguar los efectos del medio y expresar su potencial, independientemente del ambiente donde se desarrollen. Estos resultados son acordes con la afirmación de Muñoz (1978), quien menciona que el sistema riego-sequía es un procedimiento eficiente para detectar genotipos resistentes a condiciones de humedad deficiente.

Por otro lado Tatum (1954) señala que uno de los criterios para seleccionar formas tolerantes a sequía es el rendimiento sobresaliente de los genotipos en evaluación; lo anterior coincide con el rendimiento exhibido por las líneas S_1 de este estudio. También fue característico de las progenies S_1 su porte bajo en el ambiente de temporal, lo anterior coincide con lo observado por Rosic (1963).

En el sistema riego-sequía se seleccionaron sólo cuatro líneas S_1 que se consideran aptas para utilizarse en temporal de acuerdo con sus índices de sequía (0.96-1.03) y siguiendo el criterio de clasificación de Fischer, et al. (1984), quienes señalan que un índice de sequía > 1 indica que hay una resistencia relativa a sequía. Al respecto, Flores (1990) subraya la efectividad del sistema riego-sequía para seleccionar genotipos aptos para explotarse en condiciones de escasa precipitación pluvial.

De acuerdo con los resultados de esta investigación puede señalarse la posibilidad de generar en corto plazo híbridos y variedades que resulten superiores al híbrido AN-310, el cual se recomienda para diferentes regiones temporaleras del centro-norte de México.

Cuadro 4. Líneas seleccionadas bajo riego y sequía considerando su índice de sequía (IS), aptitud combinatoria general (ACG) y caracteres agronómicos.

	Altura (cm)		Acame (%)		Mazpod	Rendmaz		
Líneas	Pta.	Maz.	Raiz	Tallo	(%)	(t ha^{-1})	ACG	IS
(NP S3 GI)F2-4	154	72	7	6	26	5.86	1.04	0.96
(NP S3 GI) F2-10	168	85	9	3	20	5.56	0.74	1.04
(NP S3 GII) F2-64	159	83	12	9	30	5.34	0.52	1.01
(NP S3 GII) F2-60	137	72	2	13	41	5.33	0.52	1.00
Media	155	78	8	8	29	5.52		
Media General	154	78	8	9	33	4.45		

Pta.: planta, Maz.: mazorca, Mazpod: mazorca podrida, Rend: rendimiento

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Identification of Drought Tolerance in Elite Tropical Highland Maize Germplasm

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Abstract

Drought is extremely common in the tropical highlands. An estimated 2.8 million ha (81%) in this mega-environment is planted to maize genotypes that are usually or frequently subject to moisture stress. Most local varieties have an anthesis-silking interval (ASI) of 5-12 days under moderate stress and show very poor root development. Improved CIMMYT populations have much improved root strength and a reduced ASI -- both traits derived from temperate and subtropical germplasm. Besides improving yield, ASI and root strength, we are also developing populations that are considerably early maturing than the local varieties to escape drought stress. Farmers in the tropical highlands also plant deep (20-25 cm) to utilize residual moisture. Ability to emerge from deep planting is attributed to mesocotyl elongation. CIMMYT has developed elite highland germplasm with capacity to emerge from deep planting. Some highland germplasm (e.g., 'Michoacan 21') also possess a putative latente trait which results in a cessation of plant growth when drought stress occurs during the early vegetative stages, followed by enhanced recovery when the rains come. A breeding methodology developed for improving drought tolerance in lowland tropical germplasm at CIMMYT is currently being used in selected highland germplasm. A total of 100 S_1 *lines derived from tropical highland early white semi-dent germplasm were subjected to drought stress and the best and worst fractions, based on ASI, yield and other traits, were selected and used to form synthetics. Additionally, we have modified the interpopulation improvement scheme for Populations 901 and 902 (early white semi-dent) to incorporate selection for drought tolerance as well as for nitrogen use efficiency. Calera 9185, a drought tolerant variety, was formed based on evaluation of full-sib progenies from Pop. 85 under terminal drought at Calera, Zacatecas, Mexico, during 1991. The breeding strategy used in improving germplasm for the tropical highlands is to pyramid traits, such as drought tolerance and nitrogen use efficiency, along with other important resistance genes for biotic stresses in elite high-yielding germplasm.*

Drought is extremely common in the tropical highlands, with an estimated 2.8 million hectares (81%) of maize frequently subjected to moisture stress. Although most of these areas receive less than 1000 mm of rainfall annually (in fact, some receive as little as 350 mm per year), evapotranspiration is relatively lower under the cool temperatures of highland environments. The prevalent *criollo* (landrace) varieties have anthesis-silking intervals (ASI) of 5-12 d under moderate stress, and generally exhibit poor root development. Improved CIMMYT populations have been shown to have much better root strength and a reduced ASI -- both traits derived from temperate and subtropical germplasm (Eagles and Lothrop, 1994). Besides improving grain yield, ASI and root strength, we are also developing populations that are considerably earlier maturing than the local *criollos*, in the belief that these populations can be managed to escape drought stress by manipulating planting dates.

Farmers in the tropical highlands typically plant seed deep (20-25 cm) to utilize residual soil moisture. The ability to emerge from these depths is attributed to mesocotyl elongation. CIMMYT has developed elite highland germplasm with capacity to emerge from deep planting. Some highland germplasm (e.g., Michoacan 21) also possess a *latente* trait which results in a temporary slowing or cessation of plant growth when drought stress occurs during the establishment and vegetative stages, and this is followed by enhanced recovery when the rains come.

A breeding methodology developed for improving drought tolerance in tropical and subtropical germplasm at CIMMYT (e.g., Bolaños and Edmeades, 1993; Edmeades et al., 1997) is currently being used in selected highland germplasm. This paper discusses results from the screening of elite highland germplasm for drought tolerance as well as the incorporation of selection for drought tolerance in the breeding scheme used to improve two heterotic populations for the tropical highlands.

Screening of Elite Highland Germplasm for Drought Tolerance

Population 85 is an early-maturing semi-dent highland population with white grain color and good adaptation to the warmer highlands of Mexico. Ten superior full-sib families from this population were combined to form the experimental variety, Calera 9185, which performs well under drought stress. The ten families were selected in 1991 based on their performance in progeny trials at Calera, Zacatecas, Mexico, an environment with a short rainy season where naturally-occurring drought conditions are frequently severe (Luna and Gutiérrez, 1997). During the 1995 winter season 100 S_1 lines derived from tropical highland early white semi-dent germplasm (mainly Pop. 85) were evaluated under two levels of drought stress (severe and intermediate) at Tlaltizapán, Morelos, Mexico. In reality, because of variation in soil depth between the two selection blocks, the two water regimes resulted in almost identical stress levels. Two replicates were planted under each water regime in an alpha-lattice design. Data were recorded for the primary trait of shelled grain yield and for the following secondary traits: anthesis date, ASI, ears per plant, senescence rate, tassel size, and leaf rolling. For the last three traits, low scores indicated delayed senescence, small tassels or little leaf rolling, while large scores were indicative of rapid senescence, large tassels or strongly rolled leaves. The mean, standard error, coefficient of variation and range for each trait are presented in Table 1.

We observed large and significant ($P<0.05$) differences among families for grain yield and for each of the secondary traits (Table 1). This was likely due to the fact that little targeted selection for drought tolerance has occurred in the past in this elite germplasm. Grain yields averaged 1.41 (range 0.49 to 2.30) t/ha and 1.49 (range 0.18 to 3.20) t/ha under severe and intermediate stress regimes, respectively. For ASI, there was a range of 15 d and 16 d under the two irrigation regimes. Similar wide ranges were observed for the other traits under both stress levels. It was interesting to note that under intermediate stress the range of variation for the traits was higher than under severe stress, suggesting that for this population greater gains can be made in this environment.

A high positive correlation was observed between ears per plant and grain yield, though correlations between grain yield and other

Table 1. The performance of 100 inbred lines under severe and intermediate drought stress at Tlaltizapán during the 1995 winter season.

Trait	Mean	SE	CV (%)	Maximum	Minimum
Severe stress					
Anthesis date (d)	64.8	1.67	2.57	69.5	60.5
ASI (d)	3.07	2.51	81.7	13.0	-2.0
Ears/plant	0.91	0.12	13.2	1.15	0.55
Grain yield (t/ha)	1.41	0.38	26.8	2.30	0.49
Senescence†	6.71	0.69	10.3	8.37	4.42
Tassel size‡	3.21	0.89	27.8	4.94	1.42
Intermediate stress					
Anthesis date (d)	65.0	2.45	3.77	73.1	60.5
ASI (d)	4.27	2.99	70.1	14.5	-1.5
Ears/plant	0.80	0.20	24.85	1.29	0.26
Grain yield (t/ha)	1.49	0.63	42.17	3.20	0.18
Leaf rolling¶	2.66	0.91	34.15	5.02	0.91
Senescence†	5.02	1.72	34.21	8.38	1.87
Tassel size‡	3.00	0.89	29.81	5.01	1.00

† Score of senescence: 1 = 10% canopy senesced; 10 = 100% canopy senesced

‡ Score of tassel size: 1 = small tassel; 5 = large tassel

¶ Score of leaf rolling: 1 = leaves completely unrolled; 5 = leaves completely rolled secondary traits were generally weaker (Table 2). Large negative correlations were also observed between ASI and ears per plant and ASI and grain yield, especially under severe drought stress at flowering. Anthesis date and grain yield were negatively correlated; i.e., the early families were the highest yielding — very likely because they escaped the drought stress that was managed to coincide with flowering. The 10 best and 10 worst families for drought tolerance were selected based on an index involving the different traits. These families (S_1 lines) were intermated to form synthetics during the 1995 main season at El Batán, Mexico, and the new drought tolerant synthetic was named Batán 9585 Sequía.

Incorporation of Selection for Drought and Low-N Tolerance into a Modified Reciprocal Recurrent Selection (MRRS) Scheme

Two white semi-dent heterotic populations (Populations 902 and 903) were formed in 1994 using germplasm that is adapted to the tropical highlands and is being improved using MRRS. Since drought and low soil fertility (especially N) are major constraints in these ecologies, we have incorporated selection for both drought and low-N tolerance in the breeding schemes used to improve these populations. Approximately 500 S_1 lines are planted in an isolation block during the winter season in Tlaltizapán, Morelos, every other year, and topcross progenies are formed using the opposite population or synthetic as a tester. Simultaneously the same number of S_1 lines are planted for evaluation under drought using two different stress levels (severe and intermediate). Using an index of different traits, 190 families are selected for tolerance to drought and only topcrosses from these families are evaluated in progeny trials the following season. We have also used the drought evaluation data to form drought-tolerant synthetics, using the 10 best S_1 families under drought. Using this method, we have formed two synthetics, Tlaltizapán 96902 Seq. and Tlaltizapán 96903 Seq. During the main season, the progeny trials are evaluated under low N and control high N conditions in the highland environments of El. Batán. At the same time, the corresponding S_2 families are evaluated for *per se* performance under low and normal levels of soil nitrogen. Using this approach, we are able to improve the population simultaneously for drought tolerance and N-use efficiency. We have also formed four low-N tolerant synthetics (two each from Populations 902 and 903) using S_3 lines, based on data collected in 1996 at El Batán, Mexico. The synthetics are formed based on (i) *per se* performance of the corresponding S_2 lines, and (ii) the corresponding S_1 topcross performance. We are thus able to identify inbreds that possess special traits, such as drought tolerance and N use efficiency, and verify their performance in hybrid combination.

Conclusions

- Substantial variability exists in highland germplasm for drought tolerance and for the expression of traits related to tolerance, indicating that there is ample opportunity for improving tolerance via selection.
- Drought tolerant germplasm, including Calera 9185, Batán 9585 Sequía, Tlaltizapán 96902 Seq. and Tlaltizapán 96903 Seq., are expected to be very useful to Mexican highland farmers who grow maize in areas frequently affected by drought.

Table 2. Linear correlation coefficients among traits observed in 100 S_1 families of Pop. 85, grown under two water regimes in Tlaltizapán, Mexico, 1995-96. Values above the diagonal are from the intermediate stress regime, while those below the diagonal are from the severely stressed regime. Symbols * and ** indicate significance at $P < 0.05$ and $P < 0.01$.

	Anthesis date	ASI	Lodging %	Ears per plant	Grain yield	Senesc. score[†]	Tassel size[‡]
Anthesis date		0.277 **	0.008	-0.356 **	-0.375 **	-0.161	0.287 **
ASI	0.260 **		-0.076	-0.225 *	-0.518 **	-0.004	0.322 **
Lodging %	-0.104	-0.111		-0.031	0.035	-0.111	-0.111
Ears per plant	-0.319 **	-0.547 **	0.043		0.711 **	-0.086	-0.186
Grain yield	-0.117	-0.533 **	0.180	0.702 **		-0.193	-0.228 *
Senesc. score[†]	-0.302 **	-0.248 *	0.186	0.095	0.052		0.068
Tassel size[‡]	0.349 **	0.404 **	-0.095	-0.217 *	-0.239 *	-0.019	

[†] Score: 1 = 10% leaf area senesced; 10 = 100% of leaf area senesced.

[‡] Score: 1= small tassel biomass; 5 = large tassel biomass.

- The modified reciprocal recurrent selection scheme used by CIMMYT's Tropical Highland subprogram demonstrates how selection for drought and low-N tolerance can be incorporated into an inter-population improvement effort.
- The Tropical Highland program's breeding strategy should result in the pyramiding of genes conferring drought tolerance and nitrogen use efficiency, along with genes for resistance to important biotic stresses, within elite high-yielding germplasm.

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Maize Landraces:

Sources of Tolerance to Low Soil Nitrogen?

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Abstract

A total of 209 tropical maize accessions from the CIMMYT germplasm bank were evaluated over the course of three experiments to identify sources of tolerance to N deficiency. We measured grain yield, plant height and maturity under both high and low soil nitrogen. Under low N we also measured N uptake, N harvest index, ear leaf area, and ear leaf chlorophyll concentration. Maturity and season of evaluation had large effects, so results were analyzed separately for early and late landraces in winter and summer experiments. Landraces could be grouped using cluster analysis. Accessions from certain locations tended to have similar maturities. Some Cuban accessions were characterized by superior performance under low N. We identified 54 accessions with high total N recovery, harvest index, and grain % N, from various regions. These were grouped by maturity and intercrossed to form early and late source populations. After three cycles of intercrossing as half-sibs in a low-N nursery with very slight selection pressure for ear formation and reduced plant height, the populations underwent three additional cycles of improvement with 20-50% selection pressure for yield and plant type under low N. In two evaluations where N stress reduced mean yields to 1.05 t ha^{-1}, yields of C_6 of the source populations were not significantly less than the yields of improved check varieties. Yield of the early population increased by 15% per cycle between C_4 and C_6, and that increase was 11% per cycle in the late population. With continued improvement, these source populations may provide valuable traits for low N environments.

Maize cultivar improvement has traditionally taken place in nurseries with moderate-to-high levels of soil fertility. While improvements in plant type, disease resistance, and harvest index are expected to confer an advantage under both high and low-N conditions, there may be some specific adaptations to low fertility which are not identified in unstressed nurseries. The 17,000 maize accessions in the CIMMYT germplasm bank represent a wealth of genetic variation, but individual accessions have not been evaluated for their performance under low N. The objective of this study was to identify landraces with unique performance characteristics under low N, to recombine these to form two populations (early and late), and to study improvements in performance under low N resulting for recurrent selection.

Methods and Materials

Identifying components

We screened 209 tropical lowland accessions from Latin America to identify components for a source population with specific adaptation to low soil N supply. These accessions were evaluated over the course of three separate experiments, with data collection in both high-N and low-N fields (Table 1). Water supply and pests were not limiting in these experiments. For more details on methods, see Lafitte et al. (1997).

We used principal components analysis to identify the most important traits for characterizing groups of accessions in each season. Maturity was the most important single factor, so the accessions were divided into early and late groups for further analysis. We used cluster analysis to characterize different patterns of crop response to the contrasting N levels and to see if any particular geographic region supplied cultivars with good tolerance to low N. As an example, contrasting patterns of crop response observed for early accessions screened in the summer season are shown in Table 2. Group 1, which had good N uptake but low NHI, was found only in Cuba. Group 3, with poor N recovery but high NHI, was collected in the eastern Caribbean. Group 5, with high grain N concentration but rapid senescence, comprised collections from across the region. Despite these interesting patterns, we concluded that geographic origin was not a sufficient indicator of tolerance to low N, and that actual field measurements must be used to identify components.

Principal components analysis indicated that important traits for separating groups of accessions under low N were N uptake, NHI, and grain N concentration. We identified the best 25% of the early and late accessions in each experiment for these traits. All selected accessions were in the top 10% for at least one of the traits and in the top 15% for two or three traits. The characteristics of the selected fractions for the early accessions are shown in Table 3. We avoided using grain yield as a selection criterion, because grain yield is strongly influenced by the selection history of the accession; that is, the extent to which it had been improved prior to collection.

Assembly and improvement of the source populations

We planted the selected 32 early accessions and the 22 late accessions in a low-N field and made plant-to-plant crosses among the components within each population. We obtained 270 full-sib ears for the early population (Population BN Precoz), and 209 ears for the late population (Population BN Tardio). These were sown in two isolated half-sib blocks in the following season, again in a low-N field, and 1-2 ears were collected for each family. Families were rejected only if they failed to produce ears with adequate seed. The details of subsequent cycles are shown in Table 4. The first three cycles were designed primarily to

Table 1. Details of experiments to evaluate landrace accessions. All experiments were conducted at CIMMYT's Poza Rica Experiment Station (21°N, 60 m elevation).

Experiment:	1		2		3	
Year and season:	1987 winter		1987 summer		1988 winter	
Number of accessions:	38		112		59	
Measurements:	low N[a]	high N[b]	low N	high N	low N	high N
Grain yield	x	x	x	x	x	x
Aboveground biomass	x	x	x	x	x	
Aboveground N	x	x	x	x	x	
Plant height	x	x	x	x	x	x
Ear height	x	x	x	x	x	x
Ear leaf chlorophyll	x	x	x	x	x	
Ear leaf area	x	x	x	x	x	
Stay-green	x	x	x	x	x	
50% anthesis	x	x	x	x	x	x
50% silking	x	x	x	x	x	

[a] The low-N field received no fertilizer N.
[b] The high N field received 200 kg N/ha.

Table 2. Six groups of early accessions exhibiting different patterns of performance under high and low N when evaluated in the summer season of 1987 at Poza Rica Experiment Station. Groups are characterized as high, medium, or low (H, M, or L) for each trait based on being above, within, or below the mean by half of one standard deviation.

Group number	1	2	3	4	5	6
Grain yield -N	H	L	L	H	M	M
Grain yield +N	H	M	L	H	M	M
Total N -N	H	L	L	H	M	L
Grain %N -N	H	L	H	M	H	L
NHI -N	L	L	H	H	M	M
Stay-green -N	H	H	M	L	L	M
Number of accessions	5	10	7	9	18	18

Table 3. Characteristics of the early accessions evaluated and the selected fraction for each experiment. Data are presented for grain yield at both N levels, but these were not considered during selection.

	1		2		3	
Experiment	All	selected	All	selected	All	selected
Aboveground N[a], -N	30.5	36.9	53.7	66.1	31.7	38.3
NHI, -N	0.56	0.61	0.61	0.66	0.63	0.70
Grain %N, -N	1.67	2.02	3.34	4.36	2.04	2.69
Grain yield[b], -N	1.10	1.31	1.48	1.73	1.15	1.41
Grain yield[b], +N	2.06	2.02	4.94	5.17	2.10	2.13

[a] N in kg/ha
[b] Grain yield in t/ha

mix the population without losing individual components, and selection pressure was minimal. Subsequent selection has been for improved yield and plant type under low N, and in the evaluation of C_5, a replicated nursery was used, with a selection pressure of 15-20%.

Evaluation of the source populations

Cycles of the early and late source populations were evaluated in three trials under low N at Poza Rica.

Results and Discussion

The grain yield of Pool BN Precoz under low N did not increase between C_0 and C_4, but a yield gain of 160 kg ha^{-1} cycle^{-1} (15% per cycle) was obtained between C_4 and C_6, when a stronger selection pressure was used. The best three improved populations under low N from CIMMYT's Preliminary Evaluation Trial Three were included as checks. The grain yield of C_6 under low N was comparable to that of the early check (Fig. 1).

The grain yield of Pool BN Tardio under low N increased significantly between C_2 and C_6. The gain over that period was 118 kg ha^{-1} cycle^{-1} (13% per cycle). Other traits expected to change with selection were plant and ear height and lodging. No consistent differences were observed among cycles in height, but lodging decreased by about 2.5% per cycle in both populations.

Conclusions

These results indicate that the populations BN Precoz and BN Tardio may represent promising sources of tolerance to low N environments. Their yields have quickly approached those of superior checks in low N environments. Lines are now being extracted from both source populations to facilitate the introduction of traits for tolerance to low N into improved cultivars. We now need to examine the populations for the specific traits for which they were selected: N uptake, NHI, and grain N concentration. If the populations differ significantly from improved cultivars for these traits, their value as sources of unique traits for low N environments will be clearer. We can then begin to approach a more mechanistic understanding of maize tolerance to low soil N supply, which will improve the efficiency of future selection efforts.

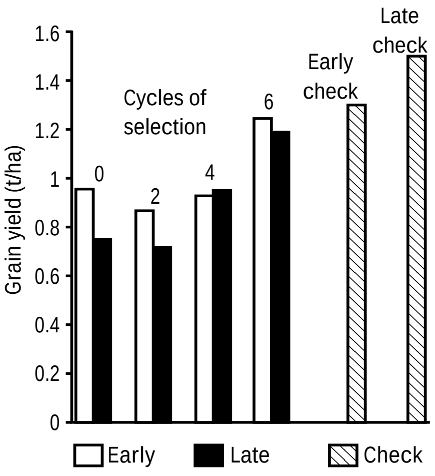

Figure 2. Mean yields of cycles of selection of early and late source populations in two trials under low N.

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Table 4. Selection procedure used in each cycle of improvement of the early and late source populations.

	Early population			Late population		
	Families screened	Families selected	Portion selected	Families screened	Families selected	Portion selected
C_0	370	324	88%	209	174	83%
C_1	364	357	98%	212	212	100%
C_2	365	357	98%	212	197	93%
C_3	360	144	40%	206	103	50%
C_4	247	100	40%	199	80	40%
C_5	195	30	15%	156	30	19%

Combining Ability for Nitrogen Use in Maize

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Abstract

Although improved nitrogen (N) use is a desirable goal of maize breeders, little is known about its inheritance. Thus, our objectives were to investigate the inheritance of several plant traits related to N use and to examine the relationship of these traits to grain yield. Fifteen single-cross hybrids produced from a diallel set of crosses among six inbred lines were grown at Champaign, Illinois, USA, in 1992 and 1993. Plants received either no supplemental N (low N) or an N rate considered sufficient for maximum yield (201 kg N ha^{-1}, high N). While significant hybrid variation was detected for all traits, the correlation with yield depended on the N supply. Harvest index, kernel number, N accumulation, and N utilization efficiency were all positively correlated with grain yield when plants were grown at low N, while only biological yield and N accumulation were correlated with yield at high N. Changes in harvest index, kernel number, and N utilization efficiency were most closely related to N-induced increases in yield. With minor exceptions, the mean squares for general and specific combining abilities (GCA and SCA) were significant for all measured traits at both levels of N. Based on the magnitude of difference between these mean squares, the majority of genetic effects were associated with GCA, indicative of additive genetic effects. Identification of traits related to high yield at low levels of N and the elucidation of their inheritance have important ramifications in maize breeding programs attempting to develop more N efficient genotypes.

Different maize cultivars grown at the same location can exhibit varying response patterns to N fertilization (Tsai et al., 1984; Smiciklas and Below, 1990; Sabata and Mason, 1992). Interest in identifying genetic differences in responsiveness to N fertilizer is intensifying, as producers and agricultural consultants see genotypic variation as one way to fine-tune N fertilizer management. There is also a desire to develop or identify genotypes that perform well under low N supply, or conversely, to find genotypes that will respond to high fertility conditions. Genotypic variation in N use is highly affected by the environment and requires controlled conditions such as hydroponics or tissue culture to be most apparent (Gentry and Below, 1993; Czyzewicz and Below, 1994; McCullough et al., 1994). Genotypic differences measured at one stage of growth or under a certain set of growth conditions may not be related to differences in N use at other times or under other environments (Teyker et al., 1989). Controversy remains as to whether genotypic differences in N use can be used to improve the management of fertilizer N in the field.

A fairly limited number of inheritance studies have evaluated parameters related to N use, such as total N accumulation, N harvest index, N translocation, and nitrate reductase activity (Katsantonis et al., 1988; Rizzi et al., 1993, 1995; Lafitte and Edmeades, 1995). Collectively, these studies have shown many N use traits to be under genetic control, with the magnitude of GCA effects comparatively larger than SCA effects, indicative of the greater importance of additive gene action. These studies also showed that physiological processes limiting yield differed according to the level of N available in the soil (e.g., low versus high) (Di Fonzo et al., 1982; Rizzi et al., 1993). Most of this work, however, has been conducted using European hybrids or landrace materials and further experimentation is needed to examine similar parameters using US lines. The objectives of this study were to investigate the effect of N supply and genotypes on various traits related to N use and productivity, and to examine the relationship of these traits to grain yield.

Materials and Methods

Fifteen single-cross maize hybrids produced from a diallel set of crosses among six inbreds were evaluated in the field in 1992 and 1993 for their response to fertilizer N. The inbreds were chosen to represent a broad base of midwest US germplasm used in hybrid production, with similar relative maturity. Our initial screening under controlled conditions showed that seedling growth of these lines differed in response to N level (data not shown). Treatments comprised the 15 hybrids grown on plots receiving no supplemental N (low N plots) or with an N rate (201 kg N ha^{-1}) considered sufficient for maximum yield. The soil type was a Drummer silty clay loam (3.1% organic matter) which had previously been shown to be responsive to N fertilizer. Nitrogen fertilizer as urea was hand applied at the V2 growth stage in granular form and immediately incorporated into the soil with cultivation followed by 2.5 cm of irrigation water. The treatments were arranged in a split plot design with hybrids as the main plots and N availability as the subplot. Four replications were used in 1992 and six in 1993. An experimental unit consisted of four rows (rows 5.4 m long and spaced 0.76 m apart) with a plant density of approximately 64,000 plants ha^{-1}.

At physiological maturity, representative plants were harvested (four per plot) and separated into aboveground stover, reproductive fractions (husk, cob, shank, and tassel), and grain. All fractions were dried to determine dry matter production, and the dry ground tissue was analyzed for N. The total amount of dry matter produced (biomass) and N acquired (N accumulation) were determined by summing the values for the various plant parts. Yield components (kernel number and kernel weight) were also determined from appropriate counts and weights of kernels. Grain yield was determined by harvesting all plants in a center unsampled row and is expressed as t ha^{-1}. The data were analyzed over the two years using a combined analysis with years and hybrids considered as fixed effects. Significant effects for hybrid and N level and hybrid by N level interaction was observed for nearly all of the parameters measured. In contrast, years by hybrids interactions were few and relatively minor (data not shown). Thus, for all data analysis and presentation, the hybrid values were averaged over the two years. General and specific combining ability effects were estimated using method 4 (F_1 hybrids no reciprocal crosses) of Griffing (1956). The Agrobase 4 statistical program was used to make the estimates.

Results

Significant differences among the hybrids were detected for all traits measured, at both levels of N (data not shown). Variation for grain yield is shown in Table 1. Yields ranged from 5.8 to 9.1 t ha^{-1} without supplemental N, and from 10.8 to 13.0 t ha^{-1} with supplemental N. Yields of all hybrids were increased by the addition of N fertilizer; increases ranged from 3.0 to 6.6 t ha^{-1}. There was no relationship between a hybrid's yield under low N and its yield under high N (r = -0.27).

The relationships between grain yield and various traits were examined by calculating simple correlation coefficients (Table 2). At the low N level, harvest index, kernel number, total N accumulation, and N utilization efficiency (grain yield divided by N accumulation) were all significantly and positively correlated with grain yield. At the high N level, only biological yield and total N accumulation were correlated with grain yield. Only the accumulation of total plant N was correlated with

Table 1. Grain yield of a diallel set of crosses among six maize inbred lines grown with low N and high N. Hybrids are ranked in descending order according to yield at low N. Values are the average of two years.

Hybrid	Low N (t ha^{-1})	High N (t ha^{-1})
LH119 x LH51	9.1	13.0
DM2 x LH82	8.8	11.8
LH119 x DM2	8.3	12.6
WF9 x LH82	8.2	11.4
LH119 x LH82	8.2	12.6
LH51 x LH82	8.1	12.1
LH51 x DM2	8.1	11.4
DM2 x WF9	7.6	12.0
Oh545 x LH82	7.4	10.9
Oh545 x DM2	7.3	11.0
LH51 x WF9	7.0	11.2
LH119 x WF9	6.4	11.0
Oh545 x WF9	6.4	11.4
LH51 x Oh545	6.4	10.8
LH119 x Oh545	5.8	12.3
Mean	7.6	11.7

grain yield at both N levels.

The magnitude of increase (percentage of change) in grain yield from supplemental N was highly correlated with N-induced changes in harvest index, kernel number, and N utilization efficiency (Table 3). In contrast, changes in biological yield, individual kernel weight, and total plant N accumulation were not related to the response of these hybrids to N fertilization.

The mean squares for general combining ability (GCA) and specific combining ability (SCA) were significant for almost all the traits examined at both N levels (data not shown). Exceptions were GCA effects for N utilization efficiency at high N, and SCA effects for total plant N accumulations at low N. Based on the magnitude of the mean squares (data not shown), the majority of genetic effects for all traits were associated with GCA.

Estimates of the GCA effects for the six inbreds are presented in Tables 4 and 5. GCA effects for grain yield differed according to the level of available N; inbreds DM2 and LH82 had high GCA effects at low N, but not at high N (Table 4). Conversely, LH119 had high GCA at high N, but not at low N. WF9 and Oh545 had negative GCA effects at both levels of N. Similar patterns of N-induced variability in GCA effects were observed for several of the other traits, especially kernel number (Table 5). For biological yield, however, GCA estimates were remarkably similar at both levels of N. Interestingly, for a given inbred and N level, the sign (positive or negative) of the GCA effects were always opposite to each other for kernel number and kernel weight.

Table 2. Phenotypic correlations (r) among grain yield and several productivity traits for a diallel set of crosses among six maize inbred lines grown with low and high N.

Plant trait	Low N	High N
Biological yield (g plant^{-1})	0.39	0.64**
Harvest index (%)	0.75**	-0.01
Kernel number (no. plant^{-1})	0.79**	0.31
Kernel weight (mg kernel^{-1})	-0.21	-0.07
N accumulation (g plant^{-1})	0.50*	0.55*
N utilization efficiency (g grain/g N)	0.75**	0.20

*, ** significant at the 0.05 and 0.01 probability levels, respectively.

Table 4. Estimates of GCA effects for grain yield, biological yield, and harvest index of six maize inbred lines grown as a diallel set of crosses with low and high N supply.

Inbred line	Grain yield		Biological yield		Harvest index	
	Low N	High N	Low N	High N	Low N	High N
	(t ha^{-1})		(g plant^{-1})		(%)	
DM2	+9.9	+1.6	+20.7	+19.1	+0.2	-2.5
LH82	+12.2	+1.0	-18.1	-14.4	+6.5	+4.1
WF9	-8.5	-5.4	-9.5	-9.7	-0.5	-0.9
LH119	+1.8	+12.6	+14.7	+15.3	-2.0	-0.4
LH51	+3.8	-1.6	+2.3	+0.8	-0.3	-1.5
Oh545	-19.3	-8.2	-10.0	-11.1	-3.9	+0.3
SE	2.3	1.9	3.6	3.2	0.6	0.3

Discussion

Our results agree with earlier findings (Katsantonis et al., 1988; Lafitte and Edmeades, 1995; Rizzi et al., 1993 and 1995) that show productivity traits related to N use are under genetic control and that maize genotypes differ in these traits. For nearly all traits, the magnitude of GCA mean squares were much larger than SCA effects, indicating that additive effects were more important than dominance effects. For many of the traits, the GCA effects differed according to the level of available N (Tables 4 and 5).

Similar to other studies (Di Fonzo et al., 1982; Rizzi et al., 1993), our data

Table 3. Phenotypic correlation coefficients (r) between the magnitude of increases in grain yield and productivity traits when supplemental N was applied to a diallel set of crosses among six maize inbred lines.

Plant trait	Correlation with percentage change in grain yield
Biological yield (g plant^{-1})	0.32
Harvest index (%)	0.94**
Kernel number (no. plant^{-1})	0.85**
Kernel weight (mg kernel^{-1})	-0.09
N accumulation (g plant^{-1})	0.19
N utilization efficiency (g grain/g N)	0.90**

** significant at the 0.01 probability level.

show that different traits were correlated to grain yield depending on the level of available N (Table 2). Only N accumulation was significantly correlated with grain yield at both levels of N. A genetic relationship between total plant N accumulation and grain yield has been reported previously (Katsantonis et al., 1988). This finding could suggest that plant N accumulation is an important trait for maximum yield, regardless of the level of available N.

Changes in harvest index, kernel number, and N utilization efficiency were all closely related to N-induced increases in yield (Tables 3 and 4). The identification of traits related to high yield at low N levels offers prospects for exploitation in maize breeding programs to develop more N efficient hybrids. Conversely, identification of traits related to grain yield at high N could allow the development or identification of hybrids responsive to high production environments.

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Table 5. Estimates of GCA effects for kernel number, kernel weight, total plant N accumulation, and N utilization efficiency for six maize inbred lines grown as a diallel set of crosses with low and high N supply.

	Kernel number		Kernel weight		N accumulation		NUE[1]
Inbred line	Low N	High N	Low N	High N	Low N	High N	Low N
	(no. plant^{-1})		(mg kernel^{-1})		(g plant^{-1})		(g g^{-1})
DM2	+38.0	-19.2	-1.8	+11.9	+0.01	+0.13	+5.2
LH82	+70.8	+87.2	-22.5	-32.6	-0.01	+0.02	+5.3
WF9	-9.2	+15.4	-5.1	-19.0	-0.06	-0.07	-0.2
LH119	-1.4	+17.9	+1.6	-0.1	+0.11	+0.12	-3.9
LH51	-37.4	-69.0	+22.2	+29.7	+0.04	-0.08	-1.7
Oh545	-60.6	-32.4	+5.7	+10.0	-0.09	-0.13	-4.8
SE	7.9	5.2	2.4	1.9	0.04	0.04	1.1

[1] GCA effects were not significant at high N.

Parámetros Genéticos de la Eficiencia en el Uso de Nitrógeno en Líneas de Maíz de Valles Altos

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Abstract

The objectives of this study were to evaluate the nitrogen (N) use, through yield and other related traits, of maize inbred lines, and to estimate the genetic parameters, general combining ability (GCA) and specific combining ability (SCA), for the traits using a diallel of crosses among these lines. Fourteen inbred lines and 91 single-cross hybrids, arranged in a Griffing's (1956) Method 4 design, were grown separately under 0 and 200 kg N/ha, using a split-plot experimental design in complete blocks. Among the inbred lines there were no significant differences between N regimes for grain yield, anthesis-silking interval, grain per ear, or barrenness. Highly significant differences were observed for all traits among crosses for N regimes, among hybrids within N regimes, and for N regime x hybrids interaction. With minor exceptions the higher yielding F_1 hybrids under 200 kg N/ha were the same under 0 kg N/ha, and the crosses showed differences of 7-20% in yield between the two N levels. Estimates of GCA and SCA were statistically significant for traits at both N levels. Inbred lines derived from local maize varieties showed smaller GCA effects than lines derived from widely-adpated populations; however, the F_1 hybrids resulting from crosses between these two classes of lines showed large SCA effects for yield and grain per N gram under both N regimes. Because SCA effects were larger under 0 N, we consider that these effects were more important under low N than under high N availability.

Introduccción

En la altiplanicie meridional de México la mayoría de las tierras de maíz presentan bajos niveles de fertilidad, de manera que para obtener altos niveles de rendimiento bajo esas condiciones se requiere la aplicación de altos niveles de fertilizante químico, principalmente N. Un maíz mejorado que presente genéticamente eficiencia en el uso de N, podría tal vez producir buen rendimiento en suelos pobres con escasa aplicación de fertilizante, o bien alto rendimiento en mejores condiciones, por su capacidad para asimilar mayores cantidades de N.

La eficiencia en el uso del N se ha definido como la producción de grano por unidad de N suministrado en el suelo y se representa como GW / NS, donde GW es el peso del grano y NS la cantidad de N suministrado (Moll et al., 1982). Existen dos componentes primarios de la eficiencia del uso de N: 1) la eficiencia de absorción Nt / NS y 2) la eficiencia con la cual el N absorbido es utilizado para producir grano GW / Nt, donde Nt es el N total en planta a la madurez (Moll et al., 1982).

Diferencias entre genotipos a dosis especificas de N han evidenciado que los caracteres relacionados con la absorción de nutrimentos son particularmente importantes cuando el suministro de N es adecuado; sin embargo, la capacidad para producir una gran cantidad de grano por unidad de N disponible en la planta es más crítica cuando el N es limitativo (Di Fonzo et al., 1982). En la caracterización de diferentes híbridos de maíz por su respuesta a la disponibilidad de N, se ha observado diferente respuesta metabólica a la deficiencia de N; sin embargo, ninguno de ellos rendirá particularmente bien bajo deficiencia de N (Tsai et al., 1990). Diferencias genotípicas del comportamiento del maíz en condiciones deficitarias de N también se han relacionado con diferencias en partición de N y biomasa dentro de la planta, especialmente en términos de cantidad de N removido de los tejidos vegetativos (Ta y Wieland, 1992). También se ha determinado que los patrones de absorción de N y su partición en la floración son críticos para el mantenimiento del número de granos en ambientes escasos de N (Pearson y Jacobs, 1987); la deficiencia de N influye tanto en la determinación del número de florecillas como en la proporción de aquellas que llegan a formar granos (Jacobs y Pearson, 1991). El suministro deficiente de N tiende a reducir la biomasa por florecilla (Lemcoff y Loomis, 1986), lo que conduce a un bajo número de granos por mazorca, síntoma típico en condiciones deficitarias de N. Entre las respuestas morfológicas y fisiológicas del maíz a condiciones con limitación de N sobresale el tamaño reducido de la planta, eficiencia reducida de la intercepción de la radiación, senescencia acelerada, movilización incrementada del N vegetativo al grano y reducida concentración del N en la planta (Muchow y Davis, 1988).

Se ha demostrado que poblaciones mejoradas por selección recíproca y de hermanos completos presentan mayor eficiencia promedio del uso de N, lo cual está asociado con un incremento en el número de mazorcas conforme se incrementa la cantidad del N aplicado (Kamprath et al., 1982); sin embargo, el incremento del rendimiento en respuesta a la aplicación de N no se debe necesariamente a una mayor eficiencia en su utilización (Anderson et al., 1985). Ciertos caracteres están estrechamente correlacionados con el rendimiento en condiciones de bajo suministro de N y se podrían combinar en un índice de selección, como son el rendimiento de grano y altura de planta con niveles bajo y alto de N, precocidad con alto N y clorofila y senescencia foliar con bajo N (Lafitte y Edmeades, 1988). Respecto a los parámetros genéticos de la eficiencia del uso de N, los efectos de dominancia tuvieron mayor contribución en la variación genética observada (Alvarado, citado por Clark y Duncan, 1991). La variación genética debida a aptitud combinatoria general, fue la preponderante con respecto a la asignación de N entre estructuras de la planta (el rendimiento y la materia seca) lo cual indica que diferencias entre cruzas podrían ser atribuidas a efectos genéticos aditivos (Rizzi et al., 1993).

En otras regiones, se ha observado variación en la absorción y aprovechamiento del N entre diferentes materiales de maíz; sin embargo, muy poco se conoce al respecto sobre maíces del altiplano mexicano; por ello se plantea el presente estudio con líneas de valles altos con los siguientes objetivos: evaluar la eficiencia en el uso de N de líneas endogámicas, y estimar los parámetros genéticos de aptitud combinatoria general y específica en los niveles de 0 y 200 kg de N / ha.

Materiales y Métodos

Para este estudio se utilizó un sistema de cruzamiento dialélico entre 14 líneas endogámicas de valles altos, de acuerdo con el método IV de Griffing (1956). Las líneas fueron previamente identificadas por su rendimiento promedio con diferentes dosis de N y densidades de siembra; específicamente se trata de siete pares de líneas hermanas, donde un par de líneas está representado por una línea de alto y otra de bajo rendimiento. De los siete pares de líneas, uno pertenece a la población Michoacan 21, cuatro a la población Tlaxcala 151, tres líneas de la Población 85 y una línea de la Población 800. Las líneas de Mich 21 y Tlax 151 son utilizadas como progenitoras en el programa de maíz de valles altos del Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP); las líneas de poblaciones son del programa de maíz del Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT).

Las líneas del INIFAP son: Mich 2115 (15), Mich 2118 (18), Tlax 15123 (23), Tlax 15125 (25), Tlax 15127 (27), Tlax 15131 (31), Tlax 15133 (33), Tlax 15136 (36), Tlax 15146 (46) y Tlax 15148 (48); y las del CIMMYT son: CML 241 (241), CML242 (242), CML 243 (243) y CML 246 (246). Los números entre paréntesis se usarán en lo sucesivo para identificar las líneas.

Para la asignación de tratamientos se utilizó un diseño experimental de parcelas divididas en bloques al azar con tres repeticiones, donde la parcela grande estuvo constituida por los niveles 0 y 200 kg de N / ha, mientras que la parcela menor fueron las 91 cruzas dialélicas y nueve testigos; para el arreglo de las cruzas se utilizó un diseño de tratamientos de latice simple 10 x 10. En el experimento con líneas la parcela menor fueron 14 líneas. La siembra se realizó en terrenos del Campo Experimental Valle de México del INIFAP en Coatlinchán, Edo. de Méx. El área experimental, con suelo areno-arcilloso profundo fue sembrada con avena sin aplicación de fertilizante durante 1993 y 1994. El análisis del suelo indicó la existencia de 2.1% de materia orgánica y 45 kg de N ha^{-1}. Se aplicaron riegos a la siembra a 40, 70y 105 días después de ésta. Los 200 kg de N se dividieron en tércios y cada uno se aplicó a la siembra, a los 20 días despues de ésta y a la floración masculina. Los testigos fueron los híbridos H-28, H-30, H-34, H36e, H38e, H-59e y las variedades VS22, V-23 y VSe. La densidad de siembra fue de 65,000 plantas/ha, distribuidas en surcos distanciados 80 cm. Se tomaron datos de iniciación de la floración masculina y femenina, altura de plantas, mazorcas por planta, peso de grano por planta, gramos de grano por peso de N y rendimiento de grano.

Se realizaron análisis de varianza y comparación múltiple de medias para los caracteres medidos. A la vez, se practicaron análisis de varianza para aptitud combinatoria y se cuantificaron los efectos de aptitud combinatoria general (ACG) y específica (ACE).

Resultados y Discusión

Comportamiento de líneas. No se detectaron diferencias estadísticas para los caracteres estimados en las líneas entre los niveles de 0 y 200 kg de N; este resultado puede ser atribuido al potencial de rendimiento reducido de las líneas, a deficiencias en su adaptación y/o a la abundancia de N en el terreno experimental. En promedio para ambos niveles de N, los rendimientos más altos correspondieron a las líneas (25), (33), (15) y (31), las cuales carecen de diferencias claras en los restantes atributos evaluados; los rendimientos más bajos fueron para las líneas que contienen cierta dosis de germoplasma subtropical, lo cual les pudo reducir adaptabilidad a valles altos (Cuadro 1).

Comportamiento de cruzas dialélicas

Con respecto a los niveles de N aplicado, se observaron diferencias altamente significativas en todos los caracteres, en el análisis de varianza conjunto para los niveles de N aplicado; pero también entre niveles de N se encontraron diferencias altamente significativas para todos los caracteres, entre cruzas y en la interacción niveles de N por cruzas, excepto para altura de planta (ALTPL) y mazorcas por planta (MAZPL). Las diferencias entre cruzas dialélicas se pueden atribuir a la variabilidad amplia que se indujo en esos híbridos con las líneas progenitoras utilizadas; la diferencia entre niveles de N se puede atribuir a que dichas variabilidad también alcanzó al potencial de rendimiento de los híbridos, el cual pudo expresarse claramente con la aplicación de los 200 kg de N. La significación estadística de la interacción niveles de N por cruzas, sugiere que existe un grupo de híbridos que responden particularmente a cada dosis de N, tanto en rendimiento (REND) como en gramos de grano por planta (GRANPL) y gramos de grano por gramo de N (GRAN*N) (Cuadro 2).

La prueba de comparación de medias (Tukey, P<0.05) para niveles de N aplicado mostró la existencia de diferencias estadísticas entre las

Cuadro 1. Rendimiento de grano y otros caracteres de las plantas y mazorcas de líneas de maíz (medias conjuntas de 0 y 200 kg de N/ha).

Líneas	Rendimiento (t ha^{-1})	Días a floración femenina	Intervalo de floración (d)	Mazorcas estériles (%)	Grano x mazorca (%)
25	3.1	78	3.0	5	81
33	2.8	75	2.0	5	79
15	2.8	82	2.5	8	77
31	2.7	78	2.7	10	76
27	2.4	80	3.0	25	73
18	2.1	84	3.0	16	77
48	2.0	75	2.0	2	78
46	1.8	77	1.7	4	80
243	1.3	77	1.2	2	84
23	1.2	81	2.2	37	76
241	1.1	78	1.0	4	84
242	0.8	77	1.5	10	80
246	0.5	88	3.2	48	80
36	0.4	88	7.0	86	65
DMS (0.05)	0.4	4.9	1.7	13.1	6.5

cruzas para los caracteres MAZPL, REND, GRANPL y GRAN*N. Respecto a la cantidad de mazorca por planta con 0 N, se observó que por cada 10 plantas una fue estéril (esto es, 6,500 plantas / ha), el rendimiento fue menor en 1 t ha^{-1} y la cantidad de GRANPL fue menor en 15 g. Los ambientes limitados de N son críticos en la determinación del número de florecillas y del número de ellas que forman grano (Jacobs y Pearson, 1991); también, se reduce la biomasa por florecilla, lo que conduce a un bajo número de granos por mazorca (Lemcoff y Loomis, 1986). Sin embargo, sin aplicación de N, el índice GRAN*N de los genotipos evaluados fue estadísticamente muy superior, lo cual puede denotar mayor eficiencia en el uso del N disponible o que el N aplicado fue bloqueado en la descomposición de residuos de las cosechas previas (Cuadro 3).

Las medias para REND y GRAN*N de las cruzas dialélicas permiten observar que cuando resultaron de líneas con germoplasma de maíces criollos de valles altos de la mesa central (INIFAP) y de líneas de las poblaciones 85 y 800 de mayor base genética y con cierta dosis de germoplasma subtropical (CIMMYT), presentaron los mayores rendimientos tanto en alta como en nula fertilización. Con 200 kg ha^{-1} de N los rendimientos de grano más altos estadísticamente fueron las 10 primeras cruzas (8.9 a 10.1 t ha^{-1}) (Cuadro 4). Sin N, las mejores cruzas produjeron de 6.7 a 8.9 t ha^{-1}. También sin N se observó que el índice de eficiencia GRAN*N de las cruzas fue más de 100% superior que con 200 kg de N ha^{-1} (Cuadro 4). Estos resultados confirman que los incrementos del rendimiento en respuesta a la aplicación de N no implican necesariamente una mayor eficiencia en su utilización (Anderson et al., 1985).

Entre ambos niveles de N hubo una gran coincidencia en las cruzas que destacaron por su mayor rendimiento. Además, las diferencias debidas al N en el rendimiento de dichas cruzas sólo varió del 7 al 20%, como sucedió con las cruzas 31x242, 33x246 y 48x246 (Cuadro 4). Este resultado sugiere que con híbridos F1 de esta constitución genética, es posible obtener rendimientos altos con o sin aplicación de N; ello aparentemente contradice que la eficiencia en el uso de N en condiciones de escasez de N sea incompatible con la eficiencia en abundancia de N (Muruli y Paulsen, 1981); tambien es posible que este comportamiento séa indicativo de un estrés ligero con 0 de N, lo cual pudo ocurrir debido a altos niveles de mineralización que aportaron una cantidad suficiente de N a la planta, ya que los niveles de materia orgánica y N total expresados en el análisis de suelo se consideran bajos. El rendimiento alto de las cruzas o híbridos F1 en ambos niveles de N, podría deberse a la constitución genética distante de las líneas de INIFAP y CIMMYT originarias. Se ha propuesto que mayores avances en el

Cuadro 2. Cuadrados medios y significación para rendimiento y otros caracteres de la planta y mazorca de cruzas de maíz, con 0 o 200 kg de N/ha y en conjunto.

F.V.	FLORM	FLORF	ALTPL	MAZPL	REND	GRANPL	GRAN*N
0 N							
Cruzas	13.5**	20.7**	1245.5**	0.06**	6926030.3**	1612.3**	1613.6**
CV%	1.3	1.4	7.2	14.5	13.4	13.5	14.4
200 N							
Cruzas	11.0**	15.5**	1072.9**	0.05**	8703550.7**	2067.6**	205.4**
CV%	2.1	2.4	6.5	10.2	10.3	9.8	10.8
0 y 200 N							
Nivel N	62.0**	49.3**	1296.5**	1.2**	153650949**	35481.6	460484.8**
Cruzas	20.6**	31.5**	2028.4**	0.1**	14848142**	3504.4**	1433.3**
N*Cruzas	3.8**	4.7**	290.0ns	0.1ns	781439**	175.5**	358.6**
CV%	1.7	1.9	6.9	12.4	11.7	11.5	15.4

FLORM: días a floración masculina, REND: rendimiento t/ha, FLORF: días a floración femenina, GRANPL: peso de grano por planta en g, ALTPL: altura de planta en cm, GRAN*N: g de grano por g de N aplicado, MAZPL: número de mazorca por planta.

Cuadro 3. Efecto de la aplicación de N sobre el rendimiento y diversos caracteres de la planta y mazorca en maices derivados de cruzamientos dialélicos.

N kg ha^{-1}	FLORM	FLORF	ALTPL	MAZPL	REND	GRANL	GRAN*N
0	73.5a	74.5a	224.1a	0.90b	5.82b	89.5b	89.3a
200	74.1a	75.1a	227.0a	0.99a	6.84a	104.9a	33.9b

Letras diferente entre columnas indican diferencias estadísticas con una P£0.05, FLORM: días a floración masculina, FLORF: días a floración femenina, ALTPL: altura de planta en cm, MAZPL: número de mazorca por planta, REND: rendimiento, t/ha, GRANPL: peso de grano por planta en g, GRAN*N: g de grano por g de N aplicado.

mejoramiento para caracteres de eficiencia en el uso de N podrían alcanzarse con procedimientos que enfaticen los efectos genéticos dominantes (Alvarado, citado por Clark y Duncan, 1991).

Aptitud combinatoria y sus efectos. El análisis de varianza para aptitud combinatoria reveló diferencias altamente significativas en aptitud combinatoria general (ACG) y en aptitud combinatoria específica (ACE) para los atributos medidos en REND y GRAN*N, en ambos niveles de N (Cuadro 5). Estos resultados concuerdan con los obtenidos para rendimiento y otros caracteres de la asignación del N en planta por Rizzi et al. (1993).

Los efectos estimados señalan que solamente las líneas 31, 241, 242, 243 y 246 presentaron valores favorables en ACG sin aplicación de N. Esas mismas líneas, más la 15 y 18, también presentaron ACG favorable con la aplicación de 200 kg ha^{-1} de N; a la vez, las líneas 15, 18, 31, 242 y 246 mejoraron su valor de ACG con la fertilización. De las 10 líneas de valles altos del INIFAP sólo una sin N y tres con fertilización presentaron valores favorables de ACG, mientras que las cuatro líneas del CIMMYT presentaron alta ACG con ambos niveles de N. Esta diferencia podría deberse a que las líneas del INIFAP son menos diversas en su composición genética, ya que en todos los casos se trata de líneas obtenidas a partir de cultivares tradicionales sobresalientes y no de poblaciones mejoradas con amplia base genética, como es el caso de las líneas del CIMMYT. Sin N, los efectos de ACG para GRAN*N fueron favorables en las mismas líneas, con las que lo fueron para REND; sin embargo, con la aplicación de N dichos efectos sólo fueron favorables en las líneas 241, 242, 243 y 246, pero con menor valor que sin N (Cuadro 6).

Respecto a los efectos estimados de ACE, en general fueron mayores sin N, tanto para REND como para GRAN*N. Sin embargo, del total de

Cuadro 4. Rendimiento medio (t ha^{-1}) y eficiencia de uso de N (g de grano por g de N aplicado) de cruzas dialélicas.

	200 kg N ha^{-1}			0 kg N ha^{-1}		
Cruza	REND (1)	GRAN*N	Cruza	REND (2)	GRAN*N	REND (2/1)
31x242	10.1	50	31x242	8.9	137	0.88
31x246	10.0	49	33x246	8.4	128	0.86
33x246	9.7	48	48x246	8.4	128	0.93
18x246	9.6	47	31x241	8.3	127	0.88
31x241	9.4	47	15x241	8.2	126	--
46x246	9.2	45	27x246	8.2	126	0.91
15x246	9.0	44	31x246	8.0	123	0.80
27x246	9.0	45	18x241	7.8	119	0.90
48x246	9.0	44	23x246	7.8	119	--
15x242	8.9	44	25x241	7.7	119	0.89
27x241	8.8	44	18x246	7.7	117	0.80
18x241	8.7	43	48x243	7.6	115	--
25x241	8.6	42	15x242	7.5	116	0.84
18x243	8.6	43	33x242	7.5	115	--
15x243	8.6	43	15x243	7.5	115	0.87
Mean	6.8	33.9	Mean	5.8	89.5	
DSH (0.05)	1.2	5.9	DSH (0.05)	1.3	19.4	

Información parcial de un juego de 91 cruzas dailélicas. REND: rendimiento t/ha, GRAN*N: g de grano por g de N aplicado.

Cuadro 5. Análisis de varianza para aptitud combinatoria para rendimiento y g de grano por g de N aplicado bajo dos niveles de N (kg ha^{-1}).

F.V.	0 REND	GRAN*N	200 REND	GRAN*N
CRUZAS	7237347.8**	1701.4**	9224525.1**	217.2**
ACG	15504253.5**	3640.5**	19636469.9**	482.3**
ACE	5841636.4**	1374.0**	7466664.3**	172.4**

REND: rendimiento kg/ha, GRAN*N: g de grano por g de N aplicado.

Cuadro 6. Efectos de la aptitud combinatoria general de líneas para rendimiento y g de grano por g de N aplicado, bajo dos niveles de N.

	REND (kg ha^{-1})		GRAN*N	
	N kg ha^{-1}			
Línea	0	200	0	200
15	-276.7	190.2	-3.2	0.4
18	-300.9	124.5	-0.7	0.7
23	-586.0	-826.6	-10.3	-3.5
25	-591.0	-519.2	-9.2	-2.3
27	-243.8	-232.8	-2.6	-8.5
31	648.5	926.8	9.7	4.8
33	-149.8	-598.9	-2.0	-3.4
36	-1250.6	-1333.9	-18.9	-6.4
46	-557.1	-637.5	-7.9	-3.0
48	-637.2	-819.1	-10.0	-4.0
241	888.0	629.8	13.9	2.7
242	463.3	557.2	8.3	2.8
243	1112.9	457.7	9.4	6.5
246	1612.1	1765.5	24.2	9.5

REND: rendimiento kg/ha, GRAN*N: g de grano por g de N aplicado.

cruzas obtenidas entre líneas del INIFAP en sólo la minoría se presentaron valores favorables de ACE, y en ninguna de las cruzas obtenidas entre líneas del CIMMYT. En cambio, todas las cruzas entre líneas del INIFAP y del CIMMYT mostraron valores altos de ACE para ambas variables (Cuadro 7). Estos resultados parecen deberse a la distancia genética entre el germoplasma de las líneas del INIFAP y del CIMMYT, la cual produjo en los cruzamientos una expresión amplia de efectos de dominancia, a diferencia de lo que ocurrió en las cruzas dentro de las líneas del INIFAP o del CIMMYT. Sin embargo, el rendimiento promedio alto en 0 de N (5.8 t ha-1) hace pensar que no hubo un estrés intenso, lo que impidio la expresión de la variabilidad genética por deficiencia de N; consecuentemente es posible que sólo se haya identificado variación genética para alta disponibilidad de N, por lo que es necesario realizar las evaluaciones del material genético en suelos de baja fertilidad comprobada de distintas localidades.

Cuadro 7. Efectos de la aptitud combinatoria específica para rendimiento y g de grano por g de N, en dos niveles de N.

	REND		GRAN	
	(kg ha^{-1})			*N
	N kg ha^{-1}			
Cruza	0	200	0	200
15x31	235.5	-149.3	3.4	0.0
15x242	1504.7	1293.5	21.2	6.9
18x31	547.1	-1370.0	5.4	-1.4
18x241	1307.6	1049.0	16.2	5.7
18x243	617.8	1157.1	13.7	1.9
25x31	-348.3	441.3	-6.1	2.7
25x242	1441.6	1126.0	13.7	4.7
31x33	974.1	572.0	15.6	2.8
31x242	1937.9	1757.8	29.2	8.5
33x246	1121.5	1681.3	15.5	8.1
48x243	1254.1	1036.4	11.0	3.6
48x246	1540.9	1166.5	26.5	4.7
241x242	-4640.5	-5019.1	-72.9	-24.3
242x243	-3448.4	-3552.0	-46.4	-22.2
243x246	-1606.2	-2200.3	-17.0	-15.8

Información parcial de un juego de 91 cruzas dialélicas. REND: rendimiento kg/ha, GRAN*N: g de grano por g de N aplicado.

Las conclusiones principales de este estudio son: 1) el rendimiento de las líneas endogámicas fue similar con independencia de la fertilización nitrogenada; 2) cruzas simples entre líneas del INIFAP con las del CIMMYT presentaron los mayores rendimientos y gramos de grano por gramo de N aplicado, con independencia de la aplicación de N; 3) las diferencias en rendimiento entre cruzas debidas a la aplicación de N variaron de 7 a 20%; 4) los cuadrados medios de ACG y ACE fueron altamente significativos para los caracteres estudiados; 5) en general, los valores de los efectos de ACE fueron mayores sin aplicación de N; 6) el aprovechamiento de N en disponibilidad limitada fue determinada principalmente por los efectos de ACE.

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Evaluación Agronómica de Líneas Autofecundadas (S_1) Obtenidas a Partir de Nueve Cultivares de Maiz para Condiciones Normales y de Bajo Contenido de N en el Suelo

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Abstract

During 1992 and 1993 a total of 298 S_1 lines of maize (245 obtained from improved varieties and 53 from Colombian landraces) were evaluated for grain yield and 12 other characteristics, including nitrogen (N) use efficiency. The objective was to identify the best lines and to integrate these with existing germplasm in an improvement program to obtain genotypes with high yield potential and good agronomic performance under conditions of high and low N availability. Evaluations were conducted at the National Research Center, Turipaná, of the Colombian Agricultural Institute (ICA) (9° N, 76° W, 13 m elevation, average temperature 28 °C, 1076 mm annual rainfall, and 83% RH). The experimental design was a randomized complete block. The interaction of genotype (line) and environment (levels of N) was not significant for the variables of major agronomic interest, i.e., grain yield, length and diameter of the ear, shelling percent, harvest index and days to silking and anthesis. From the individual and combined analyses it can be inferred that the improved materials and the Colombian landrace populations that were evaluated can both supply good lines for an improvement program in normal conditions of nitrogen fertilization, under conditions of nitrogen stress and simultaneously for both environments. A total of 25 superior white and 25 superior yellow lines were identified and recombined by color to create two base populations for recurrent selection under normal conditions and under conditions of nitrogen stress.

El maíz es uno de los cultivos de mayor arraigo y tradición en Colombia, cultivado en diversos pisos térmicos, desde el nivel del mar hasta más allá de los 2800 m de altitud, es considerado uno de los productos agrícolas de mayor consumo en el país ya que proporciona calorías y proteínas a la población (Torregroza et al., 1991).

La pobre fertilidad de los suelos es uno de los factores que conducen a los bajos rendimientos del maíz en los trópicos. El N es elemento clave para la diferenciación entre la agricultura de bajos y altos recursos, pues es el nutrimento más limitativo en la mayoría de las áreas de cultivo (Brewbaker, 1985). El N forma parte de los metabolitos esenciales de la planta (aminoácidos, proteínas, clorofilas, etc.), por lo tanto está presente en la mayoría de las reacciones fisiológicas y bioquímicas de todas las plantas (Clark, 1987). Lafitte y Edmeades (1987) indican que en maíz el rendimiento en grano puede reducirse 50% o menos dependiendo de la baja o alta disponibilidad de N en el suelo. Además, entre las respuestas morfológicas y fisiológicas sobresalientes del maíz al estrés por falta de N disponible en el suelo están: la reducción de la altura de la planta, disminución de la eficiencia para usar la radiación fotosintéticamente activa, aceleración de la senectud de la planta, incremento en la translocación del N para el llenado del grano y disminución de la concentración del

N en todas las partes vegetativas de la planta (Muchow, 1988a; Muchow, 1988b; Muchow y Davis, 1988).

Ceballos y Pandey (1991a, b) indican que en zonas marginales, el maíz es generalmente un cultivo secundario de subsistencia, con un pobre manejo agronómico, provisión limitada de recursos y poco uso de insumos. Aunque esta última condición puede ser benéfica, pues el productor requiere menor subsidio, puede ocurrir que al adoptar sólo parte del "paquete tecnológico", como las semillas mejoradas en lugar de los cultivares criollos, obtenga mayores pérdidas debido al uso de la tecnología subóptima con la que cuenta.

En Colombia entre 50 y 70% de las tierras de clima cálido tienen contenidos bajos o medios de materia orgánica, en general, menos de 3% (Muñoz, 1995). En un estudio realizado por Garcés y Humanez (1994), en el CI Turipaná, Cereté-Córdoba (Colombia) durante el segundo semestre de 1992, se detectaron diferencias significativas en el rendimiento de grano, peso de 1000 semillas y granos por hilera entre ocho cultivares criollos y siete mejorados cuando se desarrollaron con dosis de 45 y 180 kg de N/ha.

El objetivo del presente trabajo fue identificar líneas S_1 en poblaciones de amplia base genética y potencial de rendimiento eficiente para la utilización del nitrógeno, que puedan ser incorporadas a un programa de mejoramiento genético para la obtención final de cultivares con buenos rendimientos en condiciones de óptimo y subóptimo suministro de insumos y manejo agronómico; estos cultivares representarían una alternativa para el pequeño, mediano y gran productor.

Materiales y Métodos

El trabajo se realizó durante 1992-1993 en el CI Turipaná, Cereté-Córdoba, Colombia (8º51' latitud N, 13 msnm, 28 ºC, 1076 mm de precipitación), en suelo plano, de origen aluvial, con pendiente menor a 2%, textura franco-arcillo-limosa (FAL) y clasificado taxonómicamente como Typic-Eutropept.

Para la formación de las líneas S_1 se utilizaron como parentales los cultivares criollos CORD 320, VALL 343, VALL 380 y los comerciales ICA V106, ICA V109, ICA V156, ICA V155, ICA V258 e ICA V157 y como testigos en la evaluación de las líneas se sembraron todos los parentales y además los cultivares ICA V305, ICA V354, L237 y L238. La selección de los parentales se hizo con base en la evaluación agronómica de quince genotipos de maíz bajo dos dosis de nitrógeno: 45 y 180 kg de N/ha realizada por Garcés y Humanez (1994) en el CI Turipaná durante el segundo semestre de 1992, los cuales se sembraron en el primer semestre de 1993 en el mismo Centro de Investigaciones arriba anotado. Se hicieron todas las autofecundaciones posibles y se seleccionaron para la evaluación 298 líneas S_1 de acuerdo con el aspecto de la planta y la mazorca. Esta evaluación se efectuó con dos ensayos de rendimiento en el CI Turipaná, uno con baja disponibilidad de N y otro con fertilización nitrogenada. El primero se desarrolló en un lote que previamente se había sembrado con alta densidad de sorgo (para extraer la mayor cantidad posible de N del suelo), sin residuos vegetales, sin arar ni rastrillar, para no incorporar residuos orgánicos que pudiesen aportar nitrógeno; con las siguientes características antes de la siembra: M.O. 2.43%, pH 6.82, P 9.82 ppm, S 16.0 ppm, K 0.39 ppm, y CIC 11.90 meq/100g. A los 13 d después de la siembra se aplicó 1 g por sitio de superfosfato triple. El segundo ensayo se desarrolló en un lote con las siguientes características antes de la siembra: M.O. 1.22, pH 6.49, S 200 ppm, P 12.76 ppm, K 0.22 ppm, y CIC 11.72 meq/100g; se fertilizó 15 d después de la siembra con 1.1 g de superfosfato triple más 1.6 g de urea por sitio y a los 30 d con 1.6 g de urea por sitio, lo que correspondió a 120 kg N/ha.

El estudio se realizó bajo el diseño de bloques completos al azar con dos repeticiones por nivel de N (ambiente); se evaluó el rendimiento; días a floración femenina (DFF), altura de mazorca superior (Amz) (cm), porcentaje de desgrane (%D), índice de cosecha (IC), rendimiento biológico por planta (RB, g/plant) y coincidencia de la floración masculina y femenina (Coinf) (d).

Los datos se sometieron a análisis de varianza según la función FACTOR de MSTATC (MSTAT, 1988). Se hicieron particiones ortogonales de los grados de libertad del análisis de varianza general y se halló el coeficiente de correlación simple entre el rendimiento de grano/ha y cinco caracteres agronómicos.

Resultados y Discusión

Entre las 298 líneas S_1 se seleccionaron 25 blancas y 25 amarillas que con base en el rendimiento de grano constituyeron la fracción superior en el análisis combinado (promedio de los rendimientos con y sin adición de N; Cuadros 1 y 2); entre las blancas siete líneas fueron identificadas por su mayor rendimiento significativo en ambas condiciones de N y en el análisis combinado (Cuadro 1); además 12 de ellas fueron seleccionadas simultáneamente para el combinado y el ambiente con N, en tanto que para el ambiente con estrés de nitrógeno se seleccionaron cinco líneas S_1.

Entre las líneas amarillas 10 formaron parte de las 25 mejores líneas simultáneamente para ambas condiciones de N y el análisis combinado, nueve en el ambiente con N y cuatro en el ambiente sin N adicionado.

Con adición de N, se observó que entre las líneas el mayor rendimiento promedio de grano lo tuvo la línea amarilla CORD 320 ϕ 4 (5.2 t/ha) y el menor la línea blanca mejorada ICA V155 ϕ 18 (0.53 t/ha), además la familia CORD 320 ϕ 4 presentó dos días de diferencia entre la floración femenina y la masculina (Cuadro 3). Dentro de las líneas se observó que el rendimiento de grano osciló entre 5.1 t/ha para ICA V155 ϕ 30 e ICA V109 ϕ 15 y 0.53 t/ha para ICA V155 ϕ 18, las dos primeras tuvieron una diferencia de dos días entre la floración femenina y masculina y tuvieron el mayor índice de cosecha con 53.9 y 46.7%; únicamente dentro del grupo de líneas amarillas se encontró diferencia estadística significativa en el rendimiento de grano.

Cuadro 1. Medias de las mejores 25 líneas blancas ordenadas de mayor a menor rendimiento de acuerdo al análisis combinado de dos ambientes de nitrógeno. CI Turipaná, 1993B.

Genealogía	Rendimiento (t/ha)
ICA V155 ∅ 5	3.09
ICA V155 ∅ 30	2.95
ICA V157 ∅1	2.73
ICA V258 ∅26	2.68
ICA V157 ∅22	2.62
ICA V258 ∅20	2.61
ICA V258 ∅16	2.54
ICA V156 ∅10	2.50
ICA V258 ∅ 8	2.33
ICA V258 ∅22	2.28
ICA V258 ∅9	2.28
ICA V155 ∅36	2.24
ICA V258 ∅18	2.19
ICA V155 ∅21	2.18
ICA V157 ∅3	2.17
ICA V258 ∅13	2.17
ICA V155 ∅2	2.14
ICA V155 ∅17	2.14
ICA V155 ∅19	2.08
ICA V156 ∅45	2.07
ICA V156 ∅43	2.01
ICA V156 ∅3	2.01
ICA V155 ∅16	2.00
ICA V156 ∅23	1.98
ICA V258 ∅1	1.97
Promedio de 25 Líneas	2.32
Promedio de 298 Líneas	1.43
CV (%)	14.7

Cuadro 2. Medias de las mejores 25 líneas amarillas ordenadas de mayor a menor rendimiento de acuerdo al análisis combinado de dos ambientes de nitrógeno. CI Turipaná, 1993B.

Genealogía	Rendimiento (t/ha)
ICA V109 ∅ 15	3.12
ICA V106 ∅ 4	2.96
CORD 320 ∅ 4	2.85
VALL 343 ∅ 10	2.57
ICA V109 ∅ 6	2.47
ICA V109 ∅ 17	2.44
VALL 343 ∅ 23	2.41
VALL 343 ∅ 18	2.25
VALL 343 ∅ 2	2.23
ICA V106 ∅ 42	2.12
VALL 343 ∅ 17	1.91
ICA V106 ∅ 21	1.90
ICA V109 ∅ 53	1.89
CORD 320 ∅ 2	1.88
VALL 343 ∅ 1	1.83
CORD 320 ∅ 8	1.82
VALL 343 ∅ 13	1.81
ICA V109 ∅ 48	1.80
CORD 320 ∅ 3	1.77
ICA V106 ∅ 15	1.76
CORD 320 ∅ 14	1.76
ICA V106 ∅ 11	1.75
ICA V109 ∅ 54	1.73
ICA V109 ∅ 30	1.71
ICA V106 ∅ 1	1.71
Promedio de 25 Líneas	2.10
Promedio de 298 Líneas	1.43
CV (%)	14.7

Entre las líneas blancas ICA V155 ϕ 30 tuvo el mayor rendimiento promedio (5.20 t/ha) y el más bajo la línea ICA V155 ϕ 18 (0.53 t/ha); además, entre las 25 líneas del Cuadro 1 la mayor y menor frecuencia correspondió a los genotipos mejorados ICA V155 e ICA V258 con nueve familias S_1 y al cultivar criollo VALL 380 con una línea S_1. En el grupo de líneas amarillas el rendimiento de grano osciló entre 5.20 y 0.65 t/ha para la familia criolla CORD 320 ϕ 4 y la familia mejorada ICA V106 ϕ 43, respectivamente. Dentro de la fracción superior de 25 líneas ordenadas de mayor a menor rendimiento la más alta y baja frecuencia correspondió a los genotipos ICA V109 con 11 líneas S_1 y CORD 320 e ICA V106 con tres líneas S_1 cada uno. Es importante resaltar que la frecuencia de líneas amarillas fue prácticamente igual para los cultivares mejorados y los criollos con 14 y 11, respectivamente,

Cuadro 3. Rango de medias para siete caracteres agronómicos observados en 298 líneas S_1 de maíz evaluadas con fertilización normal de N, ordenadas de acuerdo al mayor y menor rendimiento de grano. CI Turipaná, 1993B.

Genealogía	Líneas 1/	Rend. (t/ha)	IC	%D	AMz	DFF	Coinf.	RB (g/pl)
ICA V155 ∅ 30	LVMB NS	5.10	53.9	0.86	72	54	2	175.52
ICA V155 ∅ 18	LVMB	0.53	18.4	0.61	60	58	3	116.50
Testigo 2/		6.10	50.7	0.82	73	52	1	267.17
ICA V109 ∅ 15	LVMA *	5.14	46.7	0.84	96	54	2	226.63
ICA V106 ∅ 43	LVMA	0.65	25.6	0.60	45	57	2	138.11
Testigo 2/		6.10	48.8	0.81	91	54	1	301.27
VALL 380 ∅ 13	LVCB NS	3.10	41.6	0.76	141	56	1	116.50
VALL 380 ∅ 15	LVCB	0.72	37.6	0.72	94	62	5	142.79
Testigo 2/		3.40	50.3	0.86	141	58	2	149.23
CORD 320 ∅ 4	LVCA	5.20 **	38.3	0.82	100	60	2	259.25
VALL 343 ∅ 15	LVCA	1.09	30.6	0.77	60	57	1	75.09
Testigo 2/		3.10	49.9	0.88	106	55	1	187.06
Testigo general 3/		6.10	52.6	0.88	73	52	1	301.27

1/ LVMB Líneas de variedades mejoradas blancas
LVMA Líneas de variedades mejoradas amarillas
LVCB Líneas de variedades mejoradas blancas
LVCA Líneas de variedades mejoradas amarillas
2/ Mejor testigo parental relativo por grupo
3/ Mejor testigo general nivel de nitrógeno
**, * Significancia al 1 y 5% de probabilidad respectivamente; NS No significativo (Comparación de medias de rendimiento arriba y de bajo de los símbolos).

Cuadro 4. Rango de medias para siete caracteres agronómicos observados en 298 líneas S_1 de maíz evaluadas en ambiente con estrés de N, ordenadas de acuerdo al mayor y menor rendimiento de grano. CI Turipaná, 1993B.

Genealogía	Líneas 1/	Rend. (t/ha)	IC	%D	AMz	DFF	Coinf.	RB (g/pl)
ICA V258 ∅ 18	LVMB NS	2.20	48.8	0.77	46	69	7	102.50
ICA V258 ∅ 19	LVMB	0.13	7.5	0.34	39	68	3	31.50
Testigo 2/		1.87	42.0	0.85	37	60	2	115.03
ICA V106 ∅4	LVMA NS	1.78	46.1	0.78	51	64	4	94.67
ICA V109 ∅ 39	LVMA	0.17	12.7	0.73	41	66	1	28.00
Testigo 2/		1.55	42.0	0.78	47	61	2	87.26
VALL 380 ∅ 7	LVCB NS	1.44	46.2	0.79	35	66	3	71.50
VALL 380 ∅ 4	LVCB	0.31	22.1	0.61	78	66	4	30.50
Testigo /2		0.34	15.4	0.64	69	68	4	45.50
VALL 343 ∅ 19	LVCA NS	1.75	45.1	0.83	45	67	5	90.75
VALL 343 ∅ 24	LVCA	0.32	11.9	0.63	57	63	3	54.83
Testigo 2/		1.34	48.8	0.80	65	63	3	115.75
Testigo general 3/		1.87	48.8	0.85	37	60	2	115.75

1/ LVMB Líneas de variedades mejoradas blancas
LVMA Líneas de variedades mejoradas amarillas
LVCB Líneas de variedades criollas blancas
LVCA Líneas de variedades criollas amarillas
2/ Mejor testigo parental relativo por grupo
3/ Mejor testigo general nivel de nitrógeno
NS No significativo (Comparación de medias de rendimiento arriba y de bajo de los símbolos).

y entre los cultivares criollos destacó la colección VALL 343 con ocho líneas S_1.

En el ambiente con estrés de N (Cuadro 4), se observó que entre las 298 líneas S_1, el rendimiento de grano osciló entre 2.2 t/ha y 0.13 t/ha para las familias blancas de variedades mejoradas ICA V258 ϕ 18 e ICA V258 ϕ 19, respectivamente, la primera destacó también por su mejor índice de cosecha (48.8%), mayor rendimiento biológico y una diferencia entre floración femenina y masculina de siete días, y de todas la última es una característica agronómica indeseable.

Dentro de los cultivares criollos y las líneas blancas y amarillas hubo fluctuaciones del rendimiento entre 1.75 (VALL 343 ϕ 19) y 0.3 (VALL 380 ϕ 4), 2.2 (ICA V258 v 18) y 0.13 (ICA V258 ϕ 19) y 1.78 (ICA V106 ϕ 4) y 0.17 t/ha (ICA V109 ϕ 39), respectivamente, pero esas diferencias no resultaron estadísticamente significativas. Además, entre las 25 líneas que constituyeron la fracción superior del rendimiento de grano, la mayor frecuencia correspondió a la variedad mejorada ICA V156 con 10 líneas S_1 y la menor a la colección criolla VALL 380 con una línea S_1, en las líneas amarillas correspondió a la variedad mejorada ICA V109 con 13 familias S_1 y la menor al genotipo criollo CORD 320 con una familia S_1, observándose que la frecuencia de líneas mejoradas fue ampliamente superior a la de líneas criollas con 19 y seis familias respectivamente, sobresaliendo dentro de los genotipos criollos la colección VALL 343 con cinco líneas S_1.

El análisis combinado (Cuadro 5) mostró que dentro del conjunto de 298 líneas el rendimiento de grano resultó estadísticamente diferente entre todos los grupos de familias S_1 y osciló entre 3.12 y 0.42 t/ha para la línea amarilla mejorada ICA V109 ϕ 15 y la línea blanca mejorada ICA V156 ϕ 16.

Dentro de las líneas S_1 provenientes de los cultivares criollos el rendimiento de grano varió de 2.85 a 0.57 t/ha para las familias CORD 320 ϕ 4 y VALL 380 ϕ15, respectivamente. En la fracción superior (Cuadro 1) de 25 líneas blancas el rendimiento de grano osciló entre 3.09 y 1.97 t/ha para las líneas ICA V155 f 5 e ICA V258 ϕ 1, respectivamente, y la mayor y menor frecuencia correspondió a las variedades mejoradas ICA V258 e ICA V157 con nueve y tres líneas S_1, respectivamente, y no quedó incluida ninguna familia proveniente de los cultivares criollos.

Cuadro 5. Rango de medias para siete caracteres agronómicos observados en 298 líneas S_1 de maíz, ordenadas de acuerdo al mayor y menor rendimiento de grano, datos del análisis combinado de dos ambientes de N. CI Turipaná, 1993B.

Genealogía	Líneas 1/	Rend. (t/ha)	IC	%D	AMz	DFF	Coinf.	RB (g/pl)
ICA V155 ∅ 5	LVMB	3.09 **	46.1	0.78	72	58	2	146.10
ICA V156 ∅ 16	LVMB	0.42	13.1	0.52	62	62	3	68.62
Testigo 2/		3.90	46.3	0.81	60	58	2	191.03
ICA V109 ∅ 15	LVMA	3.12 **	33.5	0.80	76	60	4	162.73
ICA V109 ∅ 39	LVMA	0.50	17.1	0.63	54	62	0	59.96
Testigo 2/		3.70	42.6	0.79	74	58	1	194.27
VALL 380 ∅ 13	LVCB	1.85 **	39.7	0.70	111	63	4	96.06
VALL 380 ∅ 15	LVCB	0.57	35.8	0.77	73	65	4	36.19
Testigo 2/		1.90	32.8	0.75	105	63	3	97.36
CORD 320 ∅ 4	LVCA	2.85 **	31.8	0.73	76	67	6	151.37
VALL 343 ∅ 22	LVCA	0.87	26.8	0.72	53	59	2	68.00
Testigo 2/		2.10	49.3	0.84	85	59	1	151.40
Testigo general 3/		3.90	49.3	0.84	60	57	1	194.27

1/ LVMB Líneas de variedades mejoradas blancas
LVMA Líneas de variedades mejoradas amarillas
LVCB Líneas de variedades criollas blancas
LVCA Líneas de variedades criollas amarillas
2/ Mejor testigo parental relativo por grupo
3/ Mejor testigo general nivel de nitrógeno
** Significancia al 1% de probabilidad (Comparación de medias de rendimiento arriba y de bajo de los símbolos).

Cuadro 6. Coeficiente de correlación del rendimiento de grano con cinco caracteres agronómicos, datos del análisis combinado de dos ambientes de nitrógeno. CI Turipaná, 1993B.

Caracteres agronómicos	Todos los genotipos	Líneas 1/	LVM	LVMB	LVMA	LVC	LVCB	LVCA	Testigos
AMz	0.68**	0.67**	0.71**	0.72**	0.72**	0.63**	0.63**	0.71**	0.68**
DFF	-0.60**	-0.60**	-0.60**	-0.61**	-0.61**	-0.62**	-0.67**	-0.61**	-0.78**
RB/planta	0.91**	0.90**	0.90**	0.90**	0.90**	0.90**	0.91**	0.90**	0.95**
IC	0.70**	0.70**	0.73**	0.73**	0.74**	0.58**	0.53**	0.59**	0.69**
%D	0.44**	0.46**	0.45**	0.45**	0.49**	0.51**	0.53**	0.50**	0.49**

** Significancia al 1% de probabilidad

1/ LVM Líneas de variedades mejoradas
LVMB Líneas de variedades mejoradas blancas
LVMA Líneas de variedades mejoradas amarillas
LVC Líneas de variedades criollas
LVCB Líneas de variedades criollas blancas
LVCA Líneas de variedades criollas amarillas

Entre las mejores 25 líneas amarillas (Cuadro 2) el rendimiento del grano varió entre 3.12 y 1.71 t/ha en las familias mejoradas ICA V109 ϕ 15 e ICA V106 ϕ 1, y la mayor frecuencia de líneas correspondió a los genotipos VALL 343 e ICA V109, con siete y la menor al cultivar criollo CORD 320, con cinco.

Según los resultados del Cuadro 6 el rendimiento de grano para el conjunto de líneas evaluadas presentó la más alta asociación con rendimiento biológico/planta y con el índice de cosecha con valores de r = 0.90 y 0.70, respectivamente.

Conclusiones

1. La respuesta diferencial de las líneas S_1 a la fertilización nitrogenada observada permite inferir que tanto los cultivares criollos como los mejorados pueden aportar buenas líneas en uno u otro ambiente, esto amplía la posibilidad del mejoramiento genético para aumentar la

frecuencia génica y seleccionar genotipos tolerantes a la limitada disponibilidad de N en el suelo y eficientes en su uso.

2. Los caracteres más importantes en el mejoramiento del rendimiento de las líneas S_1 con y sin estrés de N son: a) rendimiento biológico por planta con y sin estrés de N, b) índice de cosecha en condiciones de estrés de N y c) altura de mazorca en condiciones normales de N en el suelo.
3. La mayor frecuencia de líneas S_1 con y sin estrés de N encontrada en el cultivar criollo VALL 343 de acuerdo con el rendimiento de grano, indica que es la que posee mayores posibilidades para el mejoramiento, dentro de los tres cultivares criollos evaluados en el presente estudio.

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What is Yield?

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Abstract

During the past 70 years, genetic yielding ability of maize hybrids adapted to central Iowa (USA) has increased at a linear rate of about 74 kg/ha/yr, according to trials conducted during 1991-1994. Comparisons of 36 widely grown hybrids released at intervals from 1934 to 1991 show continuing improvements in tolerance to abiotic and biotic stresses such as heat and drought, excessively cool and wet weather, low soil fertility, high density planting, root and stalk rot, and European corn borer (Ostrinia nubilalis). The hybrid series also exhibited linear increases in erect leaf habit and grain starch percent, and a linear decrease in grain protein percent. These continuing changes in plant architecture and grain composition conceivably can increase efficiency of grain production under stresses of high density planting, unfavorable weather, or low soil fertility. Maximum yield potential per plant has neither increased nor decreased during the past 70 years, as measured on non-stressed plants grown at very low densities (1 plant/m^2). Results of the 1991-1994 trials agree with the hypothesis that increased grain yielding ability of widely successful maize hybrids for central Iowa is due primarily to improved tolerance of abiotic and biotic stresses, coupled with maintenance of the ability to maximize yield per plant under non-stress growing conditions.

During the past 70 years, maize breeders at Pioneer Hi-Bred International, Inc., have continually altered hybrid genotypes for better adaptation to central Iowa soils and climate, and to changing farming practices. Breeding started in the mid-1920s, and continues today. Since the beginning, the goal of breeders has been to produce hybrids with more grain yield potential, greater stability of yield, and with plant and grain traits desired by farmers and end-users.

The goal of the experiment reported herein is to measure the rates of improvement (if any) in traits the breeders intended to change and to look for changes that also may have occurred in other traits. Measuring and characterizing the changes can help breeders to understand in detail how they have changed the genetic yield potential of the maize plant during the past 70 years, and may help them as they plan future courses of action to increase yield and dependability of hybrid maize. This experiment is one of a continuing series. It complements similar experiments on hybrid maize conducted by other researchers in Iowa and elsewhere (Castleberry et al., 1983; Derieux et al., 1987; Duvick, 1977; Duvick, 1984; Duvick, 1992; Eyhérabide et al., 1994; Russell, 1991; Tollenaar, 1991).

Materials and Methods

Performance trials of 36 hybrids released consecutively during the years 1934-1991 and one open-pollinated variety typical of farm use in 1930 (Table 1) were conducted in central Iowa in 1991-1994. All hybrids were developed and released by Pioneer Hi-Bred International, Inc. Each hybrid was widely grown in central Iowa in its time. In each season, trials were planted in three locations in central Iowa, at three densities (30, 54 and 79 thousand plants/ha), one replication per density. The lowest density was

Table 1. List of hybrids and year of release. RYD = Reid Yellow Dent, an open-pollinated variety.

Hybrid	Year	Hybrid	Year	Hybrid	Year
RYD	1930	301B	1952	3517	1971
351	1934	354	1953	3366	1972
307	1936	329	1954	3301A	1974
317	1937	354A	1958	3529	1975
330	1939	328	1959	3541	1975
336	1940	3618	1961	3382	1976
340	1941	3306	1963	3377	1982
339	1942	3376	1965	3378	1983
344	1945	3390	1967	3475	1984
352	1946	3571	1968	3379	1988
350B	1948	3334	1969	3362	1989
347	1950	3388	1970	3417	1990
				3394	1991

typical for central Iowa in the 1930s, the middle density was typical of the 1960s, and the highest density was typical for maize grown on the best land in the 1990s. Plots consisted of 2 rows 0.76 m apart and 6.3 m long. Scores and counts were taken for several agronomically important traits, as well as for other traits of interest. In 1992 grain samples were saved for chemical analysis. Additional locations were planted in 1993 to provide plants for measurement of harvest index, and in 1992 and 1994 for artificial inoculation or infestation to provide special disease and insect ratings. Data also are presented for trials of a subset of the 36 hybrids in this experiment, grown in several midwestern states in 1978. They compared performance of the hybrids at two levels of nitrogen fertilization: 90 and 269 kg N / ha.

Results

Trial results show that during the past 70 years genetic yielding ability of hybrids adapted to central Iowa has improved at a linear rate of about 74 kg / ha / yr (Fig. 1). Linear improvements in yield were exhibited in each year of the test (Fig. 2). Growing conditions varied markedly among seasons: 1991 was too hot and dry, 1993 was too cold and wet, and 1992 and 1994 were nearly ideal for high grain yield. All three trial locations were affected by drought in 1991 and water-logging in 1993. Rate of improvement in yield was greatest in high yield seasons and least in low yield seasons (Fig. 2), and greatest at high plant density and least at low plant density (Fig. 3). The hybrids showed linear improvement in grain yield when subjected to drought, water-logged soils, soils deficient in nitrogen (Table 2), or conditions promoting maximum yields. They showed linear improvements in resistance to root lodging, premature death and stalk rot, second generation European corn borer (*Ostrinia nubilalis*), the stresses of high density planting, and stress-induced silk delay and barrenness. The hybrids have shown linear reductions in tassel size. Since about 1960 they have shown a linear reduction in grain protein percentage and linear increases in leaf erectness, harvest index and grain starch percentage. There was little or no change over time in growing degree units to anthesis, grain moisture percent at harvest, plant and ear height, leaf number per plant, leaf area per plant, fodder weight per plant, grain test weight, grain oil percent, resistance to

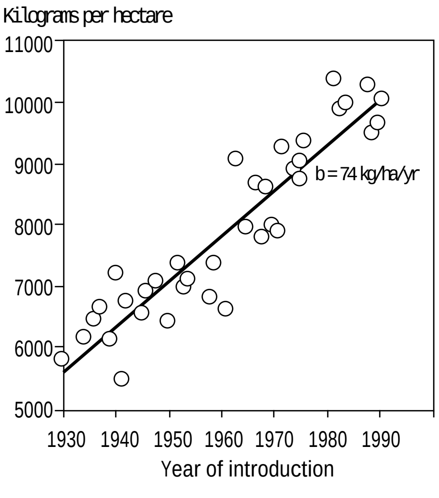


Figure 1. Grain yield per hybrid regressed on year of hybrid introduction. Averages of four years, three locations and three densities per year. Yield per hybrid is that for the planting density giving highest average yield, and was used when fitting the regression. The 1930 entry is Reid Yellow Dent, an open-pollinated variety.

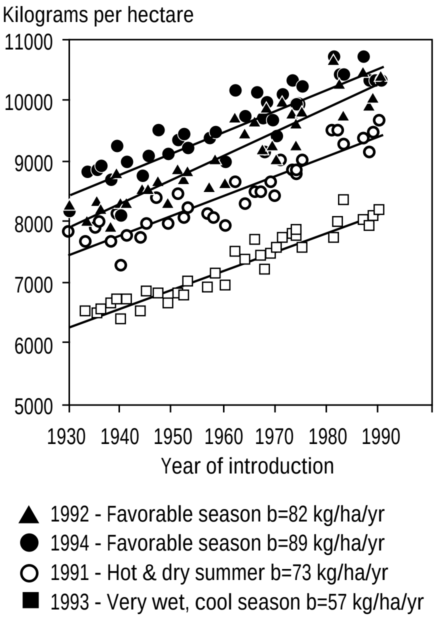
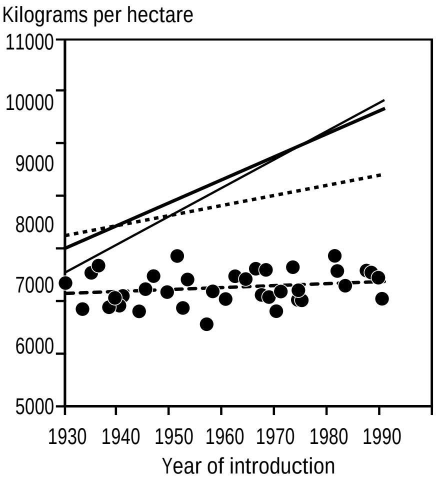


Figure 2. Grain yield per hybrid regressed on year of hybrid introduction in four separate years, 1991-1994. Yields are averages of three densities: 30, 54, and 79 thousand plants/ha. Yield per hybrid is for the density with highest average yield, and was used to fit the regression for each year.



Density	r^2	b
79 k pl/ha	0.86	110 kg/ha/yr
54 k pl/ha	0.80	88 kg/ha/yr
30 k pl/ha	0.56	39 kg/ha/yr
10 k pl/ha	0.06	9 kg/ha/yr

Figure 3. Grain yield per hybrid regressed on year of hybrid introduction at each of four planting densities, namely 10, 30, 54 and 79 thousand plants/ha. Data are from three locations, 1994.

leaf feeding by first generation of European corn borer, or resistance to Northern Corn Leaf Blight (*E. turcicum*). There was no increase in grain yield over time when hybrids were grown at very low densities (1 plant / m^2). Hybrids differed significantly in yielding ability at the very low density, but yield differences were not associated with year of hybrid release (Fig. 3). Planting at very low density reduces stress to a minimum and allows maximum grain production per plant.

Discussion

Results of this experiment agree with the hypothesis that increased stress resistance is the primary cause of increased yielding ability of hybrids developed for central Iowa during the past 70 years. A secondary cause of increased yielding ability appears to be changes that increase efficiency of grain production; e.g., smaller tassels and reduced grain protein percent. Maximum grain production per plant in the absence of stress was unchanged. The newer hybrids, therefore, can still produce increased amounts of grain per plant when growing conditions are better than average; i.e., breeding for stress tolerance has not reduced ability to maximize yield in the absence of stress. Many or most of the changes measured were for traits not subject to direct selection by breeders; the changes seem to have been produced by indirect selection. They probably are a consequence of intense selection for superior yielding ability over a broad spectrum of on-farm growing conditions; i.e., for dependable high yield.

It probably is important to note that each hybrid in this experiment proved its worth in its era on thousands of farms during a period of several years, each of these years differing in the nature of the stress experienced. This is why each of them was a sales leader. Many other hybrids with equally good records in the breeders' yield trials were released at the same time as these successful hybrids, but they failed to stand up under large-scale, rigorous, multiple-season tests.

Several traits did not change over time. They are of two kinds: those which the breeders intentionally held constant, such as plant height and grain moisture at harvest, and those which stayed constant in the absence

Table 2. Regressions (b) of trait on year of introduction of 36 hybrids and one open-pollinated variety, introduced from 1930 to 1991, and evaluated in trials 1991-1994.

Trait	Years	Density (',000 ha^{-1})	b	r^2
Grain yield	1978	{269 kg N}	+53 kg/ha/yr	0.59
Grain yield[†]	1978	{90 kg N}	+66 kg/ha/yr	0.84
Leaf angle score	1991-4	30, 54, 79	+1.0 score/10 yr	0.65
Non-tillered plants, %	1992 & 4	30, 54, 79	+4%/10 yr	0.48
Tassel weight	1992	30, 54, 79	-0.5 gm/10 yr	0.70
Tassel branch no.	1992	30, 54, 79	-2.5 branch/10 yr	0.66
Staygreen score[‡]	1991-4	30, 54, 79	+0.6 score/10 yr	0.66
Not stalk-lodged, %	1991-4	30, 54, 79	+3%/10 yr	0.68
Not root-lodged, %	1991-2	30, 54, 79	+9%/10 yr	0.66
ECB2 damage score	1992 & 4	30, 54, 79	+0.5 score/10 yr	0.58
ECB2 tunnel length	1992	30, 54, 79	-0.6 in./10 yr	0.46
Silk delay GDU	1991-4	30, 54, 79	-6 GDU/10 yr	0.61
Ears per 100 plants	1992 & 4	30, 54, 79	+2 ears/10 yr	0.74
Rows per ear	1992	30, 54, 79	-0.5 row/10 yr	0.36
Kernels per row	1992	30, 54, 79	+0.4 kernels/10 yr	0.06
Kernels per ear	1992	30, 54, 79	-11 kernels/10 yr	0.11
100 Kernel weight	1992	30, 54, 79	+0.7 g/10 yr	0.31
Grain protein, %	1992	30, 54, 79	-0.3%/10 yr	0.68
Grain starch, %	1992	30, 54, 79	+0.3%/10 yr	0.56
Harvest index, %	1993	10, 54	+1%/10 yr	0.42
50% silk, GDU	1991-4	30, 54, 79	-5 GDU/10 yr	0.16
50% anthesis, GDU	1991-4	30, 54, 79	+1 GDU/10 yr	0.01
Plant height	1991-4	30, 54, 79	-2 cm/10 yr	0.23
Ear height	1991-4	30, 54, 79	-3 cm/10 yr	0.33
Ear node	1992	30, 54, 79	+0.1 node/10 yr	0.05
Leaf area/plant	1992	30, 54, 79	-16 cm^2/10 yr	0.00
Fodder weight/plant	1993	10, 54	+12 gm/10 yr	0.00
NLB score	1994	30, 54, 79	+0.7 score/10 yr	0.34
ECB1 leaf feed score	1994	30, 54, 79	+0.3 score/10 yr	0.19
Grain oil, %	1992	30, 54, 79	-0.0 %/10 yr	0.07
Test weight	1991-4	30, 54, 79	+0.2 lb/10 yr	0.10

[†] Yield under low nitrogen level was 77% of high N level yield in 1940 hybrids, and 88% of high N level in 1976 hybrids.

[‡] Staygreen: small scores are for rapid leaf senescence; large scores for delayed leaf senescence.

Abbreviations

GDU = growing degree units, °Cd

ECB = European Corn Borer (1 and 2 represent first and second generation)

NLB = Northern Corn Leaf Blight

of breeder attention, such as grain oil percent and resistance to leaf feeding by first generation European corn borer. One can speculate that grain oil percent stayed constant because of a minimum threshold requirement for kernel germination, and first generation corn borer resistance stayed constant because first generation borer damage in Iowa during the past 70 years, on average, caused little or no reduction in grain yield.

Future breeding plans should take into account the high probability that little or no additional reduction can be tolerated in such traits as grain protein percent or reduced tassel size, and little more progress can be made in the upright leaf habit; thus it seems likely that no further help in increasing grain yield can be expected from continued change in these traits. The best way to effect future gains in yielding ability may be to make further improvements in tolerance to high plant densities, in combination with improvements in potential yield per plant under low stress environments. Continuing yield gains also can be expected by selecting for better resistance to second (and perhaps first) generation European corn borer, and by making improvements in internal physiological traits conferring heat and drought tolerance.

Results of this retrospective experiment agree with the generally accepted premise that widespread yield testing over several years in the intended area of adaptation appears to be the best way to select for hybrids with multiple-stress resistance; i.e., hybrids with higher yield and greater dependability (Baker, 1955). Breeder trials and farmer trials (on-farm “strip tests”) are equally essential for achieving this end. However, trials conducted at multiple plant densities (e.g., high, low, and normal densities), or in specially chosen environments such as low fertility, drought, insect infestation, or disease inoculation are also very useful, and sometimes essential. They will help the breeder to characterize hybrids and identify breeding stocks with specific desirable or undesirable traits.

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Choices among Breeding Procedures and Strategies for Developing Stress Tolerant Maize Germplasm

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Abstract

Abiotic stresses, particularly those related to water and nitrogen, are widely distributed and may occur at practically all stages of crop growth. Improvement efforts through breeding are rather limited for such traits, and perhaps only international agricultural research centers, the larger private seed companies, and a few strong national programs have the necessary resources and manpower to pursue such research efficiently. In the absence of major genes, the breeding of such traits is difficult, and requires some skill in managing selection environments. Variation for stress traits has been observed in maize populations under improvement by recurrent selection, as well as among inbred lines and hybrids derived from those populations. Recurrent selection procedures for improving stress tolerance characteristics have been successfully demonstrated. Choices among various kinds of breeding procedures appropriate at different stages of the improvement process are outlined, with the appropriate time to switch from one procedure to another indicated. The merits and drawbacks of procedures involving testers in intensifying such traits are discussed. The usefulness of selecting for hybrid-oriented features in stress-tolerant populations is emphasized, as tolerance to inbreeding is itself a valuable source of general stress tolerance. The integration of selection for stress tolerance traits in the on-going improvement process is emphasized. Relative efficiency and cost-effectiveness of recurrent selection procedures are compared with evaluating elite germplasm (particularly inbreds). Results to date suggest that alleles related to stress tolerance are present in most elite maize populations (and hence in any group of inbred lines) at a relatively low frequency, and that controlled stress environments play a key part in their identification. Efficient inbred line development procedures will be indicated, and alternate strategies involving inbreeding at high plant density will be suggested to improve secondary traits known to increase stress tolerance. Finally, cost-effective procedures and strategies most appropriate for breeders operating in developing countries are emphasized.

The priority given abiotic stresses, particularly drought and low nitrogen, has increased in recent years because of increasing incidence of such stresses in tropical maize growing areas. However, it is only in the last two decades that systematic efforts to tackle such problems have begun in force. Due to the complex nature of the stresses, a proper understanding of factors resulting in the superior performance of stress-tolerant genotypes may still be far off, and several issues, particularly related to whether breeding should be done under non-stress, stress or both environments are still being debated. There is wide agreement that yield selection under stress is less efficient than under non-stress conditions, mainly because of a decline in heritability of yield under stress (Blum, 1988), so breeders will often select under both non-stress and stress conditions. Efforts directed toward improving stress tolerance in tropical maize are rather limited, mostly concentrated at CIMMYT, IITA and a few strong national maize programs.

Drought stress is unpredictable, occurring with variable intensity at any crop development stage from germination to physiological maturity, and varying by year. The most critical stage in maize for drought stress is at flowering.

Depending upon the severity, seed set and thus yield can be reduced considerably. Low nitrogen stress, on the other hand, is more predictable, since farmers normally have some prior knowledge of soil nitrogen status. A breeder has the option of applying uniform minimum rates of N to create testing environments that discriminate among genotypes. Developing stress-tolerant cultivars requires strategies and experience in managing stress environments to maximize genetic gain for desired traits.

Avoiding and Managing Stresses

In general, mechanisms that help avoid stress should be exploited wherever possible, such as intra-cultivar variability in flowering date. Some genotypes can avoid a short period of stress at flowering and / or terminal drought stress because they flower and mature early. Many management options can also be employed to minimize the effects of stress. For example, crop residues and (in China) plastic mulch have been used to diminish drought during early plant development. An important part of the solution for resource-poor farmers, however, lies in developing cultivars tolerant to stress.

Strategies for Developing Stress-Tolerant Maize Germplasm

The choice of germplasm development strategies depends largely on the breeding program's circumstances, including: available selection environments, ability to control / manage stress, availability of off-season nurseries, adequately trained personnel to conduct quality research, and the possession of necessary equipment to take measurements. We discuss options as direct, indirect, alternate or integrated strategies.

Direct strategies

These involve selection for stress tolerance under specific abiotic stress conditions. Accordingly, drought selection requires testing at rain-free sites so that drought can be managed with irrigation, or sites where testing nurseries can be planted to take advantage of reliable periods of drought. Generally, main growing seasons are rainy seasons and are not useful for drought research work. CIMMYT's drought stress research relies heavily on one dry winter site and another dry hot summer site. When using a direct strategy it is important to evaluate germplasm at more than one stress level. CIMMYT breeders and physiologists prefer to conduct selection work under three water regimes differing in severity of water deficit, partly to reduce the risk of stressing the crop too severely, and partly because selected genotypes need to perform well under both stress and non-stress conditions. If stress is too severe at flowering the value of yield data is sharply reduced since many entries yield nothing. Low N stress is more easily managed than drought stress and can be manipulated by either depleting or adding nitrogen. CIMMYT's physiology and stress breeding groups have largely utilized direct strategies in their low N tolerance work in lowland tropical germplasm grown in low and high N environments at the Poza Rica Experiment Station.

Indirect strategies

Indirect strategies do not involve planned selection under managed stress conditions. Instead, elite germplasm is characterized under randomly occurring stress conditions with the expectation that tolerance to the specific stress will be present in the source germplasm, albeit at low frequency. Lines, hybrids and open-pollinated varieties (OPVs) are commonly evaluated at multiple locations in the expectation that they will be exposed to stress occurring randomly through the life cycle and at random levels of intensity at one or more locations during this testing process. The expectation is that the selection is affected by this stress and that some level of tolerance will be found in selected elite germplasm.

Alternate strategies

These aim to select genotypes with good general tolerance to stress, but do not involve purposeful selection for tolerance to a specific stress. This stems from the discovery of a number of lines tolerant to drought and low N that were developed by selecting and inbreeding under high plant density conditions. Inbreeding has also served as a very useful tool for maize improvement. It provides a tough screen — by the time a high level of inbreeding is reached, only a limited number of genotypes have survived the process. Inbreeding depression is manifested as reduced plant development and vigor and diminished reproductive performance as a result of delayed silking, lengthened anthesis-silking interval (ASI), poor seed set and lower seed weight. Many abiotic stresses manifest a similar set of plant responses. If inbreeding functions as a general stress, then selection for tolerance to inbreeding may lead to improved general performance under a variety of stresses. Similarly, high density reduces plant performance, and high density plantings are good for selecting for reduced barrenness and lodging, and shorter ASI. Troyer and Rosenbrook (1983) reported that the superior performance of inbreds under high plant density was also observed as superior performance under high densities of hybrids derived from such lines. Selection under this stress may improve general stress tolerance as well. Both inbreeding and high plant density can easily be incorporated into a breeding program, as neither requires a specific testing environment, and the major risk a breeder runs is that of losing materials to lodging, if rain and high winds are encountered (although, if the densities are too high, poor seed set occasionally results and a generation of advance is lost).

The diminished performance associated with inbreeding and high plant density conditions renders genotypes more susceptible to other stresses. This can be seen when inbreds and hybrids are planted side by side in the same field: inbreds are normally the first to show signs of stress. Thus unplanned or low levels of the target stress can be used as screening tools. High plant density may be particularly useful for augmenting selection for drought and low N tolerance. There are other advantages to working with inbred germplasm and high plant density. Inbred lines are easier to evaluate because they are more uniform than some types of full-vigor germplasm, and in addition they are true breeding.

Integrated strategies

These involve improvement of stress traits as part of on-going population and hybrid research activities. This may require modifying schemes slightly and introducing one or more stages within an improvement cycle where the progenies can be evaluated specifically for such stresses. The advantage of integrated strategies lies in not only improving stress traits but also yield and other agronomic traits through multilocation testing.

Transferring Stress-Tolerant/ Resistant Traits

Transferring drought and low N-tolerance traits from one genotype to another is complex, since no major genes have been encountered to date, and polygenic transmission is likely the rule rather than the exception. Selection in segregating generations requires a stress environment, uniform field conditions, and additional resources and expertise presently lacking in most national programs. An important alternative to transferring such traits is the selection for increased frequency of alleles conferring stress tolerance.

Traits Contributing to Stress Tolerance

Two traits which are strongly related to yield under stress are anthesis-silking interval (ASI) and ears per plant (EPP). The maize reproductive system is quite distinct because of the separation of male and female inflorescences. Although this provides advantages, such as ease in controlling pollination and in generating seed quantities suitable for research and commercial production, the separation of reproductive organs may also account for the crop's unusual susceptibility to stress at flowering. When assimilate supply is limited under stress it is usually preferentially distributed to the tassel at the ear's expense, leading to poor pollination and partial or complete failure in seed set. This occurs with practically all kinds of stress, including drought, low soil N and P, excess moisture, low soil pH, iron deficiency, pre-flowering biotic stress and high plant density. A primary objective of any maize breeding effort should be to improve robustness in reproductive behavior under stress, and ASI is a good indicator of reproductive fitness. It is an easy trait to measure in the field, and is being used by many breeding programs. Nevertheless, underlying factors and causes need to be better understood. Ear number per plant is the component of yield most commonly affected by stress. However, there are some practical concerns regarding its use. Very poor seed set is common under stress, leading to confusion regarding what threshold (e.g., presence or absence of grains, versus some minimum acceptable nubbin size) to accept for including an ear in a count. Furthermore, the maize plant can compensate for seed and ear number by adjusting kernel weight and hence its shelling percentage. Though shelling percentage is needed for accurate estimates of yield under stress, unfortunately this information is time consuming and expensive to collect.

The types of progenies evaluated affect the rate of improvement and the ability to discriminate among genotypes for stress tolerance. Our experience suggests that selfed progenies are preferred over non-inbred progeny, because heritabilities increase with levels of inbreeding (see Bolaños and Edmeades, 1997). As noted previously, inbreeding renders genotypes more susceptible to stress and selection becomes less difficult. Under drought, for example, inbreeding increases the frequency of progenies with increased ASI (Fig. 1), making selection for short ASI somewhat easier.

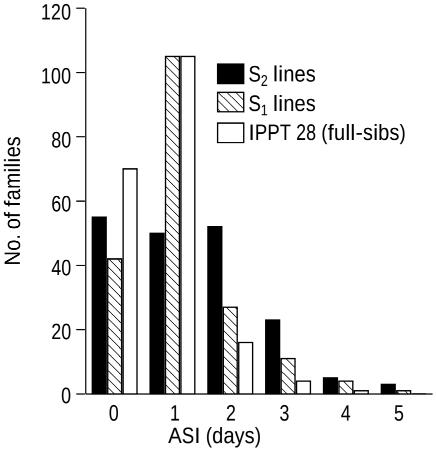

Figure 1. Distribution of anthesis-silking interval among full-sib, S_1 and S_2 progenies of Population 28 C_{10} when evaluated under drought which coincided with flowering.

Genetic Variation and Identification of Germplasm Tolerant to Drought and N Stress

Genetic variation is the key to effective improvement of any trait. Variation for both drought and low N tolerance has been encountered in all types of germplasm including OPVs, hybrids and inbred lines (Balko and Russell, 1980; Russell, 1984; Bolaños and Edmeades, 1993; Lafitte and Edmeades, 1994; Edmeades et al., 1995; Jensen, 1995, Smith et al., 1995).

CIMMYT's maize physiology group in Mexico has successfully improved several tropical maize populations for both drought and low N tolerance. In addition, the same group has formed two drought tolerant populations, DTP1 and DTP2, which have performed quite well in international experimental variety trials (see papers by Edmeades and co-workers, these proceedings, for further details).

CIMMYT's lowland tropical maize subprogram in Mexico has used indirect strategies to evaluate and identify sources of stress tolerant germplasm, particularly inbred lines and hybrids. Much of its screening work was done in close collaboration with the stress physiology group, and a sample of results is presented here. During the dry season at Tlaltizapán several promising hybrids were evaluated under intermediate stress during the 1994A and 1995A seasons. Results from a white single-cross hybrid trial conducted in 1994A and a yellow single-cross hybrid trial in 1995A are presented in Tables 1 and 2.

Table 1. Results of an evaluation of white grain, single-cross maize hybrids under drought stress, Tlaltizapán, 1994A.

Entry	Pedigree	Yield (t/ha)	ASI (d)	Ear aspect	Ears /plant
13	[(P24MH119 x 54) (S7)] / [POB21HC218 (S9)]	7.21	0.5	2.0	0.95
17	[(POB21HC114 x 38) (S7)] / [POB22TSR (S8)]	6.46	0.5	1.3	1.00
6	[POB29HC17 (S8)] / [POB21HC218 (S10)]	6.39	0.0	2.5	0.95
18	[(POB21HC114 x 38) (S7)] / [(AC7643 x 43) (S7)]	6.35	1.0	2.0	0.95
1	[POB21HC219 (S10)] / [POB43HC26 (S8)]	6.06	3.0	2.5	1.00
11	[(AC7643 x PR7722) (S7)] / [(POB21 x 21) (S7)]	5.96	0.5	2.5	0.95
12	[(AC7643 x PR7722) (S7)] / [POB21MH125 (S8)]	5.91	3.0	2.5	0.95
3	[POB21HC219 (S10)] / [POB29HC25 (S7)]	5.83	3.0	2.5	0.90
19	[POB21MH125 (S8)] / [TUX.SEQ.149 (S10)]	5.66	1.5	2.3	1.00
14	[(P24MH119 x 54) (S7)] / [(POB21 x 21) (S9)]	5.52	0.5	3.0	0.95
15	[(P24MH119 x 54) (S7)] / [TUX.SEQ.149 (S10)]	5.31	1.0	2.3	0.95
20	[POB22TSR (S8)] / [(AC7643 x 43) (S7)]	5.22	2.0	2.5	0.90
5	[POB29HC17 (S8)] / [L. DIAMANTES-8043 (S8)]	5.18	1.0	3.0	0.95
7	[POB29HC17 (S8)] / [(AC7643 x 43) (S7)]	5.10	2.0	3.0	1.00
10	[(AC7643 x PR7722) (S7)] / [POB29HC25 (S7)]	4.97	1.5	2.8	0.95
4	[POB43HC26 (S8)] / [(AC7643 x 43) (S7)]	4.85	1.5	3.0	0.95
2	[POB21HC219 (S10)] / [(AC7643 x 43) (S7)]	4.68	1.0	3.0	0.95
16	[(P24MH119 x 54) (S7)] / [(AC7643 x 43) (S7)]	4.66	3.0	2.8	1.00
8	[L. DIAMANTES-8043 (S8)] / [(AC7643 x 43) (S7)]	4.02	2.5	3.3	0.90
9	[POB21HC218 (S10)] / [POB43HC25 (S8)]	3.78	1.0	3.5	0.90
	Mean	5.46	1.5	2.6	0.95
	LSD(0.05)	1.16			
	C.V.(%)	10.8			

Table 2. Results of an evaluation of yellow grain, single-cross maize hybrids under drought stress, Tlaltizapán, 1995A.

Entry	Pedigree	Yield (t/ha)	ASI (d)	Ears/ plant
2	CML297/CML304	6.79	1.0	1.10
17	CML20/CML27	6.75	0.7	1.00
20	T4A/CML287	6.65	0.2	1.00
19	T4A/CML297	6.60	0.7	1.10
15	CML20/CML52	6.57	0.2	1.00
9	CML297/CML288	6.50	1.0	1.10
14	CML19/P24HC219	6.49	0.2	1.10
16	CML27/CML50	6.44	0.7	1.00
11	CML295/CML282	6.36	1.0	1.00
4	CML299/S.A. TSR-23	6.35	0.7	1.00
18	CML20/P27HC117	6.32	0.7	1.10
5	CML287/CML298	6.30	0.3	1.00
7	CML286/CML287	6.19	0.5	1.00
12	P24HC219/P36HC279	6.17	0.2	1.00
10	CML299/CML298	6.13	0.5	1.10
6	CML285/CML287	6.10	0.0	1.00
8	CML299/CML287	6.06	0.5	1.00
13	CML27/CML52	5.82	1.7	1.00
3	CML297/CML295	5.39	0.7	1.00
1	CML287/S.A. TSR-23	5.24	0.0	0.90
	Mean	6.26	0.6	1.03
	LSD(0.05)	1.24		
	C.V.(%)	14		

In both trials most hybrids performed well under mild drought stress, and ASI and EPP were little affected. CIMMYT's international hybrid trials white (CHTTW94) and yellow (CHTTY94) were also evaluated under mild grain filling drought stress at Tlaltizapán during the 1995A cycle. Yield performance from both the multilocation international testing and the one drought site are presented in Tables 3 and 4. International testing and drought stress ranked the hybrids differently. Nevertheless, some hybrids performed quite well under both testing conditions, including white hybrids CML258 x CML264, CML270 x CML258, and CML251 x CML267 and yellow hybrids CML287 x CML298, T2A x CML297 and CML287 x CL00331.

Promising white and yellow lines of early, intermediate and late maturity were also evaluated in drought trials at Tlaltizapán during the 1994A and 1995A seasons. Table 5 presents data on the best white and yellow lines evaluated in a trial in 1994A. Even under drought stress some of the lines yielded 2 t/ha and above. The ASI in the better performing lines ranged from 0.5 to 4.0 d with the better lines exhibiting intervals of no more than 2 d. A set of promising new white lines were evaluated in 1995A (Table 6), and here the best performing lines yielded 3 t/ha with short ASI values and quite acceptable ear aspect scores. Early yellow lines

Table 3. Performance of tropical, white grain maize hybrids in international trials (CHTTW) and under mild grain filling drought stress, 1994.

	International trial		Drought trial		
Pedigree	Yield (t/ha)	Rank	Yield (t/ha)	Rank	ASI (d)
CML264/CML273	6.9	1	4.7	9	0.2
CML247/CML274	6.9	1	4.5	11	1.2
CML247/CML254	6.9	1	4.8	8	0.4
CML264/CML258	6.7	2	5.5	4	-0.1
CML270/CML258	6.5	3	5.8	2	0.0
T2B/CML254	6.5	3	4.9	7	1.6
CML251/CML267	6.4	4	5.7	3	0.0
CML251/CML274	6.3	5	4.8	8	0.6
CML258/CML275	6.3	5	5.9	1	0.9
T2B/CML267	6.3	5	5.0	6	1.2
CML264/CML279	6.3	5	5.2	5	0.4
T2B/CL02131	6.3	5	4.6	10	1.1
T1B/CML249	6.3	5	5.2	5	0.4
T2B/CL02132	6.2	6	4.8	8	0.7
T1B/CML268	6.2	6	5.0	6	0.3
T1B/CML270	6.0	7	4.6	10	1.0
CL04316/CML251	5.9	8	5.5	4	0.6
Pop.43 (Drought tol. pop.)	5.6	9	4.9	7	1.6
Mean	6.4	5.1	0.7		

Table 4. Performance of tropical, yellow grain maize hybrids in international trials (CHTTY) and under mild grain filling drought stress, Tlaltizapán, 1995.

	International trial		Drought trial		
Pedigree	Yield (t/ha)	Rank	Yield (t/ha)	Rank	ASI (d)
CML287/CL00331	5.8	1	4.7	6	0.8
CL02808/CML287	5.5	2	4.1	10	0.4
T4A/CML297	5.5	2	4.8	5	2.7
CML287/CML298	5.5	2	5.1	2	0.1
T2A/CML297	5.4	3	4.9	4	1.3
CML299/CL00331	5.4	3	4.8	5	0.6
CML297/CML295	5.4	3	4.8	5	1.4
T2A/CL00332	5.3	4	4.2	9	1.2
CML297/CML304	5.3	4	4.5	8	1.4
T2A/CML303	5.2	5	5.0	3	0.7
T4A/CL02410	5.1	6	5.2	1	0.7
CML304/CML282	5.1	6	4.9	4	0.1
CL2807/CML285	5.0	7	4.0	11	0.8
T2A/CL02808	5.0	7	3.9	12	0.6
T4A/CML305	5.0	7	3.5	13	2.3
CML285/CL00331	5.0	7	4.9	4	0.0
CML297/CML301	4.9	8	4.6	7	0.9
POP.27 Am. Cristalino-1	4.3	9	4.2	9	0.6
Mean	5.2	4.6	0.9		

Table 5. Results of an evaluation of white and yellow grain maize inbred lines under drought stress, Tlaltizapán 1994A.

Entry	Pedigree	Yield (t/ha)	ASI (d)	Ear aspect	No. ears /plant
75	SINT.AM.TSR-93-2-2-2-2-BB-#*5	3.91	0.5	1.75	1.1
14	(21F114 x 21F38)-5-3-2-1-BB-#*5	3.52	1.5	1.25	1.0
28	POB21C6S1MH247-4-B-1-1-1-BB-#*5	2.60	0.5	2.25	1.3
20	(AC7643 x P43F7)-2-3-2-1-BB-#*5	2.26	2.0	2.75	1.0
46	POB49STEC1HC10-2-1-1-2-2-BB-#*5	2.25	1.0	2.00	0.9
56	(P22F128 x P22F25)-2-2-2-2-BB-#*5	2.06	2.0	2.25	0.9
54	POB24STEC1HC45-1-2-3-4-4-BB-#*5	2.00	2.0	2.75	1.0
34	FERKE8243-58-#-1-BB-#*5	1.95	1.5	2.50	0.8
48	POB21C6S1MH125-3-B-1-1-1-BB-#*5	1.94	3.0	2.25	1.0
22	POB29STEC1HC25-6-4-1-#-BBB-#*5	1.93	0.5	2.50	1.0
23	POB21C6S1MH125-3-B-1-1-2-BB-#*5	1.86	3.5	2.50	1.1
47	(POB43 x PORILLO8043)-5-1-2-2-BB-#*5	1.86	2.5	2.25	0.9
50	POB21C6S1MH177-2-B-4-3-1-BB-#*5	1.72	4.0	2.75	0.7
60	SINT.AM.TSR-7-4-2-2-1-BB-#*5	1.72	0.0	2.75	1.0
30	TUXSEQ-21-1-2-1-B-##-2-BB-#*5	1.71	0.0	2.75	1.0
57	(P22F128 x P22F25)-2-2-3-1-BB-#*5	1.56	1.5	2.50	0.9
49	POB21C6S1MH254-2-B-1-4-5-BB-#*5	1.55	4.0	2.50	0.8
41	TUXSEQ-149-2-BBB-##-2-BB-#*5	1.53	1.0	2.75	1.0
63	SINT.AM.TSR-19-1-2-3-1-BB-#*5	1.51	1.5	3.00	0.9
29	POB21C6S1MH254-2-B-1-4-2-BB-#*5	1.46	2.0	2.50	0.7
26	POB21C6S1MH177-2-B-4-2-1-BB-#*5	1.38	1.5	2.75	0.8
	Mean	1.92	1.7	2.44	0.9

have also been evaluated under drought (Table 7). The best performing lines yielded >2.5 t / ha. Entries 39, 41, 62, 42, 51, 43 and 40 were superior for ear aspect, and a few lines had more than one ear per plant (EPP). Both phenotypic and genotype correlations were calculated on inbred line performance data. ASI was negatively correlated with grain yield and EPP (data not shown). As expected, yield and EPP were positively correlated.

Breeding Stress-Tolerant Maize Germplasm

Important considerations in establishing a selection program for stress tolerance should be whether OPV, hybrid or both types of products are needed, and if the human, financial, and physical resources are available for experimental work. To these should be added germplasm choice, breeding methodology, selection environments, stress levels, augmenting / modifying stresses and essential data to collect. Though evaluation should take place in stress and non-stress environments,

Table 6. Results of an evaluation of white grain maize inbred lines under drought stress, Tlaltizapán, 1995A.

Entry	Pedigree	Yield (t/ha)	ASI (d)	Ear aspect
56	POB.21C5HC219-3-1-B-######-B-#	4.84	0.7	1.8
189	TUXP.SEQUIA.21-1-2-1-B-##-2-BB-f-##-B	4.62	0.9	2.0
8	POB21C6S1MH247-5-B-1-1-2-BBB-3-##-BBB-#	4.43	1.4	3.3
168	SINT.BCO.TSR-3-1-2-3-2-BBBB-##-B-B-B-#	4.30	0.2	1.8
188	POB.21C6S1MH247-4-B-1-1-1-BB-f-##-B	4.24	0.6	2.0
142	POB.49STE-C2-8-BBBB-#-B-#	4.07	0.2	1.8
99	POB25(STE)C2-51-BBBB-##-B-#	4.06	0.1	2.3
74	(21F219*43F95)-5-BBB-1-##-B-#	4.05	1.7	3.3
169	SINT.BCO.TSR-7-3-1-2-3-BB-f-##-#	3.81	2.0	2.3
186	(21F114*21F38)-5-3-2-1-BB-f-##-B	3.81	2.0	3.0
18	POB21C5HC219-3-2-2-3-B-1-1-###-B-#	3.80	5.1	2.3
58	POB21(MRRS)C1-926-2-BBBBB-B-#	3.63	0.1	1.8
16	POB21C5HC72-3-1-2-BBBB-##-2-BB-#	3.60	2.8	3.0
13	POB21C5HC216-2-3-B-####-BBB-####-BB-#	3.59	0.6	3.5
75	(21F219*25F128)-2-BBB-2-##-B-#	3.59	0.6	4.0
57	POB.21C5HC219-3-1-B-#####-B-#	3.56	1.0	2.5
134	POB49(STE)C2-8-B-B-B-B-1-B-#	3.55	0.2	3.0
141	POB.49(STE)C2-8-BBBB-##-B-#	3.54	0.6	2.8
50	POB21(MRRS)C1-321-1-BBBB-##-B-#	3.53	0.4	2.5
112	POB43C6HC133-1-5-1-B-B-B-###-B-#	3.39	0.3	3.0
	Mean	3.90	1.1	2.6

Table 7. Results of an evaluation of early maturing, yellow lines under drought stress at Tlaltizapán, 1995A.

Entry	Pedigree	Yield (t/ha)	ASI (d)	Ear aspect	Ears /plant
39	P18C19MH100#-4-1-1-1-1-B	3.37	1.0	1.0	1.08
4	POB.146 SIN-10-2-#-B	3.31	0.0	2.5	1.08
85	NEW YELLOW FLINT VARIETY-2-1-1-B	3.25	3.0	2.5	1.18
62	P18C20MH144#-2-4-1-B	3.24	1.0	1.0	1.00
79	P21C22,MH169#-1-2-1-4-B	3.17	1.0	3.0	1.27
76	P21C22,MH169#-1-2-1-1-B	3.16	0.0	2.5	1.00
5	POB.146 SIN-11-2-#-B	3.16	2.0	2.0	1.00
107	(POB.24C8HC110-1-2 x POB.146)-2-4-1-B	3.07	0.0	2.0	1.09
2	POB.146 SIN-5-6-#-B	2.97	2.0	3.0	0.82
97	TEY-DMRPOBC1-MH1#-1-1-4-B	2.87	2.0	2.5	0.92
48	P18C20MH65#-2-1-3-#-B	2.86	0.0	2.0	1.08
96	TEY-DMRPOBC1-MH1#-1-1-3-B	2.80	1.0	3.0	1.00
103	(POB.24C8HC110-1-2 x POB.146)-2-1-2-B	2.77	0.0	2.5	0.92
42	P18C19MH100#-4-1-1-1-4-B	2.77	0.0	1.5	1.00
99	TEY-DMRPOBC1-MH216#-1-3-1-B	2.75	1.0	2.0	1.00
112	(POB.36C8HC42-3-1 x SINPOB.146)-1-2-5-B	2.72	0.0	2.5	1.00
51	P18C20MH81#-2-1-1-#-B	2.66	0.0	1.5	1.08
98	TEY-DMRPOBC1-MH1#-1-1-5-B	2.62	3.0	3.0	1.09
43	P18C19MH100#-4-1-1-1-5-B	2.57	1.0	1.5	1.18
40	P18C19MH100#-4-1-1-1-2-B	2.56	2.0	1.5	0.92
	Mean	2.93	1.0	2.2	1.04

as dictated by the characteristics of the target environment, options available in selection are:

1. Selection in non-stress environments.
2. Selection in only stress environments.
3. Selection for broad adaptation to a managed combination of stress and non-stress conditions.
4. Multi-stage selection involving high density, inbreeding, complementary stress nurseries and evaluation under stress, non-stress or both.

Germplasm Choice

The selection of appropriate germplasm is critical, requiring careful consideration of all available information. A wrong choice cannot be corrected by using sound and efficient breeding methodologies. For stress tolerance traits, it is considered best to start with high performing and agronomically desirable germplasm exhibiting large variation for stress tolerance traits and having resistance to the most important pests and diseases prevailing in the target area. If hybrids are the desired product, tolerance to inbreeding, heterotic response and combining ability should also be considered. If one needs to develop a new population(s), genetic components should be incorporated which have been pre-screened for target stresses. Inbred material, if available, should be preferred over non-inbred germplasm.

Selection Environment, Progeny Type and Traits

Stress levels

Applying a single stress level is risky; if it is too severe it may cause rapid genetic drift and loss of genetic variability. Two levels of stress, plus a well-watered control to monitor yield potential, are desirable until experience in managing stress at a particular site and on a specific soil type has been obtained, or until a good level of stress tolerance is present in the germplasm.

Types of progenies and improving heritabilities

Heritabilities under stress can be considerably improved through use of better designs, more locations and more replications (see Bänziger and Lafitte, 1997). Heritabilities for yield also increase as one shifts from half-sib to full-sib and to S_1 and S_2 selfed progenies (Lamkey and Hallauer, 1987).

Trait emphasis and data collection

Characters that should receive special emphasis are grain yield, ASI, EPP and ear aspect. Ears may also be rated on a scale of 1-5 based on percentage seed set, rather than shelling all ears. In determining anthesis date, especially in inbred lines, tassels should be inspected carefully for reproductive abnormalities that may cause anthers not to dehisce. We have noted that selection for short ASI tends to increase the proportion of genotypes showing delayed dehiscence of anthers for a variety of causes, and this needs to be carefully monitored during germplasm development so that male fertility is maintained.

Breeding Alternatives for Developing Stress-Tolerant Maize Germplasm

Maize provides a wide array of breeding options with respect to germplasm products and methodologies. One choice is between intrapopulation and interpopulation improvement methods. Within intrapopulation improvement methods, choices are:

- Individual plants versus family selection.
- Non-inbred families versus selfed progenies.
- *Per se* performance versus testcross performance.
- Broad based versus narrow based testers.
- Parental versus non-parental testers.

With interpopulation improvement methods alternatives are:

- Testcrosses involving individuals versus families.
- Half-sib versus full-sib testcross progenies.
- Non-parental testers; e.g., a population, derived synthetic, single-cross hybrid, or inbred line.

Considerations in choosing among these methods are:

Individual plant selection schemes

Two common procedures are simple mass selection and stratified mass selection (Gardner, 1961). The procedures are not recommended for traits with relatively low heritability, but for highly heritable traits these can be quite effective and one or more cycles can be completed every year. The experimental area can be stratified to reduce differential fertility effects. Care must be taken at flowering to prevent pollen from undesirable plants contaminating selected plants. This scheme is particularly suited to situations where additional test sites are not available, record keeping is difficult and good seed storage facilities are lacking. A few cycles of mass selection may successfully eliminate the most susceptible fraction of the population before switching over to a family-based improvement method, though limited improvement for hybrid-oriented traits can be expected from this method. Nevertheless where human, fiscal and physical resources are limited, this is a good option.

Family-based selection (*per se*)

Here progenies such as half-sib, full-sib, S_1, S_2, etc., are evaluated. The choice of method will be guided by availability of off-season test sites, ability to store remnant seed, choice of product (variety, hybrids or both), traits, heritability, progeny seed quantities, degree of control over pollination (both parents or only one parent), and time required to complete a cycle. Family-based selection methods result in greater gains when traits under selection are complex and of low heritability, but are more demanding in resources, record keeping and overall management. Provided the timing and intensity of the target stress can be managed well, progress can be expected from any one of these methods. As with any scheme, good field execution at every step is extremely important. Half-sib improvement methods in which detasseling is commonly practiced but no progeny evaluation in replicated trials normally takes place (Vasal et al., 1982; Pandey et al., 1984) are not ideally suited for evaluation where ASI needs to be observed, though plants showing delayed silking can still be eliminated. Although replicated progeny trials of half-sib progenies can be conducted (Lonnquist, 1964), remnant seed must be used for recombination of selected families (Compton and Comstock, 1976) and seed quantity per family is limited to that from a single ear. Heritability of yield from half-sib progenies is low compared to other types of progenies, but if the trait is highly heritable (e.g., ASI, EPP), good progress may still be made without the need for hand pollination and a full cycle can be completed each year if multi-site testing is not practiced. Where resources are very limited, it is likely that this may be the most cost-effective selection scheme.

Full-sib family recurrent selection has been used extensively at CIMMYT to improve populations and to improve the drought tolerance of Tuxpeño Sequía (Bolaños and Edmeades, 1993). If off-season drought evaluations can be performed, one cycle of selection can be completed per year. The evaluation of progenies in the off-season may not be desirable (disease incidence and temperatures usually differ from the target environment), but to control drought it is perhaps the most acceptable option available. Disease resistance, however, is usually best displayed in the normal rainy season, and must be monitored carefully.

When breeding procedures are based on selfed progenies, it takes longer to complete a cycle of selection, but this approach significantly improves tolerance to inbreeding over time and generates superior inbred progenies that may be the progenitors of advanced inbred lines. Formation of many S_1 or S_2 progenies in the first phase is recommended. These can be prescreened in unreplicated observation nurseries under drought or low N and the selected fraction (perhaps only 30% of the original progenies) can be examined in more detail in replicated evaluations. Where prescreening in the main season is possible, disease susceptible progenies can be eliminated. Seed quantities can become a limiting factor and may prevent use of high plant densities in observation and progeny evaluation nurseries, though this can be solved by using selected S_2 ear bulk seed developed from each S_1 progeny. To maintain population gains over longer periods, it is recommended that no fewer than 20-50 inbred progenies be recombined (Hallauer, 1992).

Family based selection (test crosses)

Here the testcrosses of S_0 plants (Jenkins, 1940; Hull, 1945) or of S_1 or S_2 progenies are evaluated. The time required to complete a cycle of selection will thus depend on what is test crossed. Such schemes are useful when the emphasis is on combining ability, hybrid-oriented germplasm and integration of population and hybrid development. They can also be recommended where the need is to identify superior early generation lines for further inbreeding or improving a population *per se*, or to derive synthetics as byproducts of the selection process. Selection of stress traits can be emphasized during the formation and prescreening of selfed progenies as well as during test-cross evaluation.

Interpopulation Improvement Alternatives

Two commonly used methods will be discussed, namely reciprocal recurrent selection / half-sibs (RRS-HS) (Comstock et al., 1949) and reciprocal recurrent selection / full-sibs (RRS-FS) (Hallauer and Eberhart, 1970; Hallauer, 1973). Such schemes result in improved populations and superior OPV products as well as improving hybrid-oriented features of the two populations by increasing the level of heterosis between the populations. In addition these schemes allow the extraction of early-generation lines with good general combining ability (GCA), provide a sound basis for recycling early generation lines, identify superior testers on a continuous basis, and may identify future new, conventional and non-conventional hybrids. As originally described, the schemes are not particularly suitable if the populations do not tolerate inbreeding, and they ignore *per se* performance of lines and the parent populations during selection. The original schemes also recommend evaluating S_0 test crosses and recombining the parental S_1 seeds of good performing plants. The modified schemes attempt test crosses (HS or FS) on S_1 or S_2 progenies, and also permit selfed progeny evaluation for elimination of undesirable progenies. The RRS-FS schemes have an added advantage over RRS-HS in that only 50% of resources are spent on test cross progeny evaluation trials. Both original and modified schemes permit selection for drought and low N at one or more stages during the selfed progeny regeneration and evaluation stages and during the evaluation of test cross progenies. In recent years CIMMYT breeders have switched to such schemes. These types of interpopulation improvement schemes are not a necessary requirement for hybrid development, but from a long-term perspective they should generate useful early generation lines.

Integrated Strategies for Developing Stress-Tolerant Maize Germplasm

These involve the concomitant development of stress-tolerance and high yield potential as part of an on-going, intra- or inter-population improvement or hybrid development program. The extent to which selection for stress tolerance can be included in these programs depends on the availability of appropriate testing environments, the phases in progeny formation, the need for multilocation testing, the availability of a suitable stress level, and the time required to complete a selection cycle. A few strategies used by the authors will be outlined, though there are several others that can be employed.

Schemes completing one cycle of selection in one season or year (mass selection or half-sib) normally involve subjecting progenies to one stress, although high density can be superimposed in the same evaluation. In a two-phase improvement system involving recombination in one phase and regeneration of new progenies in the other, it is preferable to apply stress during progeny evaluation, perhaps in conjunction with multilocation testing. Other schemes in which a cycle of selection lasts two or more years normally comprise three phases: progeny formation; progeny evaluation; and recombination. Progeny formation may involve one, two or three steps, depending on if S_l, S_2, or testcross progenies are being formed. Prescreening of progenies may add an additional step, which could be an advantage where germplasm is intolerant of inbreeding or lacking in important agronomic characteristics. Such populations should probably pass through several cycles of inbreeding (to S_1 or S_2 level) and recombination to eliminate deleterious recessives before entering improvement schemes that depend heavily on inbred progeny performance. Opportunities for improving stress-tolerance exist at virtually all stages in these multi-stage improvement schemes, both during progeny formation and evaluation. Where facilities do not permit evaluation of large volumes of germplasm under stress, only selected selfed progenies from population improvement programs should be evaluated. Currently, CIMMYT's lowland tropical maize subprogram is evaluating selected progenies from pools and hybrid-oriented source germplasm under high density or drought at Tlaltizapán.

Inbreds, test crosses and hybrids can all be evaluated usefully under stress in a hybrid development program. Information from multilocation hybrid tests evaluated during bad years may help to identify hybrids that tolerate various stresses. Specific line evaluation nurseries for drought and low nitrogen are also recommended, since useful germplasm has been identified through such tests in the lowland tropical maize subprogram.

Development of Stress Tolerant Maize Inbreds and Hybrids

There is a misconception that hybrids perform well only under favorable environments. There is now good evidence suggesting that hybrids maintain their advantage over OPVs both in good and stress environments, and there is emerging convincing evidence that hybrids can be identified with yields up to 70% greater than those of a standard, broadly-adapted check hybrid at a mean yield level of 2.5 t/ha under drought (D. Beck, pers. comm., 1997). Types of hybrids emphasized will depend on the stage of hybrid development and seed industry infrastructure, but an evolution from non-conventional to conventional and from multiparent to two-parent hybrids seems logical. Some developing countries, such as China, Thailand and Vietnam, are already switching over to two-parent maize hybrids. Stress-tolerant hybrids may be developed both through direct and indirect strategies. Populations improved for drought tolerance have been shown to provide a higher frequency of hybrids with a given level of drought tolerance than their conventionally-selected counterparts (Edmeades et al., 1997). However, since only a few lines survive to advanced levels of inbreeding, the advantages of this strategy will also depend on the probability of obtaining superior lines from such populations.

Lines showing superior performance under drought and low N and possessing good combining ability should, without doubt, aid in the development of stress-tolerant maize hybrids. Every possible effort should be made either to develop or identify stress-tolerant lines, and high plant densities should be used to complement direct screening information on yield, ASI, barrenness and staygreen. Traits such as ASI and EPP should be emphasized when developing inbred lines, perhaps through periodic evaluation under specific stresses.

The relationship between inbred line performance and hybrid performance for stress traits is of great importance, but little published information for specific stresses is currently available. Lafitte and Edmeades (1995) reported that the correlation between S_2 *per se* and topcross performance under low N was only 0.22. Betran et al. (1997) have reported correlations, of around 0.4, between S_3 *per se* and topcross performance for some stress-related traits under drought. However, it is generally considered that inbreds with superior yields under drought and low N will result in superior hybrids under these stresses, even though these correlations are relatively weak. Part of the explanation for this is variation in inbreeding depression and in combining ability among the inbred lines in question.

Research on Stress-Tolerant Maize Testers

The choice of testers during hybrid development is very important, and can have a strong effect on the outcome of a program designed to identify stress-tolerant hybrids. Testers can be inbred, non-inbred, or a hybrid, and the choice involves a blend of theoretical and practical considerations; e.g., broad versus narrow genetic base, high versus low yield, high versus low frequency for stress tolerance traits, good versus poor GCA, one versus several testers, and related versus unrelated testers. Low gene frequency traits are theoretically attractive but are not commonly used. A desirable tester must facilitate discrimination among genotypes for combining ability (general and specific), simultaneously identify useful hybrid products for direct use, be compatible with a practical maize breeding program (Vasal et al., 1995), and discriminate among genotypes for stress-tolerance characteristics. A summary of CIMMYT's research results on testers in the lowland tropical subprogram is as follows:

1. A single tester is adequate.
2. The tester could be genetically broad or narrow, and could be an inbred, hybrid or an OPV, depending upon specific objectives and desired products.

3. If two testers are used, they should represent opposing heterotic groups.
4. The tester should be a good rather than a poor performer for yield, though perhaps a poor performer for traits related to stress tolerance.

Currently CIMMYT maize subprograms developing tropical germplasm are using two white lines (CML247 and CML254) and two yellow lines (CML287 and CL00331) as testers. Two early white lines (G15 C22 MH131#-1-3-4-1-1-BBB and G16 C19HC219-3-1-1-3-2-B-#-B) and three early yellow lines (P31 DMRP1-55-2-3-2-1-BBB, G18C19MH100#-4-1-1-BBB and G17 TSRMH5-2- 4-7-1-1-BBB) have recently been identified as appropriate testers for early maturing inbred lines. The lines from Population 31 and G17 appear to be heterotic to each other if flint hybrids are desired. Both these lines are also heterotic to the line from G18. Research on testers is continuing, and there is some information suggesting advantages in using other lines as testers for both drought and low N tolerance.

Future Considerations for Stress Work

There are several unresolved issues affecting the efficient selection for stress tolerance which merit further research:

1. Is the superiority of stress-tolerant genotypes due to favorable alleles for yield or is it due to the presence of alleles which directly affect stress tolerance?
2. How can a single level of stress be best used for evaluating potentially useful germplasm for tolerance?
3. How can ASI be minimized without drastically changing behavior of male fertility?
4. How can we best combine specific and general stress tolerances? What is their relationship?
5. How can we best combine high plant density with a specific level of drought or low N stress? Is it worth evaluating line *per se* performance at inbreeding levels greater than S_3?
6. What is the best way to modify standard selection schemes by incorporating one or more stress factors in multi-stage selection process?
7. Can a strong inbred-hybrid strategy be a better alternative for developing stress-tolerant products than developing source populations? Can the two approaches be combined?
8. Knowing that lines are more sensitive to environmental stresses, should stress-tolerance research be concentrated on inbred lines?
9. How can strategies emphasizing specific stresses be integrated with a regular hybrid-oriented program without adversely affecting other traits?
10. What is the value of additional selection parameters that measure the quality of product under stress; e.g., a score of ear aspect?
11. Standardizing data collection, particularly for EPP and ASI.
12. The use of preflowering drought stress in segregating populations during recycling of inbred lines.

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Drought Stress at Seedling Stage - Are There Genetic Solutions?

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Abstract

The feasibility of improving tropical maize for tolerance to post-emergence drought stress was examined. In 1992, CIMMYT initiated a divergent S_1 *recurrent selection program in the tropical maize population 'DTP1' for survival and biomass production under post-emergence drought stress. The present study examined (i) broad-sense heritabilities and genetic correlations between survival, biomass, leaf rolling and leaf ABA concentration in two progeny trials evaluated in different seasons under post-emergence drought stress, and (ii) progress resulting from selection in survival, biomass, leaf rolling, and leaf ABA concentration after two selection cycles. Apart from leaf rolling, selection for improved survival and biomass production under post-emergence drought stress did not result in any significant differences compared with the original population, whereas selection for decreased survival and biomass production resulted in poorer survival under post-emergence drought stress. The progeny trials confirmed low broad-sense heritabilities for survival and biomass production. Heritabilities were higher for leaf rolling and leaf ABA concentration, but there was no obvious relationship between these secondary traits and survival or biomass production. It was concluded that (i) selection for improved survival and biomass production under post-emergence drought stress is difficult because environmental variation is high under field conditions and because natural selection may have already exploited all positive genetic variation, and (ii) agronomic solutions may lead to more short-term impact than genetic solutions in reducing yield losses in tropical maize-growing areas due to post-emergence drought stress.*

Most maize in the tropics is planted at the beginning of the rainy season. With the first rains, the crop receives enough water to germinate, but plant stand is severely affected if subsequent rains are delayed. Seed supply, or the financial capacity of farmers in these areas, are often not sufficient to allow replanting after such dry spells. It is estimated that yield losses in maize due to post-emergence drought stress in some areas are as high as those due to drought stress around flowering (Edmeades et al., 1989; 1994).

As drought stress reduces water influx to the plant, plant water potential falls, pressure on cell walls (turgor) is reduced, plant growth diminishes, and wilting occurs. Plants can partially adjust their turgor under these conditions by increasing the concentration of solutes in cells under drought stress (osmotic adjustment). However, if plant water potential continues to fall and osmotic adjustment cannot maintain a positive turgor, eventually the plant wilts permanently, cell death occurs and the plant does not recover after rewatering (Hsiao, 1973). Plants respond to drought via hydraulic signals, but plant hormones, especially abscisic acid (ABA), may also induce adaptive responses before hydraulic mechanisms become effective (Zhang et al., 1987).

The tolerance of maize to post-emergence drought stress might be increased through breeding. In order to survive post-emergence drought stress, a more drought tolerant genotype would have to maintain its water status by either increasing water uptake from drying soil, by reducing water loss from leaves or by increasing tolerance to desiccation. A more extensive rooting system and increased osmotic adjustment may increase water uptake; a smaller leaf area, leaf rolling, and increased stomatal and cuticular resistance may prevent water loss from leaves; and there is evidence for genetic variation in desiccation tolerance in several species (Ludlow and Muchow, 1990;

Turner, 1986). Water conserving mechanisms which are constitutive, such as a smaller leaf area or increased stomatal resistance, tend to be detrimental to assimilation under favorable conditions and are usually not desirable breeding goals where the target environments are characterized by erratic dry spells.

Breeding for increased survival under drought is rendered difficult because genotypes which have relatively reduced water uptake under drought stress (i.e., those which experience more stress because water loss exceeds water uptake, resulting in a lower water potential) show symptoms similar to genotypes which actively maintain water uptake by metabolic adjustments. For example, solute concentrations increase with increasing drought stress (Premachandra et al., 1989) in both (i) genotypes with relatively lower water potentials and lower water uptake (passive response), and (ii) genotypes which maintain water uptake and growth by accumulating more solutes in the cells (active response) (Morgan and Condon, 1986). Although they show the same symptoms, the first class of genotypes is drought sensitive whereas the second class is drought tolerant. Similarly confounding results can also be expected for other adaptive traits such as leaf rolling, early stomatal closure, or rapid increases in ABA concentrations (e.g., Munns, 1988; Premachandra et al., 1989; Tardieu et al., 1991; Voetberg and Sharp, 1991).

Some drought adaptive traits, furthermore, are ambivalent in their effect on plant survival. Osmotic adjustment results in higher turgor which maintains stomatal aperture and thereby increases water loss (Ludlow et al., 1985), but osmotic adjustment may also maintain root growth and water uptake (Morgan and Condon, 1986). Whether genotypes having such drought adaptive traits also have increased drought survival depends on the balance between these opposing effects. Faced with these difficulties, Ludlow and Muchow (1990) concluded that traits should be grouped, instead of being considered individually when breeding for drought tolerance.

In 1992 CIMMYT initiated a divergent S_1 recurrent selection program for survival of tropical maize under post-emergence drought stress. Selection was either for increased survival and increased plant biomass, or for decreased survival and decreased plant biomass. Thus, a strategy was hypothesized whereby genotypes increase survival by maintaining biomass production and water uptake under post-emergence drought stress. In this report, we examine broad-sense heritabilities and associations between survival, biomass, leaf rolling and leaf ABA concentration in two progeny trials of these genotypes evaluated in different seasons under post-emergence drought stress, and assess genetic gain after two cycles of divergent selection.

Materials and Methods

Field site and crop husbandry

The experiments were conducted during the dry seasons of 1992-93, 1993-94 and 1994-95 at the CIMMYT experiment station near Tlaltizapán, México (18 °N, 940 m elevation). During the dry season (November to April), long-term daily temperature maxima and minima at this station average 32 and 12°C, and Penman ET_o increases during the season from 4 to 9 mm d^{-1}. The experiments in 1994-95 received 36 mm of rain at 41 d after seeding, but no rain fell on the other experiments. The soil is a calcareous vertisol (isothermic Udic Pellustert) with a pH of 7.6. Prior to sowing the soil was depleted of water by sowing the entire experimental area to either maize or Mucuna (*Mucuna* sp.) and cutting and removing it when it showed symptoms of drought stress. The experiments received 75:22 kg N:P ha^{-1} broadcast and incorporated prior to seeding, and were kept free from weeds and insects.

Germplasm

Germplasm from the CIMMYT Population ‘DTP1’ C_6 was used. DTP1 is a mixed color population that was assembled from diverse source germplasm which expressed drought tolerance when evaluated under managed drought stress at Tlaltizapán, México. The frequency of the population’s components based on adaptation are 60% lowland tropical, 22% subtropical and 18% temperate. Between cycles C_0 and C_6, DTP1 was improved under relatively mild selection pressure for general adaptation to tropical conditions and for tolerance to drought stress imposed during flowering and grain filling.

Selection procedure

Two populations were formed that trace to DTP1 C_6, one selected for increased (DTP1 SIBA) and the other for decreased (DTP1 SIWA) survival under post-emergence drought stress (Table 1). In the initial selection in 1992-93, 196 S_1 lines of DTP1 C_6 (= DTP1 SI C_0) were screened under post-emergence drought stress, and remnant seed of the best and worst fractions were each recombined by full-sib intermating. The populations were further selected in a similar manner using divergent S_1 recurrent selection for two additional cycles. Cycles bulks of DTP1 SIBA and SIWA C_0, C_1 and C_2 were formed by intermating full-sibs generated during the recombination phase in a separate, well-watered nursery.

During selection S_1 lines were screened under line-source irrigation; they were planted in rows at 90° to a sprinkler irrigation line comprising sprinklers 4.5 m apart. Experimental design in each selection cycle was an alpha (0,1) lattice with one replicate on each side of the sprinkler line. Row length was 9 m, with the beginning and end of each row at 3 m and 12 m distance from the sprinkler line. Spacing between individual seeds in the row was 10 cm and rows were 30 cm apart. A gradient of applied water from 25 to 0 mm was established on dry soil at seeding. Four to five moisture zones were identified parallel to the sprinkler line, based on amount of water applied. Zone 1 (next to the sprinklers) was the least stressed and zone 4 or 5 (most distant to the sprinklers) was the most stressed, and each zone was at least 1 m in width. Data were taken within these moisture zones.

Seed weight per progeny was determined before seeding. Live plants were counted weekly, where a plant was defined as being alive if leaves were turgid and unrolled in the morning prior to 9:30 am. Biomass was determined from both zones 1 and 3 when half the plants in the driest areas of the plot were judged dead. Both living and dead plants were collected, shoots were cut next to the seed, dried for three days at 80°C and weighed. In DTP1 SIBA we selected for increased plant counts and increased biomass. In DTP1 SIWA we selected for decreased plant counts and decreased biomass. No data were taken for biomass in 1993-94, and selection was based on plant counts alone.

A second irrigation was applied when about 50% of the plants were judged dead (directly after determining biomass). Two weeks after this water application, live plants were counted again in all zones to measure recovery. In the evaluation of DTP1 SI C_0, about 20% of the plants recovered, but all plants died in the other three experiments.

Table 1. Divergent selection scheme for good (DTP1 SIBA) and poor (DTP1 SIWA) survival of maize under post-emergence drought stress at Tlaltizapán, Mexico, between 1992 and 1995.

	DTP1 SIBA	DTP1 SIWA
Winter 1992-93	Evaluation of 196 DTP1 SI C_0 S_1's	
Winter 1992-93	Recombination of 20 best S_1's	Recombination of 20 worst S_1's
Summer 1993	Production of 144 DTP1 SIBA C_1 S_1's	Production of 144 DTP1 SIWA C_1 S_1's
Winter 1993-94	Evaluation of 144 DTP1 SIBA C_1 S_1's	Evaluation of 144 DTP1 SIWA C_1 S_1's
Winter 1993-94	Recombination of 20 best S_1's	Recombination of 20 worst S_1's
Summer 1994	Production of 225 DTP1 SIBA C_2 S_1's	
Winter 1994-95	Evaluation of 225 DTP1 SIBA C_2 S_1's	
Winter 1994-95	Recombination of 20 best S_1's	

Leaf rolling was scored on several occasions at about 11:00 am, when differences between lines were visible. Scores between 1 (unrolled leaves) and 5 (completely rolled leaves) were assigned to each zone and plot (Turner et al., 1986). During the evaluation of DTP1 SIBA C_2 S_1 progenies, abscisic acid (ABA) concentration was measured in the third youngest visible leaf harvested from 10 plants in zone 3. About 50% of the plants had shown leaf rolling at 11:00 am the day before harvest in that zone. Leaves were harvested between 6:00 and 8:00 am, and immediately put on ice. ABA concentration was assayed in freeze-dried and powdered aliquots as described by Pekic and Quarrie (1987), validated for maize leaves by Quarrie et al. (1988). Data on leaf rolling and ABA concentration were not used for selection.

Evaluation of progress

Seed of each selection cycle was formed by randomly crossing a balanced sample of seed from each recombination. DTP1 SI C_0 (the original selection cycle), DTP1 SIBA C_1 and C_2, DTP1 SIWA C_1 and C_2 and four experimental synthetics from DTP1 SI C_0 were evaluated in 1994-95. The four synthetics were formed from 10 S_1 progenies selected for either high plant counts, low leaf rolling score, high biomass, or good recovery after irrigation. The experiment was planted in an alpha (0,1) lattice design with six replicates. Line source irrigation was again used to apply a gradient of 21 to 0 mm of water at seeding. The setup of sprinklers, moisture zones, row length and seed spacing were the same as those used during selection, and plant counts, biomass, leaf rolling, and leaf ABA concentration were determined as described above.

Statistical analyses

Because live plant counts were based on a subjective assessment and decreased with time, data for analysis on plant counts were compiled by calculating a linear regression between plant counts and date of count. Predicted initial (first counting date) and final (last counting date before second irrigation) plant counts were determined with these regressions and used in further analyses. This approach reduced plant counts taken over 7 (1992-93), 6 (1993-94), and 9 (1994-95) weeks to two values only. All other data were averaged across moisture zones. Data from the evaluation of S_1 lines were analyzed with genotype, replicate and incomplete block as random factors. Broad sense heritabilities and genetic correlations between traits were determined according to Falconer (1989). Data from the evaluation of progress were analyzed with entry as a fixed factor and replicate and incomplete block as random factors. Phenotypic correlations were determined. Statistical analyses were conducted using SAS (SAS Institute, Inc., Cary, NC).

Results

Evaluation of S_1 lines (selection experiments)

There were few consistent genetic correlations among plant characteristics when correlations in DTP1 SI C_0 and DTP1 SIBA C_2 were compared (Tables 2 and 3). Genotypes with higher initial plant counts (higher germination) had more plants surviving until the final plant count; genotypes with higher seed weights or higher final plant counts produced more biomass; and genotypes with rolled leaves had slightly higher leaf ABA concentrations. There were no consistent genetic correlations between leaf rolling or ABA concentration and plant counts or biomass.

Broad-sense heritabilities for plant counts and biomass were less than broad-sense heritabilities for leaf rolling, seed weight and leaf ABA concentration (Table 4). In three of four selection experiments, final plant counts showed higher heritabilities than initial plant counts.

Evaluation of progress

Apart from leaf rolling, C_1 and C_2 of DTP1 SIBA (selection for good survival under seedling drought stress) did not differ for any characteristic from the original cycle DTP1 SI C_0, while C_1 and C_2 of DTP1 SIWA (selection for poor survival under seedling drought stress) had significantly fewer plants surviving and tended to have lower leaf ABA concentrations (Table 5). The synthetic selected for leaf rolling was the only one that significantly differed from DTP1 SI C_0 for the selected trait, with its realized heritability for leaf rolling being 0.79. Initial and final plant counts were correlated (r = 0.77**). All other phenotypic correlations were less than |0.30| and not significant (data not shown).

Table 2. Phenotypic (above diagonal) and genotypic (below diagonal) correlations among traits measured for 196 S_1 lines of DTP1 SI C_0 under post-emergence drought stress at Tlaltizapán, Mexico, 1992-93.

	Plant count			Leaf	Seed	Recovered
	Initial	Final	Biomass	rolling	weight	plants
Initial plant count		0.20**	0.17*	-0.19*	0.13	0.05
Final plant count	0.62		0.57***	-0.59***	0.12	0.37***
Biomass	0.65	0.38		-0.44***	0.15*	0.36***
Leaf rolling	-0.10	-0.21	-0.10		-0.08	-0.15*
Seed weight	-0.18	0.06	0.33	-0.19		-0.10
Recovered plants	0.31	0.51	0.05	-0.29	0.05	

*, **, *** indicate significance at P ≤ 0.05, 0.01, 0.001 for phenotypic correlations.

Table 3. Phenotypic (above diagonal) and genotypic (below diagonal) correlations measured for 225 S_1 lines of DTP1 SIBA C_2 under post-emergence drought stress at Tlaltizapán, Mexico, 1994-95.

	Plant count			Leaf	Seed	Leaf ABA
	Initial	Final	Biomass	rolling	weight	concentration
Initial plant count		0.19*	0.29***	0.15*	-0.07	0.09
Final plant count	0.49		0.24**	-0.16*	0.06	0.02
Biomass	-0.26	0.52		-0.15*	0.04	0.15*
Leaf rolling	0.34	0.02	0.12		-0.05	-0.02
Seed weight	-0.11	0.12	0.22	0.16		-0.02
Leaf ABA conc.	-0.08	0.01	-0.10	0.18	0.15	

*, **, *** indicate significance at P ≤ 0.05, 0.01, 0.001 for phenotypic correlations.

Discussion

Evaluating genotypes for improved survival under post-emergence drought stress requires the assessment of plant death. In the past, plant death has been assessed by the ability of excised leaves to rehydrate (Flower and Ludlow, 1986), by estimating the proportion of dead leaf area (Ludlow et al., 1983), by counting number of recovering plants after rewatering (Rincon Tuexi et al., 1988) or by measuring sensitive metabolic functions such as cell membrane stability (Blum and Ebercon, 1981). Drought stressed plants usually recover in the field during the night as evaporative demand of the air decreases and the interface between roots and soil is replenished with water. Evidence of the plants' ability to rehydrate during the night was taken as the criterion for measuring plant death in this study. A plant was defined as being alive if leaves were turgid and unrolled in the morning, before 9:30 am. However, this definition of a living plant did not allow accurate determination of the time when a plant could not recover further. In all selection experiments, a second irrigation was applied when about 50% of the plants were determined to be dead by this method. While about 20% of the plants from DTP1 SI C_0 recovered, all plants died in the other three experiments (data not shown). However, even though the time of death was not accurately determined by this method, the genetic correlation between recovered plants and final plant count in DTP1 SI C_0 S_1 progenies indicated that there was a highly significant relationship between what we defined as a plant remaining alive at the end of the evaluation period and genotypic differences in the ability to recover.

Table 4. Broad-sense heritabilities measured for S_1 lines of DTP1 SI, DTP1 SIBA and DTP1 SIWA under post-emergence drought stress at Tlaltizapán, Mexico, between 1992 and 1995.

	Plant count			Leaf	Seed	Recovered	Leaf ABA
	initial	final	Biomass	rolling	weight	plants	concentration
DTP1 SI C_0 S_1	0.28	0.42	0.27	0.54	0.94	0.32	NA
DTP1 SIBA C_1 S_1	0.20	0.48	NA	NA	NA	NA	NA
DTP1 SIWA C_1 S_1	0.59	0.35	NA	NA	NA	NA	NA
DTP1 SIBA C_2 S_1	0.14	0.41	0.28	0.64	0.99	NA	0.56
Mean	0.30	0.42	0.28	0.59	0.96	0.32	0.56

NA = not available.

Table 5. Characteristics of germplasm selected for either good (DTP1 SIBA) or poor (DTP1 SIWA) survival under post-emergence drought stress, and of four experimental synthetics selected for specific traits from the original population, DTP1 SI C_0. The entries were evaluated under post-emergence drought stress at Tlaltizapán, Mexico, in 1994-95.

	Plant count			Leaf	Leaf ABA
	Initial	Final	Biomass	rolling	concentration
	(no. m^{-1})		(g m^{-1})	score†	(ng g^{-1})
DTP1 SIWA C_2	7.9	5.0	24	4.1	338
DTP1 SIWA C_1	8.4	5.7	24	3.7	337
DTP1 SI C_0	9.2	6.4	25	4.2	367
DTP1 SIBA C_1	8.5	6.2	19	3.7	373
DTP1 SIBA C_2	8.7	6.6	25	3.6	371
DTP1 SI C_0 high plant count	8.9	5.6	23	3.9	393
DTP1 SI C_0 unrolled leaves	8.3	5.9	19	3.2	398
DTP1 SI C_0 high biomass	8.4	5.6	22	3.7	348
DTP1 SI C_0 good recovery	9.4	6.6	18	4.1	333
Mean	8.6	5.9	22	3.7	362
$LSD_{0.05}$	1.3	1.0	7	0.5	49
Significance of entry effect	NS	*	NS	*	+

+, * indicate significance at $P \leq 0.10, 0.05$, respectively.

† 1 to 5 score, where 1 indicates unrolled and 5 indicates completely rolled leaves.

Broad-sense heritabilities for plant counts were low and no selection gains were realized in DTP1 SIBA (selected as improved survival under post-emergence drought stress). On the other hand, selection to *reduce* survival in DTP1 SIWA was successful, suggesting that it is far easier to select for genotypes with poorer survival than to improve survival further under drought by selecting for genotypes which maintain water uptake and biomass production under post-emergence drought stress. Natural selection is likely to have applied a consistent selection pressure for survival over time. Consequently, it is possible that adaptive genes for increased water uptake and biomass production under post-emergence drought stress have already been largely exploited within these DTP stocks. The continued ability to select for poorer survival implies that heterosis and/

or epistasis should be important determinants of fitness in these droughted environments.

Another explanation that may account for the lack of progress in DTP1 SIBA is the difficulty we experienced in stressing maize seedlings equally in such field experiments. This is reflected in low heritabilities and large S_d values. Relatively small differences in soil texture, residual soil water, seeding depth or water application may have affected plant survival considerably. In the evaluation of progress, the LSD for final plant count was 17% of the mean value. With such low precision, selection gains of 8% cycle^{-1} would have to be obtained in order to be considered significant. Thus, continued selection, or selection under better controlled conditions, is needed to corroborate whether improvement in survival under post-emergence drought stress is indeed possible with these stocks.

The primary traits of interest in this study, survival under seedling drought stress and plant biomass, were difficult to assess and had a low heritability. Secondary traits with a higher heritability and a high genetic correlation to the primary traits (Falconer, 1989) may therefore be better indicators of survival under post-emergence drought stress. This study examined leaf rolling and leaf ABA concentration as indicators of survival under post-emergence drought stress. Leaf rolling and leaf ABA concentration showed higher heritabilities than plant counts, and in the case of leaf rolling, this was confirmed by significant selection gains in the synthetic 'DTP1 SI C_0 unrolled leaves'. Leaf rolling and ABA concentration were weakly correlated in the evaluation of DTP1 SIBA C_2 S_1 progenies, indicating that common mechanisms affected both traits, but to only a minor extent. Both leaf rolling and ABA production in the leaf are induced by reduced leaf turgor (Turner et al., 1986; Pierce and Raschke, 1980) and genotypes with less turgor supposedly showed increases in both leaf ABA concentration and rolling. Indeed, leaf ABA concentrations in DTP1 SIBA C_2 S_2 seedlings under well-hydrated field conditions were only about 160 ng g^{-1} and showed only small genotypic variation (Pekic and Quarrie, unpublished data). The results provided little indication that leaf ABA concentration or leaf rolling were of adaptive value for survival under post-emergence drought stress. In the evaluation of progress, the two entries with the highest (DTP1 SI C_0 good recovery) and lowest (DTP1 SIWA C_2) final plant count had the same leaf ABA concentration. 'DTP1 SI C_0 unrolled leaves' had significantly less leaf rolling than DTP1 SI C_0, however, but this did not affect the final plant count. Reduced leaf rolling was weakly related with higher final plant counts in the DTP1 SI C_0 S_1 progenies, but this was not observed in C_2, a more advanced selection cycle of the same material.. A similar relationship in DTP1 SIBA C_2 S_1 progenies might have been masked: leaf rolling seemed to increase more rapidly where more plants germinated, probably due to less water being available per plant. Thus, it should be concluded that symptoms of leaf rolling were indicative, if anything, of poorer rather than of improved capacity to survive. This is somewhat surprising in that leaf rolling is frequently considered a water-conserving mechanism which helps genotypes to survive longer on a limited amount of water (Ludlow and Muchow, 1990; Turner et al, 1986). Leaf rolling in this study may have been less the 'cause' for extended survival than the 'symptom' for genotypes with a relatively inferior water uptake. Others have shown that genotypic differences in leaf rolling can be affected not only by leaf turgor, but also by differences in the structural characteristics of leaves (Begg, 1980). Additionally, genotypic differences in the water potential and turgor at which leaves begin to roll have been observed in rice (Turner et al., 1986).

Controlled environment tests in an artificial rooting medium should avoid the difficulty of stressing maize seedlings uniformly in field experiments and would also allow rooting characteristics to be examined. In preliminary trials evidence was found for variation in relative root growth under drought in germplasm related to the stock used in this study (Pekic and Quarrie, unpublished data). If the heritabilities of traits measured under controlled conditions prove to be higher than those of seedling survival and plant biomass under drought stress in the field, progress may be achieved in selecting for improved seedling drought resistance.

In conclusion, the results show that selection for improved survival under post emergence drought stress is rendered difficult under field conditions. Secondary traits, including leaf rolling and leaf ABA concentration, have higher heritabilities than plant counts or biomass, but do not show an obvious relationship with survival. Better controlled selection conditions, other secondary plant traits, and molecular marker techniques may help to identify superior genotypes, unless genetic variability has already been exhausted through natural selection. The most effective solution in the short term to improve seedling survival under drought conditions, however, may be improved agronomic practices. Planting dates based on risk assessment or modified planting methods may lead to more short-term impact on plant stands and subsequent yield than genetic solutions aimed at reducing yield losses caused by post-emergence drought stress.

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The Importance of the Anthesis-Silking Interval in Breeding for Drought Tolerance in Tropical Maize[1]

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Abstract

Selection for improved performance under drought based on grain yield alone has often been considered inefficient, but the use of secondary traits of adaptive value whose genetic variability increases under drought can increase selection efficiency. In the course of recurrent selection for drought tolerance in six tropical maize (Zea mays L.) populations, a total of 3509 inbred progenies (S_1 to S_3 level) were evaluated in 50 separate yield trials under two or three water regimes during the dry winter seasons of 1986-90 at Tlaltizapán, México. In over 90% of the trials, ears plant^{-1}, kernels plant^{-1}, weight kernel^{-1}, anthesis-silking interval (ASI), tassel branch number and visual scores for leaf angle, leaf rolling and leaf senescence were determined. Low scores indicated erect, unrolled or green leaves. Canopy temperature, leaf chlorophyll concentration and stem-leaf-extension rate were measured in 20-50% of the trials. Across all trials, linear phenotypic correlations ($P<0.01$) between grain yield under drought and these traits, in the order listed, were 0.77, 0.90, 0.46, -0.53, -0.16, 0.06^{NS}, -0.18, -0.11, -0.27, 0.17 and 0.10. Genetic correlations were generally similar in size and sign. None of the physiological or morphological traits indicative of improved water status correlated with grain yield under drought, although some had relatively high heritabilities. Genetic variances for grain yield, kernels ear^{-1}, kernels plant^{-1} and weight kernel^{-1} decreased with increasing drought, but those for ASI and ears plant^{-1} increased. Broad-sense heritability for grain yield averaged around 0.6, but fell to values near 0.4 at very low grain yield levels. Genetic correlations between grain yield and ASI or ears plant^{-1} were weak under well-watered conditions, but approached -0.6 and 0.9, respectively, under severe moisture stress. These results show that secondary traits are not lacking genetic variability within elite maize populations. Their low correlation with grain yield may indicate that variation in grain yield under moisture stress is dominated by variation in ear-setting processes related to biomass partitioning at flowering, and much less by factors putatively linked to crop water status. Field-based selection programs for drought tolerance should consider these results.

An estimated 40% of maize sown in lowland tropical environments is reported to suffer yield reductions because of drought (Edmeades et al., 1989), and this figure is expected to increase in the future as a larger proportion of the crop is being shifted to marginal lands. Thus, the development of tropical maize cultivars with high and stable yields under drought is an important priority for CIMMYT (International Maize and Wheat Improvement Center), as access to drought-adapted cultivars may be the only affordable alternative to many small-scale farmers.

Selection under drought compared with selection under unstressed conditions has often been considered less efficient because of a decline in heritability for grain yield under stress (Rosielle and Hamblin, 1981; Blum, 1988). Johnson and Geadelmann (1989) reported that selection in maize based on grain yield under irrigation was as effective as selection under intermittent drought for increasing yield in droughted environments, but resulted in greater responsiveness in well-watered environments. Slightly

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greater gains in grain yield under drought were reported by Arboleda-Rivera and Compton (1974) when mass selection was conducted in the dry season rather than the rainy season. They also observed greater gains in yield under well-watered conditions from selections made during the rainy season.

Heritability for grain yield typically falls under drought because the genetic variance for yield decreases more rapidly than the environmental variance among plots with increasing stress. Under these conditions, secondary traits (in contrast to the primary trait, i.e., yield) whose genetic variance increases under stress or is reduced less than that of yield, can increase selection efficiency provided they have a clear adaptive value under stress, relatively high heritability and are easy to measure (Blum, 1988; Edmeades et al., 1989; Ludlow and Muchow, 1990). Physiologists and ideotype breeders have advocated the judicious incorporation of secondary traits within breeding programs (Blum, 1988; Ludlow and Muchow, 1990), but few traits have a proven contribution to increasing grain yield under stress. Evaluation of the adaptive value of a trait begins by showing that it is related to yield under drought in a field environment. However, correlation analysis between yield and secondary traits must be interpreted with care, since results are often confounded by genetic differences among genotypes for other traits or by the presence of outliers (Blum, 1988; Edmeades et al., 1989). A more effective test of the adaptive value of a trait can be done by comparison of genotypes differing only in the given trait in a nearly isogenic background (Grumet et al., 1987; Bolaños and Edmeades, 1991).

In one of the few examples of selection based on drought-adaptive traits, the lowland tropical maize population Tuxpeño Sequía underwent eight cycles of recurrent selection across three controlled levels of drought at a rainless site in México. Selections were for progenies with high yield, reduced anthesis-silking interval (ASI), increased relative stem-leaf-extension rate, cooler canopy temperature and increased staygreen, all observed under drought, and for average yield, maturity and plant height under well-watered conditions (Edmeades et al., 1987; Fischer et al., 1989). The secondary traits were thought to indicate improved ability to maintain a positive water balance under drought, and were consistent with the best available knowledge in crop physiology. Data collected during selection showed faster progress with the use of these secondary traits in addition to grain yield *per se*, and that the correlation between these and yield under drought were generally high and significant (Fischer et al., 1989).

Evaluation of changes in Tuxpeño Sequía showed gains in grain yield of around 80 to 100 kg ha^{-1} $cycle^{-1}$ across environments ranging in yield from 1.0 to 9.0 Mg ha^{-1} (Bolaños and Edmeades, 1993a; Byrne et al., 1995). The gains in yield under well-watered environments were not surprising, given that maintenance of yield potential had been a breeding objective. The only secondary trait which registered a significant change from selection was a reduction in ASI under drought, associated with an increase in ears and kernels $plant^{-1}$ (Bolaños and Edmeades, 1993b), while no progress was registered in other drought-adaptive traits for which selection pressure had been reasonably strong (Bolaños et al., 1993).

The selection scheme used in Tuxpeño Sequía provided the point of departure for similar recurrent selection schemes in other CIMMYT tropical elite maize populations (Edmeades et al., 1992). However, the lack of progress in Tuxpeño Sequía for traits indicative of improved water status under drought emphasized the need to assess the relative value of secondary traits in practical selection programs for improved performance under drought. The objectives of this study were to evaluate the usefulness of selecting for secondary physiological and morphological traits within the context of a breeding program to improve adaptation to drought in tropical maize. The paper presents genetic and environmental variances, broad-sense heritabilities, and phenotypic and genetic correlations for a series of traits used in selection in 50 progeny trials (S_1 to S_3 inbreeding level) across several water regimes from 1986-90, as part of CIMMYT's on-going recurrent selection program for drought tolerance in six elite maize populations. These results can provide information to assess the relative value of drought-adaptive secondary traits and to improve current breeding strategies for drought tolerance in tropical maize.

Materials and Methods

Progeny evaluation trials

Six elite maize populations adapted to the lowland tropics, varying in maturity, grain color and texture, are being selected under recurrent selection schemes for improved performance under drought at CIMMYT (Table 1). This paper reports data from a total of 50 trials, comprising 11 sets of S_1 progenies (166 to 250 each for a total of 2489 S_1's), five sets of S_2 progenies (64 to 164 each for a total of 623 S_2's) and four sets of S_3 progenies (46 to 135 each for a total of 397 S_3's), evaluated each under two to three water regimes in the course of routine breeding for adaptation to drought at CIMMYT (Table 2). For presentation, S_2 and S_3 progenies were grouped together.

All trials were conducted in the rain-free winter seasons (November to April) of 1986/87, 1987/88, 1988/89, 1989/90, and 1990/91 (hereafter referred to as '86, '87, '88, '89 and '90 seasons, respectively) at Tlaltizapán, México (19°N, 940 m above sea level), so the crop depended almost completely on stored and applied water. In all treatments, water was applied by sprinkler for germination, and then the soil profile was saturated by surface irrigation to alternate furrows of 80 to 120 mm of water. Thereafter, three water regimes were established:

a) Well-watered (WW), with water application every 10 d.
b) Intermediate or post-flowering stress (IS), where irrigation was suspended one to two weeks prior to anthesis.
c) Severe or pre- and post-flowering stress (SS), where irrigation was suspended three to four weeks prior to anthesis until mid or late grain filling, when one additional irrigation was made (Table 2).

Experimental design for each moisture regime was an alpha (0, 1) lattice (Patterson and Williams, 1976) in two replications, with an incomplete block size varying between 5 and 16 plots. Sowing was in rows 0.75 m apart at a density of 5.3 plants m^{-2} (LPS, P26S, DTP1, TS6 and S3C) or 6.6 plants m^{-2} (P16S and P18S), obtained by oversowing and thinning. Plot size was one row 2.5 m

Table 1. Characteristics of maize populations from which progeny trials reported in this study were derived. All are adapted to the lowland tropics and are undergoing recurrent selection for drought tolerance at CIMMYT.

Population	Days to harvest [a]	Grain color	Grain texture	Yield potential (t ha^{-1}) [b]
La Posta Sequia (LPS)	115	White	Dent	8.5
Pool 26 Sequia (P26S)	108	Yellow	Dent	7.5
Pool 16 Sequia (P16S)	95	White	Dent	6.0
Pool 18 Sequia (P18S)	90	Yellow	Dent/Flint	5.0
Tuxpeño Sequia C6 (TS6)	110	White	Dent	7.5
Drought Tolerant Pop.(DTP1)	105	Mixed	Dent/Flint	8.0

[a] For environments with daily maximum and minimum of 32 and 22 °C, respectively.
[b] Estimated grain yield under non-limiting conditions in a lowland tropical environment.

Table 2. Progeny trials reported in this study and evaluated under two or three water regimes at Tlaltizapán, México, during 1986-90, as part of CIMMYT's routine screening in breeding for drought tolerance in tropical maize. Water regimes used were: well-watered (WW), intermediate stress (IS) and severe stress (SS). Cycle number refers to when selection under drought began.

Population	Selection cycle	Number families	Stress levels	Family type	Year
La Posta Sequia (LPS)	C_0	166	WW, IS, SS	S_1	1986
	C_1	235	WW, IS, SS	S_1	1988
	C_2	222	WW, IS, SS	S_1	1990
Pool 26 Sequia (P26S)	C_0	250	WW, IS, SS	S_1	1986
	C_1	235	WW, IS, SS	S_1	1988
	C_2	222	WW, IS, SS	S_1	1990
Pool 16 Sequia (P16S)	C_1	222	WW, IS, SS	S_1	1989
Pool 18 Sequia (P18S)	C_0	250	WW, IS, SS	S_1	1987
	C_1	222	WW, IS, SS	S_1	1989
Tuxpeño Sequia C_6 (TS6)	C_0	225	WW, SS	S_1	1989
Drought Tolerant Pop.(DTP-1)	C_0	240	WW, IS, SS	S_1	1990
LPS & P26S	C_0	135	WW, SS	S_2	1988
	C_1	160	WW, SS	S_2	1989
P16S & P18S	C_0	64	WW, SS	S_2	1989
P16S & P18S	C_1	164	WW, SS	S_2	1990
TS6	C_0	100	WW, SS	S_2	1990
Conventional inbreds (S3C)	[a]	135	WW, SS	S_3	1987
LPS & P26S	C_0	90	WW, SS	S_3	1989
	C_1	126	WW, SS	S_3	1990
P16S & P18S	C_1	46	WW, SS	S_3	1990

[a] S_3 inbred lines derived from 22 lowland populations by conventional selection.

in length, comprising 10 to 12 plants. Plots were established back-to-back in strips 5 m wide, with alleys of 1.5 to 2 m between strips. Five rows separated water regimes.

Photosynthetically active radiation increased from 9.0 to 12.0 MJ m^{-2} d^{-1} and reference evapotranspiration from 4.0 to 8.0 mm d^{-1} as the cropping season progressed from November to April. Air vapor pressure varied between 1.0 to 1.2 kPa and maximum and minimum temperatures averaged 32 and 12°C, respectively. Cool temperatures early in the crop season slowed down vegetative development (flowering occurring around 80 to 85 d after sowing), but rising temperatures in March and April hastened grain-filling (maturity occurring around 135 to 145 d after sowing). The soil is a calcareous vertisol (Isothermic Udic Pellustert) 1.3 to 1.8 m in depth, with pH 7.6. Nitrogen (150 kg N ha^{-1} as urea) and phosphorus (26 kg P ha^{-1} as triple superphosphate) were applied as fertilizer, with half the N and all the P applied at sowing and the remaining N sidedressed 40 d later. Progenies received one or two foliar applications of a 1% $FeSO_4$ aqueous solution prior to flowering if symptoms of lime-induced chlorosis appeared, and the crop was kept free from weeds, insects, and diseases.

Measurements

The border plant nearest the alley in each plot was not used for measurements. In each plot of WW and SS treatments in 10 trials, starting 2-3 weeks before flowering, the youngest visible leaf in the whorl of four plants was marked by cutting 5 cm off the leaf tip. The height from ground to cut tip was measured, and one week later the measurement was repeated on the same leaf. The absolute increment in height under SS was divided by that under WW for the same family and replicate to give the relative stem-leaf-extension rate, which was considered relatively independent of genetic differences in potential elongation rate (Fischer et al., 1989).

Canopy-to-air temperature differentials were determined by taking two to three readings of sunlit leaves near the center of each plot in four trials under SS, using a hand-held infrared thermometer (Model AG-42, Teletemp Corp., Fullerton, California) having a field of view of 2.5°. Measurements were performed between 1200 and 1500 h on mainly hot, clear, still days. Readings were taken before flowering when the crop first showed signs of leaf rolling, or after tassel emergence, taking care not to include tassels in the field of view. The instrument was pointed away from the sun at a 20° depression angle and at a 20° incidence angle to the direction of the row. During measurements, two observers proceeded in opposite directions through each replicate. Readings were averaged to minimize the effects due to time of observation.

Chlorophyll concentration (µg cm^{-2}) of fully exposed leaves, positioned midway between the ear leaf and the top of the plant, were measured *in situ* in eight trials, using a portable chlorophyll photometer (Design Electronics, Palmerston North, New Zealand) (Hardacre et al., 1984). Measurements were taken from near the center of one leaf (avoiding the central midrib) from each of six plants per plot, on one to three occasions during the latter half of the grain-filling stage. Calibration of the instrument was by regression of instrument readings on values obtained by chemical extraction (Arnon, 1949) from the same leaves, using leaves ranging widely in chlorophyll concentrations.

Visual scores of leaf rolling were recorded from each plot under drought in 20 trials on one or two occasions before anthesis, when differences in leaf rolling were obvious. Scores of leaf senescence of lower leaves were taken in each plot in 40 trials on two or three occasions about 7 d apart, near the end of the grain-filling stage, when progeny differences were obvious. Senescence scores were adjusted by covariance for flowering date, but this did not improve their correlation to grain yield, so the data is not included. Scores of leaf angle were recorded at one time immediately prior to anthesis in well-watered treatments of 20 trials. All scores on each occasion were given by two independent observers, using a scale of 1 (unrolled, green or erect) to 5 (rolled, dead, or lax). Repeated scores for each trait were averaged before analysis.

Beginning when flowering started, the cumulative number of plants that had anthesed or silked were observed daily, and days to 50% anthesis and 50% silking recorded when 50% or more of the plants in a plot had done so. A plant was considered to have anthesed or silked if at least one extruded anther or silk was visible. The anthesis-silking interval (ASI) was calculated as the days to 50% silking minus days to 50% anthesis. Some plots under severe moisture stress failed to reach 50% silking approximately 30 to 40 d after 50% anthesis, and were declared missing values.

Three weeks after anthesis in well-watered treatments, plant height (from ground to point of flag leaf insertion) was measured in 20 trials and the number of primary tassel branches counted on four plants per plot in 15 trials. In all trials, at maturity, lodged plants, plant stand and ear number were counted. An ear was considered fertile if it had one or more grains on the rachis. Grain yield was measured by hand-harvesting each plot, air-drying ears, and shelling and weighing grain. Grain weights were corrected for moisture by taking fresh weights of 100 randomly chosen kernels per plot during shelling, and drying to constant weight in a forced-air oven at 80°C, and then used to determine weight kernel^{-1}, kernels plant^{-1} and kernels ear^{-1}.

Data analysis

Data were first tested for normality, and ASI was normalized using the transformation of $\log_e \sqrt{(ASI + 10)}$. Analyses of variance of each trial were conducted and lattice-adjusted means were computed for each water regime within each progeny trial, and used to identify superior progenies for recombination. Under SS, many plots failed to reach 50% silking 30 to 40 d after anthesis, with a large proportion of barren plants. In such cases, weight kernel^{-1} on barren plants and ASI when plots failed to reach 50% silking were treated as missing values, and analyzed as a randomized complete block design. Broad-sense heritability (h^2) for a specific trait in each progeny trial and in each water regime was estimated as $h^2 = \sigma^2_g / [\sigma^2_g + \sigma^2_e / r]$, where σ^2_g and σ^2_e are estimates of genetic and environmental variance, respectively, and r is the number of replications (Hallauer and Miranda, 1981). Genetic correlations between pairs of traits were estimated as $r_{x,y} = \sigma^2_{x,y} / \sqrt{(\sigma^2_x . \sigma^2_y)}$, where $\sigma s^2_{x,y}$ is the covariance of two traits, x and y, each with variances of σ^2_x and σ^2_y (Singh and Chaudhary, 1979). Variance components for calculations of heritability and genetic correlations were obtained from the randomized complete block design analysis. Although methods exist for estimating heritabilities from lattice designs (Singh and Ceccarelli, 1995), in these trials the improvement in relative efficiency of lattice designs over randomized complete blocks was usually only 5% and never more than 25%.

Results

Performance across water regimes

Across the S_1 progeny trials, grain yield averaged 2.49, 0.95 and 0.35 Mg ha^{-1} under WW, IS and SS treatments, respectively (Table 3). The drought treatments imposed reduced yield severely to 38 and 14% of well-watered levels. The $S_{2,3}$ progenies were evaluated only across WW and SS, with mean yields of 2.13 and 0.51 Mg ha^{-1}, respectively. For both types of progenies, the reduction in yield under drought was accompanied by a reduction in all yield components (Table 3). Drought treatments markedly increased barrenness, as ears plant^{-1} averaged 0.95, 0.69 and 0.46 for S_1 progenies under WW, IS and SS treatments, respectively. The number of kernels ear^{-1} were also reduced in almost the same proportions to 267, 183 and 116,

Table 3. Mean and standard deviation for several traits for 50 progeny trials (166-250 S_1 or 46-160 $S_{2,3}$ progenies each) from six tropical maize populations under two or three water regimes (WW, IS and SS refer to well-watered, intermediate and severe stress, respectively) at Tlaltizapán, México, 1986-90. Standard deviations were computed from mean values obtained in each individual trial.

Trait	S_1 progeny			$S_{2,3}$ progeny		Across
	WW	IS	SS	WW	SS	all
No. of trials	11	10	11	9	9	50
No. of progenies	2489	2264	2489	1020	1020	9282
Mean of selected traits						
Grain yield (t ha^{-1})	2.49±0.56	0.95±0.37	0.35±0.19	2.13±0.49	0.51±0.27	1.31±0.97
Ears plant^{-1}	0.95±0.06	0.69Ò0.14	0.46±0.16	0.94±0.06	0.62±0.17	0.73±0.23
Kernels ear^{-1}	267±45	183±41	116±21	219±49	84±30	183±76
Kernels plant^{-1}	255±57	130±52	56±26	203±58	46±26	146±95
Weight kernel^{-1} (mg)	188±26	136±13	115±32	184±13	146±19	153±37
Days to anthesis (d)	84.1±7.7	84.2±7.7	83.3±7.5	-[a]	87.6±6.8	84.5±7.3
Anthesis-silking interval (d)	2.3±1.2	4.6±1.8	8.3±4.7	1.6±1.1	5.6±3.6	4.5±3.7

[a] Not measured.

respectively. Kernels plant^{-1} reflected the effects of combined reductions in ears plant^{-1} and kernels ear^{-1}. Individual kernel weight was less affected by drought than kernels plant^{-1}, and averaged 189, 134 and 98 mg kernel^{-1}, respectively, under the WW, IS and SS regimes. Similar reduction in all yield components were observed in the $S_{2,3}$ progenies under drought (Table 3).

Days to 50% anthesis was unaffected by drought, but the duration from sowing to 50% silking was progressively delayed by increasing drought (data not shown). Consequently, in the S_1 progenies, ASI increased from 2.3 d in the WW regime to 4.6 and 8.3 d under the IS and SS treatments, respectively (Table 3). Similar but smaller increases were observed in the $S_{2,3}$ progenies. It should be noted that mean ASI under drought shows a systematic underestimation of its value, since many plots did not reach 50% silking, and were treated as missing values in the analysis. For example, if plots which did not reach 50% silking had been assigned an arbitrary value of 50 d for ASI (i.e., the approximate length of the grain-filling stage), mean ASI under SS for the S_1 progenies would have been 17.7 d rather than 8.3 d (data not shown).

The dependence of grain yield on its components across all trials was strong, both S_1 and $S_{2,3}$ progenies showing similar relationships (Fig. 1). Across all trials, grain yield was linearly related to weight kernel^{-1} (r^2 = 0.74**) and kernels ear^{-1} (r^2 = 0.89**), with apparent lower limits of 83 mg kernel^{-1} and 78 kernels ear^{-1}, respectively. In general, $S_{2,3}$ progenies had larger but fewer kernels (Table 3). The relationship between grain yield and ears plant^{-1} was curvilinear and strong (r^2 = 0.94**), and so was the relationship between yield and ASI (r^2 = 0.70**). Grain yield decreased to less than 20% of its well-watered levels as ASI increased from 0 to 5 d, and then declined asymptotically to almost zero yields as ASI increased further (Fig. 1).

Within individual trials of S_1 progenies, grain yield in any water regime was significantly ($P<0.001$) but not highly correlated with grain yield in either of the other two water regimes. Phenotypic correlation coefficients were higher when comparing stress treatments adjacent in severity (IS vs. WW or IS vs. SS) than when comparing treatments farthest apart in severity (SS vs. WW) (data not shown). Across all trials, corresponding correlations were 0.44, 0.44 and 0.33 ($P<0.001$), suggesting that changes in the relative ranking of progeny varied as the severity of stresses being compared increased. This was confirmed also by a highly significant family x stress level interaction for grain yield in most trials (data not shown).

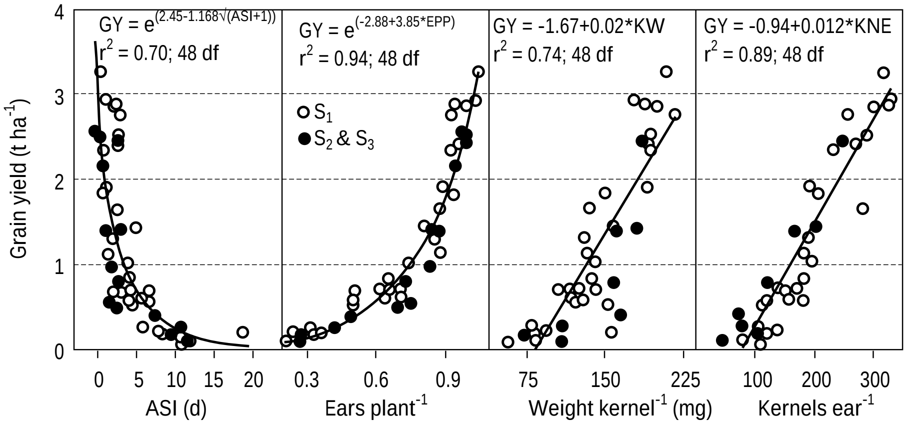

Figure 1. Grain yield as a function of mean anthesis-silking interval (ASI), ears plant^{-1}, weight kernel^{-1} and kernels ear^{-1} for 50 progeny trials (166-250 S_1 or 46-160 $S_{2,3}$ progenies each across two replicates) from six tropical maize populations under a range of water regimes at Tlaltizapán, México, 1986-90. Each data point is the mean for the trial.

Genetic and environmental variances and broad-sense heritabilities across water regimes

Changes in the magnitude of genetic (σ^2_g) and error (σ^2_e) variances, as well as the estimated corresponding broad-sense heritability (h^2) of specific traits plotted as a function of trial mean grain yield are presented in Figure 2. Since all trials were conducted in an almost completely rain-free environment, mean grain yield level was taken to reflect mainly water availability. Linear regressions were fitted to indicate trend by S_1 and $S_{2,3}$ progenies.

In general, consistent with expectations, values of σ^2_g were greater for $S_{2,3}$ than for S_1 progenies, but both types of progenies had similar values of σ^2_e for all traits examined (Fig. 2). Genetic variances for grain yield, kernels ear^{-1} and weight kernel^{-1} increased with increasing yield levels, while variances for ears plant^{-1} and ASI decreased. Stress level had small effects on σ^2_g for days to anthesis. In general the changes in magnitude of σ^2_g and σ^2_e with increasing yield were in the same direction and of similar magnitude for all traits. Exceptions were kernels ear^{-1} and weight kernel^{-1} where increases in σ^2_g with increasing availability of water were accompanied by no change or a slight decline in σ^2_e.

In all cases and for all traits, $S_{2,3}$ progenies had larger heritabilities (by around 0.10 to 0.15) than S_1 progenies across all yield levels without any crossover interaction (Fig. 2 and Table 4). The heritability for grain yield showed a general tendency to decrease with increasing moisture stress (Fig. 2), from around 0.60 in well-watered environments to values of 0.40 or less at very low yield levels. The heritability of kernels ear^{-1} and weight kernel^{-1} was around 0.60 under well-watered conditions, but also decreased with increasing stress (Fig. 2). In contrast, the heritability for ASI and ears plant^{-1} either increased or remained fairly constant with increasing moisture stress and declining yield levels. The heritability for days to anthesis remained fairly constant across all moisture regimes.

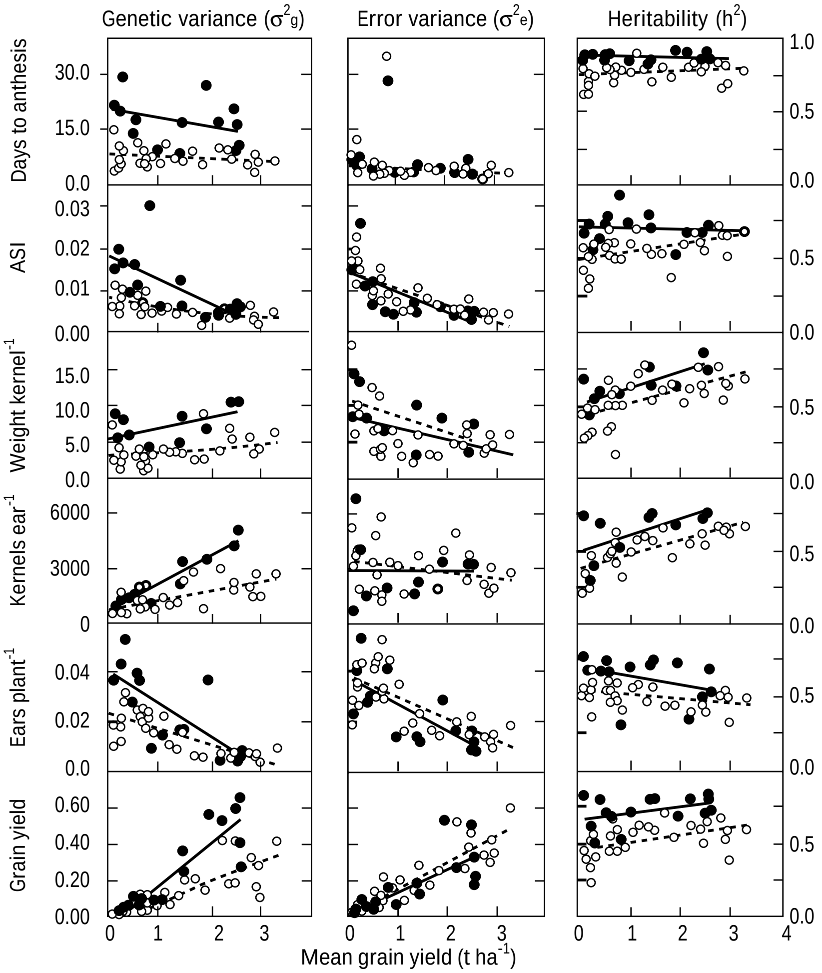

Figure 2. Genetic and environmental variances and broad-sense heritabilities for several traits as a function of mean grain yield for 50 progeny trials (166-250 S_1 or 46-160 $S_{2,3}$ progenies each across two replicates) from six tropical maize populations under a range of water regimes at Tlaltizapán, México, 1986-90. Linear regressions are shown to indicate trend, broken lines for S_1 progenies and solid lines for $S_{2,3}$ progenies.

The largest heritabilities across all water regimes were generally those for phenological and morphological traits, such as days to anthesis (0.80), leaf angle score (0.78), tassel branch number (0.79) and plant height (0.70) (Table 4). Mean heritabilities of grain yield and its components ranged from 0.50 to 0.60, for leaf rolling, leaf senescence, relative stem-leaf-extension rate and lodging. The lowest heritability estimate across trials was for canopy temperature (0.27). There was a small tendency for the heritability for leaf rolling to increase with stress level, while the heritabilities of lodging, leaf senescence score and leaf chlorophyll concentration were unaffected by changes in water availability (Table 4).

Correlations between traits used in selection and grain yield

There were no consistent differences between the genetic correlations (r_g) of most traits with grain yield computed for S_1 progenies versus those computed for $S_{2,3}$ progenies. Genetic correlations between grain yield and kernels ear^{-1}, ears plant^{-1} and kernels plant^{-1} were consistently high (0.7 to 0.8) and positive, while that with weight kernel^{-1} was positive but small (0.22±0.16) (Fig. 3, Table 5). The genetic correlation between grain yield and kernels ear^{-1}, kernels plant^{-1} and weight kernel^{-1}, respectively, showed non-significant trends as water availability changed (Fig. 3). However, the value of $r_{GY.EPP}$ (between grain yield and ears plant^{-1})

Table 4. Broad-sense heritability estimates for several traits for 4 to 50 progeny trials (166-250 S_1 or 46-160 $S_{2,3}$ progenies each) from six tropical maize populations under two or three water regimes (WW, IS and SS refer to well-watered, intermediate and severe stress, respectively) at Tlaltizapán, México, 1986-90. Standard deviations were computed from mean values obtained in each individual trial.

Trait	No. trials	S_1 progeny			$S_{2,3}$ progeny		Across all
		WW	IS	SS	WW	SS	
Grain yield	50	0.57±0.08	0.57±0.08	0.43±0.10	0.76±0.05	0.66±0.11	0.59±0.14
Ears plant^{-1}	50	0.45±0.07	0.52±0.07	0.54±0.08	0.59±0.14	0.64±0.14	0.54±0.12
Kernels ear^{-1}	40	0.59±0.07	0.51±0.10	0.39±0.13	0.73±0.03	0.53±0.18	0.54±0.15
Kernels plant^{-1}	40	0.63±0.05	0.61±0.04	0.47±0.08	0.76±0.05	0.62±0.18	0.60±0.12
Weight kernel^{-1}	40	0.66±0.08	0.50±0.15	0.43±0.14	0.72±0.10	0.56±0.09	0.56±0.15
Days to anthesis	50	0.78±0.06	0.79±0.05	0.72±0.08	0.88±0.03	0.87±0.02	0.80±0.08
Anthesis-silking interval	50	0.60±0.10	0.55±0.07	0.51±0.12	0.69±0.07	0.71±0.11	0.60±0.12
Lodging	50	0.47±0.14	0.53±0.11	0.50±0.12	0.67±0.08	0.67±0.06	0.55±0.13
Leaf rolling score	20	-[a]	0.37±0.10	0.52±0.09	-[a]	0.70±0.10	0.56±0.15
Leaf senescence score	40	0.60±0.08	0.54±0.09	0.54±0.08	0.67±0.22	0.63±0.12	0.58±0.11
Leaf angle score	20	0.74±0.07	-[a]	-[a]	0.81±0.03	-[a]	0.78±0.05
Leaf-stem extension rate	10	-[b]	-[b]	0.45±0.10	-[b]	0.75±0.03	0.56±0.12
Canopy temperature	4	-[a]	-[a]	0.25±0.05	-[a]	-[a]	0.27±0.05
Tassel branch number	15	0.82±0.04	-[a]	-[a]	0.84±0.03	-[a]	0.79±0.13
Leaf chlorophyll conc.	8	0.52±0.31	0.57[c]	0.52±0.12	-[a]	0.77[c]	0.56±0.20
Plant height	20	0.60±0.09	-[a]	-[a]	0.84±0.06	-[a]	0.70±0.14

[a] Not measured.

[b] Value for stem-leaf-extension rate only shown under SS.

[c] Data available only from one trial.

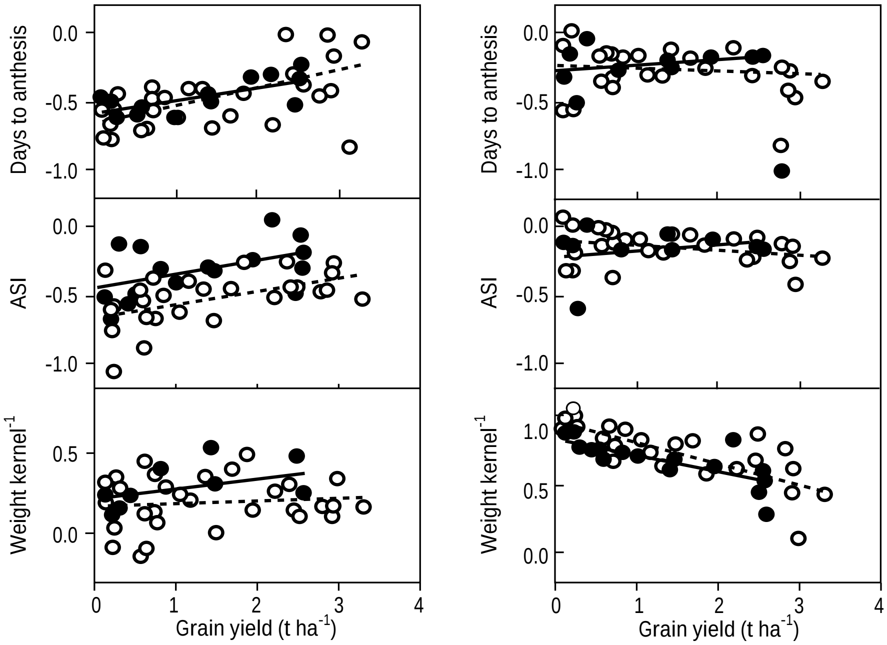

Figure 3. Genetic correlation between grain yield and several traits as a function of mean grain yield for 50 progeny trials (166-250 S_1 or 46-160 $S_{2,3}$ progenies each across two replicates) from six tropical maize populations under a range of water regimes at Tlaltizapán, México, 1986-90. Linear regressions are shown to indicate trend, broken lines for S_1 progenies and solid lines for $S_{2,3}$ progenies.

increased from values of around 0.5 under well-watered conditions to near 1.0 as grain yield fell to almost zero. The magnitude of the genetic correlation between grain yield and ears plant^{-1} was also shown as a function of ASI and ears plant^{-1} (Fig. 4). Curves fitted to these relationships indicated that $r_{GY.EPP}$ increased very rapidly to almost 1.0 (0.8 to 1.0) as mean ASI exceeded 5 d or mean ears plant^{-1} fell below 0.7 for each trial with increasing moisture stress.

Flowering parameters were also quite strongly associated with grain yield across all moisture regimes. The value of $r_{GY.AD}$ (between grain yield and days to anthesis) averaged -0.47±0.18 across all trials (Table 5), suggesting that earlier-flowering progenies were associated with high grain yields. Similarly, the value of $r_{GY.ASI}$ averaged -0.48±0.21, indicating that a short ASI was linked to high grain yield under stress. However, both days to anthesis and ASI correlated more strongly and more negatively with grain yield as moisture stress intensified and yield levels declined (Fig. 3). Data shows that the genetic correlation of grain yield and ASI ($r_{GY.ASI}$) was apparently higher for S_1 than for $S_{2,3}$ progenies at the same yield level (Fig. 3). This observation may imply that the relationship between ASI and yield may not hold as the inbreeding level advances in progenies.

Among other traits and yield, genetic correlations were extremely low and inconsistent (Table 5). Only canopy temperature (-0.22±0.11) and plant height (0.29±0.21) showed genetic correlations with grain yield larger than their standard deviations in absolute terms. Thus, tassel branch number, leaf chlorophyll concentration, relative stem-leaf-extension rate, and scores for leaf angle, rolling and senescence showed little genetic correlation with yield. In general, phenotypic correlation between grain yield under SS and other traits were a little smaller but similar in sign to the mean values of the corresponding genetic correlation, suggesting that environmental correlation for the same traits were relatively small (Falconer, 1981). Exceptions were for weight kernel^{-1} where the phenotypic correlation was 0.46 versus 0.14 for the genetic correlation with grain yield under SS, and for relative stem-leaf-extension rate where the two correlations were small but of opposite signs.

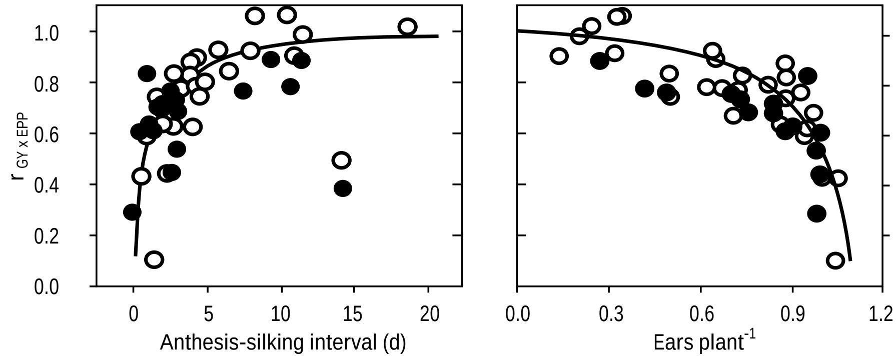

Figure 4. Genetic correlation between grain yield and ears plant^{-1} (r_{GYxEPP}) plotted against mean anthesis-silking interval (ASI) and mean ears plant^{-1} for 50 progeny trials (166-250 S_1 or 46-160 $S_{2,3}$ progenies each across two replicates) from six tropical maize populations under a range of water regimes at Tlaltizapán, México, 1986-90.

Discussion

For selection, each water regime served a different purpose. Well-watered treatments allowed for monitoring of yield potential, maturity and plant morphology (e.g., tassel size, leaf angle and plant height). The post-flowering stress (IS) treatment allowed for manifestation of the genetic variability for rates of canopy senescence, weight kernel^{-1}, ears plant^{-1} and yield. The severe stress (SS) treatment revealed the genetic variation for ASI and ears plant^{-1} (i.e., barrenness), as well as for secondary physiological and morphological drought-adaptive traits (leaf rolling, rates of leaf

Table 5. Genetic correlations (r_g) of several traits with grain yield for 4 to 50 progeny trials (166-250 S_1 or 46-160 $S_{2,3}$ progenies each) from six tropical maize populations under two or three water regimes (WW, IS and SS refer to well-watered, intermediate and severe stress, respectively) at Tlaltizapán, México, 1986-90. Standard deviations were computed from mean values obtained in each individual trial. The phenotypic correlation (r_p) for the same traits and grain yield under WW and SS for S_1 progenies only is also shown.

		Genetic correlations (r_g) with grain yield						Phenotypic (r_p) correlation w/ yield	
	No.	S_1 progeny			$S_{2,3}$ progeny		Across		
Trait	trials	WW	IS	SS	WW	SS	all	WW	SS
Ears plant^{-1}	50	0.58±0.21	0.82±0.06	0.90±0.14	0.58±0.16	0.77±0.07	0.73±0.19	0.49	0.77
Kernels ear^{-1}	40	0.71±0.11	0.78±0.10	0.71±0.22	0.81±0.03	0.74±0.17	0.75±0.13	0.70	0.50
Kernels plant^{-1}	40	0.79±0.10	0.88±0.11	0.86±0.15	0.86±0.05	0.79±0.23	0.84±0.13	0.89	0.90
Weight kernel^{-1}	40	0.23±0.12	0.20±0.18	0.14±0.17	0.35±0.17	0.23±0.11	0.22±0.16	0.31	0.46
Days to anthesis	50	-0.32±0.22	-0.56±0.12	-0.58±0.12	-0.38±0.10	-0.55±0.06	-0.47±0.18	-0.28	-0.40
Anthesis-silking interval	50	-0.42±0.11	-0.64±0.15	-0.60±0.24	-0.24±0.16	-0.41±0.20	-0.48±0.21	-0.35	-0.53
Lodging	50	0.10±0.17	0.16±0.28	-0.03±0.15	-0.11±0.09	0.03±0.26	0.04±0.22	0.04	-0.08
Leaf rolling score	20	-[a]	-0.10±0.21	-0.03±0.15	-[a]	-0.14±0.18	-0.08±0.18	-[a]	-0.18
Leaf senescence score	40	-0.09±0.24	0.15±0.11	0.14±0.15	-0.08[d]	0.04±0.18	0.07±0.18	-0.14	-0.11
Leaf angle score	20	0.07±0.14	-[a]	-[a]	0.05±0.13	-0.28±0.19	0.02±0.17	0.06	0.06
Leaf-stem extension rate	10	-[b]	-[b]	-0.08±0.33	-[b]	-0.24±0.21	-0.11±0.29	-[a]	0.10
Canopy temperature	4	0.26[c]	-[a]	-0.20±0.15	-[a]	-[a]	-0.22±0.11	-[a]	-0.27
Tassel branch number	15	-0.14±0.17	-[a]	-[a]	0.27±0.11	0.15[c]	-0.02±0.24	-0.05	-0.16
Leaf chlorophyll conc.	8	0.19±0.14	0.21[c]	0.11±0.24	-[a]	0.03[c]	0.15±0.16	0.22	0.17
Plant height	20	0.24±0.23	-[a]	-[a]	0.38±0.15	-[a]	0.29±0.21	0.26	0.02

[a] Not measured.

[b] Value for stem-leaf-extension rate only shown under SS.

[c] Data available only from one trial.

senescence, relative stem-leaf-extension rates, canopy temperatures, osmotic adjustment), but reduced the genetic variation for grain yield.

Yield components, morphological and phenological traits

In the present study, more than 75% of the variation in grain yield under drought was accounted for by variation in ears and kernels plant^{-1} (Table 5). High correlations between grain yield and its components are normally found because of lack of independence among them (Blum, 1988). Nonetheless, correlation analysis showed that ears and kernels plant^{-1} were more important determinants of grain yield than weight kernel^{-1}. Individual kernel weight seemed to play a more important role in determining yield only under well-watered environments. As stress increased, the dependence of grain yield on ears plant^{-1} increased more than on kernels ear^{-1}. For example, ears plant^{-1} accounted for 24% of the variation in grain yield in the WW treatments but 59% in SS, while that for kernels ear^{-1} declined from 49 to 25% (based on phenotypic correlation coefficients, Table 5). The value of the genetic correlation points to a stronger underlying relationship between grain yield and ears plant^{-1} ($r_{GY.EPP}$ = 0.90±0.14) under severe stress. This value is somewhat larger than reported by Guei and Wassom (1992) in a separate study of LPS and P26S.

Of the remaining traits, only ASI showed a strong and consistent genetic correlation to grain yield under drought (Table 5). The phenotypic correlation between grain yield and ASI reported here (-0.53** across S_1 trials under drought; Table 5) is considerably greater than the one reported for full-sib progenies by Fischer et al. (1989) at the same site. In addition, the corresponding genetic correlation (-0.60±0.24) points to a strong underlying dependence of yield on ASI. Both grain yield and ASI have similar heritabilities (Table 4), and variation in ASI accounted for 70% of the variation in grain yield across all trials reported here, similar to a value of 76% reported for Tuxpeño Sequía (Bolaños and Edmeades, 1993b). The relationship between grain yield and ASI from this study encompassing 3509 progenies (Fig. 1) was very similar to that established for Tuxpeño Sequía (Bolaños and Edmeades, 1993b), a South Africa hybrid (DuPlessis and Dijkhuis, 1967) and for a Corn Belt hybrid under density stress (Edmeades and Daynard, 1979), suggesting that this relationship could be ubiquitous in maize. Delayed silking has been associated with barrenness (Herrero and Johnson, 1981), and appears to reflect reduced partitioning of assimilates to the developing ear at flowering (Edmeades et al., 1993). Selection for improved performance under drought in tropical populations has been accompanied by large reductions in ASI (Bolaños and Edmeades, 1993b; Edmeades et al., 1996).

Moisture stress at flowering destabilizes grain yield by increasing barrenness, suggesting that the ability of a cultivar to produce an ear under stress is the most important characteristic associated with drought tolerance. This provides justification for CIMMYT's continued emphasis on moisture stress during the flowering period when ears and kernels plant^{-1} are determined in maize. A corollary is that the crop must additionally retain its capacity to yield well in favorable environments, or it will be quickly disregarded by farmers (Edmeades et al., 1992).

Since moisture stress increased with time within IS and SS trials, it penalized late-flowering progenies. This accounts for the consistent negative correlation between days to 50% anthesis and grain yield, becoming more negative with increasing intensity of stress (Table 5; Fig. 3). Populations selected only for grain yield under drought would drift earlier, i.e., 2-3 d cycle^{-1} because of the strong negative correlation between these two variables. Early maturity is clearly a trait of considerable importance in providing a stable but relatively low grain yield in regions where the length of the growing season varies markedly because of rainfall (Blum, 1988; Ludlow and Muchow, 1990). Selecting progenies that simply escape moisture stress by flowering early should be avoided in programs that focus on simultaneously increasing yield potential *and* tolerance.

Other morphological traits were very weakly associated with grain yield under stress. A small but significant negative phenotypic correlation between tassel branch number and grain yield was observed. Tassel size is highly heritable (Table 4) and can be easily altered by selection (Fischer et al., 1987). Selection for drought tolerance in Tuxpeño Sequía led to a reduction in tassel size (Bolaños and Edmeades, 1993b), even though it was an unselected trait. In other maize studies, reduced tassel size was also associated with improved partitioning toward the ear (Fischer et al., 1987). The fact that $_{rGY.TBN}$ is essentially zero suggests that its phenotypic correlation is the result of an environmental correlation reflecting competition between ears and tassels for available resources at flowering.

The moderate association found between yield and plant height under unstressed conditions (r=0.28**) may be an artifact of the use of single-row plots for evaluation, taller progenies capturing additional radiation when surrounded by shorter neighbors. Such advantage, however, would not be expressed in large plots. Selection for improved performance under drought in Tuxpeño Sequía resulted in a slight reduction in plant height (Bolaños et al., 1993), suggesting that this genetic correlation may reverse sign under drought. Lodging showed no consistent association with grain yield in this study, possibly because it occurred towards the end of grain-filling when assimilates were being remobilized from the stem to the grain.

Traits indicative of crop water status

Traits used during selection had only a weak association with grain yield under stress (Table 5). This was unexpected as these traits were thought to be indicators of increased crop water status (Blum, 1988; Ludlow and Muchow, 1990). Several studies comparing maize cultivars under drought have shown that increases in grain yield and biomass were correlated with the ability to maintain higher leaf water potential or leaf turgor under drought, either because of improved soil water uptake or through osmotic adjustment (Ackerson, 1983; Lorens et al., 1987). Leaf and stem elongation has been shown to be very sensitive to changes in plant and soil water status (Hsiao et al., 1970; Westgate and Boyer, 1985), and Sobrado (1986) reported a strong relationship between leaf expansion rate and predawn leaf turgor potential in tropical maize cultivars. In the present study the relative stem-leaf-extension rate was barely associated with grain yield under stress. In addition, despite direct selection for the trait, no changes were detected after eight cycles of selection in Tuxpeño Sequía (Bolaños et al., 1993), and its use has been discontinued at CIMMYT (Edmeades et al., 1992).

Water stress accelerates leaf senescence, and cultivars with osmotic adjustment have been shown to have delayed senescence under drought (Aparicio-Tejo and Boyer, 1983). However, osmotic adjustment in 204 maize cultivars under drought in Tlaltizapán was small, and selection for low osmotic potential in two maize populations (P16S and P18S) demonstrated little adaptive value for the trait under drought (Bolaños and Edmeades, 1991). The lack of association between green leaf longevity and grain yield observed in these trials, and the apparent lack of progress in selecting for this trait in Tuxpeño Sequía (Bolaños et al., 1993), may indicate that increased demands for N by the larger ear resulting from selection are met by remobilization of N from the leaves, thereby inducing senescence (Muchow, 1994). Droughted plants are usually lighter green than their unstressed counterparts (Wilson and Allison, 1978), with a lower level of leaf N and chlorophyll concentration (unpublished data, 1991). This is probably because N uptake is restricted in very dry soil. The weak positive genetic correlation between leaf chlorophyll concentration and grain yield (r=0.15**) was consistent across stress levels (Table 5).

Genetic variation in canopy temperature reflects in part variation in rates of transpiration, and the trait has been used effectively as a selection tool for drought tolerance of wheat and sorghum (Blum et al., 1982; Blum, 1988). The weak (although consistent) association between cooler canopies and high grain yield obtained in the present study may reflect measurement difficulties with an instrument of low acceptance angle in single-row plots of leaf area indices of 1.5 to 3 in which interference by background and the effects of wind, cloud cover and time of observation were not satisfactorily controlled.

Leaf rolling has been associated with maize cultivars having low leaf water status (Sobrado, 1987), though not for rice (Turner et al., 1986) nor for sorghum (Blum et al., 1989). Ackerson (1983) noted that leaf rolling occurred at a higher leaf water potential in a drought-tolerant *latente* maize hybrid than in a normal commercial hybrid. In addition, no association could be established between leaf rolling score and predawn leaf water potential in other studies of maize progenies (J. Bolaños, unpublished data, 1991). Leaf rolling is a moderately heritable trait under stress (h^2=0.70 for $S_{2,3}$ progenies and h^2=0.56 for S_1 progenies, Table 4), but it may reflect morphological and anatomical differences among progenies in the capacity of leaves to roll. Erect leaves, because of the resultant reduction in mean incident radiation flux per unit leaf surface (Duncan, 1971), could be associated with higher yield under stress because of increased water-use efficiency and possible decreases in photooxidation. However, no association was found between leaf angle score and yield. One possible reason could be that the benefits of erect leaves were masked by low leaf area indices characteristic of single-row progeny evaluation trials.

The weak correlations between traits indicative of crop water status and grain yield under drought found in this study contrast with strong correlations between yield and low canopy temperatures (-0.40* for C_2 and -0.73** for C_3), high relative stem-leaf-extension rates (0.35* for C_2 and 0.39** for C_3) and delayed foliar senescence (-0.38** for C_2 and -0.48** for C_3), reported by Fischer et al. (1989) during evaluations of cycles 2 and 3 of Tuxpeño Sequía at the same site. However, a detailed evaluation of gains from selection after eight cycles of selection found no change in any of these traits (Bolaños et al., 1993). Reasons for these differences are not clear. One reason could be the type of progenies under observation, full-sibs in the case of Tuxpeño Sequía, compared to S_1 and $S_{2,3}$ progenies in this study. Weak relationships may also result from the use of single-row plots for progeny evaluations, because traits that provide a competitive advantage in single-row plots, such as height, aggressive rooting and lax leaves, may provide little or no yield advantage in well-bordered plots, and may actually be disadvantageous under drought. A recent study of progenies under low N concluded that small plots are not a major source of environmental error during selection (Bänziger et al., 1995).

Implications for tropical maize improvement

Data from this study shows that secondary traits are not lacking genetic variability in broadly based elite maize populations. Their low correlation with yield may indicate that variation in grain yield under stress was dominated by variation in ear-setting processes related to biomass partitioning at flowering, and less by factors putatively linked to crop water status. It seems likely that ASI (and / or barrenness) is masking the possible contributions of drought-adaptive traits to grain yield under drought, which implies that little gain can be expected from these drought-adaptive traits until ASI is substantially reduced and grain yield stabilized under drought.

As selection tools, both ASI and ears plant^{-1} increase in utility as stress intensifies and genetic differences become larger. For example, days to 50% anthesis and silking are measured with an accuracy of no more than ± 1 d, giving an accuracy for ASI of ± 2 d. Therefore, under unstressed conditions, ASI may be 1 to 3 d, and the error of measurement becomes 100-200% of the mean. When genotypes are planted at high densities (Edmeades and Daynard, 1979), or are exposed to drought during their floral development, silk delay may extend ASI from 5 to 20 d and many families will fail to reach 50% silking. The error of measurement then falls to 10-40% of the mean, and the genetic variability for ASI can be identified more precisely. The same argument also applies to ears plant^{-1}. By careful management of stress levels it is possible for the breeder to observe and exploit this variability.

These results endorse the use of a well-watered environment and one with a severe moisture stress timed to coincide with flowering. The first exposes sufficient genetic variability for yield so that progress for this trait through direct selection can be maintained. Under drought, gains are maintained mainly by selection for ASI and ears plant^{-1}, whose genetic variability increases, and to a lesser extent by yield itself. Declines in heritability of grain yield with increasing moisture stress are offset by concomitant increases in the heritabilities and σ^2_g of ASI and ears plant^{-1} and in the magnitude of the genetic correlation between grain yield, ears plant^{-1} and ASI under drought. To maximize expected genetic gain, drought should be managed so mean ASI exceeds 5 d and mean ears plant^{-1} drops below 0.7, at normal planting densities. During selection, care should be exercised to avoid selecting early-flowering escapes. Depending on resources available, the researcher may then add a third intermediate stress level and observe other aspects of a stress-tolerant ideotype.

Other physiological and morphological traits appear to have little adaptive value for improving performance of maize under drought at the present time, but may assume greater importance once barrenness is substantially reduced and grain yield under stress stabilized. At this point, it is possible that reduced tassel size, erect, green, unrolled leaves with enhanced longevity, and other traits indicative of improved crop water status under drought may assume greater importance during selection. Given that the genetic variability in ASI seems to be related to variation in biomass partitioning to the developing ear rather than to changes in crop water status, selection for grain yield *per se* may be done more efficiently using carefully managed drought as a selection environment, than by direct selection under unstressed conditions.

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From Landrace to Hybrid: Strategies for the Use of Source Populations and Lines in the Development of Drought Tolerant Cultivars

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Abstract

Significant yield reductions caused by drought are common occurrences in maize production fields throughout the world. Although breeding efforts aimed at developing drought-tolerant cultivars are justified in many of these regions, the complexity of the task and the scarcity of resources are often prohibitive. This paper will present principles learned and give an account of germplasm developed, based on our experience with drought-tolerant breeding at CIMMYT. Strategies discussed leading to more efficient development of drought tolerant cultivars include: a) field management of drought stress; b) source population development; c) utilization and introgression of "exotic" drought tolerant sources; d) appropriate recurrent selection schemes; e) use of secondary traits and selection indices; f) line development; and g) hybrid formation and testing.

Development of Drought Tolerant Breeding Populations

CIMMYT has taken two approaches to develop source populations for drought tolerance (DT). One involves recurrent selection with elite populations, in the belief that there is a low frequency of alleles conferring DT in most elite germplasm. The second approach is to evaluate an array of putative DT sources, including cultivars and landraces, followed by recombination of the best of these into a new breeding population which can then be further improved for agronomic performance (Edmeades et al., 1997b). NARS have similar alternatives: the frequency of alleles conferring DT in local 'adapted' germplasm can be improved; 'unadapted' but drought tolerant populations can be improved for local adaptation; and new populations can be formed by introgressing DT source population germplasm into locally adapted germplasm (Fig. 1).

Local 'adapted' germplasm

Evaluation and selection for drought tolerance in local populations can provide useful germplasm. In Thailand, 3 DT synthetic varieties, DR 9401, 02, and 03, have been developed by selecting S_1 families from the maize population KK-DR (Manupeerapan et al., 1997). In West and Central Africa two populations, DRT-EW (Early white dent) and DRT-EY (Early yellow flint), were created from landraces and improved varieties from semi-arid West African countries (Badu-Apraku et al., 1997).

Source populations ('unadapted?' germplasm)

The usefulness of these populations depends on the balance between their tolerance and their adaptation. Susceptibility to other abiotic and/or biotic stresses often restricts their usefulness, though this can usually be improved through selection. Moreover, adaptive traits, such as maturity and disease resistance generally have high heritabilities and are regulated by fewer genes than yield. The CIMMYT drought network provides a good opportunity to evaluate source populations in the target area, and has been used in this manner (Edmeades et al., 1997a). Open-pollinated varieties (OPVs), progeny trials, and recently topcross progeny trials provide a wide range of tolerant source material that can be evaluated under local conditions.

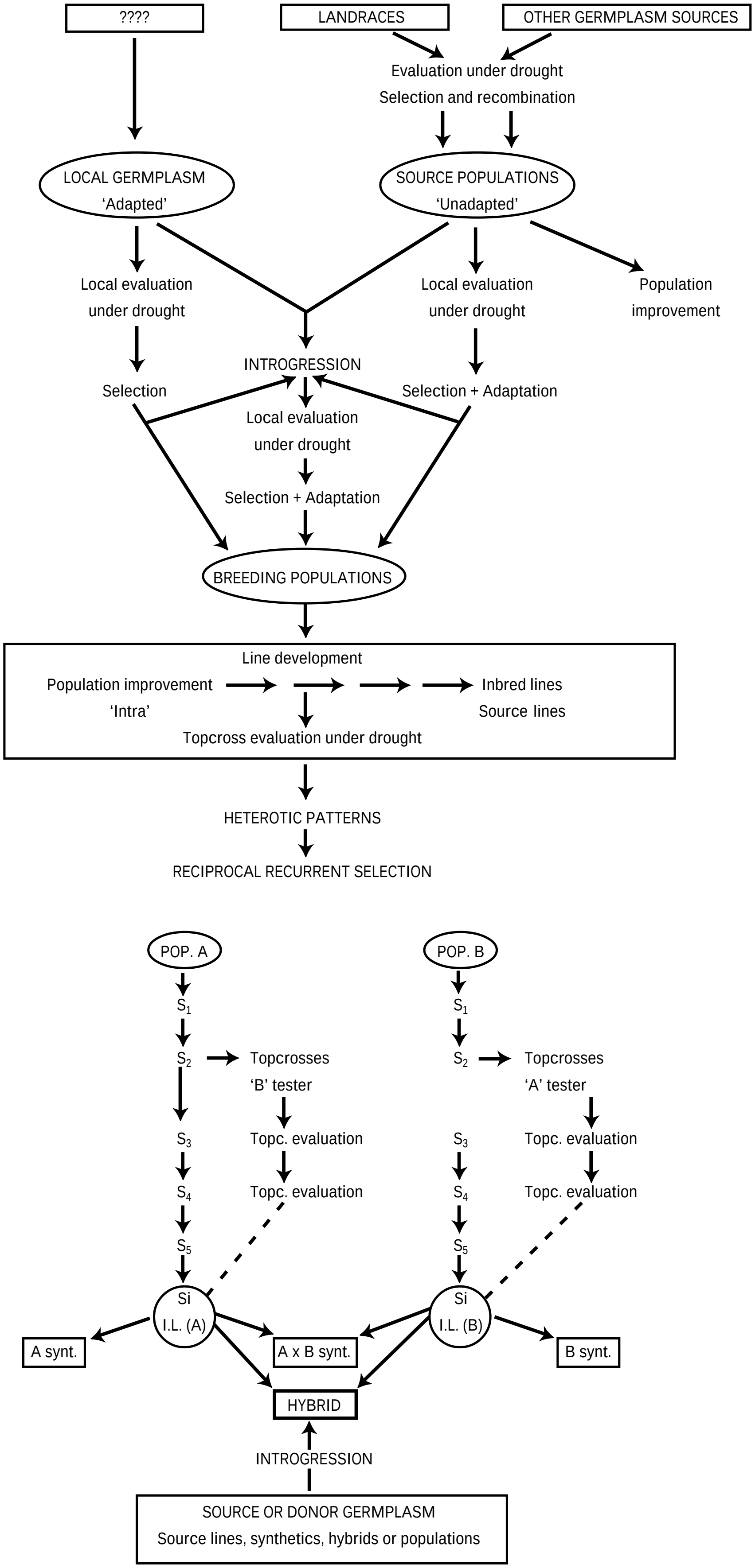

Figure 1. Development of breeding populations from local and source germplasm, RRS and line development and improvement.

Based on their performance, a decision can be made to use the source populations *per se* or to cross them with locally-adapted material.

In Ecuador, two varieties, 'INIAP-540" and 'INIAP-542', were developed by recombining two selections of S_1 families, one each from 'Tuxpeño Sequía C_6' (TS6) and 'Pool 26 Sequía C_1' (Reyes et al., 1997). In Central America, the population 'TS6 x BS19' is under S_2 recurrent selection (Brizuela et al., 1997). In West and Central Africa, 12 drought tolerant early varieties have been extracted from Pool 16 DT, which has been selected for 8 cycles of recurrent selection for DT after its conversion to streak resistance (Badu-Apraku et al., 1997). In Bolivia, a selection of the best S_3-S_4 lines developed by the CIMMYT hybrid program was made based on their topcross performance with a local variety, 'IBO-128', under both drought stressed and normal conditions (Claure et al., 1997). In Ethiopia, two maize varieties 'ACV3' (originated from early maturing collections from North America and Europe) and 'ACV6' (originated from maize collections from USA and Africa) are proposed for release (Yitbarek, 1997). In Vietnam, 'Tuxpeño Sequía', 'Pool 16 Sequía' and 'Pool 18 Sequía' are being used as direct genetic resources to extract inbred lines and to develop drought-tolerant composites in the breeding program (Tinh, 1997).

Formation of new germplasm complexes through introgression

The third and more complex strategy is to develop a new breeding population by introgressing locally adapted germplasm with a source DT population. This approach raises several issues: which source population should be used? What proportion of local and source material is appropriate? How much recombination is necessary before the population is ready for intense selection? And how can molecular markers (MM) facilitate this process?

Incorporation of drought tolerance from 'exotic' material into locally-adapted breeding material is being considered a valid strategy in South Africa (Magson, 1997). In Kenya, locally adapted Katumani and Makueni populations were combined with CIMMYT drought tolerant germplasm (Mugo and Njoroge, 1997). The Kenya Seed Company has screened lines from early-maturing local and introduced CIMMYT germplasm to develop two heterotic populations, KSDA and KSDB. Dryland Hybrids 01 and 02, developed from crosses of lines from these populations, outperformed check entries 'Katumani Composite B' and 'Dryland Composite 1', and have been recently released (Ndambuki, 1997). At CIMMYT, the source population 'DTP2' was created by introgression of new sources of DT into 'DTP1' (Edmeades et al., 1997b). In Indonesia, a local drought tolerant population, 'Cetek', has been used in crosses with other varieties and Pool 2, a population developed by crossing local varieties with Suwan 2, is under selection for DT (Dahlan et al., 1997). In Cameroon, seven varieties from West Africa and CIMMYT were crossed in a partial diallel fashion in order to form two reciprocal DT populations (The et al., 1997).

Which source population(s) to use? - Goodman (1985) indicated the choice of breeding material is a major determinant of the future success or failure of a breeding program. Broad or general adaptation (tropical, subtropical, highland), grain characteristics (color, texture), genetic components and their geographic origin, *per se* performance, combining ability and heterotic pattern, and degree of tolerance in the source populations are relevant information needed to make an appropriate selection. For CIMMYT source DT populations a catalog is available which includes information about adaptation, thermal time to flower, photoperiod sensitivity, type of heterotic response, agronomic type, specific tolerance, grain type, components of the population, selection history, and *per se* performance, where these are known (Edmeades et al., 1995).

Available information can be used to identify breeding materials for an initial evaluation in the target environment. Such an evaluation might be of: The population *per se*; the selfed population *per se*; diallel of local and exotic populations; and population x tester topcross combinations (Geadelmann, 1984). The CIMMYT drought network has provided one way for NARS scientists to evaluate source populations *per se*. Selfed population evaluations could identify favorable recessive alleles for some adaptive qualitative traits (e.g., downy mildew or *Striga* resistance), or eliminate unfavorable recessive alleles. Variety cross diallels have been used to estimate combining ability of populations possessing different levels of exotic germplasm (Crossa et al., 1987; Michelini and Hallauer, 1993). Testcrosses of source populations with a local elite tester are also recommended, especially if that tester's heterotic response is known, though a diallel evaluation has the added advantage of being able to identify completely new heterotic patterns (Geadelmann, 1984).

Biometrical methods can be applied to all the information collected in the preliminary evaluation in order to analyze GxE, to organize the material and to make decisions for the introgression process. Principal component analysis, cluster analysis, factor analysis, AMMI analysis and linear regression are all methods useful for analyzing GxE interaction of source populations in target environments (Crossa, 1990) in an attempt to identify a stable broadly-adapted source material. Diallel information can be used to estimate genetic diversity among local and source populations (Hanson and Casas, 1968) and to evaluate complementation among them (Hanson and Casas, 1981; Hanson, 1983). Prediction methods can be used for selecting composites formed from within a set of local and source populations, and usually take into consideration the predicted mean and potential variability (Miranda-Filho, 1974; Calvalho et al., 1980; Vencovsky et al., 1973), as well as the contribution of varieties to the composite mean of new breeding populations (Miranda-Filho and Chaves, 1991).

What proportion of 'local' versus 'source' germplasm? **-** In the new breeding population the proportion of source germplasm can vary from: 12.5% (BC_2 with local germplasm as recurrent parent); 25% (BC_1 with local germplasm as recurrent parent); 50% (F_2 population); 75% (BC_1 with the source population as recurrent parent); and 87.5% (BC_2 with the source population as recurrent parent). In theoretical studies examining the introgression of 'exotic' into adapted germplasm, Dudley (1982) concluded that at least one generation of backcrossing to the adapted parent (25% 'exotic') would be appropriate, and additional backcrossing was possibly justified when diversity between the parental populations was large. This is in agreement with various researchers' empirical results (Geadelmann, 1984). However, 100% 'exotic' populations such as BS16 (100% ETO) have been successfully adapted to Corn Belt conditions after several cycles of mass selection for early flowering (Hallauer, 1978) while other exotic populations have been used directly as a source of inbred lines (Goodman, 1985). Michelini and Hallauer (1993), by regressing grain yield on percentage of exotic germplasm in several crosses (0%, 25%, 50%, 75% and 100% exotic), concluded that 50% exotic germplasm provided the best means of retaining and combining favorable alleles from an exotic source with local germplasm. When evaluating inbred progenies (S_1, S_2) developed from populations with some degree of exotic germplasm, mean grain yield was lower for introgressed populations than for adapted populations but genetic variation was increased by introgression, resulting in higher predicted gains (Crossa et al., 1987; Eagles and Hardacre, 1990).

In our case the proportion of 'source' germplasm will depend on the balance between the adaptation of the source population(s) and the drought tolerance level of the local population (s). Multilocation evaluation of source populations and CIMMYT Preliminary Evaluation Trials (PETs) suggest that some source populations, such as La Posta Sequía C_3, show good stability across a range of environments (Edmeades et al., 1997c), though a preliminary evaluation is still needed to determine adaptation and relative performance under drought of source germplasm. Crossa (1989) discussed the probability of fixation for one favorable gene (one locus) and for two independent genes (two loci) from different base populations (F_2, BC_1, BC_2) at different effective population sizes (Ne), gene frequencies in local and source populations, and intensities of selection (i). Ho and Comstock (1980) showed that when Ne is large enough and local and source populations do not differ much in performance, the F_2 population should be used as a base foundation population. If the difference in performance between parents is large, one backcross to the superior germplasm would be the appropriate choice. Similar results were found by Bridges and Gardner (1987) for both long-term and short-term selection goals.

How much recombination in 'local x source' populations? **-** There is general agreement regarding the beneficial effects of several generations of intermating with mild phenotypic selection following the introgression process, but before intense inbreeding and selection is initiated (Geadelmann, 1984). High linkage disequilibrium along with intense selection could result in the loss of favorable alleles. On the other hand, random mating with mild selection allows the separation of useful and undesirable linked alleles (Eagles et al., 1989). During recombination it is important to maintain an adequate effective population size to avoid genetic drift (Hallauer and Miranda, 1988). The loss of time needed for recombination can be partially offset by initiating mild selection for adaptation and possibly DT. We recommend at least three generations of recombination under local conditions before initiating any inbreeding.

Molecular marker (MM)-monitored introgression. Strategies for marker-based introgression of drought tolerance **-** Molecular markers have the potential to increase efficiency of the introgression process by:

1. Providing additional information on the relationship between source and local populations, and their genetic diversity.
2. Facilitating the introgression into local populations of specific genomic regions associated with DT in the source population.
3. Increasing the probabililty of recovering transgressive segregants for DT while maintaining adaptation.

DNA fingerprinting can be used to select source populations that generate maximum diversity and minimum duplication with local populations. Once the source population has been identified and crossed with a local population, if quantitative trait loci (QTLs) for DT in the source population are known then markers can be used directly to recover progenies carrying the DT regions. If QTLs for DT have as yet not been identified, the 'local x source' cross has to be characterized for marker genotypes as well as for DT and adaptation. Hybridization among different germplasm sources (local vs. source) creates a desired degree of genetic disequilibrium that can be exploited to identify QTLs. Because such a cross between populations produces unique genotypes that can not be replicated to reduce environmental error (especially important under drought stress) or that may be lost after marker characterization is completed, it will usually be more efficient to use a mapping population formed from the cross of 'local x source' inbred lines, partially-inbred lines, or doubled haploids, even though this requires additional time and resources (Edwards, 1992). Once the association between MMs and QTL has been made, new cycles of recombination and selection can be monitored by MMs to increase the frequency of favorable alleles in the progenies. However, the probability of recombination between the markers and QTLs increases with the additional cycles so marker-assisted selection should be emphasized during the early cycles.

At CIMMYT, there is on-going research to identify genomic regions responsible for drought tolerance. Ribaut et al. (1996) identified QTL for the anthesis-silking interval (ASI), an important secondary trait in selection for drought tolerance (Edmeades et al., 1992). Changes in allelic frequencies in 'Tuxpeño Sequía' during cycles of selection have paralleled changes in QTL for drought tolerance, identified using MMs (Ribaut et al., 1997b). In the future it should be possible to assist NARS in their search for DT by offering these QTL as a product, along with the methodologies to identify and transfer them (Ribaut et al., 1997a).

Population Improvement

Intrapopulation improvement methods have been effective at improving the DT of source populations (Edmeades et al., 1997d), and have increased the probability of developing superior DT inbred lines from those populations (Edmeades et al., 1997c). Vasal et al. (1997) have discussed the effectiveness of, and potential choices among, breeding procedures which are recommended at different stages of a breeding program. Here a more hybrid-oriented breeding methodology will be presented.

Heterotic patterns

Lee (1995) defines a heterotic group as "a collection of germplasm which, when crossed to germplasm external to its group (usually another heterotic group), tends to exhibit a higher degree of heterosis (on average) than when crossed to a member of its own group". Identification of such heterotic patterns may be conducted using a population. If the heterotic pattern is already known we can classify new material by crossing it with an appropriate representative tester from each heterotic group. Heterotic patterns for temperate maize are well established, and include Reid's Yellow Dent x Lancaster Surecropper in USA, and European flints x USA dents in Europe. These patterns have had a relatively long evolutionary development process resulting in significant genetic distance between the groups. Common heterotic patterns with tropical maize include Tuxpeño in combination with either ETO Composite, Suwan 1, Cateto, or Cuban Flints. Each of these represents a broader germplasm base and shorter evolutionary history than those of the heterotic groups identified in temperate maize.

In CIMMYT an extensive characterization of lowland tropical and subtropical maize germplasm was done in order to develop hybrid-oriented populations (Beck et al., 1990; Crossa et al., 1990; Vasal et al., 1992a, b). Although results generally showed low levels of interpopulation heterosis, several heterotic pairs have been identified for use in reciprocal recurrent population improvement schemes (e.g., Population 21 (Tuxpeño) and Population 32 (ETO). The issue of whether to establish a heterotic pattern for DT is a difficult one, and the authors are not aware of any published work on this subject. If we use inbred line-based synthetics or existing elite DT populations, these will probably need to be assigned to a heterotic group suited to the needs of the national program. Here there are two choices: (i) use testers for existing heterotic groups to characterize incoming germplasm; or (ii) to create new DT heterotic groups. In (i) the testers will largely represent normal conditions, and in (ii) the testers will maximize heterosis under drought (see section on appropriate testers). In CIMMYT, for example, we are using CML 247 and CML 254 as white tropical inbred line testers under drought, but CML 254 has more inherent DT than CML 247, creating a bias in favor of CML 254 when materials are assigned to heterotic patterns based on performance under severe drought stress. Once heterotic groups are defined, either the reciprocal population, or lines/hybrids developed from it, can be used as a tester. Definition of heterotic responses of source germplasm will undoubtedly increase the efficiency with which it can be utilized in national breeding programs.

Reciprocal recurrent selection breeding method proposals

Interpopulation recurrent selection methods, such as reciprocal recurrent selection (RRS) can maximize potential benefits of heterosis, and usually build on previous intrapopulation improvement efforts (Fig. 1). Intrapopulation methods (e.g., mass selection, half-sib, full-sib and S_1/S_2 recurrent selection) have generally been more effective than interpopulation approaches at improving population means *per se* for mono- and oligogenic traits such as insect and disease resistance, plant height, tassel size, anthesis-silking interval, and for improving yield itself (Pandey and Gardner, 1992). After initial improvement using intrapopulation selection, a switch to RRS is proposed in order to create favorable complementary allele combinations in both heterotic populations. These combinations will exploit heterosis by emphasizing both non-additive as well as additive gene effects.

Two RRS schemes are presented for DT improvement, based on that proposed by Eberhart et al. (1996). These are reciprocal full-sib selection (FS) and reciprocal recurrent selection (RRS) (Fig.2; Fig. 3). Alternating rainy (RS) and dry seasons (DS) in a given year are used in the schemes presented. The basic difference between FS and RRS is that only one set of n (S_2-A x S_2-B) crosses needs to be evaluated in FS, vs two sets (n S_2-A x B tester + n S_2-B x A tester) in RRS. One disadvantage of FS is that hand pollinations are required (S_2 lines from A and B are paired according to maturity), whereas with RRS the S_2 testcross formation can be done using isolation blocks. Under both schemes during the first RS season (RS1), selection for highly heritable traits such as maturity, ASI, disease resistance and plant height can be done among S_0 plants in both populations. In the DS2 season, S_1 families will be evaluated under intermediate drought stress and/or high densities and selected for agronomic traits with low to moderate heritability, such as yield, grain quality, and lodging resistance. In the RS2 season, S_2 lines will be used to form either FS families (FS) or testcrosses (RRS), while simultaneously another set of these S_2's are advanced to S_3. FS families or testcrosses can be evaluated in season DS3 under well-watered and controlled drought stress conditions. Based on trial data, a superior set of S_2 lines from Population A and B, sown from remnant seed, will be recombined separately to form the next cycle of selection for each population. In the initial cycles of RRS the opposite

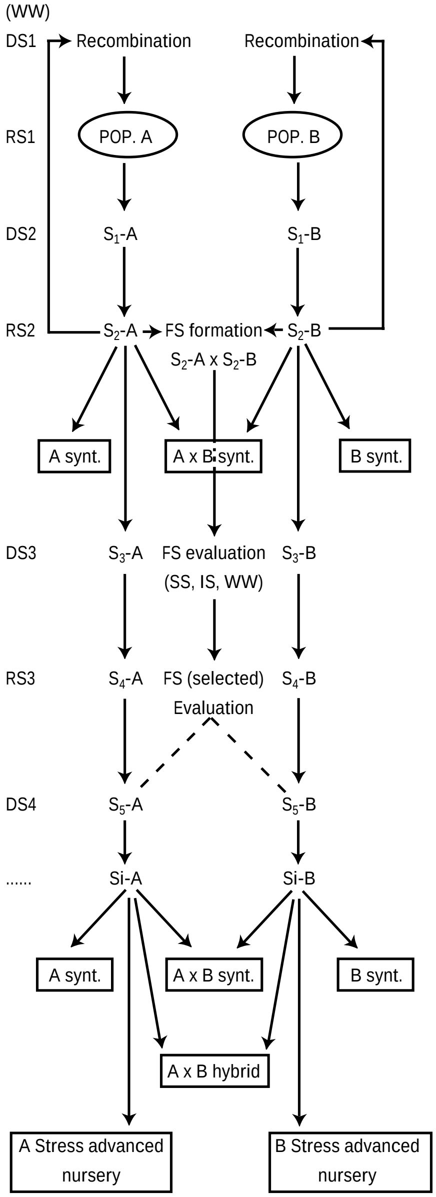

Figure 2. Reciprocal full-sib selection scheme for drought tolerance.

population can be used as a tester, but in later cycles a single-cross or line tester formed from the opposite population should be used. Genetic gain formulae for each method, and factors affecting that gain, have been presented by Hallauer and Miranda (1988) and Eberhart et al. (1996).

In comparisons among intra- and interpopulation schemes, the average observed genetic gain per cycle were found to be similar (Hallauer and Miranda, 1988), though genetic gain per year was generally higher for the intra-population schemes.

Nevertheless, the value of RRS must be judged by the improved heterosis among reciprocal populations and the increased probability of obtaining superior A x B hybrids. The value of RRS in selection specifically for drought tolerance remains unanswered.

Breeding Methodology

Breeding methodology at CIMMYT

Once the initial DT breeding population(s) are formed, other issues, such as the product goal (variety, synthetic, or hybrid), must be addressed. Open-pollinated varieties, compared with hybrids, require less development time, have lower seed costs, and are often more stable but lower yielding. Increased pressure for input use efficiency and for yield, and increased availability of tropically-adapted, hybrid-oriented germplasm have led to increased demand for hybrid development. In response CIMMYT, including the stress breeding unit, has significantly increased its resources devoted to developing hybrid-oriented germplasm for major maize ecologies (Vasal et al., 1997) in a program in which the production of hybrids and OPVs is carefully integrated.

Field drought stress evaluations - These are critical to a successful DT breeding program, where reliable expression of DT traits is essential to progress. In our work, dry season nurseries with controlled applications of irrigation water have been used to evaluate lines and hybrids. The soil profile is fully charged at planting and stress progressively develops as water is used during the growing season. Three moisture regimes used are: well-watered with target yield = 100%, to allow full expression of yield potential; mild flowering and severe grain filling stress with target yield = 50%, where irrigation is withheld from early flowering to maturity; and severe flowering and grain filling stress with target yield = 10-20%, where water is withheld from about 3 weeks before flowering until maturity. One useful alternative is to use only one water regime with

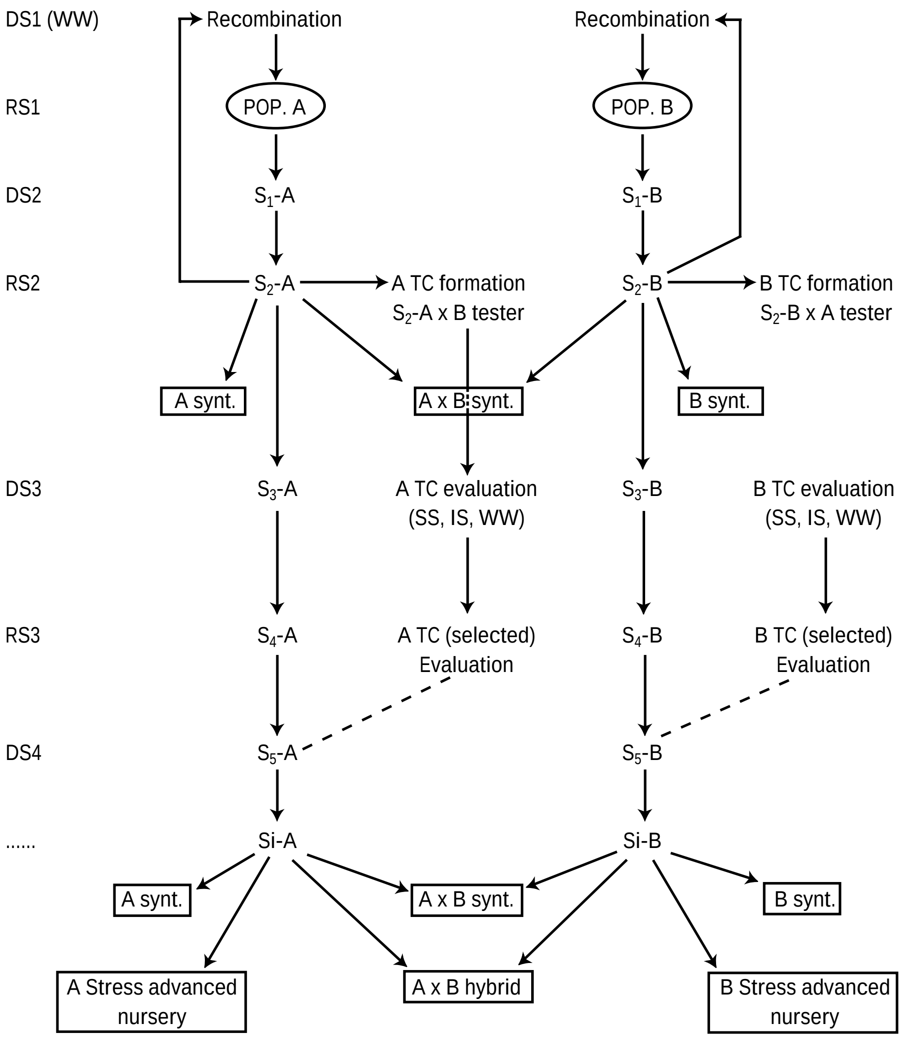

Figure 3. Reciprocal recurrent selection scheme for drought tolerance.

target yield = 75% at normal plant density, and combine this with a higher plant density (2 times normal) to obtain a considerably greater stress level. High plant densities are known to increase the anthesis-silking interval (ASI) and this is commonly used by plant breeders in temperate environments to improve overall stress tolerance in segregating nurseries. The relationship between high density tolerance, ASI, and DT seems clearer in temperate germplasm but is still a matter of debate in tropical germplasm, where the correlation between ASI under high density and under drought has been reported to only be 0.3-0.4 (Edmeades et al., 1992). Our goal in stress management is to expose genetic variability for traits indicative of drought tolerance or susceptibility including yield, barrenness, leaf rolling, upper leaf firing, lower leaf senescence, tassel blasting and ASI. A standardized selection index of these traits and others such as root and stalk lodging is used to select superior families. Alpha (0,1) lattice designs are routinely used to adjust for within-block variation caused by soil variation. The importance of correct timing of stress through careful water management, the ability to rapidly evaluate primary and secondary traits, the use of procedures that integrate these data into a single value for selection purposes (Barreto et al. 1997), and the effective control of experimental error, cannot be overemphasized.

DT population improvement - The CIMMYT Maize Program has successfully developed a series of tropically-adapted DT populations using half-sib, full-sib, and S$_1$ recurrent selection (Edmeades et al., 1997b). We are now attempting to build on the population improvement foundation established by both breeders and physiologists to develop lines, synthetics, and hybrids tolerant to drought.

Development of drought tolerant lines and hybrids - S$_1$ recurrent selection has the added advantage over other methods of providing early generation lines for further hybrid development. A modified two-stage S$_1$ recurrent selection scheme has been used where a large number (500-1,000) of S$_1$ families from a given population were prescreened under summer drought and heat stress at Ciudad Obregon, Mexico (Fig. 4). The superior 200-250 families are grown from remnant seed at CIMMYT's experiment station in Tlaltizapán during the winter dry season under three water regimes and 50 superior S$_1$ lines were recombined to form the next cycle of the population (Edmeades et al., 1997b). Remnant seed of the 50 selected S$_1$s have also been sown in our breeding nursery and advanced by selfing to S$_3$, while being tested for *per se* performance under drought. Combining ability evaluations were first conducted with S$_3$ lines derived from the populations La Posta Sequia C$_3$ (LPS) and TS6 (two tropical, drought tolerant populations of Tuxpeño origin) crossed onto two testers (experimental varieties representing the Tuxpeño (Across 9021) and ETO (Across 9032) heterotic groups). The topcross hybrids were evaluated under both droughted and normal conditions over two seasons, while the original S$_3$ lines were advanced by selfing to S$_5$. Superior lines based on *per se* and topcross tests are being evaluated in new hybrid combinations with elite tester lines from the tropical lowland program. These lines are also being used to form synthetics and we have begun a small effort in recycling these materials. Elite lines have been recently released as CIMMYT maize lines (CMLs; Table 1).

Correlation between line and hybrid performance - The relationship between performance of inbred lines and their hybrids is an important issue in hybrid development. Brown (1967) concluded that selection for improved plant type in lines made no

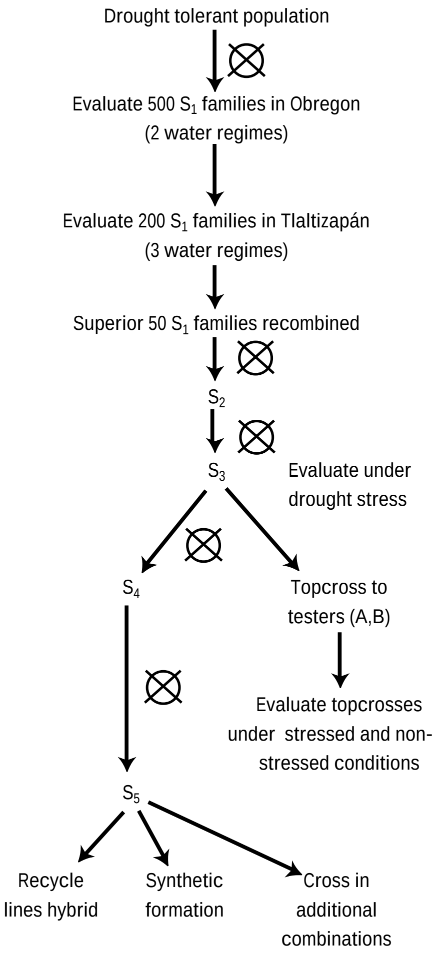

Figure 4. General breeding scheme for drought tolerance population improvement and line development used at CIMMYT.

contribution to yield of the lines in hybrid combinations. Other studies have shown small positive gains in combining ability with lines selected for improved plant type. Hallauer and Miranda (1988) concluded that visual selection of *per se* line performance has value in developing vigorous lines suited to economic seed production. There is evidence that, under stress conditions imposed through high plant densities, the relationship between line and hybrid performance is somewhat stronger than under non-stress conditions. In a study of 200 tropical inbred lines and topcrosses evaluated under non-stress and drought stress conditions, Betrán et al. (1995) showed that their performances were significantly and positively correlated under the same stress but not between stress levels. Under a stress provided by low soil nitrogen, S_2 line and topcross yields for 80 entries were not significantly associated (r = 0.22 ns) (Lafitte and Edmeades, 1995). These findings imply that selection of lines for *per se* performance under stress may be justified to the $S_{2\text{-}3}$ level, but with higher levels of inbreeding selection, should be based on hybrid performance.

Appropriate testers - The choice of tester is critical yet difficult. Hallauer (1975) indicated that a suitable tester should provide simplicity of use and information that correctly classifies the relative merit of lines and should maximize genetic gain. Of great interest here is how the given tester line classifies materials as stress intensifies from low to intense drought stress. For DT we are currently using as testers elite inbred lines developed by CIMMYT´s conventional lowland tropical breeding program. Testers have similar adaptation, maturity, and grain color characteristics as the material under test. These are:

Line No.	Grain color	Maturity	Pedigree	Drought tol.
CML 247	White	Late	(G24F119*G24F54)-6-4-1-1-BB-f	Susc.
CML 254	White	Late	TuxSeq-21-1-2-1-B-##-2-BB-f	Interm.
CML 287	Yellow	Late	(P24F26*P27F1)-4-1-B-1-1-BB-f	Susc.
CL00331	Yellow	Late	Sint.Am.TSR-23-3-1-1-1-BB-f-#	Susc.

Using these testers promotes germplasm flow among the various CIMMYT breeding programs, allows us to test our stress tolerant lines with the best elite germplasm, provides good separation into heterotic groups, and allows us to use common isolation blocks with the conventional breeding programs to form large numbers of topcrosses efficiently. There are some disadvantages to using these testers, since they confine us to a specific heterotic pattern and raise the question of "dosage"; i.e., is it necessary that both parents of a hybrid contribute stress tolerance, to obtain a tolerant hybrid? We recently initiated combining ability studies with early maturing tropical lines, using as testers an S_6 line developed by the lowland tropical subprogram from Pool 15 and an S_4 line developed from Pool 16. With yellow-grained materials derived from Pool 18 Sequía, we are using an elite flint single cross consisting of lines from Pool 17 and Population 31 as the tester.

Table 1. Recently released CMLs adapted to the lowland tropics and carrying drought tolerance.

CML No.	Pedigree	Grain* texture	GCA+	Heterotic# pattern	Special resistance/tolerance
White Grained					
339	La Posta SeqC3-H297-2-1-1-1-3-#-#-B-B	F	Excellent	B	Drought
340	La Posta SeqC3-H20-4-1-1-2-3-#-#-B-B	SD	Good-Exc	A/B	Drought
341	La Posta SeqC3-H1-2-2-2-1-1-#-#-B-B	SD	Excellent	A/B	Mod. Drought, Low N
342	La Posta SeqC3-H1-2-2-3-2-1-#-#-B-B	SD	Excellent	A/B	Mod. Drought, Low N
343	La Posta SeqC3-H17-1-2-3-2-1-#-#-B-B	SF	Excellent	A/B	Mod. Drought
344	TS6C1-F118-1-2-3-1-2-#-#-B-B	SF	Good	A/B	Mod. Drought, Low N
Yellow Grained					
347	G26SeqC3-H71-1-1-2-1-B	SD	Good	A/B	Mod. Drought
348	G26SeqC3-H83-1-1-2-1-B	SF	Good	B	Mod. Drought

* F=flint, SF=Semi-flint, SD=Semi-dent
+ General combining ability
# A= Tuxpeño type
B= Non-Tuxpeño, ETO, type

Dosage effects - A project involving a diallel among stress tolerant and susceptible lines aims to determine the genetic control and modes of action for DT, to examine dosage rate and hybrid vigor effects for DT, determine the relationship between line *per se* and hybrid performance under drought stress and normal conditions, and to identify single crosses for developing second cycle lines that combine DT and good agronomic performance. Ten superior lines from LPS and TS6, along with seven elite lines from the lowland tropical subprogram, were crossed in all possible combinations and the resulting hybrids are being evaluated under a range of moisture levels.

Reciprocal recurrent selection - This was designed to improve cross performance between two heterotic populations, and may be appropriate for programs geared toward hybrid development (Hallauer and Miranda, 1988). We are gathering combining ability information on DT lines in various studies, including the DT network and other hybrid evaluations, and this could be used to form two heterotic DT synthetic populations. We will form two heterotic white-grained DT populations, which may then be improved using the modified S_2 testcross reciprocal recurrent selection scheme previously described.

CIMMYT Source Material

Recently released CMLs carrying drought tolerance

CIMMYT has recently made available to research partners several lines with moderate-to-good DT (Table 1). All lines have tropical adaptation and are late maturing. Most white-grained lines were derived from the La Posta Sequía population; the yellow-grained lines come from Pool 26 Sequía. Grain texture, general combining ability, heterotic pattern, DT, and reaction of lines under low nitrogen conditions are indicated by material in Table 1.

Line and hybrid improvement by introgression

Here we discuss strategies to improve line and hybrid performance. Our most important decision is what source germplasm (lines, synthetics, populations, hybrids, etc) is most likely to contribute the most favorable genetic factors for DT to the elite recipient line or hybrid? Several methods of selection of the donor source have been described by Dudley (1982, 1984a, b, 1987), Gerloff and Smith (1988), Bernardo (1990), Metz (1994), and Hohls et al. (1995). The objective is to identify source germplasm (P_w) with the highest frequency of favorable dominant alleles which are not present in an elite hybrid (P_1 x P_2). Dudley (1984a, 1987) established four different classes of loci for the two parental inbred lines: class i loci (homozygous favorable in both P_1 and P_2), class j loci (homozygous favorable in P_1 and homozygous unfavorable in P_2), class k loci (homozygous unfavorable in P_1 and homozygous favorable in P_2) and class l loci (homozygous unfavorable in both P_1 and P_2). The frequency of favorable alleles at class l loci (p_l) and its number ($l\mu$) estimates the number of favorable alleles that P_w can provide to P_1 or P_2 to improve the hybrid. Dudley (1987) proposed the statistic $l\mu' p_l$ (DS) to select the P_w with the highest frequencies of favorable alleles not present in P_1 or P_2. The estimator was: $[(P_w \times P_1 - P_1)(P_1 \times P_2 - P_2) - (P_w \times P_2 - P_2)(P_1 \times P_2 - P_1)]/[2(P_1 - P_2)]$.

Gerloff and Smith (1988) proposed two additional statistics: the upper bound (UBND) = minimum ($P_w \times P_1 - P_1$, $P_w \times P_2 - P_2$), and the testcross to the single cross [TC(SC) = P_w x (P_1 x P_2). Estimation of DS and UBND requires evaluation of the testcrosses of the source material to the two inbreds and the inbreds themselves (inbred performance could be a limitation). TC(SC) calculation, however, requires only the evaluation of the three-way crosses of potential P_ws with the target single-cross, but does not provide information about the heterotic group of P_w. DS, UBND and TC(SC) statistics were evaluated to identify donor inbred lines (Misevic, 1989a, b) and commercial hybrids as sources of favorable alleles (Misevic, 1990). Bernardo (1990) pointed out that there is a risk of losing favorable alleles present in a single cross while new favorable alleles are being transferred from P_w to P_1 or P_2. Bernardo (1990) devised the NI (net improvement) statistic, which estimates the number of favorable alleles that can be gained from P_w minus the number of favorable alleles that can be lost from P_1 or P_2 ,and can be calculated as the maximum of $[(P_1 \times P_w - P_1 \times P_2)/2, (P_2 \times P_w - P_1 \times P_2)/2]$. NI requires similar evaluations as DS and UBND.

Metz (1994) proposed two statistics, PNG_g and PNG_{ceg}, to estimate the genetic probability of a net gain of favorable alleles from P_w regardless of its relationship with P_1 and P_2. With the same purpose Hohls et al. (1995) presented an unbiased estimator, ma(B + G), based on a combining ability model and free from the assumption of complete dominance. General combining ability, GCA (Sprague and Tatum, 1942), also could be used to identify the best source when GCA has been estimated under local drought conditions.

As an example, we assume our goal is to improve the performance under drought stress of the tropical white CIMMYT single cross CML247 x CML254 (P_1 x P_2) (or any other local hybrid). We have several DT sources including five advanced lines from $LPSC_3$ and five advanced lines from $TS6C_2$ (P_ws). Both sets of lines will be crossed with CML247, CML254, and CML247 x CML254. Hybrids plus parental lines will be evaluated in local environments under drought stress. Calculation of the estimates defined above will provide criteria to select the best source line(s) to improve the drought tolerance of this specific hybrid.

Once the source is identified, what is the best method of incorporating new alleles from the donor (D) to the recipient (R) line?. After the initial cross between R x D is made, selection and/or inbreeding can be initiated either immediately or after one or more backcrosses. Dudley (1982, 1984b) examined the most efficient method of transferring alleles from the D to the R parent, considering different generations (F_2, BC_1F_2, BC_2F_2, BC_3F_2), level of dominance (additive, partial dominance, complete dominance), and the proportion of loci homozygous and favorable for R and D (50-50, 70-30, 80-20, 90-10, 95-5). Dudley (1984b) noted the advantages of backcrossing if one parent has more loci with favorable alleles than the other, the parents are diverse, or the level of dominance is high. Selection before inbreeding will increase the probability of developing lines superior to either parent.

These recommendations can be applied using our example with CML 247 as the R line. First, define the degree of DT necessary for the target environment. If tolerance to severe drought stress is the goal, one or more backcrosses to the D line are recommended. If intermediate drought stress is desired, the F_1 (50% CML 247 and 50% D) may be the more appropriate starting population. Several generations of recombination of the chosen population before initiating inbreeding under drought stress conditions would increase the chances of obtaining inbreds with DT *and* good agronomic performance. However, Lamkey et al. (1995) indicated that in second cycle breeding when inbreds from the same heterotic pattern are used as potential donors, favorable epistatic gene combinations can be maintained by limiting recombination before selection and inbreeding.

Molecular markers (MMs) can be used during different phases of line and hybrid development by facilitating *a priori* selection of parents for source populations, estimating genetic distance among lines and hence helping assign lines to heterotic patterns, and assisting in identification of the best hybrid combinations (Lee, 1995). MMs could be used to estimate the number and location of those regions with favorable alleles and to provide the basis for MM-assisted enhancement of DT or improvement of a superior line such as CML 247 (in our example). Thus marker-assisted backcrossing would reduce the number of backcross generations and ensure the recovery of the favorable CML 247 alleles as well as the DT donor alleles (Ribaut et al., 1997a). With marker-assisted backcrossing, up to six independent markers (or QTLs) can be transferred, using closely flanking markers. However, if the number of regions is significantly larger than six it may be necessary to initiate backcrosses using subgroups of lines (Edwards, 1992). An interesting alternative to marker-assisted backcrossing would be to conduct cycles or recurrent selection using the F_2 population as a starting population and trying to accumulate DT factors in the new progenies. This is related to an increase in the probability of developing superior inbred lines if selection is made before inbreeding (Dudley, 1984b), but recognizes that flanking markers provide a better chance of maintaining favorable DT genes and to increase their frequencies.

Conclusions

In summary, we have presented principles along with examples for the development of DT populations. Three breeding approaches described included the identification and development of local 'adapted' populations, the use of source DT populations, and the formation of new germplasm complexes through introgression. We described our DT breeding work at CIMMYT involving careful integration of population improvement with line and hybrid development. Information regarding the recent release of CMLs with DT is presented. Theoretical ideas and practical examples on methodologies for introgression at the inbred line level and the use of molecular markers in improving efficiency in DT breeding are presented.

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Relationship Between Line and Topcross Performance Under Drought and Non-Stressed Conditions in Tropical Maize

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Abstract

Maize grain losses due to drought in the tropics may reach 24 m tons per year. 'Tuxpeño Sequía C_6' (TS6) and 'La Posta Sequía' (LPS) are two white-grained tropical populations that have been improved for drought tolerance at flowering and grain filling, using a recurrent S_1 selection scheme under three water regimes: well-watered, intermediate drought stress and severe drought stress. Population improvement accomplished by recurrent selection has shown that increased grain yield under drought stress is highly associated with reductions in anthesis-silking interval (ASI) and barrenness. The objective of this study was to estimate the relationships among yield and secondary traits under managed stress environments between S_3 lines derived from TS6 C_1 and LPS C_3 and their topcrosses with Tuxpeño and non-Tuxpeño testers. Phenotypic correlations between topcross grain yield and line grain yield, ASI and barrenness, as well as high heritabilities for these traits (>0.50), suggest that selection for a reduction in ASI and barrenness in the lines, together with line per se yield performance under drought, could be used to select stress tolerant hybrids.

Maize grain losses due to drought in the tropics may reach 24 m tons per year, equivalent to 17% of well-watered production (Edmeades et al., 1992). Improvements in drought tolerance at flowering in open-pollinated varieties have been accomplished by recurrent selection using managed stress environments (Bolaños and Edmeades, 1993; Byrne et al., 1995). The value of individual secondary traits such as ears per plant, anthesis-silking interval (ASI) and senescence has been demonstrated by linear phenotypic correlations and divergent selection (Bolaños et al., 1993).

Inbred line information indicative of hybrid performance is desirable to reduce hybrid trial evaluation. Development of stress tolerant hybrids requires selection for certain traits during inbred line development. In order for this selection to be effective we need to know the relationship between inbred lines and hybrids under drought stress. This study compared lines and topcrosses developed from two drought-tolerant populations, examined the relationship between lines developed from drought-tolerant populations and their topcrosses under normal and stressed conditions, and evaluated the importance of secondary traits in a hybrid breeding program.

Materials and Methods

One hundred S_3 lines derived from TS6 C_1 ('Tuxpeño Sequía C_6') and 100 LPS C_3 ('La Posta Sequía') and their topcrosses with Tuxpeño (Ac9021) and non-Tuxpeño (Ac9032) testers were used. TS6 and LPS are two white-grained tropical populations that had been improved for drought tolerance at flowering and grain filling, following a recurrent S_1 selection scheme under drought and well watered conditions. Ac9021 and Ac9032 are two experimental varieties derived from Population 21 (Tuxpeño) and Population 32 (ETO), respectively.

Lines and topcrosses were evaluated under three water regimes in the rainfree winter environment at the CIMMYT experiment station at Tlaltizapán, Mexico (940 masl). The three water regimes used were: WW (Well-watered; normal conditions); IS

(Intermediate drought stress, with water stress during late flowering and throughout grain filling); and SS (Severe drought stress, with no water applied from 3 weeks before silking till maturity). The materials were also evaluated at CIMMYT's station at Poza Rica, Mexico (60 masl), under well-watered, lowland tropical wet season conditions.

Traits measured included AD, days from sowing to 50% of the plants shedding pollen; SD, days from sowing to 50% of the plants with silks emerged from the husk; ASI, which was taken as SD-AD; EPP, ears per plant (total number of harvested ears/total number of plants); GY, oven-dry grain yield obtained from shelled grain (SS and IS treatments) or by assuming a shelling percentage of 80% in well-watered plots; and SEN, leaf senescence scored as the proportion of total leaf area which is dead. Individual and combined analyses of variance of alpha (0,1) lattice designs in two reps per environment were conducted with the SAS MIXED procedure (SAS Institute Inc., 1992). Lattice-adjusted means were used to calculate simple phenotypic correlations among lines and topcrosses. Grain yield was adjusted (AGY) to a constant flowering date by covariance. The SAS STEPWISE procedure was used to relate line traits to topcross performance.

Results and Discussion

Among lines, grain yield reduction from WW to SS was 90% (Table 1, Fig. 1). LPS lines suffered greater grain yield reduction (92%) than TS6 lines (88%), though LPS lines performed better than TS6 lines under well-watered conditions (Fig. 2). Heritabilities of grain yield and secondary traits were similar (>0.50) in SS and WW conditions. Grain yield reduction among topcrosses from WW to SS was 70% (Table 2, Fig. 3). Grain yield reduction for LPS topcrosses was 19% from WW to IS and 73% from WW to SS. Grain yield reduction for TS6 topcrosses was 20% from WW to IS and 67% from WW to SS. LPS topcrosses were superior under WW and IS conditions and TS6 topcrosses were superior under SS (Fig. 4). TS6 C_1 has a longer breeding history for drought tolerance (six cycles of full-sib recurrent selection + one cycle of S_1 recurrent selection) than LPS C_3 (three cycles of S_1 recurrent selection), which is reflected in line and topcross performance. Heritability for grain yield decreased when drought stress increased (Table 2).

Topcross GY under SS was significantly correlated with all line traits under SS as well as with line AD under WW (Table 3). AGY correlations were lower than GY

Table 1. Performance of maize inbred lines derived from LPS C_3 and TS6 C_1 under drought stress and well-watered conditions, Tlaltizapán, Mexico.

	GY (t/ha)	EPP	AD (d)	ASI (d)	SEN (%)
Severe stress (SS)					
Mean	0.39 ± 0.01	0.61 ± 0.01	96.5 ± 0.14	-0.99 ± 0.2	64 ± 0.4
LPS C_3	0.33 ± 0.02	0.58 ± 0.02	98.1 ± 0.28	-0.30 ± 0.4	57 ± 0.9
TS6 C_1	0.44 ± 0.02	0.64 ± 0.02	94.9 ± 0.28	-1.69 ± 0.4	71 ± 0.9
Heritability	0.64	0.62	0.83	0.61	0.76
Well-watered (WW)					
Mean	3.96 ± 0.05	1.31 ± 0.01	91.9 ± 0.10	-0.65 ± 0.09	36 ± 0.5
LPS C_3	4.05 ± 0.10	1.30 ± 0.03	93.6 ± 0.21	-0.63 ± 0.18	34 ± 1.0
TS6 C_1	3.88 ± 0.10	1.32 ± 0.03	90.2 ± 0.21	-0.68 ± 0.18	39 ± 1.0
Heritability	0.61	0.58	0.83	0.54	0.60

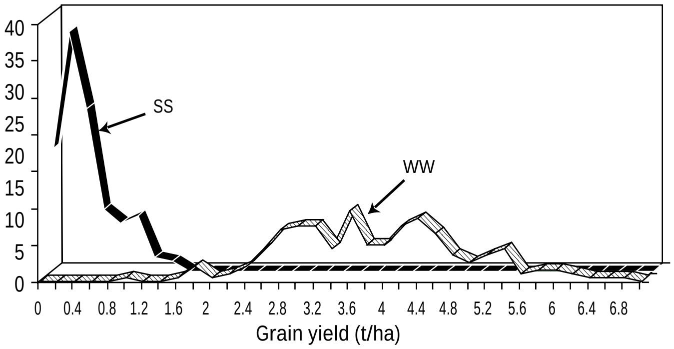

Figure 1. Frequency distribution for line GY under SS and WW water regimes.

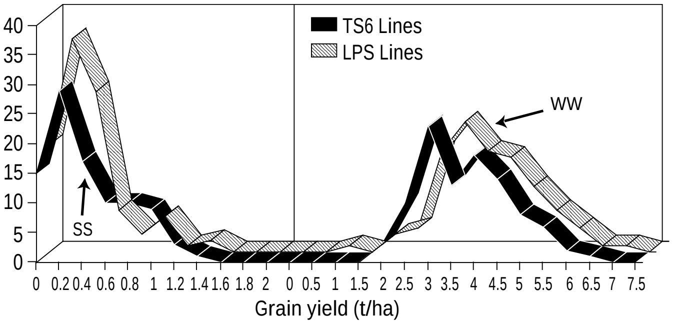

Figure 2. Frequency distribution for GY in LPS and TS6 lines under WW and SS water regimes.

correlations. Correlation of line ASI under SS with topcross GY and AGY was significant only under SS conditions. Line AD showed a negative correlation with topcross GY under SS and a positive correlation under WW. Line SEN under SS was negatively correlated with topcross GY under IS. Line AD and ASI under SS together explained 34% of topcross GY under SS (Table 4). Line SEN under SS explained 8% of topcross GY under IS. Line GY under WW explained some variation

Table 2. Performance of maize topcrosses derived from LPS C_3 and TS6 C_1 lines under two levels of drought stress and well-watered conditions, Tlaltizapán, Mexico.

	GY (t/ha)	EPP	AD (d)	ASI (d)	SEN (%)
Severe stress (SS)					
LPS C_3	1.82 ± 0.04	0.87 ± 0.01	86.0 ± 0.12	1.70 ± 0.13	46 ± 0.4
TS6 C_1	2.09 ± 0.03	0.93 ± 0.01	85.4 ± 0.12	0.63 ± 0.10	45 ± 0.4
Heritability	0.28	0.25	0.79	0.39	0.38
Intermediate stress (IS)					
LPS C_3	5.39 ± 0.10	0.99 ± 0.01	82.9 ± 0.12	-0.34 ± 0.10	39.7 ± 1.0
TS6 C_1	5.10 ± 0.06	1.02 ± 0.01	80.4 ± 0.11	-0.36 ± 0.07	65.1 ± 0.7
Heritability	0.33	0.32	0.77	0.38	0.29
Well-watered (WW)					
LPS C_3	6.67 ± 0.07	1.05 ± 0.01	64.3 ± 0.20	0.00 ± 0.08	
TS6 C_1	6.38 ± 0.06	1.03 ± 0.01	64.1 ± 0.08	0.01 ± 0.06	
Heritability	0.50	0.41	0.76	0.42	

Table 3. Phenotypic correlations between grain yield (GY) of topcrosses under severe drought stress (SS), intermediate drought stress (IS), and well watered conditions (WW), and grain yield adjusted for flowering date effects (AGY), against line traits under SS and WW water regimes, Tlaltizapán, Mexico.

	Topcross GY under SS	Topcross AGY under SS	Topcross GY under IS	Topcross GY under WW
Line traits under SS				
GY	0.43**	0.17*	0.05	- 0.22**
AGY	0.25**	0.07	0.04	0.16*
EPP	0.36**	0.17*	0.03	- 0.15
AD	- 0.44**	- 0.16*	0.00	0.23**
ASI	- 0.22**	- 0.18**	0.11	0.07
SEN	0.22**	0.12	- 0.27**	- 0.30**
Line traits under WW				
GY	0.06	0.03	0.20**	0.19**
EPP	- 0.02	0.05	0.05	0.10
AD	- 0.51**	- 0.19**	0.08	0.35**
ASI	- 0.01	0.02	0.20**	0.09

* significant at $P = 0.05$; ** significant at $P < 0.01$

Table 4. Line traits under severe drought stress (SS) selected by stepwise regression to explain variation in topcross grain yield (GY) under SS, intermediate drought stress (IS), and well-watered conditions (WW), Tlaltizapán, Mexico.

Top-cross	Line traits, SS	b	SE(b)	Pr>T
SS	AD	- 0.044	0.004	0.0001
	ASI	- 0.033	0.005	0.0001
	$R^2 = 0.34$			
IS	SEN	- 0.014	0.003	0.0001
	$R^2 = 0.08$			
WW	SEN	- 0.011	0.003	0.0001
	GY	- 0.263	0.090	0.0035
	$R^2 = 0.13$			

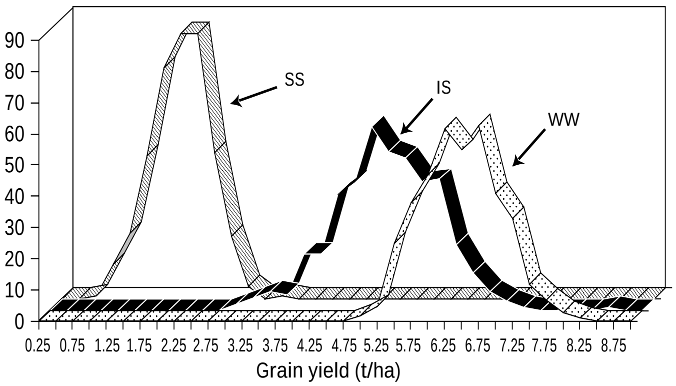

Figure 3. Frequency distribution for topcross GY under SS, IS and WW water regimes.

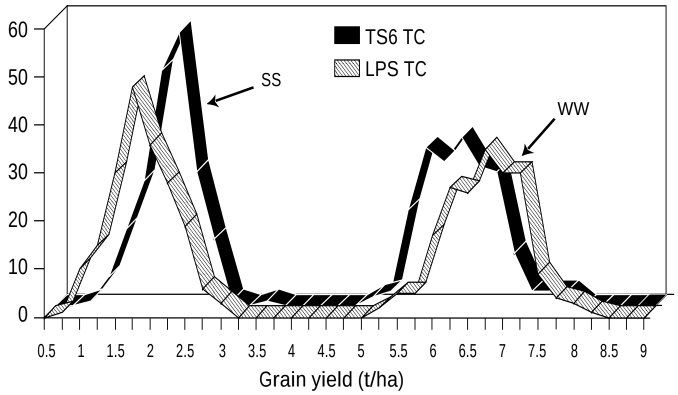

Figure 4. Frequency distribution for LPS and TS6 line topcrosses under SS and WW water regimes.

in topcross grain yield under IS and WW but not under SS (Table 5).

Conclusions

TS6 lines and topcrosses are superior to LPS lines and topcrosses under severe drought stress, but inferior under IS and WW even when GY was corrected for AD. Line traits under SS are more strongly correlated with topcross performance under severe drought stress than are line traits under normal conditions. Selection for a reduction in ASI, senescence and barrenness in lines under severe drought stress could be used to enhance the chances of selecting drought tolerant hybrids.

Table 5. Line traits under well-watered conditions (WW) selected by stepwise regression to explain variation in topcross grain yield (GY) under severe drought stress (SS), intermediate drought stress (IS), and WW, Tlaltizapán, Mexico.

Topcross	Line traits, WW	b	SE(b)	Pr>T
SS	AD	- 0.054	0.006	0.0001
	$R^2 = 0.26$			
IS	GY	0.152	0.040	0.0002
	AD	0.027	0.012	0.0224
	ASI	0.075	0.021	0.0005
	$R^2 = 0.11$			
WW	GY	0.131	0.029	0.0001
	AD	0.056	0.008	0.0001
	ASI	0.039	0.015	0.0117
	$R^2 = 0.13$			

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Breeding for Yield Stability in a Commercial Program in the USA

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Abstract

Moisture stress is probably the greatest yield limiting factor in maize production throughout the world. Although the US Corn Belt contains a lot of highly productive land, significant portions of the region encounter some moisture stress during most growing seasons. Maize producers in the USA demand hybrids with high yield potential, wide adaptation, and stable performance. Improving tolerance to moisture stress while maintaining high yield potential helps satisfy this demand. Several techniques are commonly utilized in commercial maize breeding programs in the USA to select for improved drought tolerance. Most of these involve the evaluation of segregating material for flowering synchrony under artificially high plant densities. In arid regions, it is possible to grow nurseries under moisture limited or non-irrigated conditions to evaluate leaf firing, premature death and ear development. Characterization of yield stability generally involves evaluation of hybrids at a number of locations combined with some type of regression analysis. These methods, combined with recycling of improved germplasm, have served to improve stress tolerance in much of the germplasm currently in use in commercial maize breeding programs in the USA.

Inadequate moisture during the growing season is probably the greatest yield limiting factor in the USA and throughout the world. Maize producers in the USA demand hybrids with both high yield potential and consistent performance. Several factors complicate selection for tolerance to moisture stress, including the issue of how tolerance is defined and evaluated. Every drought event differs by year and location in timing of onset, severity, and duration. Drought is often accompanied by high temperatures and the response demonstrated by plants is confounded by these two factors. When farmers discuss drought, they often say that today’s hybrids are more drought tolerant than those available in the past. Data show that the drought tolerance of maize hybrids has improved. My objective in this presentation is to share with you how we go about selecting for tolerance to heat and drought stress in germplasm adapted to the US Corn Belt. I will draw on my own experiences and also what I have learned from breeders within the Ciba organization and from other commercial breeders in the USA.

US Maize Production

Each year approximately 32 million hectares of maize are grown in the USA. Data provided by Dr. K.R. Lamkey, USDA-ARS, Iowa State University (Fig. 1), shows maize yields versus time from 1866 to 1995. These data demonstrate that from 1866 to the early 1930s average yields in the USA remained unchanged. From the early 1930s to around 1960 average yields showed a steady increase. Major factors contributing to this increase were the introduction, rapid acceptance, and improvement of double-cross hybrids. From 1960 to the present average yields have continued to increase, but at an increased rate. The increased gain seen after 1960 corresponds mainly to the introduction of single-cross hybrids and the increased use of nitrogen-based fertilizer.

Hallauer et al. (1988) summarized 13 studies designed to estimate the total increase in maize yield and the portion attributable to genetic improvement. Total yield gain over all studies was 0.093 t/ha/yr, while genetic gain ranged from 33 to 89% of this amount and averaged 0.062 t/ha/yr. Several authors have indicated that more recently developed hybrids have improved tolerance to heat and drought stress than hybrids developed in earlier eras of breeding (Duvick, 1984; Carlone and Russell, 1987).

Climatology

The US Corn Belt is located in the central part of the country from Indiana through Nebraska and contains parts of Minnesota, Iowa, Missouri, and Kansas (Fig. 2). Although the region has large areas of highly productive land, the maize crop grown on significant portions of that area can be expected to suffer some degree of moisture stress during the growing season. Palmer Drought Index (Palmer, 1965) values averaged from 1896 to 1995 show that at some point during the growing season 26% of the area in the Great Plains is under moderate or severe drought stress. During the same period 27% of the Missouri River Basin and 25% of the upper Mississippi River Basin showed at least moderate drought stress (Fig. 3) (Data provided by M.D. Svoboda, National Drought Mitigation Center, University of Nebraska-Lincoln).

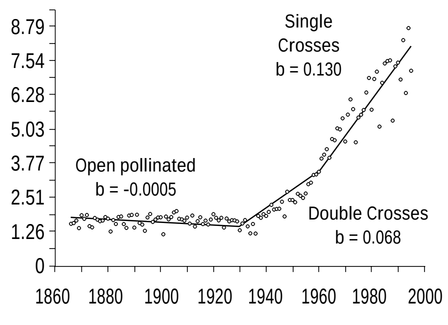

Figure 1. US maize yields and cultivar types - 1866 to 1995.

Generally, precipitation decreases from southeast to northwest in the USA and temperature decreases from south to north.

During the growing season, the moisture requirements of the maize crop must come from soil reserves, precipitation, and in some areas irrigation. In the Corn Belt, soil moisture reserves at planting typically range from excessive to adequate in the East and from adequate to insufficient in the West. Annual precipitation in the East averages about 900 mm/yr, tapering off to an average of about 500 mm/yr in the West. Thunderstorms account for more than 70% of total annual precipitation in much of the Western Corn Belt (Williams and Wai-lok, 1996). These storms are relatively short lived with intense rainfall, much of which may run off. This region is also characterized by lower relative humidity than the Central and Eastern portions. The occurrence of moisture stress across large portions of the maize producing areas throughout the USA, coupled with producer's demands for stable hybrids, makes tolerance to heat and drought stress a requirement of most commercial hybrids.

Selection for Yield Stability

Improving tolerance of maize germplasm to heat and drought stress has helped improve the stability of yield of current hybrids.

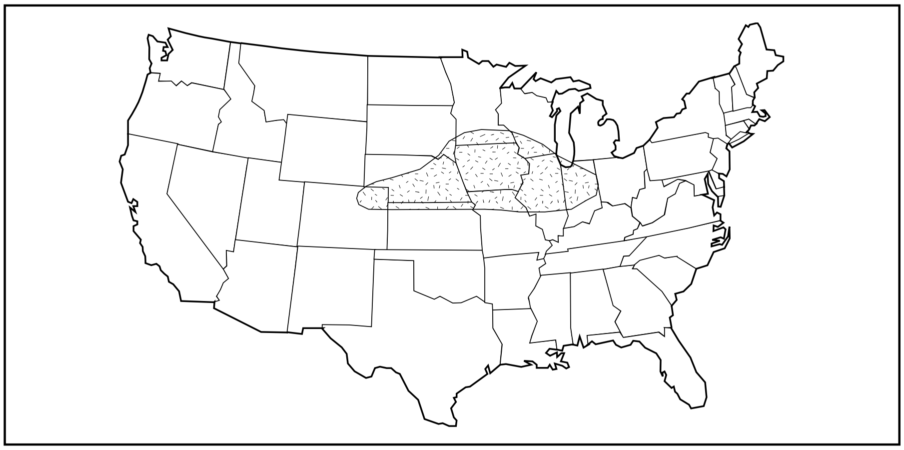

Figure 2. Primary maize producing region of the USA.

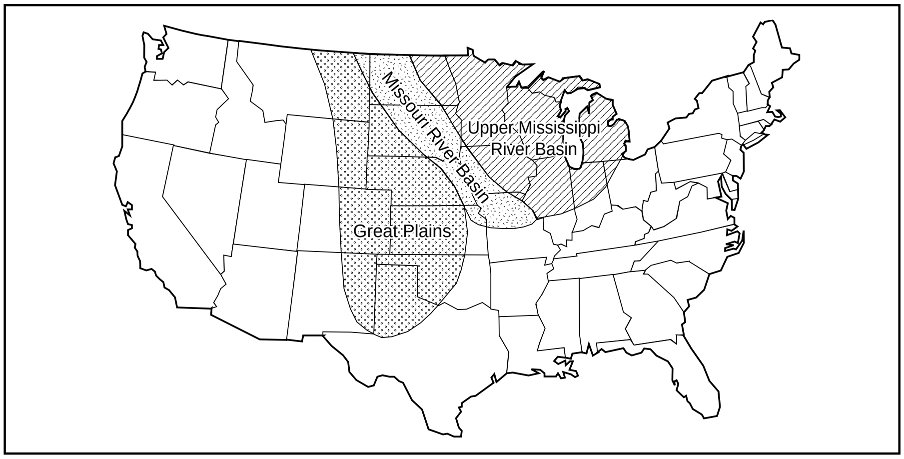

Figure 3. Major climatological zones of the US Corn Belt.

Indirect selection for tolerance to heat and drought stress has occurred in maize since its domestication. Differential reproduction of stress tolerant genotypes in more stressful years increased the frequency of favorable alleles in landrace varieties. As breeding programs evolved, inbreeding and selection occurred in hot, dry environments in some years. In most seasons, some yield testing locations in a commercial program will suffer from drought stress.

Choice of germplasm is the most critical decision a breeder makes. The probability of developing a useful inbred from a breeding population is determined to a large degree by the components of that population. As a population is developed, a breeder needs a clear idea of the desired result from that population. A tester must be identified to evaluate new lines in hybrid combinations. The tester should be commercially acceptable and complement weaknesses of new lines so the introduction of a new product is not delayed.

From a commercial standpoint an inbred line must possess several characteristics. First, and of greatest importance, it must have combining ability for yield. The line should also have wide enough adaptation to allow its use across a broad range of environments. Seed parents need adequate yield and an acceptable distribution of seed sizes. Pollen parents need to produce good quantities of pollen and have an adequate duration of shed. Tolerance to heat and drought stress is desired in both seed parents and pollinators because these stresses affect flowering in lines. A poor nick, or asynchrony of flowering, between pollen and seed parents will greatly reduce yields in seed production fields. Hot, dry conditions during vegetative development may increase barrenness in seed parents or lead to tassel blasting and sterility in pollinators. Susceptibility of inbreds to stress increases the risk associated with producing a particular hybrid.

Several techniques are commonly used in commercial maize breeding programs in the USA to select for stress tolerance during the development of inbred lines. Growing segregating material at 20 to 50% greater than normal plant density is almost universally practiced in the industry. At these densities, competition for nutrients and moisture is increased. Troyer and Rosenbrook (1983) concluded that testing hybrids at higher plant densities increased barrenness, stalk and root lodging, and ear droppage. The range of performance among hybrids increased, making selection among them easier. The same conclusion holds true for inbreds. Increasing plant density increases barrenness and lodging, making it easier to differentiate among lines. Most breeders also use techniques to select against asynchronous flowering. In working nurseries, pollinating crews are instructed not to cut back ear shoots to expose silks. This provides selection for flowering synchrony and also some selection against long silk channels. Extended silk channels can result in delayed silk emergence in stressed environments.

Among commercial breeders located in more arid environments of the Western Corn Belt, the use of dryland or limited irrigation observation nurseries is fairly common. Segregating material is grown in these nurseries and observations are collected for traits including leaf rolling, leaf tissue firing , tassel blasting, flowering synchrony, barrenness, ear development, and premature death. Observations are made within breeding populations and parental components are included as checks within nurseries.

Leaf rolling occurs as turgor is lost in leaves when a plant’s demand for water exceeds the available supply. In most seasons, leaves roll as temperatures rise and evaporative demand increases during the day. Consequently, leaf rolling is best rated from mid-morning to early afternoon. Turgor is generally regained during the night. Within a population, lines that roll earliest in the day are regarded as those that are least able to maintain turgor and are discarded. Leaf rolling in itself is not a clear indicator of susceptibility to drought. Lines with a B73 background are usually among the first to exhibit leaf rolling. In many cases, however, they are also more reliable in producing ears (i.e., they resist barrenness) than lines from other backgrounds that show later leaf rolling. A second trait that is often scored in observation nurseries is leaf firing (or scalding), which is usually first observed on the tips of upper leaves. Upper leaf firing is an indication of the inability of a plant to transpire enough water to keep leaves cool. The leaves then overheat and the tissue dies. Depending on environmental conditions such as temperature, wind speed and relative humidity, many commercially acceptable lines will exhibit some upper leaf firing. If conditions permit, we try to obtain ratings of leaf firing over time to determine the progression of tissue necrosis.

In extreme cases of heat and drought stress, differing degrees of tassel blasting or sterility are observed. Lines that exhibit tassel blasting are discarded because they present an unacceptable level of risk in production situations. Delay of silk emergence is an excellent indicator of moisture stress tolerance. As mentioned earlier, techniques to enforce flowering synchrony are almost universally used in breeding nurseries in commercial programs. Lines that exhibit asynchronous flowering under moisture stress are selected against. Another trait studied in dryland observation nurseries is barrenness and ear development. Plants at the ends of rows have less competition than those in the middle. Larger ears and less barrenness are typically seen on end plants. Lines that maintain a more consistent ear size throughout the row, and that show less barrenness are selected. Lines that die prematurely are discarded because their grain fill period is limited.

Hybrid Evaluation

A stable hybrid shows relatively less interaction with variable environments. Tolerance to drought is one trait that adds to the stability of a hybrid. Evaluating and characterizing tolerance of a hybrid to drought in a field oriented program where water supply is not controlled is difficult. Every time drought is encountered circumstances differ.

The major factor complicating evaluation of hybrids in drought-prone areas is the inability to control the amount of precipitation received during the growing season. In 1994, many locations in the Western Corn Belt received timely and adequate rainfall, and temperatures were moderate. Yields at our dryland testing locations were equal to irrigated yields in the same area. In extremely dry years like 1988, non-irrigated yields were reduced to levels of 1 to 2 t/ha and it was impossible to differentiate among hybrids for yield.

Testing in stress environments decreases mean performance. Generally, genetic variance decreases and genotype x environment interactions increase, reducing gain from selection. Rosielle and Hamblin (1981) concluded that the best allocation of testing resources is to choose locations representative of the production conditions for which a breeder hopes to improve a trait. It is important that the breeder develop a target environment for a hybrid being evaluated. Sprague (1955) concluded the most efficient use of a given number of plots will be to provide as extensive a sampling of locations as possible even though this may require limited replication per individual test. Over the years, my program has moved in the direction of minimizing replications at a location and maximizing locations. We stratify our initial testing among locations that have over the years shown low, medium, and high yield levels.

Hybrids that flower before stress occurs or before it becomes severe may show less effect than those that flower later. In 1995, Ciba hybrid 4394 performed better than expected under what was characterized as fairly severe drought. We began the year with a soil profile fully charged with water at most locations. There was no precipitation from early June until late August. At many locations soil moisture was adequate to carry this hybrid through flowering with little moisture stress. Although this hybrid is susceptible to pre-flowering moisture stress, it handles heat well, and consequently performed well under these conditions. Later flowering hybrids in the same trials were more severely penalized because less soil moisture was available when they reached anthesis.

Stability Analysis

Stability analysis provides a method to characterize the response of a hybrid to varying environmental conditions. A number of approaches to stability analysis have been developed. By far the most common technique in the commercial sector is based on the analysis developed by Eberhart and Russell (1966). In this analysis the yields of a specific hybrid from many locations are regressed on the mean yield of all hybrids grown at the same set of locations. Maize breeders in the USA who use this analysis tend to define a stable hybrid as being one with high mean performance, a regression coefficient of close to 1.0 and small deviations from regression. Both Jensen and Cavalieri (1983) and Hallauer et al. (1988) have noted that a large number of locations are necessary to obtain reliable estimates of stability of a hybrid. Gama and Hallauer (1980) suggested that breeders first select high yielding hybrids, and as more data becomes available, select the most stable hybrids from among those with high yield. Developing maize hybrids with yield stability is difficult, but necessary. A farmer will remember a hybrid that failed and the company that sold it to him for many years.

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Changes in Allelic Frequencies in a Tropical Maize Population Under Selection for Drought Tolerance

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Abstract

Selection for grain yield under severe water stress has often been considered inefficient because heritability generally declines as yield is reduced while environmental variance remains the same or increases. Under these conditions selection for secondary traits correlated with yield, such as the anthesis-silking interval (ASI), may increase selection efficiency. Although ASI is a simple trait to measure in the field and has a relatively high heritability, it is not always possible to provide the stress levels required for efficient selection of this trait. CIMMYT physiologists conducted eight cycles of full-sib recurrent selection during the dry season for drought tolerance in the population 'Tuxpeño Sequía' based mainly on an index comprising increased grain yield and reduced ASI. In this study, we quantified changes in allelic frequencies over cycles of selection at loci of known map position. Through these changes identification of alleles involved in the expression of short or long ASI was possible, and may provide a rapid diagnostic tool in the future for screening lines or plants with potential drought tolerance in Tuxpeño germplasm. Changes in allele frequencies over cycles of selection (C_0, C_4 and C_8; 116 plants randomly chosen from each cycle) were estimated using molecular markers. Loci distributed over the maize genome were assayed using RFLPs. Special attention was given to genomic regions responsible for expression of ASI, identified in a previous study using a cross between two inbreds derived mainly from Tuxpeño germplasm. There is strong evidence that the alleles of these two inbred lines are also present in this population. Allelic frequencies that either increased, decreased or remained stable were recorded for C_8 relative to C_0. Some major allele frequency changes were detected at loci located in genomic regions responsible for ASI expression, and the effects of these frequency changes were estimated. Implications of this analysis concerning the improvement of open-pollinated populations or lines using molecular markers are discussed.

Drought is a major source of grain yield decrease in cereals, especially in developing countries. For maize in the tropics, this loss has been estimated to be around 17% annually, with regional losses reaching 70% under extreme conditions, compared with well-watered production (Edmeades et al., 1995). In maize, when drought occurs before and during flowering, a delay between pollen shedding and silk emergence is observed (Hall et al., 1982; Bolaños and Edmeades, 1993a; 1993b). This increase in the anthesis-silking interval (ASI) has been associated with a grain yield decrease under drought (Du Plessis and Dijkhuis, 1967; Bolaños and Edmeades, 1993b). Selection for grain yield under water stress has often been considered inefficient because genetic variance declines more rapidly than environmental variance, reducing heritability. Under such conditions selection for secondary traits correlated to grain yield, such as ASI, appears to increase selection efficiency (Bolaños et al., 1993). Even though ASI is a relatively simple trait to measure in the field, selection for a short ASI requires carefully managed levels of drought stress at critical times during each crop season, which severely limits its use in many breeding programs. The use of molecular markers to improve the efficiency of selection for this trait without the need for specific field conditions may provide a cost-effective alternative for improving drought tolerance in maize populations. This study sought to quantify changes in allele frequency over eight cycles of full-sib recurrent selection for drought tolerance in the population Tuxpeño Sequía. The magnitude and genomic position of allelic frequency changes were compared with the location of QTL previously identified for the expression of ASI and yield under drought, with a view to using this information to increase the efficiency of population improvement for these traits.

Materials and Methods

F_2 segregating population used for mapping ASI

Two tropical maize inbreds were selected: P_1 was extracted from 'Across 7643', has a short ASI and is relatively drought tolerant; P_2 was extracted from a varietal cross, 'Across 7729 x TZSRW', has a long ASI and is drought susceptible.

Table 1. Numbers of individual F_2 families involved in genotyping, and $F_{2:3}$ families used for the ASI observation in the field.

	Genotyping	ASI (per plant)
	F_2	$F_{2:3}$
P_1 x P_2	234	242

Table 2. Numbers of plants from each selection cycle of Tuxpeño Sequía involved in the allelic identification, and the numbers of full-sib families used in the evaluation of ASI in the original conventional selection scheme.

	Genotyping No. of plants	ASI evaluation No. of families
Cycle 0	116	250
Cycle 4	116	250
Cycle 8	116	250

Full-sib recurrent selection

Eight cycles of full-sib recurrent selection (30-40% selection intensity per cycle) were conducted in the tropical maize population Tuxpeño Sequía. Major selection criteria included ASI (time between silking of 50% of plants and pollen shedding of 50% of plants) on a per family basis (Fig. 1), grain yield, and ear number per plant.

Field evaluation of ASI in the present study

We recorded ASI for individual plants as the time between the extrusion of the first anther(s) and of the first silks. A total of 250 families plus 6 checks were observed in two replications per water regime, in a 16 x 16 simple lattice design. Individual plant data were recorded on 10 plants/plot, each plot being a single row 2.5 m in length. The three water regimes used were severe drought stress at flowering (SS); intermediate drought stress at flowering (IS); and well-watered conditions (WW). The trials were conducted at Tlaltizapán, Morelos, Mexico, elevation 940 masl, in the rain-free winter season, where temperatures vary from 4 to 39°C.

Genotyping using RFLPs

See Hoisington et al. (1994) for details of methods used. In brief DNA was digested with *Eco RI* or *Hind III* restriction enzymes. Probes tested were from the University of Missouri Columbia (UMC), Brookhaven National Laboratory (BNL) and Native Plants Incorporated (NPI); their presence was detected by a chemiluminescent reaction.

Results and Discussion

To date, 32 probes have been used to screen the three selection cycles (C_0, C_4 and C_8). At any one locus the number of alleles identified was between 3 and 7. No significant changes in allelic frequencies were observed for around 30% of the probes. The greatest changes in allelic frequencies were detected on chromosomes 1, 2, 6, 7, 9 and 10 (see Tables 3 and 4 as examples). In general, the direction of these changes was consistent across C_0, C_4 and C_8, and the intensity of the changes was more marked between C_4 and C_8. The alleles in the F_2 mapping population were almost

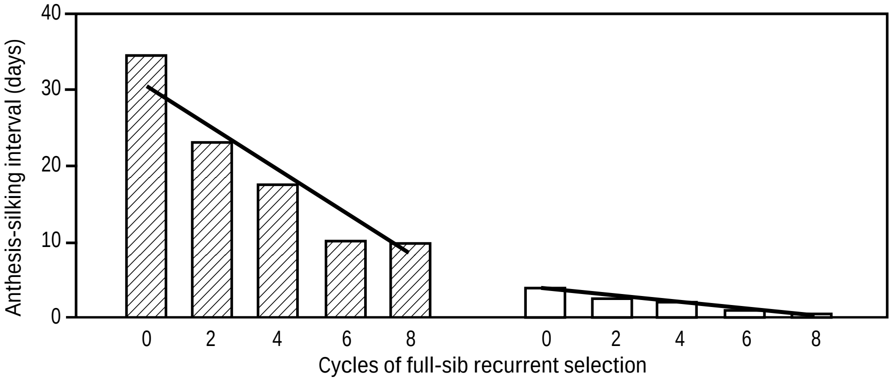

Figure 1. Anthesis-silking interval (ASI) for cycles of selection in Tuxpeño Sequía (C_0, C_2, C_4, C_6 and C_8), grown under droughted and well-watered conditions. Lines represent the fitted regression of ASI on cycles of selection. Numbers refer to least squares estimates of rate of change per selection cycle in absolute values and as a percentage of the mean (modified after Bolaños and Edmeades, 1993b).

always present in Tuxpeño Sequía as well. Major changes in allelic frequencies were found at loci close to the four most important QTL associated with ASI, as identified in the F_2 population (Fig. 2) (Ribaut et al., 1996). At three of these four QTL, the frequency of the allele involved in the expression of a short ASI in the F_2 population increased with cycles of selection.

Conclusions and Perspectives

Results applicable to breeders

The genomic regions associated with the traits that the breeder has been selecting for have been identified. The degree of genetic diversity after n cycles of selection could be evaluated to estimate whether significant genetic gains can still be made through further cycles of selection. Few fixed genomic regions have been identified. During eight cycles of selection the number of alleles per locus has decreased, though from the results obtained for C_8 genetic progress for drought improvement seems still possible.

Strategy for marker-assisted selection in maize populations

After a few cycles of full-sib recurrent selection alleles which increase in frequency at specific loci can be identified. The latest selection cycle of the population can then be screened using molecular markers to select those individuals that have favorable alleles at specific loci. Recombination of these individuals should bring the population to an advanced level for the trait(s) of interest. Further details of a proposed marker-assisted selection scheme for populations, based on the results in this paper, are presented in Ribaut et al.(1997), the following paper in this proceedings.

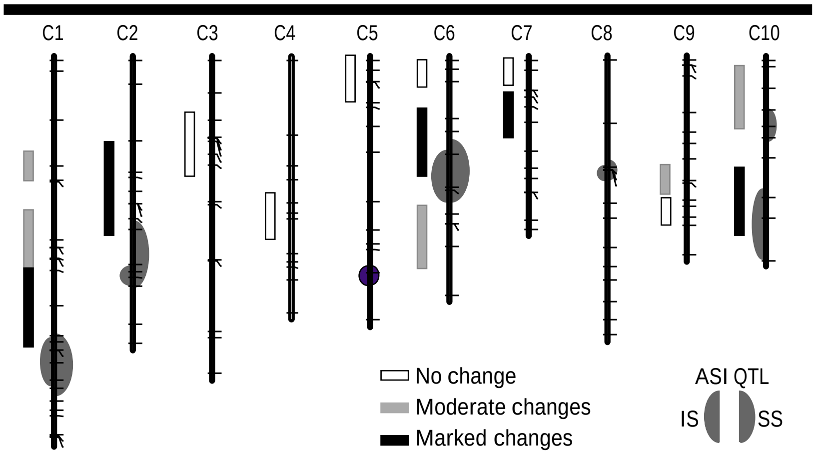

Figure 2. Changes in allelic frequencies in a tropical population (Tuxpeño Sequía) over cycles of selection to improve drought tolerance. Vertical bars indicate the position on the map where allelic frequency changes were quantified, as well as the intensity of these changes. Location of ASI QTL detected in an F_2 population (Ac7643 x Ac7729/TZSRW) under intermediate (IS) and severe drought stress (SS) in 1994 are represented by ellipses for LOD scores higher than 2.0. The width of the ellipses is proportional to the percentage of phenotypic variance explained by that QTL.

Table 3. Allelic frequencies at two loci on chromosomes 2 and 10 in three selection cycles of population Tuxpeño Sequía.

Chromosome	Locus		Cycle 0	Cycle 4	Cycle 8
2	*umc371*				
	Allele 1		0.18 ± 0.03	0.18 ± 0.03	0.06 ± 0.02
	Allele 2		0.11 ± 0.02	0.09 ± 0.02	0.01 ± 0.01
	Allele 3		0.04 ± 0.01	0.08 ± 0.02	0.10 ± 0.02
	Allele 4	P_2	0.32 ± 0.03	0.31 ± 0.03	0.56 ± 0.03
	Allele 5	P_1	0.36 ± 0.03	0.32 ± 0.03	0.25 ± 0.03
10	*bnl7.49*				
	Allele 1		0.01 ± 0.01	0.05 ± 0.01	0.00
	Allele 2		0.37 ± 0.03	0.35 ± 0.03	0.22 ± 0.03
	Allele 3	P_1	0.22 ± 0.03	0.41 ± 0.03	0.44 ± 0.03
	Allele 4	P_2	0.17 ± 0.03	0.05 ± 0.01	0.14 ± 0.03
	Allele 5		0.01 ± 0.01	0.01 ± 0.01	0.06 ± 0.02
	Allele 6		0.22 ± 0.03	0.12 ± 0.02	0.10 ± 0.02

Table 4. Allelic frequencies at two loci on chromosome 6 in three selection cycles of population Tuxpeño Sequía.

Chromosome	Locus		Cycle 0	Cycle 4	Cycle 8
6	*umc379*				
	Allele 1	P_2	0.65 ± 0.03	0.65 ± 0.03	0.67 ± 0.03
	Allele 2		0.04 ± 0.01	0.00	0.09 ± 0.02
	Allele 3		0.00	0.01 ± 0.01	0.00
	Allele 4	P_1P_2	0.31 ± 0.03	0.34 ± 0.03	0.24 ± 0.03
6	*umc132*				
	Allele 1	P_1	0.32 ± 0.03	0.28 ± 0.03	0.44 ± 0.03
	Allele 2		0.00	0.03 ± 0.01	0.00
	Allele 3	P_2	0.42 ± 0.03	0.44 ± 0.03	0.32 ± 0.03
	Allele 4		0.00	0.05 ± 0.01	0.03 ± 0.01
	Allele 5		0.25 ± 0.03	0.22 ± 0.03	0.21 ± 0.03

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Identification and Transfer of ASI Quantitative Trait Loci (QTL): A Strategy to Improve Drought Tolerance in Maize Lines and Populations

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Abstract

When drought stress occurs just before or during flowering in maize, it delays silking and increases the anthesis-silking interval (ASI). Strong evidence associates an increased ASI with reduced grain yields in maize. In the present study, molecular markers were used to identify genomic segments responsible for the expression of ASI in maize, with the aim of using this information in marker-assisted selection (MAS) for reduced ASI. An F_2 population of 260 individuals was genotyped at 150 loci. In 1992 and 1994, F_3 families were evaluated under several water regimes in the field for ASI, several morphological traits, yield components and physiological drought variables. For ASI, six QTL (LOD scores greater than 2.5) were identified on chromosomes 1, 2, 5, 6, 8 and 10. These QTL account together for approximately 50% of the phenotypic variability which represented a change of 10.5 d for ASI. Transgressive segregation was observed for this trait. The four QTL segments contributed by the short-ASI line were responsible for a 6.8 d reduction in ASI, represented around 7% of the linkage map, and were stable over years and stress levels. Based mainly on these results and on the identification of QTL involved in the expression of grain yield, three different MAS projects are now being conducted at CIMMYT. These schemes, one based on backcrossing, another on line development from F_3 families, and a third on changes in allelic frequencies in open-pollinated populations are discussed. Preliminary results suggest that MAS based on a strategy combining QTL identified under drought for ASI and grain weight should be a powerful tool to improve drought tolerance of tropical maize inbred lines, and perhaps also of open-pollinated populations.

Drought is an important climatic phenomenon which ranks as the second most severe limitation, after soil infertility, to maize production in developing countries (Edmeades et al., 1992). Even in areas where average rainfall is considered adequate for maize growth, in some years rainfall variation can result in big yield reductions over large regions. In general, breeding under stress conditions is difficult to manage because of difficulties in providing adequate field conditions for expression of the trait(s) of interest, and because heritability of yield decreases as the level of stress increases, making selection for yield under stress more inefficient than under well-watered conditions (Blum, 1988). Moreover, only one dry crop season per year is available in the tropics, making selection even more time consuming.

When drought stress occurs just before or during the flowering in maize, a delay in silk emergence is observed, resulting in an increase in anthesis-silking interval (ASI) (Hall et al., 1982; Westgate and Bassetti, 1990; Bolaños and Edmeades, 1993b). This asynchrony between male and female flowering dates is strongly associated with grain yield decreases in maize under drought conditions (DuPlessis and Dijkhuis, 1967). Selection for reduced ASI in tropical open-pollinated varieties has been shown to be well correlated with improved yield under drought stress (Bolaños and Edmeades, 1993b). While ASI is a simple trait and has a relatively high heritability, selection for ASI is best achieved under carefully managed drought conditions, which severely limits its use in many breeding programs. Molecular markers are being used to identify genomic segments responsible for expression of ASI, as well as other morphological traits related to yield, with the aim of using this information in marker-assisted selection (MAS) for reduced ASI.

The first use in plants of a restriction fragment length polymorphism (RFLP) linkage map to identify genomic regions responsible for expression of quantitative trait loci (QTL) was reported in 1988 for tomatoes (Paterson et al., 1988). This method allows researchers to break down quantitative traits into their Mendelian components, thus increasing the understanding of trait inheritance and gene action. Among crop plants, maize is particularly well suited for quantitative trait mapping, since it has a very high degree of molecular polymorphism. Molecular markers have been extensively used to obtain genetic linkage maps and to identify QTL of the genome of temperate maize. However, few studies on quantitative trait inheritance have been conducted under abiotic stresses. This present study reports on CIMMYT's attempts to improve drought tolerance in tropical maize using molecular markers, thereby demonstrating the potential of molecular genetic dissection of QTL and of marker-assisted selection. Two marker-assisted selection projects based mainly on ASI QTL to improve drought tolerance in maize lines and populations are now under way.

Preliminary Study

From a cross between two tropical lines (P_1 with a short ASI and a reasonable level of drought tolerance; and P_2 with a long ASI and drought susceptible), an F_2 population of 260 individuals was genotyped. Based on the polymorphisms identified at 150 different loci, a RFLP linkage map was constructed using the MAPMAKER software (Lander et al., 1987). F_3 families derived from the F_2 plants were evaluated for ASI in the field under several water regimes. Several morphological traits, yield components, and physiological drought variables were measured in 1992 and 1994. It was possible to identify QTL involved in trait expression by comparing field data with the allelic distribution at loci along the genome using two complementary mathematical approaches: Simple Interval Mapping (SIM; MAPMAKER/QTL) (Lander and Botstein, 1989) and Composite Interval Mapping (CIM) (Zeng, 1994). Seven QTL (likelihood threshold, LOD score, greater than 2.5) for ASI were identified on chromosomes 1 (with two QTL), 2, 5, 6, 8 and 10. These QTL accounted for approximately 50% of the phenotypic variability, which represented a change in ASI of 10.5 d. Transgressive segregation was observed for ASI. Five QTL segments contributed by P_1, the short ASI line, were responsible for a 7 d reduction in ASI, and were stable over years and stress levels (Ribaut et al., 1996). QTL involved in the expression of yield components, such as grain weight, ears per plant and grain number, were not consistently identified across stress levels and explained only a low percentage of the phenotypic variance for these traits. From these first QTL analyses, it can be concluded that:

1. The identification of molecular markers of interest at QTL peaks associated with ASI and yield components has to be achieved using field data obtained under drought.
2. MAS for drought tolerance using only the QTL involved in the expression of yield components under drought would not be efficient.
3. MAS using only QTL involved in the expression of secondary traits of interest, such as ASI, would not be the most efficient either, since at one important genomic position the allele contributing to an ASI reduction contributed also to a grain yield decrease (Fig. 1).

The most successful MAS strategy should take into account the "best QTL" for different traits, in the form of an index. These QTL should be stable across environments, account for a large percentage of the phenotypic variance, and, if not involved directly in the expression of yield, should be involved in the expression of traits significantly correlated with yield.

Recombinant Inbred Lines

Two hundred and forty recombinant inbred lines (RILs) were developed by selfing plants from consecutive generations of an F_2 population (P_1 x P_2). In the 1996A dry season these RILs were planted in CIMMYT's station at Tlaltizapán under two water stress levels. Morphological traits and yield components mapped at the F_2 level were measured again in the field and mapped at the S_5 level. Analysis of these data is now under way and should allow a better understanding of the genetic control of the traits; their inheritance, gene action and level, and stability of expression across different water regimes. Moreover, by comparing the QTL identified at different levels of homozygosity (S_1 and S_5), we should obtain information on the effects of inbreeding on QTL mapping. RILs also allow more precise definition of the genomic position of QTL involved in the expression of traits of interest, such as ASI. Based on preliminary results obtained from the two parental lines, we are focusing our efforts on mapping the following physiological components: relative water content, osmotic adjustment, chlorophyll content and root capacitance. An experiment under well-watered conditions is planned for the 1996 summer cycle.

Marker-assisted Selection Project 1: Line Improvement

The first MAS project (Fig. 2) is based on a backcrossing scheme using P_1 as the donor line and CML247 as the recurrent line. CML247 is an elite, lowland tropical line developed by CIMMYT, with outstanding combining ability, good yield *per se* under well-watered conditions, but with a relatively long ASI and significantly reduced yield under drought. Presently, QTL are being identified by combining genetic data from the F_2 population with data from F_3 family evaluation in the field under severe stress conditions. Preliminary results indicate that QTL for ASI are quite consistent between the two crosses. Of the five QTL previously identified in P_1 (Ribaut et al., 1996), only the QTL on chromosome 6 was not detected. The QTL on the short arm of the chromosome 1 was shifted by 40 cM in the new cross, and the three other QTL on chromosomes 2, 8 and 10 were in similar position in both crosses. A new QTL for ASI was detected on the short arm of chromosome 3. These results

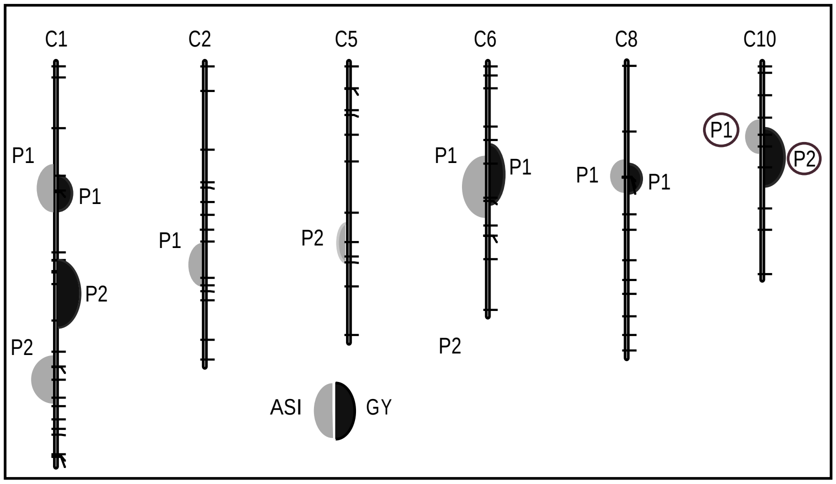

Figure 1. Location on maize chromosomes of the anthesis-silking interval (ASI) and grain weight (GY) QTL detected using composite interval mapping, based on combined data sets from field evaluations under intermediate and severe drought stress. Genomic regions responsible for the expression of ASI and GY are represented by ellipses for LOD scores higher than 2.0. The width of the ellipse is proportional to the percentage of phenotypic variance explained by that QTL. The parental line contributing the allele for a short ASI or better yield is indicated for each QTL.

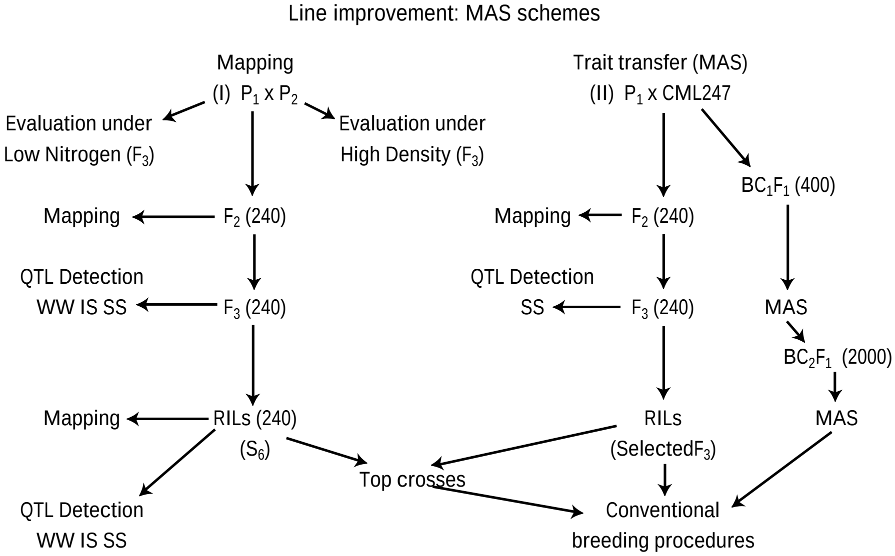

Figure 2. Summary of the on-going project of drought tolerance improvement in maize lines using molecular markers. The left part of the scheme presents the preliminary study with P_1 and P_2 as parental lines used to identify QTL under several water regimes at F_2 and recombinant inbred line (RIL) genetic levels. The right side presents the marker-assisted selection (MAS) backcrossing scheme, using P_1 as the donor line and CML247 as the recurrent line. WW, IS and SS indicate evaluations conducted under well watered, intermediate and severe water stress conditions, respectively. Numbers in parentheses refer to the numbers of lines evaluated at each stage.

demonstrate that it is essential to make a new genetic map when a new recurrent line is used, although only a single good quality field trial under drought conditions may be sufficient to map the QTL. Based on these findings, we are selecting individuals among 400 backcrossed plants (BC_1F_1) that were RFLP genotyped. In the next backcross cycle (BC_2F_1) we intend to select among 2,000 plants using polymerase chain reaction (PCR)-based markers to transfer to CML247 only the QTL of importance, such as those associated with a short ASI, and thereby increase the yield of the line and its crosses under drought.

Marker-assisted Selection Project 2: Population Improvement

CIMMYT physiologists conducted eight cycles of full-sib recurrent selection in the population "Tuxpeño Sequía" during dry seasons in Mexico (Bolaños and Edmeades, 1993a). Selection was based mainly on an index comprising increased grain yield under drought, maintenance of the sowing-anthesis interval (to avoid escapes due to earliness), and reduced ASI. In Project 2 (Fig. 3), we quantified changes in allelic frequencies over cycles of selection at loci of known map position. The most significant allelic shifts occurred at or near the QTL previously detected for ASI (Ribaut et al., 1995; Ribaut et al, 1997). It can be postulated that these changes result from the selection pressure applied by breeders to reduce ASI while increasing various yield components under drought. It is intriguing to speculate whether plant selection based on the presence of the alleles that increased in frequency could provide improvement of drought tolerance in a shorter time than that taken by conventional selection. Project 2 tries to answer this question by evaluating the gain from MAS on 400 plants from Cycles C_0 and C_4 (Fig. 3).

Results obtained to date suggest that MAS based on a strategy combining QTL identified under drought for ASI and grain weight should be successful at improving drought tolerance of tropical maize inbred lines and open-pollinated populations. Improvement should progress more rapidly than is possible using conventional methods and should not alter significantly the combining ability of elite lines or populations.

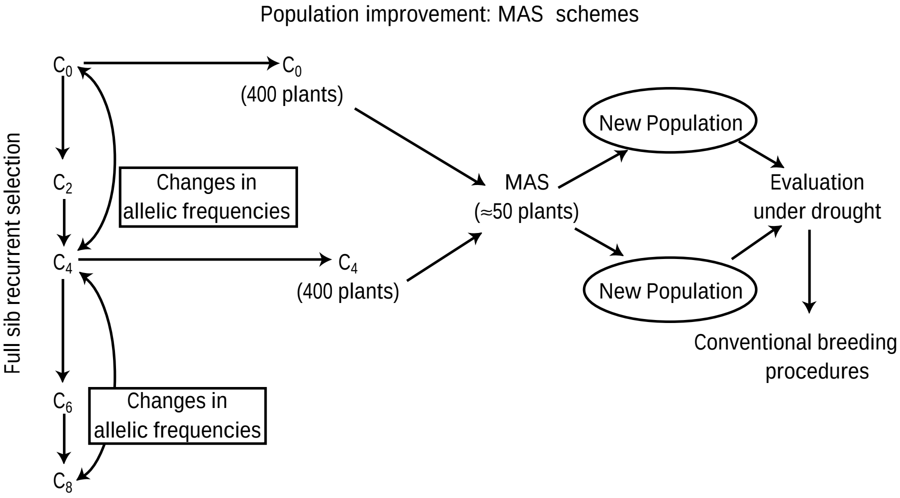

Figure 3. Summary of the on-going project of drought improvement in a maize open-pollinated population using molecular markers. The left part of the scheme represents the eight cycles of full-sib recurrent selection conducted by CIMMYT breeders. Allelic frequency changes between C_0 and C_4, and C_4 and C_8 are being quantified. The right side presents the marker-assisted selection (MAS) scheme from 400 plants of C_0 and C_4, the selection being based on favorable or neutral alleles identified at genomic regions of interest.

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Breeding for N-stressed Environments: How Useful are Low-N Selection Environments and Secondary Traits?

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Abstract

The present study examines (i) to what extent alpha (0,1) lattice designs and secondary traits improve selection efficiency under low N, and (ii) whether selection under high N is an efficient approach for increasing grain yields under low N. Grain yield and the secondary traits anthesis-silking interval (ASI), number of ears per plant, leaf chlorophyll concentration and leaf senescence of 19 maize trials grown under low N and 14 under high N conditions were analyzed. Broad-sense heritabilities of traits, genetic correlations between environments and traits and predicted response to selection were calculated. The results indicate that (i) alpha (0,1) lattice designs and secondary traits can considerably increase the efficiency of selection for grain yield in maize breeding programs targeting low N environments, and that (ii) if the N stress present in the target environment leads to a yield reduction greater than about 40%, a breeding program should include low N selection environments in order to maximize selection gains for that target environment.

Most maize breeding is conducted under high yielding conditions where heritability and genotypic variance for grain yield, and therefore potential selection gains, are high (Rosielle and Hamblin, 1981). However, a considerable proportion of all maize in the tropics is produced under low N conditions, raising the need for efficient selection methods that improve grain yields under low N. Improved statistical designs and secondary traits have been suggested as ways of increasing selection efficiency under low N. On the other hand, most maize breeding programs have chosen the approach to select for grain yield under high N conditions where heritability and genotypic variance for grain yield are high, in the expectation that this is also a way to increase grain yields under low N. The present study examines (i) to what extent alpha (0,1) lattice designs and secondary traits improve selection efficiency under low N, and (ii) whether selection under high N is an efficient approach for increasing grain yields under low N.

Materials and Methods

Data were analyzed for 19 replicated maize progeny trials where genotype was a random factor. Fourteen of these experiments were grown simultaneously under low and high N and five experiments were only grown under low N. They were evaluated at CIMMYT's experiment station at Poza Rica, Veracruz, México (21 °N, 60 m elevation), between 1986 and 1995. The low N experiments were conducted in fields which were depleted of N by continuously growing maize and removing the biomass after each crop, and no N was applied. Two hundred kg N ha^{-1} was applied under high N. Low and high N fields were adjacent to each other and, except for N fertilization, management was the same for both N levels. Experimental designs were alpha (0,1) lattices (Patterson and Williams, 1976), with two replications at each N level.

Anthesis-silking interval was calculated as (silking date - anthesis date). Chlorophyll concentration of the ear leaf of five bordered plants per plot was measured approximately 2 weeks after anthesis with a portable photometer

(Hardacre et al., 1984; Minolta, 1989). Leaf senescence was determined either by counting the number of green leaves remaining below the ear on five bordered plants at approximately 3 and 5 weeks after anthesis (Exp. 1 to 10), or by visually estimating the percentage of leaf area remaining in each plot on two to three occasions during grain filling (Exp. 10 to 19). The number of ears per plant was determined at harvest, and grain yield was measured from shelled, dried ears.

Statistical analyses followed procedures described by Falconer (1989). Each experiment was analyzed separately. To assess the value of using alpha (0,1) lattice designs, each low N experiment was analyzed as a randomized complete block design and as a lattice design, and broad-sense heritabilities of grain yield and predicted responses of grain yield to selection were compared between these designs. Broad-sense heritability (h^2) was calculated as:

$$h^2 = \sigma_G^2/(\sigma_G^2+\sigma_E^2/r)$$

where σ_G^2 is the genetic variance, σ_E^2 is the error variance, and r is the number of replications in the experiment. Predicted response to selection was calculated as

$$R = h * \sigma_G$$

assuming a standardized selection differential of 1.0.

To assess the value of secondary traits under low N, data on grain yield, ASI, ears per plant, leaf chlorophyll concentration and leaf senescence were combined using a Smith-Hazel index. The efficiency of index selection was calculated by dividing the predicted response to index selection by the predicted response of selection for grain yield alone (Lin, 1978; Wells and Kofoid, 1986):

$$\text{Efficiency of index selection} = \mathbf{b}G/[h_{GY}*\sigma_{G(GY)}]$$

where **b** is the vector of index weights, *G* is the genotypic variance-covariance matrix between grain yield and traits included in selection, h_{GY} is the square root of the heritability for grain yield and $\sigma_{G(GY)}$ is the square root of the genetic variance.

To compare selection under high N with selection under low N as a means of increasing grain yields under low N, broad-sense heritabilities and genetic correlations between grain yields under low and high N were computed. Efficiency of high N selection was then calculated by dividing the predicted response of grain yield under low N to selection under high N by the predicted response of selection under low N to selection under low N:

$$\text{Efficiency of selection under high N} = r_G h_{\text{High N}}/h_{\text{Low N}}$$

where r_G is the genetic correlation between grain yield under low and high N, and $h_{\text{High N}}$ and $h_{\text{Low N}}$ are the square roots of the heritability for grain yield under low and high N.

Additive and non-additive effects were not separated, and genotype x environment interactions resulting from effects other than nitrogen were ignored. Further details can be found in Bänziger et al. (1997) and Bänziger and Lafitte (1997).

Results and Discussion

The value of improved designs

Broad-sense heritabilities for grain yield averaged 0.33 (low N) and 0.54 (high N) across 14 experiments using a randomized complete block design (Table 1). Alpha (0,1) lattice designs increased broad-sense heritabilities by 33% (low N) and 15% (high N) on average, and increased predicted response of grain yield to selection by 19% (low N) and 12% (high N) on average. Error variance was larger under low vs. high N, when randomized complete block designs were used, but decreased relatively more under low vs. high N when data were analyzed as alpha (0,1) lattices, resulting in similar error variances under low and high N.

The value of improved statistical designs (complete and incomplete lattice designs, spatial designs) is

Table 1. Broad-sense heritability (h^2), genetic variance (σ_G^2), error variance (σ_E^2) and predicted response to selection (R; assuming a standardized selection differential of 1.0) for 14 maize experiments conducted under low and high N at Poza Rica between 1986 and 1995 when analyzed as randomized complete block designs (RCBD), as alpha (0,1) lattice designs, and when alpha (0,1) lattice designs were combined with index selection.

Experiment	h^2	σ_G^2	σ_E^2	R
		$(t\ ha^{-1})^2$		$t\ ha^{-1}$
Low N				
RCBD	0.33	0.12	0.70	0.19
Lattice	0.44	0.12	0.38	0.22
Lattice + Index	0.26			
High N				
RCBD	0.54	0.30	0.52	0.40
Lattice	0.62	0.32	0.39	0.44

well established (see Kempton et al., 1994; Patterson and Williams, 1976). The use of alpha (0,1) lattice designs in this study resulted in an improved estimation of broad-sense heritability and in a larger predicted selection gain under low and high N. The relative advantage of the improved design was higher under low N. Low N fields are usually subject to larger error variation, probably due to inherent differences in soil fertility (Lafitte et al., 1997). Alpha (0,1) lattice designs (and other improved designs) may compensate for this effect. CIMMYT has developed publicly available software that designs and analyzes alpha (0,1) lattices (Barreto et al., 1997).

The value of secondary traits

The identification of secondary traits with adaptive value under low N has been described elsewhere (Bänziger and Lafitte, 1997). The present study assesses to what extent simultaneous selection for grain yield, ASI, ears per plant, leaf chlorophyll concentration and leaf senescence (using a Smith-Hazel selection index) improve predicted selection gains of grain yield under low N over selection for grain yield alone. A Smith-Hazel index calculates weights for each trait used in selection based on the phenotypic and genotypic covariance between that trait and grain yield, and thereby optimizes predicted progress for grain yield (Lin, 1978).

Index selection that includes grain yield as one trait cannot lead to smaller selection gains than selection for grain yield alone. Consequently, the efficiency of index selection must be greater than 1.0. Across 19 experiments, the efficiency of index selection averaged 1.14; i.e., index selection increased predicted selection gains under low N by 14% on average over selection for grain yield alone. Because the efficiency of index selection was calculated as $\mathbf{b}G/h_{GY}{*}s_{G(GY)}$, the efficiency of index selection was necessarily the highest where the broad-sense heritability of grain yield was low (Fig. 1).

With the reduced set of 14 experiments presented in Table 1, the use of alpha (0,1) lattice designs and index selection together increased predicted selection gains by 36% on average, indicating that improved statistical designs and secondary traits can considerably increase selection gains under low N.

Efficiency of selection under high N vs. selection under low N

The efficiency of selection under high vs. low N for increasing grain yields under low N is determined by the broad-sense heritabilities of grain yield under low and high N and the genetic correlation between grain yields under low and high N (Falconer, 1989). Broad-sense heritabilities of grain yield under low and high N are presented in Table 1. Broad-sense heritabilities under high N exceeded those under low N by 41% on average. For the same 14 experiments, genetic correlations between grain yield under low and high N averaged 0.38. They systematically decreased with increasing N stress intensity (Fig. 2), indicating that as N stress under low N increased, there was less agreement in ranking for yield between genotypes that performed well under high N versus those that performed well under low N. As a result, the efficiency of selection under high N for improving grain yield under low N also decreased with increasing N stress (Fig. 3). At an index efficiency of 1.0, selection under low and high N will be equally

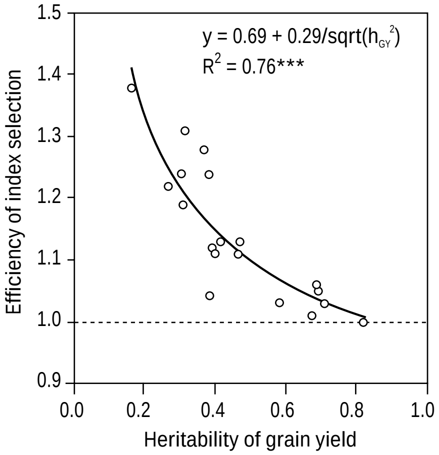

Figure 1. The efficiency of index selection for the grain yield, anthesis-silking interval, ears per plant, leaf chlorophyll concentration, and leaf senescence, compared with selection for grain yield alone, plotted against the heritability of grain yield for 19 maize experiments evaluated under low N at Poza Rica, México, between 1986 and 1995.

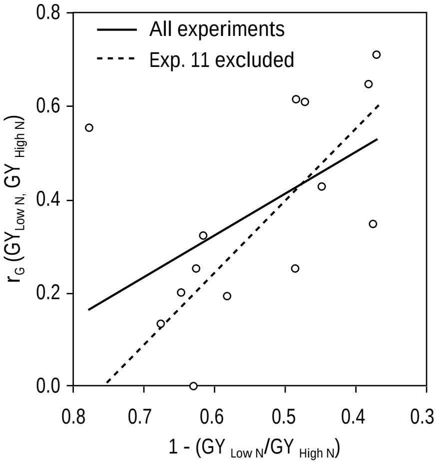

Figure 2. Genetic correlations (r_G) between grain yields under low and high N of grain yield vs. relative yield reduction under low N (1- ($GY_{Low\ N}/GY_{High\ N}$)) for 14 maize progeny trials evaluated at Poza Rica, México, between 1986 and 1995. Regressions are shown for the combined dataset from all trials ($y = 0.86 - 0.90x$; $R^2 = 0.27$; $n = 14$) and with Exp. 11 excluded ($y = 1.19 - 1.58x$; $R^2 = 0.62^{***}$; $n = 13$).

efficient. The regression (Fig. 3) predicted this to be the case when the relative yield reduction under low N exceeded 23%. However, it was at a relative yield reduction under low N of 43% that selection under low N was predicted to be significantly superior ($P < 0.05$) to selection under high N for improving grain yields under low N.

Breeders usually select under high N conditions, where heritability and genotypic variance for grain yield and, therefore, potential selection gains for high N conditions are high. The present results show that this strategy is not the best one for low N target environments. Selection under low N for increasing grain yields under low N was superior to selection under high N in all the experiments examined (Fig. 3). Where yields in the target environment were reduced by more than 43% due to N stress, low N selection was significantly superior to high N selection.

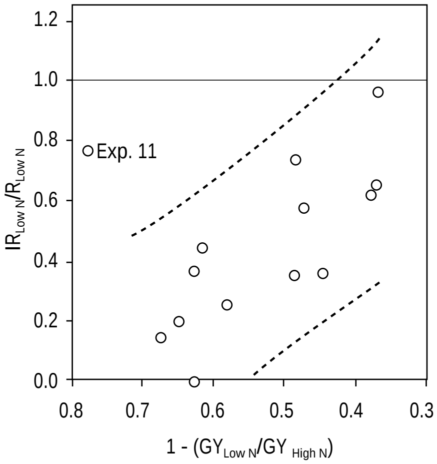

Figure 3. Relative efficiency of indirect selection under high N vs. direct selection under low N for improving grain yield under low N ($IR_{Low N}/R_{Low N}$) as a function of relative yield reduction under low N ($1- (GY_{Low N}/GY_{High N})$) for 14 maize progeny trials evaluated at Poza Rica, México between 1986 and 1995. Regression and confidence interval of regression were calculated with Exp. 11 excluded. The equation for the regression was: $y = 1.45 - 1.92x$ ($R^2 = 0.65$***; $n = 13$).

Conclusions

The results of this across-experiment analysis indicate that if the reduction in yield due to N stress in farmers' fields in target areas exceeds about 40%, a breeding program should include low N selection environments to maximize selection gains for that target environment. Selection gains under low N can be considerably enhanced if improved statistical designs (e.g., alpha [0,1] lattices) and secondary traits are used when evaluating genotypes in low N selection experiments.

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Drought and Low N Testing Networks - Past, Present and Future

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Abstract

A goal of the UNDP Stress Project has been to establish networks of collaborating scientists interested in developing drought- or low N-tolerant maize germplasm. These complement the activities of several other general or stress-related testing networks that CIMMYT has developed. The objectives of these networks are to: a) improve national program awareness of, and access to, germplasm possessing superior levels of tolerance to these stresses; b) broaden adaptation of CIMMYT's stress-tolerant source germplasm; and c) exchange germplasm and information among network members. Three sets of trials (1989; 1992; 1995-96) have been shipped to members of the drought tolerance network, and one set (1995-96) to low N-tolerance network members. Participants in the networks total around 32 in 26 countries for drought and 20 in 15 countries for low N. The first and second sets of drought trials were of late and early open-pollinated varieties (OPVs), along with a progeny trial of 222 S_1 *families from the Drought Tolerant Population-1 (DTP1). Enthusiasm for the networks was shown by the seed requests which followed these trials, and the marked improvement in data received over the years. In the 1992 trials the highest yielding entries across sites were La Posta Sequia* C_3 *(late), a DTP1 early selection and Pool 18 Sequía* C_3 *(early). The composition of the trials has now changed, along with CIMMYT's breeding strategy. The 1995-96 drought trials consist of two topcross progeny trials (yellow; white) and three variety trials (late; early and extra-early, hybrids and OPVs in the same trial, plus two to three collaborator-supplied checks). Trials shipped to Low N network participants consist of two topcross progeny trials, the same early variety trial (drought tolerant germplasm performs well under low N), and a late-maturity variety trial consisting of low N-tolerant entries. CIMMYT will continue to develop and test germplasm with improved levels of drought and N-tolerance at sites which are specifically managed to provide genetic expression for stress-tolerant traits. Such sites will be linked to regional breeding programs so that germplasm with greater local adaptation becomes the focus of improvement.*

Over the past 23 years CIMMYT has maintained a large network of cooperators in around 90 countries who have worked together with CIMMYT breeders to test new maize varieties and segregating progenies in 300-500 trials per year as part of the International Maize Testing Unit's activities. Products of this network's activities are broadly-adapted maize germplasm for general use and information on performance. Other smaller global germplasm development networks operating at varying levels of organization address the issues of soil acidity and insect resistance. At a regional level, testing networks for germplasm adapted to region-specific environmental challenges exist in South Asia and southern and eastern Africa. Regional agronomy networks focusing on common maize production problems and coordinated by CIMMYT staff also operate in Central America and the Caribbean and in East Africa. The abiotic stress research program at CIMMYT, with UNDP support, has become a part of the general germplasm improvement effort by establishing two networks of cooperators with specific interest in the development of genetic sources of tolerance to drought or low N that can be used directly or in combination with locally-adapted germplasm.

Objectives of the Drought and Low N Networks

a) Improve national program awareness of and access to germplasm possessing superior levels of tolerance to these stresses and to selection methods of proven efficiency; give national programs a stake in the development process and a sense of common ownership of the germplasm. Cooperators are encouraged to contribute germplasm and new methods. Hybrids are being included along with OPVs in trials this year, so collaborators can compare products with differing levels of vigor under stress.

b) Broaden the adaptation of CIMMYT's stress-tolerant source germplasm. Information derived from network trials has been used to identify fractions of populations and cultivars that are broadly adapted. Results from Tuxpeño Sequía (Byrne et al., 1995) suggest that > 85% of the gains in drought tolerance observed at CIMMYT's station at Tlaltizapán, México, in the winter season are also observed at other international sites, but exposure to the range of diseases that stress-tolerant maize encounters is a necessity if these sources are to be used.

c) Provide a forum for exchange of germplasm and information among network members through publications describing this research at regional and global meetings.

Characteristics of Present Drought and Low N Networks

Currently the Drought Network consists of 32 participants in 26 countries, and the Low N Network has 20 participating members in 15 countries. Collaborators are specifically interested in genetic tolerance to the target stress. They are generally divided into ***development*** cooperators at fewer, key sites, and ***testing*** cooperators at many sites**.** Development cooperators are those with the capacity to evaluate progeny trials (S_1 or full-sib families; topcross progenies) under conditions of controlled drought or low N stress, while testing cooperators generally provide a test site for already-developed germplasm at a location where drought or low N stress is likely to occur. Development cooperators generally have access to a uniform level test site, with access to supplemental irrigation and near a meteorological station, and are usually willing to observe stress-specific traits, such as the anthesis-silking interval (ASI), staygreen and leaf rolling, as well as shelled grain yields. Instrumentation for measuring the level of water stress or N content of plant parts has not been required; crop yield and visual symptoms are adequate indicators of the level of stress experienced.

Both networks are global in scope, and around 80% of the germplasm being tested originates from CIMMYT. CIMMYT staff coordinate the selection of entries in each trial, their shipment, data analysis and reporting. Trials are always distributed to participants on request, and shipments of trials to Drought Network participants have occurred about once every three years (1989; 1992; 1995-96). The first shipment to the Low N Network took place in 1995-96. Following each round of trials a comprehensive report has been issued (Edmeades et al., 1991, 1995), though it has been generally too late arriving to maintain interest of collaborating staff. In the latest round of network testing, preliminary reports of each trial are supplied to collaborating scientists as the trial data are analyzed. There has also been periodic distribution of additional information, such as reprints or reports from local tests of stress-tolerant sources, though no regular newsletter is issued and no formal means of cooperator feedback exists. The Drought Tolerance Network has sponsored one training course of 19 cooperators for 4 weeks in 1993, and both networks have sponsored one International Symposium in 1996 (these proceedings). Funding of network activities has been with UNDP support, and there are some doubts about future activities since UNDP funding ends in December, 1996.

Performance of networks to date

In 1989 56 trials were requested and shipped to Drought Network participants. In 1992 this number increased to 80, and in 1995-96 it increased further to around 110 trials. Shipments of trials to the newly-formed Low N Network totaled about 60 trials in 1995-96. Around 60% of sites have returned usable data, similar to the return rate from CIMMYT's conventional maize testing network. Trials are lost mainly because the cooperator is unable to sow them, or they arrive too late for a specific sowing date and are forgotten or will not germinate adequately the following year.

A marked improvement in the quality of trials was observed from 1989 to 1992. Participants in the 1992 trials tested under a wider range of water stress levels, and took better observations on traits such as ASI and the degree of foliar senescence under stress. Seed shipments (excluding trial shipments) have increased from 169 individual genotypes in 1992 to 1,818 in 1996. Much of this increase has been in hybrid-oriented products derived from populations that have formed the basis of network trials to date.

Methods and Materials

Progeny evaluations

A total of 225 S_1 progenies of DTP1 (C_5 in 1989; C_6 in 1992) have been evaluated in replicated trials at 7-10 locations by collaborators. This population was formed from a collection of source germplasm which demonstrated drought tolerance under tests conducted in Mexico, or which had putative drought tolerance based on trials conducted by national programs (Edmeades et al., 1997a). Plot size was normally 1 row 5 m long, rows 0.75-0.80 m apart, and plants were usually 25 cm apart in the row (53,000 plants/ha). Actual densities ranged from 40,000 plants/ha to 53,000 plants/ha. Cooperators at most locations recorded days to 50% anthesis, 50% silking, scores of foliar senescence, stand counts at harvest, lodging, ear number, grain moisture at harvest, and shelled grain yield from a bordered plot area (3.19 m^2). The relative efficiency of the lattice design (alpha (0,1) design; see Patterson and Williams, 1976) compared with a randomized complete block design ranged from 0% to 82% (average 15%). Selections comprising the 10 best families across sites (to create Across 92DTP1) and the 35 best families (for recombination of the population) over all sites were done using a selection index based on yields at each site, weighted according to the level of drought experienced at each site, as well as ASI where it had been carefully observed. A number of site-specific experimental varieties were formed by recombining the 10 best progenies identified via a selection index based on all data observed at that site, and these have been re-tested in variety trials at many more sites. This population, while performing quite adequately under drought, has a number of agronomic problems, chiefly its mixed grain color and inadequate disease resistance and husk cover. Progenies of the DTP populations were not, therefore, tested internationally in 1995-96; instead topcross progenies of elite stress tolerant source germplasm were distributed.

Evaluation of varieties and hybrids

Most of these have been varieties or population bulks derived from source populations selected specifically for tolerance to these stresses, and are fully described in Edmeades et al. (1991, 1995). Entries were stratified by maturity into separate trials, one early and the other late. Two to three site-specific check entries from the collaborating national program were included to give an indication of the adaptation of CIMMYT germplasm and to help network participants identify promising germplasm developed by other research programs. For example, in the second round of drought testing, the performance of hybrid H430 (developed by CIRNO, Mexico, and which performed well in Obregón) was highlighted, and the hybrid been included in the current round of testing at all sites. As well as testing varieties, the latest trials under test include both varieties and hybrids, so that collaborators can decide whether hybrids outyield varieties at all yield levels or whether these two classes of germplasm exhibit crossover behavior as stress levels intensify. Plot size is normally 4 rows 5 m long, rows 0.75-0.80 m apart, and the plants are usually 20-25 cm apart in the row (53-66,000 plants/ha). Cooperators are asked to record similar data as in progeny trials and shelled grain yield from a bordered plot area (6.4 m^2). The relative efficiency of the lattice design compared with a randomized complete block design ranged from 0% to 50% (average 10%) for the early maturing trial and from 0 - 91% (average 19%) for the late maturing trial. The types of trials currently being tested by both networks and the demand for these trials are shown in Table 1.

Statistical analysis

Routine analyses of variance were conducted at each site, and data were combined for across-location analyses. Stability of performance across sites was examined in the following ways (Edmeades et al., 1995):

(1) ***Joint linear regressions*** (Eberhart and Russell, 1966) **-** Yield of an individual genotype was regressed on mean yield of all genotypes at each site. A desirable genotype for drought-prone areas is one with a high positive y-intercept, a slope of near 1.0 or greater (i.e., has the capacity to exploit high yielding environments, but yields well under stress), and low deviations from the regression.

(2) ***Average rank across sites, and the standard error of the rank*** **-** A desirable cultivar is one with a low average rank and a low standard error of that rank.

(3) ***Superiority index*** (Lin and Binns, 1988) **-** This measure is suited to the situation where there are a balanced number of entries common to all sites, even though local checks differ at each site. The maximum yield of any cultivar at each location is computed and used as the standard for the site. The superiority of a specific entry is computed from the mean square of the difference between this standard and the specific cultivar performance, added up over sites. The measure includes both genetic and genotype x environment effects, and thus should identify broadly adapted cultivars. The smaller the value, the better the cultivar.

Examples of Results of Network Trials

These have been reported in detail by Edmeades et al. (1991, 1995, 1997a) and Crossa et al. (1997), and only recent highlights are reported here.

Early variety trial

A total of 21 trials (or 60%) returned useful results.

Severely stressed sites: mean yields <1.75 t/ha (7 sites) **-** Although yield differences among entries were non-significant (Table 2), the highest yielders were those which flowered earliest. In these low rainfall, severely-stressed environments, the primary requirement is escape, followed by tolerance. Nonetheless, the ASI of these sites averaged 4.4 d, indicating quite severe stress at flowering, and barrenness was widespread. Santa Rosa 8330 RE provided an exception, being 3-4 d later to flower but as high yielding as the early-flowering entries Pool 16 C_{20} and Pool 18 Sequía $C_{3.}$ Yields were positively associated with ears per plant (r = 0.81**) and weakly and negatively with anthesis date (r = -0.37 NS) and the ASI (r = -0.46 NS). Ears per plant showed a strong negative association with ASI (r = -0.83**). The capacity to resist barrenness is an important selection criterion in these environments and is strongly related to a short ASI under stress. In general check entries were not the highest yielding in these trials, suggesting that some of the Mexican drought tolerant entries may prove useful in these environments.

Moderately moisture-stressed sites with yields between 1.75 and 3.0 t/ha (8 sites) **-** These types of environment must be regarded as those in which drought *tolerance* (rather than escape) is the most important trait. They were slightly less stressed at flowering than the low-yielding sites (ASI=2.6 d vs. 4.4 d). The superior cultivars across sites were the CIMMYT entries DTP1 C_5 Early Selection, Pool 18 Sequía C_3, TEYF, Pool 16 C_{20} and TIWD. There was again a strong association of grain yield with ears per plant (r = 0.75**) and with ASI

Table 1. Type and demand for trials announced in 1995-96.

Trial	Stress	Type[a]	Color	Maturity	Entries	Reps	Sets requested[b]
DLTWT	drt	topcross	W	late	100	2	10
DLTYT	drt	topcross	Y	late	36	2	12
DLTC	drt	OPV/hybrid	W/Y	late	30	4	24
DETC	drt	OPV/hybrid	W/Y	early	25	4	24
DEETC	drt	OPV	W/Y	v. early	12	3	27
NLTWT	low N	topcross	W	late	56	2	3
NLTYT	low N	topcross	Y	late	32	2	10
NLTC	low N	OPV/hybrid	W/Y	late	20	4	23
NETC	low N	OPV/hybrid	W/Y	early	24	4	22
Total							165

[a] OPV = open-pollinated variety

[b] As of January 31, 1996

(r= -0.63*). A large correlation between ears per plant and ASI was again observed (r = -0.83**). Results in these environments emphasize the continuing need for selecting against barrenness by identifying plants with a short ASI under stress at flowering.

Relatively unstressed sites with yields from 3.0 to 6.0 t/ha (6 sites) - When analysis was conducted across these high-yielding sites (Table 2), the highest yielding cultivars were generally the latest flowering (correlation between grain yield and days to anthesis was 0.80**). In these environments drought tolerance is unimportant and yield potential, itself proportional to crop maturity, becomes the trait which dominates performance. It was apparent that DTP1 C_5 Early Selection has a high yield potential and performs well (0.5 t ha^{-1}, or 12% better than the average of local checks) in well-watered conditions.

Across all sites (21 sites) - Genotype differences were significant (*P*= 0.04) (Table 2). The highest yielding cultivar was DTP1 C_5 Early Selection, followed by Pool 18 Sequía C_3 and the average performance of Local check #1. Joint linear regression analysis of grain yield suggested that Pool 18 Sequía C_3 and Pool 16 C_{20} were stable, since they had a positive intercept and a slope near 1.00, whereas DTP1 C_5 Early Selection and TIWD Drt. Tol. Pop. C_0 were all characterized by zero or negative intercepts and slopes of greater than 1.0, indicating that they were better adapted to high yielding environments (Edmeades et al., 1995). Analysis of ranks showed that Pool 18 Sequía C_3 was consistently ranked near the top of cultivar performance. DTP1 C_5 Early Selection showed a relatively high SE of rank, suggesting instability associated with its later maturity. Lin and Binn's superiority index identified Pool 18 Sequía C_3 and DTP1 C_5 Early Selection as stable and superior, followed by Pool 16 C_{20} and selections from Pool 18 Sequía (Table 2). Correlations among important traits across sites (data not shown) showed that grain yield was positively associated with ears per plant (r = 0.68***) and negatively with anthesis date (r = - 0.33***), showing the importance of escape in these environments, and negatively with ASI (r = -0.34***), indicating a continued need for drought tolerance in this germplasm. This trial indicates that, in areas requiring early yellow flint or dent varieties, Pool 18 Sequía C_3 was the cultivar of choice, though local selection for suitable texture will be required. For early white dent areas, Pool 16 C_{20} Syn. 1 seems very suitable, and for flint areas, Santa Rosa 8330 or TEWF Drt. Tol. Syn 2 seems appropriate. In the longer term, DTP1 C_5 Early Selection is a promising source of drought-tolerant yield-responsive germplasm.

Table 2. Across-site means of various characteristics observed in 12 early maturing drought tolerant maize genotypes, two reference genotypes (RE), and two local check genotypes. Superiority index (Lin and Binns, 1988) is smallest for entries that are the most stable across sites.

	Grain yield at sites with stress level: All sites (t ha^{-1})	Low (t ha^{-1})	Moderate (t ha^{-1})	Severe (t ha^{-1})	Superiority index	Anthesis date (d)	ASI (d)	Ears per plant	Rotted ears (%)	Senesc. score (1 to 5^a)
DTP1 C_5 Early Sel.	2.63	4.63	2.70	0.89	53.1	59.4	3.59	0.80	10.6	2.59
Pool 18 Sequía C_3	2.53	4.10	2.67	0.99	52.3	54.5	2.29	0.83	7.7	2.71
Local Check 1	2.50	4.18	2.38	0.94	69.9	58.3	3.56	0.76	6.6	2.80
Pool 16 C_{20} Syn. 1	2.47	4.05	2.58	1.03	57.5	54.2	2.64	0.83	8.5	2.65
Pool 18 Seq. C_2 Low TBN	2.41	4.08	2.43	0.98	66.5	55.5	2.08	0.83	7.2	2.82
TIWD Drt. Tol. Pop. C_0	2.41	4.31	2.48	0.67	80.0	59.7	4.41	0.75	10.0	2.49
Pool 18 Seq. C_2 Best ASI	2.35	4.00	2.45	0.79	68.3	55.0	1.96	0.84	9.0	2.81
TEYF Drt Tol. Syn. 2	2.31	3.65	2.59	0.86	91.7	53.7	2.49	0.82	8.9	2.80
Santa Rosa 8330 RE	2.29	4.18	1.90	1.00	94.2	58.7	3.45	0.78	7.8	2.49
TEWF Drt Tol. Syn. 2	2.27	3.89	2.37	0.79	84.0	55.2	2.78	0.80	9.0	2.71
Across 8331 RE	2.20	4.12	1.90	0.83	107.2	58.5	3.57	0.76	10.7	2.63
Local Check 2	2.17	4.09	1.82	0.69	129.7	58.3	3.89	0.70	8.9	2.81
Mean	2.38	4.11	2.36	0.87	79.5	56.8	3.06	0.79	8.8	2.69
Number of sites	21	6	7	7	21	21	21	21	15	9
Prob. F test	0.04	0.10	0.00	0.20		0.00	0.00	0.00	0.45	0.67
LSD (0.05)	0.28	0.51	0.48	0.40		1.8	1.25	0.07	3.6	0.40

Source: Edmeades et al. (1995)

[a] Score of 1 = green; 5 = dead

Late variety trial

A total of 19 trials (or 58%) provided usable results.

Severely stressed sites with mean yields <2.0 t/ha (5 sites) - Cultivar differences were non-significant (*P*=0.22) but mean yields were only 1.01 t/ha (Table 3). The highest yielding cultivar was Pool 26 Sequía C_3, which was 3 d earlier to flower than other entries in this trial. Escape is an important mechanism in these harsh and uncertain environments. Barrenness was widespread, with ears per plant averaging only 0.57, and ASI averaging 4.7 d. The performance of TS6 C_1 was uncharacteristically poor. Correlations between grain yield and ears per plant (r = -0.86**), ASI (r = -0.71**) and anthesis date (r = -0.59*) were strong and negative, and suggest that the outcome of stress which occurs at flowering or is terminal is a key to yield determination. The correlation between ASI and ears per plant was r = -0.70**.

Moderately moisture-stressed sites with yields between 2.0 and 4.0 t/ha (7 sites) - This is the main target environment for drought-tolerant cultivars. Entry differences for yield were non-significant (*P* = 0.22) (Table 3). Local checks took the top two yield positions, followed by Across 89DTP1, TS6 C_1, Ilonga 89DTP1 and La Posta Sequía C_3. The performance of Pool 26 Sequía was disappointing, suggesting that yield potential was more important than escape in these environments. Stress at flowering was apparently mild (ASI was 2.4 d, half that of the severely stressed trial set), and ears per plant remained high. Consequently, grain yields showed a positive association with days to flower (r = 0.69**) and no association with ASI or ears per plant.

Relatively unstressed sites with yields from 4.0 to 6.5 t/ha (7 sites) - These sites primarily measured yield potential and broad adaptation rather

Table 3. Across-site means of various characteristics observed in 20 late-maturing drought tolerant maize genotypes, two reference genotypes (RE), and three local check genotypes. Superiority index (Lin and Binns, 1988) is smallest for entries that are the most stable across sites.

	Grain yield at sites with stress level:									
	All sites ($t\ ha^{-1}$)	Low ($t\ ha^{-1}$)	Moderate ($t\ ha^{-1}$)	Severe ($t\ ha^{-1}$)	Superiority index	Anthesis date (d)	ASI (d)	Ears per plant	Rotted ears (%)	Senesc. score (1 to 5[a])
La Posta Sequía C_3	3.58	6.06	2.95	0.99	78.6	64.5	2.45	0.87	12.7	3.32
Local check #2	3.56	5.68	3.36	0.88	86.0	63.6	2.85	0.85	5.8	3.36
Across 8627 RE	3.42	5.53	2.91	1.17	82.3	62.8	2.34	0.92	8.4	3.11
Ngabu 89DTP1	3.36	5.48	2.86	1.08	71.4	61.6	2.58	0.84	13.7	3.25
Sinematiali 89DTP1	3.36	5.55	2.85	1.00	68.9	61.2	2.44	0.85	15.6	3.40
DTP2 C_4	3.35	5.57	2.75	1.08	73.1	60.5	2.32	0.85	16.0	3.28
Local check #1	3.34	5.23	3.06	1.08	60.2	62.8	2.40	0.84	10.1	3.16
Sete Lagoas 89DTP1	3.34	5.56	2.70	1.13	73.4	61.4	2.16	0.85	13.6	3.22
TS6 C_1	3.31	5.57	2.99	0.58	117.9	64.2	2.24	0.80	13.0	3.12
Ilonga 89DTP1	3.30	5.29	2.98	0.97	76.7	61.7	2.58	0.84	14.1	3.21
Across 89DTP1	3.30	5.13	3.04	1.09	78.5	60.9	2.30	0.89	12.5	3.20
La Lujosa 89DTP1	3.29	5.37	2.87	0.95	84.0	61.2	2.54	0.84	12.8	3.29
Tak Fa (1) 89DTP1	3.28	5.25	2.94	1.01	79.2	60.8	3.21	0.84	14.7	3.17
Awassa 89DTP1	3.26	5.39	2.82	0.89	91.9	61.2	2.97	0.82	16.6	3.39
Local check #3	3.25	5.36	2.80	0.92	102.2	62.4	2.83	0.80	9.4	3.40
Golden Valley 89 DTP1	3.21	5.31	2.59	1.15	103.9	62.0	2.34	0.84	18.7	3.23
Farako Ba 8625 RE	3.20	5.51	2.48	0.96	98.4	61.4	2.49	0.87	12.4	2.99
Delhi 89DTP1	3.17	5.14	2.76	1.01	94.6	60.8	2.84	0.82	13.0	3.35
Harare 89DTP1	3.11	5.16	2.66	0.87	117.6	62.0	2.80	0.83	14.0	3.20
Pool 26 Sequía C_3	2.93	4.61	2.36	1.37	156.6	58.4	2.33	0.87	12.5	3.34
Mean	3.30	5.39	2.84	1.01	89.8	61.8	2.55	0.85	13.0	3.25
Number of sites	19	7	7	5	19	19	19	19	12	10
Prob. F test	0.06	0.02	0.22	0.22		0.00	0.62	0.01	0.00	0.32
LSD (0.05)	0.32	0.58	0.55	0.39		1.36	0.83	0.06	4.1	0.29

Source: Edmeades et al. (1995)

[a] Score of 1 = green; 5 = dead

than drought tolerance. Cultivar differences for yield were significant ($P<0.02$) (Table 3). The four highest yielding entries were La Posta Sequía C_3, local check #2, TS6 C_1 and DTP2 C_4, followed by two site-specific selections from DTP1. The short ASI (1.3 d), high mean ears per plant (0.99) and the positive correlation between grain yield and days to flower ($r = 0.68^{**}$) attest to the general lack of moisture stress at these sites.

Across all sites (19 sites) - Analysis (Table 3) showed that La Posta Sequía C_3 was equal in grain yield to the average performance of local check #2, though it outyielded the best local check in 8 of the 19 locations and demonstrated consistently good general performance. Across 8627 RE, a CIMMYT check entry of long standing, demonstrated its broad adaptation and high yield, while two site-specific selections of DTP1, Ngabu (1) 89DTP1 and Sinematiali 89DTP1, slightly outyielded local check #1 and the newer population, DTP2 C_4. All DTP selections, however, suffered from high levels of ear rots compared with the local checks, and this requires immediate improvement. Joint linear regression (data not shown) revealed that Across 8627 RE, Across 89DTP1, and Delhi 89DTP1 had positive intercepts and slopes near 1.0 and that La Posta Sequía C_3 and TS6 C_1 showed slopes greater than 1.0 and negative intercepts, with La Posta Sequia C_3 being the better of these two. Lowest mean ranks for yield were reported for Sinematiali 89DTP1, DTP2 C_4, and Across 89DTP1, followed by La Posta Sequía C_3. The superiority index identified Sinematiali 89DTP1, Ngabu (1) 89DTP1, DTP2 C_4, Sete Lagoas 89DTP1, Ilonga 89DTP1 and Across 89DTP1 as superior non-check cultivars, followed by La Posta Sequía C_3. Correlation analysis showed a clear dependence of grain yield on ears per plant ($r = 0.71^{***}$) and on ASI ($r = -0.51^{***}$), but none on anthesis date (data not shown). Ears per plant was closely associated with ASI in this trial set ($r = -0.55^{***}$). For programs requiring drought-tolerant late white dent lowland tropical germplasm, La Posta Sequía C_3 is the cultivar of choice. For late yellow flint areas, Across 8627 performed well and should be considered. In the more subtropical lowland areas, Ngabu (1) 89DTP1 or Sinematiali 89DTP1 are white flint/dent alternatives, and Sete Lagoas 89DTP1 a yellow dent possibility. White and yellow versions of both DTP populations are now available, and offer new possibilities of high yielding broadly adapted source germplasm (Edmeades et al., 1997a).

Site Selection, Management of Stress and Selection Procedures

A uniform site greatly increases the efficiency of the selection process for both drought and low N, and it is well worth investing effort in identifying such sites before the processes of testing and selection begin. The shortcomings of a site caused by lack of uniformity can, to some extent, be offset by an efficient design, and we recommend the use of alpha (0,1) lattice designs (Patterson and Williams, 1976) or row and column designs (Patterson and Robinson, 1989). Such designs provide a considerable increase in efficiency (often >20%) at no additional cost in seed or land.

When selecting a site for drought research, the emphasis should be on locations where rain will not interfere at critical stages of growth. A dry winter season where irrigation is available to manipulate stress levels near flowering is often the best choice, provided selections are tested subsequently in the normal rainy season. Studies by Byrne et al. (1995) indicated that around 85% of gains made in dry winter environments were transferable to the normal rainy season. Do not be afraid to reduce yields by 60-70% with a stress applied at flowering, since genetic variation for tolerance and for ear growth under stress is not clearly revealed until stress levels become severe. If a dry season nursery is not feasible because of cold winter conditions, then very early sowing with irrigation in the regular crop season can be an effective way to ensure heat and drought stress at flowering. Where irrigation is not possible, very late sowing in the middle of the season may expose the crop to stress at flowering and to terminal stress during grain filling as the rains end. High plant densities can also be used to amplify the intensity of an otherwise moderate drought stress. Where resources are scarce, data should not be collected on the less important secondary traits (see Edmeades et al., 1997b); rather the focus should be on good water management and the observation of shelled grain yield, anthesis and ears per plant, and, if resources permit, ASI.

When selecting for low N tolerance, indigenous N of the plot area should be reduced until yields are less than 50% of unstressed levels (Lafitte et al., 1997). This is usually done by growing several crops (2-3 are usually all that is needed) of maize planted at high plant density with no added N fertilizer, and cutting and removing the entire crop from the area. When N levels have been reduced sufficiently, the crop for selection is grown with no added N fertilizer but with supplemental P and other nutrients added to avoid deficiencies from non-N sources. Crop residues can be removed to further reduce fertility, though sometimes fertility can become too low over time (e.g., when yields are <20% of potential) and emergency N (at around 20-25 kg N/ha) must be applied to save the crop. Often N stress early in the season, or even at flowering, is not very severe. Stress at this stage can be intensified by using an intercrop (e.g., sorghum) that can be removed when the stress level becomes sufficiently severe. High plant density also increases the level of N deficiency, and thinning can be delayed to induce an early N stress. Where resources are scarce, emphasis should be on observing shelled grain yield, anthesis date, ears per plant and a visual score of staygreen on one or two occasions during the latter half of grain filling (Bänziger and Lafitte, 1997).

Where several traits are observed and collaborators want to make their own selections, or where data from several sites are combined, the use of a selection index that combines data from all measured traits and sites (e.g., Barreto et al., 1997) has led to increased selection efficiency compared with the use of grain yield alone (Bänziger and Lafitte, 1997).

Future Trends in Drought and Low N Networks

- Regional devolution of stress-tolerance research is needed. It is clear that drought and low N-tolerant germplasm distributed from CIMMYT's breeding program in Mexico needs further selection for adaptation to regional challenges; e.g., resistance to downy mildew, streak virus, the stunt virus complex, ear rots, and better husk cover. Source germplasm developed in Mexico should be transferred to the regions for regional adaptation, though a more effective strategy will be for regional breeding programs to improve tolerance to drought and low N in adapted germplasm using the selection methodology developed at CIMMYT headquarters (Edmeades et al., 1997c). A full integration of conventional improvement and breeding for abiotic stress tolerance in regional breeding programs and regional testing networks is now required, since the phase of methods development is now reducing in importance. Joint reporting of results, planning and decision making through region planning meetings already occurs; decisions regarding which germplasm should be improved for stress tolerance would simply become another item on the agenda at these gatherings. Two such networks will be operational in eastern and southern Africa by the end of 1997, but other regions are less well served. A regional focus will also help ensure the testing of genotypes appropriate to regional needs and a faster turn around of data analysis and reporting, since in general the trials are all sown at the same time of the year and results should be therefore available before the subsequent year's trials are assembled. Since donor funds are increasingly being placed in the major geographic regions before decisions are being taken on their distribution, regionalized breeding schemes have greater donor appeal today than in the 1980s.
- Greater investments in site development and stress management are needed if regional testing and development networks are to be effective. The provision of reliable irrigation facilities greatly improves efficiency of selection for drought tolerance during the dry season, and the identification and development of sites with spatially-uniform low N conditions will greatly benefit selection for tolerance to that stress.
- Sources should not be of mixed grain color if they are to be used by national programs, since most have neither the resources or the patience to separate white and yellow genotypes.
- As national programs move in the direction of inbred lines, hybrids and intellectual property rights, the free exchange among national programs of inbreds will become sharply reduced. CIMMYT is uniquely placed to serve as the

"honest broker" in the exchange of unique sources of stress tolerance among national program, either through hybrid products, source populations, or through synthetics from inbred lines provided in trust by national programs.

- Better relations with quarantine authorities, and more regional uniformity and rationality in quarantine regulations will greatly facilitate germplasm exchange within regions where diseases are fairly uniformly distributed. CIMMYT can help this process. Research programs and quarantine authorities must work together to enhance overall crop improvement, rather than reverting to purely bureaucratic and regulatory roles that often are competitive rather than collaborative.

CIMMYT's Role in Fulfilling Network Goals

Regional network activities

CIMMYT can assist in the facilitation and execution of regional testing networks focusing on selection for stress tolerance by:

- Coordination of network activities such as selection of entries for trials, development of fieldbooks, packaging and dispatch, inspection, analysis of data across locations, and reporting.
- Development and distribution of regionally-adapted genetic diversity for stress tolerance.
- Management and reporting of regionally-focused donor funds for national program support.
- Strategic research on stress management and selection techniques that have a regional orientation.
- Adaptation of exotic germplasm introduced as a source of stress tolerance from CIMMYT headquarters, from other regional maize breeding programs, or from private sector sources.
- Application of biotechnology tools, such as the conversion of elite regionally-adapted but susceptible inbred lines to tolerance through the transfer of traits such as short ASI under stress (Ribaut et al., 1997).
- Information exchange through sponsored regional conferences and their proceedings, and joint planning meetings.
- Fostering seed and information exchanges, and arranging for testing sites with regional private seed companies on behalf of national program clients in the region.

Headquarters research activities

There is a continuing role for CIMMYT's stress-oriented breeding and research programs at headquarters in the following areas:

- Development of highly stress-tolerant sources that may initially have poor agronomic characteristics and very narrow adaptation, but which could be used in marker-assisted backcrossing programs.
- Development of broadly-adapted elite source germplasm through recurrent selection (Edmeades et al., 1997c).
- Stress definition: the incidence, intensity, nature and distribution of drought and low N stresses, and their global and regional costs, using tools provided by GIS and crop process models (White and Elings, 1997).
- Distribution of broadly adapted source germplasm (populations; inbred lines) to regional centers for regional adaptation, for introgression into locally-adapted populations, or for use as a line in a hybrid or synthetic.
- Higher-risk strategic research on improved selection methodology and biotechnology. Examples are marker-assisted selection for specific traits; determination of the value of additional secondary traits, such as ABA.

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Recurrent Selection Under Managed Drought Stress Improves Grain Yields in Tropical Maize

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Abstract

After soil fertility, drought is the major abiotic stress limiting maize production in the tropics, and is the most important source of variation in yield over time. Eight cycles of recurrent full-sib (FS) selection or up to four cycles of recurrent S_1 selection were practiced on one early-maturing and three late-maturing maize populations adapted to the tropical lowlands. By controlling irrigation in an otherwise dry season, drought stress was applied at flowering and during grain filling. Well-watered nurseries were used to ensure that yield potential was maintained. Selection was for an index of traits that sought to: increase grain yield, reduce anthesis-silking interval (ASI), reduce barrenness, delay senescence, reduce tassel size and increase leaf angle while leaving male flowering date unaltered. Traits related to yield and flowering behavior received the greatest weighting. Gains ranged from 80-108 (mean 94) kg ha^{-1} yr^{-1} under FS selection, and from 73-144 (mean 111) kg ha^{-1} yr^{-1} under S_1 recurrent selection, when selections were evaluated at a yield level of 1.5-2.4 t ha^{-1} (annual gains >5%). Under well-watered conditions (5.6-8.0 t ha^{-1}), gains were from 38-108 (mean 73) kg ha^{-1} yr^{-1} from FS and from 27-89 (mean 59) kg ha^{-1} yr^{-1} from S_1 selection. Yield increases were associated strongly with reduced ASI, reduced barrenness and increased harvest index; mildly with delayed leaf senescence and reduced tassel size; and not at all with changes in leaf angle. Biomass production under all conditions and plant water status under drought were unaffected by selection. Reductions in ASI were associated with faster ear growth rates, suggesting an increased partitioning of assimilates to the growing ear. Floret number has declined with selection, but in one population mean floret size at 50% anthesis doubled. This was associated with a marked increase in floret survival under stress. We conclude that it is possible through selection to increase grain yields under severe drought stress (mean yield of 2 t ha^{-1}) by 25-40%, while at the same time increasing yield potential by around 5-10%. The key to success is carefully managed drought stress coinciding with flowering and the choice of elite germplasm, followed by selection for grain yield, ears per plant, ASI, staygreen and a constant anthesis date. **Acknowledgement**: *Parts of the contents of this paper have been presented in various forms elsewhere (Edmeades et al., 1992, 1993, 1997a, b).*

Drought and low fertility are two of the major causes of maize yield loss in the tropics. CIMMYT's megaenvironment study (CIMMYT, 1988), and the application of arbitrary loss estimates to each moisture stress class suggests that global losses of maize grain to drought in the tropics may total 24 million tons per year, or around 17% of well-watered production (Edmeades et al., 1992). Losses in the lowland tropics, which alone may total 15 million tons annually, are most severe where annual rainfall is less than 500 mm, and can be especially severe on shallow, sandy soils. The normal inter-seasonal fluctuations in rainfall have been associated closely with variation in average national maize yields across large production regions in eastern and southern Africa (Rötter, 1993; Edmeades et al., 1997a), demonstrating that drought is a pervasive cause of yield instability in maize-based cropping systems in most years and environments.

Despite the fact that the yields of sorghum and millet are often more stable than maize in variable rainfall environments, they are usually lower in good years, and consumer preference often demands that maize be grown instead.

Ludlow and Muchow (1990) noted that the first essential step in breeding for stable production in water-limited environments is to ensure that crop phenology matches the seasonal supply of crop-available water. If the rainy season is reliable but very short, then escape through earliness is a desirable breeding goal. Evolutionary pressures and farmer selection have resulted in the development of early maturing maize cultivars in dry tropical areas of Indonesia, Kenya, Mexico, Colombia, etc. These escape drought but are usually relatively low yielding when rainfall is not limiting. A more productive strategy would be to develop a later-maturing cultivar with a higher yield under optimal conditions and a yield under drought which is stabilized by reducing the effects of drought on grain number and size. It is this latter approach which is the focus of the research reported here, since we regard earliness as a relatively simple trait from a selection viewpoint.

The probability of drought is highest at the start and end of the growing season. At planting farmers have management alternatives to loss of stand at planting, such as replanting with a shorter duration cultivar or a different species. Field selection for improved establishment in a drying soil has met with mixed success, and gains have been small, perhaps at a cost to grain yield under unstressed conditions, while stress levels have proven difficult to manage (Bänziger et al., 1997).

Variation in kernel number per plant is normally responsible for most of the variation in grain yield, and kernel number is determined by events which occur near flowering when maize is most susceptible to drought. Grain yield loss is around twice as great from a single stress day experienced around flowering than at any other time (Shaw, 1976; Grant et al., 1989; NeSmith and Ritchie, 1992), and although the probability of drought stress is lower at silking, its consequences on yield can be severe, since it is too late in the season for replanting. This susceptibility is probably because of the spatial separation of male and female flowers on the plant, a reduced proportion of assimilates partitioned to the ear versus the tassel when the plant is stressed at flowering (Edmeades et al., 1993), and direct effects of water deficits on enzyme and hormone activities in the newly-fertilized ovary (Westgate, 1997). Abortion of fertilized kernels shortly after pollination seems to be due to a reduced flux of assimilates, especially sucrose, to the developing kernel (Schussler and Westgate, 1995; Zinselmeier et al., 1995b). Schussler and Westgate (1995) and Zinselmeier et al. (1995a) have reported that drought at flowering also affects the carbohydrate metabolism of the developing ovule, further reducing sucrose flux to the newly formed seed. This suggests that a reduction in the growth of competing organs (stems, tassels, perhaps surface roots) at flowering might also increase the flow of current assimilate to the ear and contribute to drought tolerance. The greater degree of drought tolerance of short plant selections under drought (Fischer et al., 1983) supports this hypothesis.

An easily observed indicator of this assimilate flow, and hence the growth rate of the ear under stress, is anthesis-silking interval (ASI), which lengthens as photosynthesis per plant is reduced by stresses that reduce photosynthesis per plant (DuPlessis and Dijkhuis, 1967; Bolaños and Edmeades, 1993b). There is a strong relationship between ASI and kernels or ears per plant (Bolaños and Edmeades, 1997). In one study an increase in ASI of 1 d was associated with a 28% reduction, a 3 d increase with 55%, and a 5 d increase with a 69% reduction in kernels per plant (Bolaños and Edmeades, 1993b). In a severely drought-stressed field it is common, therefore, to find a significant proportion of plants, perhaps 30-50%, that are completely barren. Pollen shortage is usually not the reason for this (Westgate and Bassetti, 1991), though research by Westgate and others suggests that grain yields in the northern Corn Belt can be predicted accurately by measures of pollen shed intensity and silk growth in the field (Westgate, pers. comm., 1996). They found that pollen densities of less than 100 grains cm^{-2} d^{-1} were associated with inadequate grain set on any given day during flowering. For a hybrid this coincides with an ASI of >7 d (Bassetti and Westgate, 1994), though in open-pollinated varieties with greater variation in flowering date an

ASI of 10-12 d could probably be tolerated before pollen supply limits grain set. Pollen viability is normally little affected by plant water status, but is reduced by temperatures greater than 38-40°C (Schoper et al., 1986). Tassel blasting is commonly observed in fields when temperatures exceed this level.

Provided an ear has been established on the plant, the maintenance of a green functional canopy and a capacity to remobilize carbohydrates stored in the stem and husk (Blum, 1988) should contribute to high yield under terminal stress. Associations between foliar "staygreen" and yield are, however, often weak (Bolaños and Edmeades, 1997; Edmeades et al., 1997c). Erect leaves should, theoretically, have a higher water use efficiency than lax leaves, since they intercept radiation in a more efficient manner, but selection for this trait is merited only if total radiation interception does not decline.

Because variation in grain yield under drought stress is strongly associated with variation in kernels per plant, much emphasis in our program has been placed on the exploitation of genetic variability for tolerance to drought stress at flowering, and to a lesser extent during grain filling. We describe here highlights of the results of recurrent selection for improved drought tolerance in several tropical maize populations that spans more than 20 years of field research. Detailed accounts of each study can be found in Fischer et al., 1983, 1989; Bolaños and Edmeades, 1993a, b, 1997; Bolaños et al., 1993; Edmeades et al., 1993; Byrne et al., 1995; Edmeades et al., 1995. These reports have been complemented recently by considerable research on drought tolerance in hybrid-oriented germplasm (Beck et al., 1997; Vasal et al., 1997).

Methods and Materials

Selection procedures

These have been extensively described elsewhere (Bolaños and Edmeades, 1993a, b; Bolaños et al., 1993; Bolaños and Edmeades, 1997; Edmeades et al., 1997b). In summary, selection began in the elite lowland tropical white dent population, Tuxpeño Sequía, in 1975. This population underwent eight cycles of recurrent selection among full-sib families in the rain-free winter season at Tlaltizapán, Mexico, where timing and intensity of stress can be managed by irrigation. Each of 250 families was grown in single-row plots under three regimes of increasing drought intensity, namely well-watered (WW), intermediate stress (IS; water withdrawn during late flowering and throughout grain filling), and severe stress (SS; no water applied from 3 wk before silking onwards). Selection of the best 60-80 families was based on an ideotype with high grain yield under SS and IS, high leaf and stem extension rates under drought, delayed foliar senescence under SS and IS, and reduced canopy temperatures and ASI under IS and SS. Each cycle of full-sib selection required one year to complete.

Improvement commenced in a new and diverse group of five elite maize populations in 1985-86, using a recurrent S_1 selection scheme (Table 1). Three of these populations (La Posta Sequía; Pool 26 Sequía and TS6) are late-maturing, and two (Pool 16; Pool 18 Sequía) are early-maturing. Within each selection cycle 500-600 S_1 families were prescreened under drought and heat in the Sonoran Desert at Cd. Obregón, Sonora, in northwest Mexico. The superior 200- 220

Table 1. Description of populations under S_1 recurrent selection for improved drought tolerance. All are adapted to the lowland tropics, though DTP-W and DTP-Y lack some disease resistances necessary for lowland environments and are better suited to some subtropical environments.

Population name	Days to harvest[a]	Grain color	Grain texture	Cycles[b] completed	Comments
La Posta Sequía	115	W	dent	5	Selection continuing
TS6	112	W	dent	4 (+6)	Selection continuing with Central American national programs
Pool 26 Sequía	105	Y	dent	3	Selection stopped at C_3
Pool 16 Sequía	90	W	dent	2	Selection stopped at C_2 and merged with CIMMYT's Pool 16
Pool 16 BN	90	W	dent	1	Was Pool 16 C_{20}; now simultaneous selection for drought and low N
Pool 18 Sequía	90	Y	flint/dent	4	Selection continuing
DTP-W	109	W	flint/dent	4 (+4)	Selection continuing
DTP-Y	109	Y	flint/dent	4 (+4)	Selection continuing

[a] Time from planting to around 25% grain moisture in the lowland tropics at sea-level in summer.

[b] Cycles in parentheses refer to selection by half- or full-sib methods. Updated to July, 1997.

families thus identified were grown in Tlaltizapán during winter from remnant seed under the three water regimes described, and the best 50 S_1 families recombined to form the subsequent cycle of selection. The stress level tolerated by S_1 families is less than that for full-sib families, so water was applied once after flowering in the SS treatment to ensure that kernels set under stress would be filled. Each of the managed selection environments was used to expose genetic variation for a specific trait. The dry heat of Obregón (temperatures often exceed 37°C) exposed variation for upper leaf senescence, tassel sterility and barrenness. At Tlaltizapán the well-watered environment allowed expression of yield potential, while the IS regime exposed genetic variation for lower leaf senescence and for grain yield. Under the SS regime, variation in grain yield was small, but genetic variability for ears per plant (barrenness) and for ASI was exposed. The heritability for grain yield of S_1 families remained in the range of 0.5-0.6 until yields fell to below 20% of the well-watered control. Selection was principally for increased shelled grain yield, ears per plant, and staygreen under stress, and for decreased ASI and tassel sterility. Less important traits were upright unrolled leaves, small tassels and lodging resistance. Two years were needed to complete a cycle of two-stage recurrent S_1 selection. Elite S_1 lines were advanced to S_2 and S_3 under drought stress, then topcrossed to two testers to assign them to heterotic groups. Lines were then advanced to S_5 while evaluation of topcrosses took place (Beck et al., 1997).

During the selection process several studies were conducted on the adaptive value and realized heritability of a number of secondary traits, using correlation analysis and divergent selection. Results of these studies (Edmeades et al., 1997c) were used to modify the array of traits being used in selection and to alter the weights assigned to each in the selection index used to identify superior families for recombinations (Barreto et al., 1997).

Results and Discussion

Evaluation of progress

Evaluations of C_1, C_2, C_4, C_6 and C_8 of Tuxpeño Sequía were conducted in two seasons from 1987-89 in large plots at the selection site, using the three water regimes described. Irrigation regimes were grouped over years into droughted and well-watered environments. Grain yield increased at a rate of 108 kg ha^{-1} cycle^{-1} at yield levels ranging from 1 to 8 t ha^{-1}, and the same rate of gain was observed under well-watered and drought stressed conditions. At a yield level of 2 t ha^{-1} this represented a gain of 6.3% cycle^{-1} (Bolaños and Edmeades, 1993a). These same genotypes and some conventionally-selected checks were grown in 12 environments, seven of which were rainfed and outside Mexico. Gains averaged 90 kg ha^{-1} cycle^{-1} across all sites at a mean yield level of 5.6 t ha^{-1} (Byrne et al., 1995). This indicated that 83% of the gains from selection in a dry winter environment were observed in a more normal production situation in the summer rainy season. Evaluations demonstrated that eight cycles of selection have resulted in a 35% increase in yield for a farmer whose yields are reduced from 6 to 2 t ha^{-1} by drought occurring near flowering and during grain filling.

In populations subjected to S_1 recurrent selection, gains were evaluated after 1-3 selection cycles. Gains per cycle were expected to be larger than those under full-sib selection because selection intensity was greater (35% of best families selected in the full-sib scheme, versus 8% in the S_1 scheme). Cycles of selection of La Posta Sequia (C_0, C_1, C_2 and C_3) and Pool 26 Sequia (C_1, C_2 and C_3) were compared with the conventionally-improved versions of these populations (Pop. 43 C_9 and Pool 23 C_{23}) and with Tuxpeño Sequía C_0 and C_8 and TS6 C_1 (first cycle of S_1 recurrent selection in Tuxpeño Sequía C_6) along with some check cultivars (Edmeades et al., 1995; Table 2). Average yields of the environments varied from 1.01 to 10.40 t ha^{-1}. Five environments were droughted during flowering and grain filling, and the other five were well-watered. Mean yields were 2.35 t ha^{-1} and 8.0 t ha^{-1}, respectively. Yield gains in La Posta Sequía and Pool 26 Sequía averaged 259 kg ha^{-1} (12.4%) cycle^{-1} under drought, and 115 kg ha^{-1} (1.5%) cycle^{-1} under well-watered conditions (Table 2). Yield improvements under drought were paralleled by increases in ears per plant of around 0.075 cycle^{-1} and in harvest index, while ASI declined by 1.3 d cycle^{-1}. Populations became earlier to flower by 0.7 d cycle^{-1}, despite our objective of keeping the time from sowing to anthesis constant during selection.

Conventional selection, using international progeny evaluation at mainly well-watered sites, did not increase drought tolerance; Pop. 43 C_9 and Pool 26 C_{23} became later by about 1 d cycle^{-1} but improvements in yield were only observed under well-watered conditions. Gains of Tuxpeño Sequía C_8 versus C_0 in this evaluation were slightly lower than those reported previously (Bolaños and Edmeades, 1993a; Byrne at al., 1995), though TS6 C_1 represented an important improvement over Tuxpeño Sequía C_8 under all environments (Table 2). Principal component analysis of yields in the 10 different environments showed that well-watered and droughted environments were generally orthogonal (Chapman et al., 1997), interpreted by the authors as meaning that selection in only well-watered environments is unlikely to give improvements in yield under drought. They concluded from these and other analyses that selection for drought tolerance has improved broad adaptation, as well as specific adaptation to dry environments.

In a similar set of trials to those described above, rates of progress were determined in Pool 18 Sequía (C_0 - C_3) and in Pool 16 Sequía (C_0 - C_2) (Table 3). Gains averaged 146 kg ha^{-1} (10.3%) cycle^{-1} under drought, 126 kg ha^{-1} (2.4%) cycle^{-1} under well-watered conditions, and 134 kg ha^{-1} (3.8%) cycle^{-1} across sites. This contrasted with a slight loss in yield (-3.2%) under drought and a 2.4% cycle^{-1} yield increase under well-watered conditions in Pop. 31 which had been improved by conventional selection based on the international testing of progenies at sites where drought was a random occurrence.

Table 2. Grain yield and other traits of cycles of selection of three late-maturing maize populations and six check entries when grown at five droughted sites or at five well-watered locations in Mexico (adapted from Edmeades et al., 1995).

	Yield, droughted	Yield, well-watered	Anthesis date, droughted	ASI, droughted	Ears per plant, droughted	Harvest index, droughted
	t ha^{-1}		d		no no^{-1}	
Test sites	5	5	5	5	5	2
La Posta Seq. C_0	1.91	8.22	83.6	6.7	0.76	0.10
La Posta Seq. C_1	1.95	8.30	83.4	6.1	0.79	0.09
La Posta Seq. C_2	2.38	8.45	82.4	4.2	0.88	0.14
La Posta Seq. C_3	2.53	8.35	82.3	3.4	0.95	0.18
Pop. 43 C_9	1.74	8.00	86.0	7.0	0.79	0.09
Pool 26 Seq. C_1	2.25	7.52	78.0	5.8	0.83	0.16
Pool 26 Seq. C_2	2.59	7.81	77.5	3.7	0.95	0.18
Pool 26 Seq. C_3	2.82	7.87	76.2	2.8	0.98	0.24
Pool 26 C_{23}	2.14	7.97	81.6	5.9	0.81	0.12
Tuxp. Seq. C_0	1.75	7.48	82.6	6.4	0.73	0.12
Tuxp. Seq. C_8	2.39	7.78	80.0	2.9	0.93	0.22
TL89DTP1 C_5	3.11	7.91	76.0	1.7	1.00	0.27
DTP2 C_2	2.78	8.11	76.1	2.8	1.01	0.27
TS6 C_1	2.69	8.19	80.8	1.9	0.95	0.24
TLWD-EL	2.35	7.63	84.5	6.8	0.83	0.13
Mean	2.35	7.96	80.6	4.5	0.88	0.17
LSD (0.05)	0.35	0.39	0.56	1.34	0.07	0.06
Selection gains cycle^{-1}						
La Posta Sequía	0.229**	0.053ns	-0.52**	-1.18**	0.07**	0.03**
Pool 26 Sequía	0.288**	0.177*	-0.93**	-1.50**	0.08**	0.04*
Tuxpeño Sequía	0.080**	0.038**	-0.32**	-0.44**	0.02**	0.01**

A comparison of advanced selection cycles from these populations with that of check entries in international drought network trials has shown that La Posta Sequia C_3, Pool 18 Sequía C_3 and Pool 16 C_{20} were stable and high yielding, though the yields of Tuxpeño Sequía and Pool 26 Sequia C_3 were unstable over environments (Edmeades et al., 1997d).

What changed with selection?

Gains were largely the result of reduced barrenness (i.e., increased ears per plant) under drought, and an associated increase in harvest index (Table 2), given that total biomass production was unaffected by selection. In Tuxpeño Sequía tassel size was reduced, and root biomass in the top 50 cm of soil declined by 35%, though neither of these traits was selected for directly. There was no change in any trait indicative of plant water status in Tuxpeño (e.g., predawn or noon water potential; osmotic adjustment; canopy temperature, water extraction profiles) (Bolaños and Edmeades, 1993b; Bolaños et al., 1993). Detailed analysis of C_0 and C_8 has shown that the photosynthetic system of C_8 recovers more rapidly from drought stress, and has a slightly higher radiation use efficiency (Raya et al., 1997; Manda et al., 1997). In all cases anthesis date became slightly earlier, and ASI became shorter under drought (Tables 2, 4). Eight cycles of selection in Tuxpeño Sequía led to significantly faster spikelet and ear growth but also to a 21% reduction in final spikelet number (Table 5; Fig. 1). Larger spikelet size was not a result of earlier initiation of ears in relation to tassels, but was rather due to an increase in ear relative growth rate and a decrease in tassel relative growth rate, especially under water stress at flowering (Tables 4, 5). Under low N stress Tuxpeño Sequía C_8 also initiated fewer spikelets, had a 5 d longer lag phase during grain filling, and had considerably larger kernels when the linear phase of grain growth began (Table 5). Thus fewer spikelets were formed, grew more rapidly, and were ultimately more successful in forming grain. Preliminary data suggests that these changes in ear growth have also occurred in the other late-maturing populations under improvement for drought tolerance.

The ASI trait has been mapped and appears to be coded at relatively few important loci on the maize genome (Ribaut et al., 1997b). Changes in ASI due to selection in Tuxpeño Sequía have been related to changes in allelic frequency at genome map positions associated with changes in ASI under drought in an unrelated mapping population (Ribaut et al., 1997a). Marker-assisted selection could speed the transfer of regions carrying these loci to elite inbred lines and populations, and thus reduce the time and perhaps the cost associated with conventional breeding procedures for drought tolerance.

Relationship of drought tolerance to tolerance of other abiotic stresses

Recent studies have shown that drought tolerant selections also perform well under low N conditions. Gains observed under low N averaged 210 kg^{-1} ha^{-1} cycle^{-1} for S_1 selection and 86 kg ha^{-1} cycle^{-1} for full-sib selection, values which were very similar to those observed under drought (Lafitte et al., 1997). Selection for improved partitioning of assimilates to the developing ear using drought stress at flowering as

Table 3. Grain yield of 11 early-maturing genotypes, and selection gains in two populations (Pool 18 Sequía; Pool 16 Sequía) selected for drought tolerance and in one conventionally-selected population (Pop. 31) when evaluated with two check cultivars in droughted and well-watered environments in Mexico (source: Edmeades and Deutsch, 1994).

Genotype name	Drought sites mean	Well-watered sites mean	Across sites mean
	t ha^{-1}		
Sites	6	4	10
Pool 18 Seq. C_0	1.42	5.30	3.54
Pool 18 Seq. C_1	1.51	5.64	3.76
Pool 18 Seq. C_2	1.67	5.47	3.74
Pool 18 Seq. C_3	1.85	5.78	4.00
Pop. 31 C_2	1.55	5.60	3.76
Pop. 31 C_5	1.40	6.00	3.91
Pool 16 Seq. C_0	1.06	5.43	3.44
Pool 16 Seq. C_1	1.27	5.62	3.64
Pool 16 C_{20}	1.85	6.29	4.27
SPE C_6, F_2 Best all	1.19	5.70	3.65
TEYF Drt Synthetic 2	1.68	5.34	3.68
Mean	1.46	5.64	3.74
Selection gains			
Pool 18 Sequía (vs. C_0)			
t ha^{-1} cycle^{-1}	0.146**	0.126**	0.134**
Gain % cycle^{-1}	10.3	2.4	3.8
Pool 16 Sequía (vs. C_0)			
t ha^{-1} cycle^{-1}	0.204**	0.198**	0.201**
Gain % cycle^{-1}	19.2	3.6	5.8
Population 31 (C_2 vs. C_5)			
t ha^{-1} cycle^{-1}	-0.050	0.133**	0.050
Gain % cycle^{-1}	-3.2	2.4	1.3

**, * denotes selection gains significant at $P < 0.01$, $P < 0.05$, respectively.

Table 4. Days from planting to tassel initiation (TI), ear initiation (EI), anthesis date (AD), and the anthesis-silking interval (ASI) for C_0, C_4 and C_8 of Tuxpeño Sequía. Data are means across five trials at high plant density, mild and severe drought, when grown at Tlaltizapán, México, 1988-90. Durations are summer season equivalents (modified from Edmeades et al., 1993).

	TI	EI	AD	ASI
	d			
Tuxpeño Sequía C_0	27.8	38.0	63.3	12.1
Tuxpeño Sequía C_4	27.2	37.4	61.3	8.1
Tuxpeño Sequía C_8	26.2	36.3	60.8	2.5
Rate change cycle^{-1a}	-0.23***	-0.26***	-0.34***	-1.14**

***, ** denotes gains significant at $P < 0.001$, $P < 0.01$, respectively.

[a] Rates of gain computed from data collected from C_0, C_2, C_4, C_6 and C_8.

the selection screen, therefore, can simultaneously improve tolerance to drought and to low N. In a recent study Uhart and Andrade (1995) noted that under moderate levels of N stress the effects of N on grain number were mediated through effects on carbon metabolism. Progeny trials conducted in Pool 16 BN under severe drought and low N stresses have shown a correlation between ASI observed under low N and under drought of around 0.45 ($P < 0.01$) (unpublished data, 1995). Under severe levels of N deficiency, then, it seems likely that ASI may also be an indicator of partitioning patterns of N as well, though the relatively low correlation suggests that each may be under separate genetic control; this possibility is now being investigated.

Other trials have shown that advanced selection cycles of Tuxpeño Sequía suffer significantly less yield reduction than C_0 when exposed to a 53% reduction in radiation intensity for two weeks either side of silking (Edmeades et al., 1992). Tolerance to high plant density showed a non-significant tendency to increase with selection in this population (unpublished data, 1992).

Role of the selection environment

A key factor in the success of this selection program has been the availability of facilities where drought stress can be carefully managed. Gains are only possible when the genetic variation for tolerance, through whatever mechanism, can be observed (Bolaños and Edmeades, 1997). In these studies this led to the use of an atypical winter season selection site with adequate irrigation supply, but selection gain x environment interaction was small and only 17% of the gains reported in the winter season were lost when germplasm was transferred to the normal summer production environment (Byrne et al., 1995). Improvement in drought tolerance by this mechanism was significantly greater than that resulting from selection based on international testing of progenies at sites where drought was a random occurrence, and, when drought tolerance is the principal goal of improvement, considerably cheaper.

Choice of traits and germplasm

Given the importance of the last half of the crop life cycle in determining yield, and the large correlation between kernels per plant and grain yield under drought stress (r = 0.9**; Bolaños and Edmeades, 1997), our focus on factors affecting kernel set under drought seems justified. Where resources are very limited, selection should be based on a minimum dataset comprising anthesis date, ears per plant and shelled grain yields under a moderate to severe drought stress imposed at flowering and during grain filling. Observation of anthesis date is simply to avoid the unwitting selection of early flowering escapes. With more resources, the observation of silking date (hence ASI) and leaf senescence and an extra managed stress environment are logical additions (Edmeades et al.,

Table 5. Parameters of: A: spikelet initiation and growth under high plant density, and mild and severe water stress; and B: spikelet and kernel growth under low nitrogen in Cycle 0 and Cycle 8 of Tuxpeño Sequía when grown in Mexico, 1989-92.

	Tuxpeno Sequía		
	Cycle 0	Cycle 8	Significance
A: High density and mild, severe drought (Source: Edmeades et al., 1993)			
Duration of spikelet initiation (d)	15.3	13.7	*
Spikelet initiation rate (d^{-1})	46.6	42.7	NS
Spikelets ear^{-1} at 50% anthesis	715	586	***
Biomass spikelet^{-1} at 50% anthesis (mg)	0.60	1.74	*
Ear RGR around anthesis ($g\ g^{-1}\ d^{-1}$)[a]	0.383	0.421	***
Tassel RGR around anthesis ($g\ g^{-1}\ d^{-1}$)[a]	0.282	0.216	**
B: Low nitrogen (Source: Lafitte and Edmeades, 1995)			
Biomass spikelet^{-1} at 50% silking (mg)	1.1	1.4	*
Spikelets ear^{-1} at 50% silking	529	445	*
Duration of lag period grain growth (d)	15	20	+
Biomass spikelet end of lag phase (mg)	33	63	*

***,**, *, +, NS: denote differences significant at $P < 0.001$, $P < 0.01$, $P < 0.05$, $P < 0.10$ and $P > 0.10$, respectively.

[a] RGR = relative growth rate

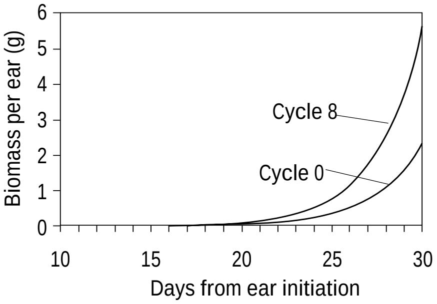

Figure 1. Ear biomass versus time after ear initiation for Cycle 0 and Cycle 8 of Tuxpeño Sequía. Fitted curves are from data collected under high plant density, mild and severe drought stress (modified from Edmeades et al., 1993)

1997c). Our evidence suggests that selection using these criteria will result in stabilized and improved yields of maize exposed to mid-season and terminal drought in highly variable rainfall environments.

For national programs the correct choice of germplasm for recurrent selection is critical. Landraces normally have a number of agronomic defects that may take years of selection to correct, and for this reason it is recommended that selection begin in *elite* adapted germplasm (Edmeades et al., 1997f).

Development of stress tolerant hybrids

Recent studies have shown that stress-tolerant hybrids are developed with a greater frequency from stress-tolerant source populations than from their conventionally-selected genetic counterparts (Edmeades et al., 1997e). The probability of deriving a hybrid that yielded more than 1.55 t ha^{-1} under mid-season drought was 0.08 for Tuxpeño Sequía C_0 and 0.31 for TS6 C_2. (TS6 C_2 is approximately equivalent to Tuxpeño Sequía C_8). For yields greater than 1.05 t ha^{-1} under drought these probabilities are 0.44 and 0.81 for the same populations. The chances of obtaining a hybrid with a yield 30-50% greater than the mean for all hybrids evaluated under moderate-to-severe drought stress was 3-5 times greater when lines were derived from drought-tolerant sources, compared with conventionally-selected source populations. These data help the breeder judge the appropriate level of investment in developing stress-tolerant source populations within a hybrid breeding program.

Future research for yield stability in environments characterized by mid-season stress

Considerable emphasis has been placed on the use of the trait ASI, based on its consistent and strong association with grain yield under drought. It is, however, important to remember that variation in ASI accounts for only 25-35% of the variation in grain yield under drought. There remains ample scope for the identification of additional secondary traits that explain the residual variance in grain yield. These might include: relatively slow expansion of green leaf area to conserve soil moisture throughout the crop life cycle; reduced growth of organs such as stem, husk, tassel and superficial roots during flowering; a well developed deep but uniformly distributed root system for both water and N uptake, resulting in an extended grain filling period; prolificacy under low planting densities; remobilization of stored reserves in the stem (Blum, 1988; Edmeades et al., 1997b). Others which show theoretical benefits, such as small tassel size (reduces shading and direct competition with the ear for assimilates at flowering), osmotic adjustment, and increased leaf uprightness have shown little association with yield (Bolaños and Edmeades, 1997). The lack of association may be partly due to our use of small single row plots with inadequate bordering when evaluating families, though bordering in single vs. multiple row plots has been discounted as a significant factor influencing cultivar performance under low N (Bänziger et al., 1995).

Models can give the breeder a first estimate of the potential value of additional secondary traits such as those listed here. Models can also play a very useful role in a drought breeding program by matching crop phenology to season length and sowing date.

Drought tolerance and its role in dry environments

Duvick (1995) has proposed that the major goals of tropical maize breeding in the near future should be stabilized yield and broadened adaptation through increased stress tolerance. Results presented here suggest one way of accomplishing this. Gains have averaged about 100 kg ha^{-1} yr^{-1} or about 5% per year. Selection can increase grain yields by about 35% under conditions where drought during the flowering and grain filling period has reduced yields by about two thirds, while yields under well-watered conditions increased at rates similar to those obtained by conventional selection. The value of earliness as an escape mechanism cannot be ignored. In cases where rainfall intensity and duration are highly variable it may be appropriate to grow a mixture of an early-maturing cultivar with one which is later-maturing but drought-tolerant (Edmeades et al., 1997a). In the event of severe drought the early component escapes the drought; under moderate stress, the drought-tolerant component provides a stable and increased yield. Should the rains be plentiful, the later-maturing component can exploit these through its higher yield potential.

On a note of caution, it should be recalled that even though genetic gains in tolerance reported here are important, they may only raise yields under drought from 2 t ha^{-1} to 2.7 t ha^{-1}. Careful crop management practices will in all likelihood add at least as much or more yield, as is the case for low N environments (Waddington and Heisey, 1997). The remainder of the gap between droughted and well-watered yield (often a further 2 - 5 t ha^{-1} of grain) can only come from additional water applied to the crop.

Summary

- Drought destabilizes maize grain production in the tropics. It can be especially serious when it coincides with establishment, flowering or grain filling. A reduction in drought susceptibility increases production and economic stability of rural economies, and should therefore reduce the level of chronic food deficits in drought-prone production areas.
- The interval between anthesis and silking (ASI) is a sensitive and heritable indicator of partitioning to the growing ear at flowering. A long ASI is generally equated with drought susceptibility, and low harvest index, slow ear growth and barrenness under drought. A short ASI is associated with fewer but larger florets that grow more rapidly at anthesis and which are therefore more tolerant of reductions in photosynthesis caused by drought or other stresses. Differences in ASI reflect partitioning differences to the ear rather than variability in plant water status.
- Gains in grain yield under mid-season drought from recurrent selection have averaged about 100 kg ha^{-1} yr^{-1} or about 5% per year. They have been due to reduced barrenness, increased kernels per ear and an increased harvest index (i.e., the establishment of a bigger sink). Gains have been associated with a sharply reduced ASI, small improvements in staygreen and radiation use efficiency, some reduction in root length density of superficial roots, but not with changes in plant water status. Gains in yield were also observed under well-watered conditions, so there is no yield penalty associated with improvements in tolerance to drought at flowering. Selection for improved drought tolerance has also resulted in similar improvements in performance under low N, and increased tolerance to shading.
- Water deficits, whose timing and intensity are controlled by managed applications of irrigation water in an otherwise rain-free environment, provide a reliable and efficient means of displaying genetic variation for ASI and barrenness, provided the stress is severe enough to reduce yields to 20% of unstressed controls or less. At this stress level barrenness and ASI serve as suitable surrogates for grain yield, since heritability of grain yield is relatively low. About 80% of the selection gains made under this selection system are transferable to a normal rainfed environment. Care must be exercised to avoid selecting early-flowering escapes.
- National programs should concentrate on identifying stress-tolerant alleles which exist at a low but significant frequency in most elite adapted populations, and increasing their frequency through selection, rather than searching for tolerance in unimproved local cultivars. Source populations carrying drought tolerance from diverse backgrounds are available from CIMMYT.
- The minimum dataset when selecting for drought tolerance comprises days to anthesis, ears per plant and shelled grain yield. As resources permit, add ASI and leaf senescence.

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Selección de Líneas de Maíz Tolerantes al Calor y la Sequía para Híbridos Adaptados al Verano Árido y Caliente de los Valles Irrigados del Noroeste de México

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Abstract

Planting maize in the summer-fall cycle in northwest Mexico represents a profitable option, permitting a rotation with wheat and the possibility of producing 10-14 t/ha of grain per year on some 250,000 ha of irrigated land. The environmental conditions in northwest Mexico (with summer temperatures above 35ºC) require maize hybrids and synthetics tolerant to extreme heat and drought. The Yaqui Valley possesses the ideal conditions – especially in the spring-summer and summer-fall periods — to evaluate and select parents adapted to such environments. Parent lines were developed by growing out materials in two adjacent nurseries, one with normal and the other with limited irrigation (the latter simulating drought conditions). The following methods were used to identify the parents: 1) progenies with differing levels of inbreeding, as those with full vigor did not express the differences which could be observed in the self-pollinated progenies; 2) simple visual ranking scales to classify the progenies' response to firing and leaf rolling; 3) measurement of the number of plants of each progeny which produced silks before and after irrigation in the drought trial; 4) selection under drought of progenies with erect leaves and without firing or leaf rolling; 5) selection of progenies with reduced anthesis-silking intervals; and 6) advancement of the selected progenies to the next level of inbreeding and selection for other desirable traits, in particular resistance to pathogens in the normal irrigated nursery (especially in the fall-winter cycle). Finally, various lines in this selection process were used to produce synthetics and hybrids H-430, H-431 and PNS-4019, which permit profitable maize production in northwest Mexico. Two of these synthetics formed part of the CIMMYT population DPT1.

En muchas regiones del mundo ya sea en condiciones de precipitación natural (temporal) o bajo riego, el cultivo del maíz puede ser afectado en cualquier etapa de su desarrollo por temperaturas elevadas y tensión hídrica concomitante. Especialmente en temporal, estas circunstancias contribuyen a un elevado porcentaje de siniestros. Es por esto, que para muchos programas nacionales e internacionales ha sido y es prioritaria la obtención de plasma germinal que prospere con éxito relativo en tales condiciones.

En el noroeste de México, el cultivo de maíz bajo riego puede ser una opción rentable en alguna o en varias de las cuatro estaciones del año. Por esto, es indispensable que los híbridos de maíz posean tolerancia al calor excesivo y al estrés hídrico que provocan las altas temperaturas de los ciclos invierno-primavera, primavera-verano, y especialmente verano-otoño. La obtención de híbridos de maíz para el ciclo verano-otoño reviste especial importancia porque constituye junto con el cultivo de sorgo las únicas opciones rentables para esta época del año, ya que el cultivo de soya y ajonjolí se ha abandonado por su vulnerabilidad al insecto *Bemisia argentifolii*, (mosquita blanca) lo que deja disponibles 250,000 ha de riego dependiente de la disponibilidad de agua en las presas. Además, esta opción tiene la gran ventaja de permitir la rotación con trigo, para una producción total de granos de 10 a 14 t anuales, de las que aproximadamente la mitad corresponde a cada cultivo. Finalmente, es factible la secuencia maíz de verano-otoño y trigo de invierno-primavera, como lo han demostrado algunos productores innovadores, mediante esquemas de labranza reducida y de conservación de millones de toneladas de rastrojo, evitando la quema y contribuyendo a una agricultura sustentable con mejor equilibrio ecológico.

El noroeste de México tiene climas que van desde los secos (BW), cálidos o semicálidos (h’)hs(x’), hasta los semicálidos subhúmedos (Aw’(w)). El Valle del Yaqui en el sur de Sonora, sede del proyecto de maíz del noroeste, se caracteriza por tener temperaturas máximas de abril a octubre que fluctúan alrededor de los 40ºC, precipitación anual de 270 mm, acumulada entre julio y octubre; evaporación potencial anual de 2 m; baja humedad relativa entre abril y julio y vientos secos y cálidos desde mediados de marzo hasta mediados de junio (Cuadro 1). De vez en cuando esta región se ve afectada por los ciclones que pueden presentarse entre agosto y octubre.

Materiales y Métodos

Entre la primavera de 1983 y el otoño de 1986 se condujeron trabajos de evaluación y selección, siguiendo el esquema riego-sequía, de progenies de las poblaciones Tuxpeño 1, Mezcla Tropical Blanca, ETO Blanco, Blanco Dentado 2 y Pool 24, obtenidas del CIMMYT.

El procedimiento utilizado consistió en preparar viveros contiguos de las líneas con riego normal y bajo estrés de sequía, en suelo de textura arcillosa. La siembra se hizo en suelo seco, depositando dos semillas cada 20 cm, en surcos de 5 m de largo por progenie y separados a 75 cm, para una densidad de unas 66,000 plantas por ha. Antes del primer cultivo se raleó a una planta por sitio, quedando 26 plantas por surco. Se fertilizó antes de la siembra con la fórmula N-P-K 150-50-00. Después de la siembra se regaron los viveros (riego de germinación) en la misma fecha. El vivero de riego normal recibió además del riego de germinación cinco riegos de auxilio para una lámina total de 65 cm. El vivero de sequía después del riego de germinación, no recibió agua hasta que las líneas en el vivero de riego normal iniciaron la floración masculina. Más o menos tres semanas después de la siembra se labró el suelo para eliminar las arvenses y sellar las grietas del suelo, propiciar la conservación del agua y que el estrés hídrico fuera más gradual.

Las líneas que mostraron tolerancia al estrés de calor y sequía, en lo posible se avanzaron en el vivero de riego de Sn a Sn+1. Cuando no se tuvo éxito por interferencia de plagas o porque aún en riego normal se foguearon las espigas, o no hubo producción de estigmas, se recurrió a semilla remanente para continuar la evaluación y selección en el siguiente ciclo, aprovechándose para incorporar nuevas líneas.

Cuadro 1. Parámetros climatológicos del Valle del Yaqui (Periodo 1944-1990)

	Temperatura								Hum.		Largo
	Máxima		Mínima		Precipitación			Evap.	Rel.	Rad.	Dias en
	Maxi.*	Media	Media	Mini.**	Media	mm	Dias	mm	%	***	Horas
Enero	34.0	24.1	6.8	-5.5	15.4	19.7	2.4	76.4	72	305	11.5
Febrero	37.0	25.8	7.1	-4.0	16.4	8.7	1.4	93.1	69	404	12.1
Marzo	40.0	28.1	8.3	2.0	18.2	4.0	0.9	137.5	66	504	12.6
Abril	43.0	31.6	10.8	-2.0	21.2	2.1	0.4	193.4	57	581	13.7
Mayo	46.0	33.8	14.1	4.0	24.0	0.6	0.3	247.0	51	—	14.4
Junio	46.0	35.8	22.6	7.6	30.0	3.3	0.9	267.6	57	—	14.7
Julio	44.0	36.0	24.1	15.0	30.1	58.2	5.8	231.8	59	—	14.5
Agosto	48.0	36.0	24.0	15.0	30.0	74.5	6.0	210.2	72	—	13.8
Septiembre	46.0	36.0	22.9	8.4	29.4	45.1	3.4	184.6	72	—	13.1
Octubre	46.0	34.0	17.8	2.0	25.9	28.5	1.6	164.0	64	—	12.2
Noviembre	41.0	29.9	11.0	-1.0	20.5	10.1	1.2	117.5	61	345	11.6
Diciembre	36.0	25.4	8.0	-4.0	16.7	21.1	2.2	81.3	68	285	11.3
Total Anual	42.2	31.4	14.8	-5.5	23.0	269.9	26.1	200.3	64		13.0

* Máxima, Maximorum

** Mínima, Minimorum

*** Radiación solar en calorias por m^2 por día

Para evaluar la respuesta de las progenies al fogueo y al enrollamiento de las hojas, se utilizó una escala de apreciación visual que va del 1 al 9. La calificación de 9 se otorgaba a aquellas progenies que no mostraban síntomas de enrollamiento o fogueo hasta la calificación de uno para aquellas con enrollamiento o fogueo severo (Cuadro 2).

Otro parámetro utilizado en el vivero de sequía fue la emisión de estigmas, el cual fue cuantificado para cada línea considerando: a) los emitidos antes del riego; b) los emitidos después del riego; y c) las plantas que no emitieron estigmas o plantas horras. La suma de las tres cantidades fue el total de plantas por progenie.

Se detectó una reducción notable en la altura de planta y mazorca en el vivero de sequía al comparar lo registrado en ambos viveros. Aunque esas reducciones no fueron parámetros utilizados, las diferencias observadas entre líneas y entre poblaciones al ser sometidas al estrés hídrico y térmico, indican una respuesta que pudiera tener algún valor en la selección.

Finalmente en el ciclo otoño-invierno se clasificaron de acuerdo al ángulo foliar las progenies provenientes de las diferentes poblaciones en progenies con hojas erectas y en progenies con hojas laxas. Estas clases se subdividieron en semi-erectas o semi-laxas y de cada uno se separaron las hojas anchas o angostas.

Resultados y Discusión

Enrollamiento foliar en relación con la producción de estigmas

En el ciclo primavera-verano de 1985, la siembra se realizó el 25 de abril y se evaluaron 845 progenies provenientes de las poblaciones Blanco Dentado 2 (Pob.49), Mezcla Tropical Blanca (Pob. 22), La Posta (Pob. 43), Tuxpeño 1 (Pob.21) y Pool 24. En promedio, cada una de estas progenies quedó representada por 16-17 plantas.

En el otoño-invierno de 1986, la siembra se realizó el 5 de septiembre y se evaluaron 764 progenies derivadas de las poblaciones Blanco Cristalino Precoz (Pob. 30), Blanco Dentado 2 (Pob.49), Tuxpeño 1 (Pob.21), ETO Blanco (Pob.32) y Mezcla Tropical Blanca (Pob.22). En esta evaluación, cada progenie quedó representada en promedio por 18 a 21 plantas.

Para analizar la respuesta a la sequía se calcularon los porcentajes en cada nivel de enrollamiento foliar de las plantas con y sin estigmas, antes y después del riego y de las que no produjeron estigmas.

En ambos ciclos en los que se ilustra el proceso descrito, se apreció una clara tendencia en el vivero de sequía a incrementar gradualmente el número de plantas que produjeron estigmas antes del riego y un descenso gradual de las plantas que no los produjeron, a medida que la intensidad de enrollamiento foliar disminuía (Cuadros 3 y 4). Este comportamiento parece indicar que la selección contra el enrollamiento foliar propicia la obtención de progenies que son capaces de producir estigmas en condiciones de estrés severo. Si esta hipótesis se confirma sería de gran valor en la selección de progenies tolerantes al calor y a la tensión hídrica. Sin embargo, Troyer (1983) reconoció la posibilidad de mayor tolerancia al calor de los genotipos que se enrollan.

Fogueo foliar en relación con la producción de estigmas

Para analizar la respuesta a las temperaturas superiores a los 35ºC, pero inferiores a las máximas del ciclo primavera-verano, en el ciclo otoño-invierno de 1985-86 de las progenies de cinco poblaciones

Cuadro 2. Escala visual de apreciación para evaluar el enrollamiento y fogueo foliar en maíz

Escala		
CIANO	CIMMYT	Aspectos de las hojas (enrollamiento)
8-9	1	Sin enrollamiento u hojas superiores ligeramente enrolladas
6-7	2	Cuarto superior de las plantas con hojas enrolladas
4-5	3	Mitad superior de las plantas con hojas enrolladas
2-3	4	Los tres cuartos superiores de las plantas con hojas enrolladas
1	5	Todas las hojas completamente enrolladas
		Aspectos de las hojas (fogueo)
8-9	1	Sin fogueo o las dos hojas superiores ligeramente dañadas
6-7	2	Una o dos hojas superiores dañadas
4-5	3	Tres a cuatro hojas superiores dañadas
2-3	4	Cinco a seis hojas supriores dañadas
1	5	La mayoría de las hojas dañadas

(Pobs.: 21, 22, 30, 32 y 49) se evaluó el fogueo foliar antes de la iniciación de la floración. Se observó que aparentemente el fogueo foliar tiene poca influencia en la emisión de estigmas antes del riego (Cuadro 5). Sin embargo, después del riego se observó un incremento gradual de las plantas con producción de estigmas y una disminución de las que no produjeron, a medida que disminuyó la intensidad del daño por fogueo foliar, debido a las caída de la temperaturas máximas a fines de octubre y principios de noviembre. Por otro lado, en el ciclo de primavera-verano, la floración ocurre en junio o julio; la desecación es mucho más intensa y la producción de estigmas menos abundante.

Enrollamiento foliar en relación con el ángulo de las hojas

En el ciclo primavera-verano de 1985, se clasificaron 675 progenies de cinco poblaciones, de acuerdo con la posición de las hojas respecto al tallo, en progenies con hojas erectas o con hojas laxas, para cada nivel de enrollamiento foliar (Cuadro 6).

Cuadro 3. Enrollamiento foliar en relación con la producción de estigmas, en el vivero de sequía, en la Población 49, Blanco Dentado-2 (S4 y S5) en la primavera-verano, 1985; y en la Población 22, Mezcla Tropical Blanca (S2-S5) en el otoño-invierno 1985-86. Valle del Yaqui, Sonora, México

Parámetro	Intensidad de enrollamiento foliar (1-9)*					
	5	6	7	8	9	Totales
			Población 49, Blanco Dentado-2			
Número de familias	39	107	66	12	——	224
Número de plantas	713	1831	1127	215	——	3886
Plantas con estigmas antes riego (%)	143 (20)	582 (32)	356 (31)	108 (50)	——	1189 (31)
Plantas con estigmas después riego (%)	399 (56)	903 (49)	842 (43)	78 (36)	——	1862 (48)
Plantas sin estigmas (%)	171 (24)	346 (19)	289 (26)	29 (14)	——	835 (21)
			Población 22, Mezcla Tropical Blanca			
Número de familias	13	47	49	70	38	217
Número de plantas	291	1060	1064	1487	768	4670
Plantas con estigmas antes riego (%)	90 (31)	360 (34)	394 (37)	625 (42)	307 (40)	1776 (38)
Plantas con estigmas después riego (%)	61 (21)	233 (21)	245 (23)	297 (20)	177 (23)	1003 (21)
Plantas sin estigmas (%)	140 (48)	477 (45)	425 (40)	565 (38)	284 (37)	1891 (41)
IAE (sequia) días**	13	14	8	9	6	

1= Máximo enrollamiento, 9= Sin enrollamiento

** IAE= Intervalo Antesis-Estigmas

Cuadro 4. Porcentaje de plantas con estigmas en relación con el enrollamiento foliar, en el vivero de sequía, en la primavera-verano de 1985, y en el otoño invierno de 1985-86 Valle del Yaqui, Sonora, México.

Parámetro	Intensidad de enrollamiento foliar (1-9)*					
	4	5	6	7	8	9
			Primavera-Verano de 1985**			
Antes del riego	-	10	12	19	30	-
Después del riego	-	49	59	56	51	-
No produjeron estigmas	-	41	29	25	19	-
			Otoño-Invierno 1985-86***			
Antes del riego	24	47	46	54	60	67
Después del riego	18	19	19	18	14	10
No produjeron estigmas	58	34	35	28	26	23

* 1= Máximo enrollamiento, 9= Sin enrollamiento

** Información consolidada de las poblaciones, Blanco Cristalino Precoz, Blanco Dentado-2, Tuxpeño 1, ETO Blanco y Mezcla Tropical Blanca

*** Información consolidada de las poblaciones, Blanco Dentado-2, Mezcla Tropical Blanca, La Posta, Tuxpeño 1, y Pool 24.

Cuadro 5. Porcentaje de plantas con estigmas en relación con la intensidad de fogueo foliar en el vivero de sequía, Valle del Yaqui, Sonora, México. Otoño-Invierno 1985-86

Parámetro	Intensidad de fogueo foliar (1-9)*						
	4	5	6	7	8	9	Media
Antes del riego	48	43	47	48	48	56	49
Después del riego	10	14	17	15	18	18	15
No produjeron estigmas	42	43	36	37	34	26	36

* 1 = Máximo fogueo, 9 = Sin fogueo

Con excepción de ETO Blanco en las otras cuatro poblaciones se registró un gran número de progenies con hojas erectas en cualquier nivel de enrollamiento y un predominio de éstas a medida que la intensidad del enrollamiento descendió. Esta tendencia fue particularmente notoria en Pool 24 y Tuxpeño 1. Al respecto, Troyer (1983) ha recomendado la selección de plantas con hojas erectas propensas al enrollamiento, en nuestro caso se ha dado preferencia a las que no se enrollan, considerando que estas permanecen activas a pesar del estrés. Debe aclararse que dentro de cada tipo se consideraron las subdivisiones que toman en cuenta el ancho de las hojas, por ejemplo, erecta-ancha, erecta-angosta, semi-erecta ancha o angosta y los tipos intermedios.

Enrollamiento foliar en relación con los días de intervalo entre la antesis y la emisión de estigmas (IAE)

En el ciclo otoño-invierno de 1985-86 se evaluó, tanto en riego como sequía, el intervalo entre la antesis y la emisión de estigmas cuando se registró 50% de floración masculina y femenina en las cinco poblaciones ya citadas (Cuadro 7). El intervalo promedio en el vivero de sequía fue de 10 días en enrollamiento intenso, bajó a siete días en los niveles intermedios de enrollamiento y descendió a cinco días en las progenies que no sufrieron enrollamiento.

En el vivero de riego normal el IAE promedio fue de dos días en cuatro de ellas y de cuatro en Tuxpeño 1. Esta tendencia fue mas evidente en las poblaciones ETO Blanco, Blanco Dentado 2 y Mezcla Tropical Blanca. Aunque las diferencias no son notables, si sugieren un intervalo menor para las progenies que no se enrollan. El valor de la sincronización floral como indicador de tolerancia al déficit hídrico ha sido ampliamente documentado por Bolaños y Edmeades (1989) y Edmeades et al. (1992).

Enrollamiento foliar en relación con el fogueo foliar

En cuatro de las cinco poblaciones evaluadas en el ciclo otoño-invierno de 1985-86 se procuró relacionar la intensidad del fogueo con la intensidad del enrollamiento. Como ejemplo se presenta en el Cuadro 8 la información sobre la población Mezcla Tropical Blanca. La información, permite señalar que la selección simultánea contra fogueo y

Cuadro 6. Porcentaje de plantas con hojas erectas (E) y laxas (L) en relación con la intensidad del enrollamiento foliar en el vivero de sequía. Valle del Yaqui, Sonora, México. Primavera-verano de 1985.

	Intensidad de enrollamiento foliar (1-9)*										Número total de familias	
	5		6		7		8		Total			
Población	E	L	E	L	E	L	E	L	E	L	E	L
Pool 24	0	0	17	0	53	4	26	0	96	4	51	2
Tuxpeño-1	5	3	37	5	39	6	4	1	85	15	141	25
Mezcla Tropical Blanca	6	3	28	14	17	14	12	6	63	37	103	58
Blanco Dentado-2	7	11	30	18	16	13	4	1	57	43	127	97
ETO Blanco	12	14	17	26	14	20	0	7	43	57	31	40
Media	6	4	26	13	28	11	9	3	67	33	453	222

* 1= Máximo enrollamiento, 9= Sin enrollamiento

Cuadro 7. Intervalo (días) entre la antesis y la emisión de estigmas (IAE) en relación con el enrollamiento foliar, en el vivero de sequía. Valle del Yaqui, Sonora, México. Otoño-invierno 1985-86.

	Intensidad de enrollamiento foliar (1-9)*						IAE en riego
Población	4	5	6	7	8	9	
Blanco Cristalino Precoz	10	8	7	7	11	5	2
ETO Blanco	10	9	10	8	7	4	2
Blanco Dentado-2	-	5	5	4	3	2	2
Tuxpeño-1	-	-	-	9	6	7	4
Mezcla Tropical Blanca	-	13	14	8	9	6	2
Media	10	9	9	7	7	5	

* 1= Máximo enrollamiento, 9= Sin enrollamiento

Cuadro 8. Población 22, Mezcla Tropical Blanca, número de progenies en cada nivel de fogueo foliar, en relación al enrollamiento foliar en el vivero de sequía. Valle del Yaqui, Sonora, México. Otoño-Invierno, 1985-86.

Enrollamiento	Intensidad de fogueo foliar (1-9)*							
(1-9)*	3	4	5	6	7	8	9	Total
5	0	1	2	1	1	5	4	14
6	1	2	4	4	14	14	7	46
7	0	1	4	8	10	12	13	48
8	0	1	0	4	13	19	28	65
9	0	0	0	2	7	12	17	38
Total	1	5	10	19	45	62	69	211

* 1= Máximo fogueo, 9= Sin fogueo

enrollamiento aumentó en forma apreciable la frecuencia de progenies que toleran el calor y el déficit hídrico en las poblaciones 21, 22, 32 y 49.

Utilización de los productos derivados del proceso de selección

Las líneas T-39, T-40 y T-43, obtenidas por el proceso descrito han sido liberadas para su uso comercial en la producción de los híbridos H-430, H-431 y PNS-4019 (Cota et al., 1991; Ortega et al., 1993). Estas líneas también han sido adquiridas por varias empresas privadas. Las líneas T-39 y T-40 tienen hojas erectas y anchas, no se foguean ni se enrollan, aunque la espiga es susceptible al calor intenso del verano. El intervalo entre la antesis y la emisión de estigmas fue de tres días para la T-39 y uno para la T-40 y T-43. La T-43 tiene hojas semierectas y anchas y color verde pálido que es común en las líneas tolerantes al calor intenso. Las tres líneas son altamente resistentes al achaparramiento (micoplasmosis o espiroplasmosis del maíz). Las líneas T-39 y T-40 son susceptibles a la roya *Puccinia polysora* y la T-43 es resistente. La T-43 muestra mejor calidad de tallo que las otras dos.

Estos tres híbridos se ubican entre las opciones más rentables para el ciclo verano-otoño del noroeste de México cuyas temperaturas frecuentemente rebasan los 40ºC y provocan el déficit hídrico concomitante. El potencial del H-431, el híbrido mas sobresaliente para verano ha fluctuado de 4 a cerca de 6 t/ha de grano al 14% de humedad, en los veranos de 1992, 1993, 1995 y 1996 (Cuadro 9).

Existen otras líneas que aún no son comerciales, que tienen buen comportamiento bajo estrés (Y-90B80702, Y-90B84510, Y-902114, Y-902329, Y-902921, Y-904408 y Y-90B84704) y han sido evaluados recientemente en el CIMMYT (Edmeades, 1995, comunicación personal); varias de estas líneas han mostrado buena aptitud combinatoria con T-39 y el área de fisiología del CIMMYT ha incorporado a la población DTP-1, los sintéticos Obregón-Sequia 8322 y Obregón Sequía 8332 y el producto de su cruza así como el H-430 a la población DTP-2.

Cuadro 9. Rendimiento de grano al 14% de humedad de híbridos comerciales de maíz, en el ciclo muy cálido del verano-otoño del Valle del Yaqui, Sonora, México.

Ensayo II-1-3 de 1992			Ensayo DEVT-93 CIMMYT		Ensayo I.5.6 de 1996		Validaciones con agricultores			
	t/ha Grano 14% humedad		Híbrido	t/ha Grano 14% Humedad	Híbrido	t/ha Grano 14% Humedad	Híbrido	t/ha Grano 14% Humedad		
	*	**						1/	2/	3/
H-431(CSM-8810)	5.3	5.3	H-422	5.0	H-431	5.6	H-431	5.7	5.4	5.1
CM-82	4.9	4.8	H-430	4.3	C-385	5.2	PNS-4019	5.4	5.8	4.7
CM-Pacifico	4.7	5.5	H-431	4.2	A-7597	4.9	CM-82	5.1	5.5	5.0
H-430	4.5	4.9	La Posta Seq.C_3	3.5	C-343	4.7	NK-7201	4.7	—	—
CM-12	44	5.0	Pool 26-Seq.C_3	2.9	A-7420	4.6	NK-5170	4.6	—	4.4
B-810	3.9	3.6	TS6C_1	3.1	SEMESA 101	4.3	C-343	4.5	—	—
H-422	3.9	3.5	Across 89 DTP-1	2.5	C-220	4.1	H-430	4.5	—	2.7
B-555	3.3	3.3	Harare 89 DTP-1	2.5	TB-7201	4.1	C-385	4.4	5.4	—
P-3298	3.1	2.7	Gol. Val. 89 DTP-1	3.3	C-620	2.9	CM-Huracan	4.2	—	4.4
P-3292	2.9	3.0	Delhi 89 DTP-1	2.3	P-3020	2.5	A-7530	—	—	4.2
P-507	2.9	2.4	Tak-Fa(1)89 DTP-1	2.9	CM-Huracan	2.2	A-775	—	—	3.5
DMS-5%	0.7	1.0	DMS-5%	0.9	DMS-5%	1.2	H-422	—	4.2	3.0
C.V. (%)	11.0	14.0	C.V. (%)	19.0	C.V. (%)	21.0	CM-Tormenta	—	5.7	—

Fuente: Reporte técnico, proyecto maíz, primavera-verano 1992, pag. 53 y 57 CEVY-CIRNO-INIFAP.
Fecha de siembra: 01* Y 30** junio 1992
Riegos: 5, en ambos ensayos
estrés hídrico en prefloración, bajo

Fuente: CIMMYT, Maize drought Tolerance Network, 1995 report, pag.69
Fecha de siembra: 21-04-93
Fecha de cosecha: 05-08-93
Riegos: 4, estrés hídrico Intermedio en prefloración

Fuente: Reporte técnico,proyecto maize. verano-otoño 1996.CEVY CEVY-INIFAP.
Fecha de siembra: 28-06-96
Fecha de cosecha: 28-10-96
Riegos: 2, mas 376 milimetros de lluvia, estrés hídrico leve en prefloración.

Fuentes: [1] UCAY-FIRA.Club de productores
[2] USPRUS-FIRA.Club de productores
[3] UCESS-FIRA.Club de productores
Siembras: Junio: COSECHAS: octubre
[1] Agricultor: C.Valenzuela Obregón(1995)
[2] Agricultor: M.A. Ayala (1996)
[3] Agricultor: G.Alvaréz (1996)

La información que se ha reunido permite hacer las siguientes consideraciones:

1. El esquema de viveros gemelos contiguos uno en riego y el otro en sequía, en un terreno bien nivelado, con un control esmerado de los riegos, de las arvenses, etc., favorece la selección de genotipos tolerantes al calor y tensión hídrica asociada con las temperaturas altas.
2. Es muy conveniente en ambos viveros agrupar las progenies en sublotes de acuerdo con su precocidad, para dar el o los riegos en las etapas de desarrollo equivalentes.
3. Las técnicas simples y empíricas de apreciación visual de las respuestas de las plantas a condiciones de estrés son confiables en tiempo y espacio.
4. Las progenies con hojas erectas y que produjeron más estigmas, fueron las menos propensas a enrollarse.
5. La intensidad del fogueo foliar (de 1 a 4 hojas dañadas) no pareció influir, en la emisión de estigmas.
6. El intervalo entre la antesis y la emisión de estigmas tendió a ser menor en las progenies menos propensas a enrollarse.
7. La selección simultánea contra fogueo y enrollamiento aumentó apreciablemente la frecuencia de progenies tolerantes al calor y a déficit hídrico asociado a las altas temperaturas.
8. El ambiente árido y cálido también permite seleccionar contra la mala cobertura de la mazorca, contra el fogueo de la panoja e indirectamente contra la inviabilidad del polen.
9. Por último, para el Noroeste de México, las líneas tolerante al estrés térmico-e hídrico elevado, también deben poseer mejor calidad de tallo y resistencia a varios patógenos (*Micoplasmas*, *Puccinia polysora*, *Alternaria* sp. *Curvularia* sp., *Fusarium*).

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Selección Familiar de Maíces Criollos del Valle de Puebla

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Abstract

To develop a genetic basis for an in situ *maize improvement program, a project was started to select families of half-sibs among landrace varieties in the Puebla valley. In 1992, 136 maize varieties were evaluated; outstanding ones were selected within three early maturity classes. From these outstanding collections, families of half-sibs were derived and evaluated in 1993 at six locations in the Puebla valley. In specific environments, some families equalled or even surpassed the yield of the best check in each earliness class. We concluded that there is high yield potential and great genetic diversity in maize varieties of the Puebla valley which can be used, if improvement is targeted to the conditions where each genotype can express its maximum potential.*

Introducción

En el área del Plan Puebla el cultivo del maíz ocupa 68% de la superficie cultivada, principalmente en condiciones de temporal y/o humedad residual (Plan Puebla, 1992). Estas condiciones implican riesgos en la producción agrícola, por lo errático de la cantidad y distribución de las lluvias, la ocurrencia de heladas tempranas y/o tardías y la incidencia de plagas y enfermedades, entre otros.

En el mejoramiento genético de las especies vegetales se distinguen dos métodos principales, que suelen ser complementarios: la selección y la hibridación. En la selección se aprovechan los efectos genéticos aditivos y consiste en la identificación de los mejores individuos de una población y su utilización como progenitores de la siguiente generación, proceso que se repite durante varios ciclos (Márquez, 1985). Para que una variedad responda satisfactoriamente a las condiciones del ambiente para el cual se recomienda, es preciso desarrollar su mejoramiento *in situ*, bajo las mismas condiciones ambientales y de manejo de los agricultores y con la herramienta matemática más apropiada (Muñoz y Rodríguez, 1988). De acuerdo con la teoría del fitomejoramiento por nichos ecológicos (Muñoz, 1988), un programa se inicia con una exploración etnofitogenética para valorar la diversidad del germoplasma local de las especies de mayor importancia antropocéntrica en la región; continúa con la evaluación de las colecciones obtenidas y de los genotipos introducidos por lo menos en dos ambientes y dos años, después de lo cual es posible identificar el patrón varietal, con la selección y recombinación de los genotipos sobresalientes. En este contexto, se concibe al fitomejoramiento como un proceso dinámico de aplicar los métodos genotécnicos adecuados a las condiciones y necesidades de una región o de un nicho ecológico para explotar el potencial de los cultivares tradicionales y mejorados; así, apoyado en una amplia fuente de germoplasma, con este enfoque se busca el aprovechamiento óptimo y la conservación de los recursos. Con base en la información antes presentada, en este estudio se tuvo como objetivo principal definir el patrón varietal del maíz en el valle de Puebla, para iniciar un proceso de selección de las variedades locales que permita estructurar una base genética para un programa de mejoramiento *in situ*.

Materiales y Métodos

En 1992 se evaluaron 136 variantes de maíz, obtenidas en las Muestras Regionales de Semillas Criollas organizadas por el Campus Puebla del Colegio de Postgraduados. Esta evaluación se realizó en tres localidades del valle de Puebla: Capultitlán, Calpan y Ocotitlán, sembrándose el 31 de marzo, 14 abril y 7 de mayo, respectivamente; simultáneamente se derivaron familias de medios hermanos de cada una de las 136 variantes ensayadas. La selección de las mejores variantes se realizó con base en el Modelo I para evaluar resistencia a sequía, propuesto por Muñoz y Rodríguez (1988). En 1993 se evaluaron las familias derivadas de las variantes sobresalientes, dentro de cada estrato de precocidad; así, se probaron a) 78 familias de ciclo tardío, en dos ambientes considerados de alto potencial de rendimiento: Tlaltenango y Capultitlán, con siembras del 14 y 15 de abril, respectivamente; b) 97 familias de ciclo intermedio, en dos localidades cuyo potencial productivo se consideró de nivel medio: Huejotzingo y Calpan, sembrándose los días 20 y 12 de abril, cada uno; c) y 97 familias precoces, en dos localidades con ambiente restrictivo para el cultivo de maíz: Ocotitlán y Nenetzintla, cuyas siembras fueron el 30 de marzo y siete de abril, respectivamente. Las seis localidades se ubican en el valle de Puebla. Los experimentos de 1992 y 1993 se sembraron bajo el sistema de humedad residual, antes del inicio de la temporada de lluvias y el desarrollo del cultivo fue bajo condiciones de temporal. Las variables evaluadas fueron: color del grano, rendimiento de grano, días a floración masculina, días a floración femenina y altura de la planta.

Los diseños experimentales utilizados en los experimentos de 1992 fueron dos latices rectangulares 8 x 9 con tres repeticiones en cada localidad. En los ensayos de las familias, en 1993 se emplearon latices simples 10 x 10 y 9 x 9 con dos repeticiones cada uno. La unidad experimental en los ensayos de 1992 fue de dos surcos de 5 m de largo, en los ensayos de 1993 la unidad experimental fue de un surco de 5 m de largo; en ambas pruebas la densidad de población fue de 45 000 plantas ha^{-1}. La preparación del terreno y el manejo del cultivo fue de acuerdo a como lo acostumbra el agricultor de la región. Se aplicó la fórmula de fertilización 150-60-00 (N-P-K) en todos los experimentos usando como fuente de nitrógeno a la urea y como fuente de fósforo al super fosfato de calcio triple, aplicando una tercera parte del nitrógeno y todo el fósforo a la siembra y el resto del nitrógeno en la segunda labor.

Los testigos utilizados en cada grupo de precocidad fueron: en las familias tardías el híbrido HCP-1 (T1), la variedad Blanco San Pedro (T2) y un compuesto formado con las familias evaluadas (SFCT-1); en las familias intermedias los testigos fueron el híbrido HCP-1 (T1), la variedad Blanco San Pedro (T2) y el compuesto formado con las familias evaluadas (SFCI-1); los testigos empleados en las familias precoces fueron el híbrido HCP-3, la variedad Pinto Salvatori y el compuesto formado con las familias (SFCP-1). La comparación de medias se realizó aplicando la prueba de la diferencia mínima significativa (DMS), con un valor de probabilidad de 0.05.

Resultados

Caracterización del patrón varietal
El color blanco de grano predominó entre las variedades ensayadas, seguido por los maíces azules, los pintos y por último, los amarillos y rojos (Cuadro 1). Con base en los días a la floración femenina promedio se identificaron tres niveles de precocidad en el conjunto de variantes, para formar el grupo de precoces con 89 a 95 días a floración, intermedias con 96 a 100 días a floración y tardías con 101 a 105 días a floración. En la muestra estudiada predominaron las variantes intermedias (Cuadro 2). En rendimiento de grano, los maíces precoces fueron los más sobresalientes, seguidos por los intermedios y al último los tardíos. Los maíces blancos aumentaron su frecuencia en los grupos intermedios y tardíos, mientras que los maíces azules fueron más frecuentes en el grupo precoz; por otro lado, los

Cuadro 1. Frecuencia del color de grano en 136 variantes criollas de maíz del valle de Puebla, cultivadas durante 1992.

Color del grano	Frecuencia Absoluta	Relativa
Blanco	104	0.76
Azul	16	0.12
Pinto	8	0.06
Amarillo	4	0.03
Rojo	4	0.03
Total	136	1.00

maíces de color amarillo y rojo sólo estuvieron representados en el grupo precoz.

Evaluación de familias de las variantes sobresalientes

De las familias tardías hubo cuatro que en ambas localidades superaron estadísticamente en rendimiento de grano a los testigos (Cuadro 3), aunque fueron muy similares a ellos en el comportamiento de las otras variables. Con las familias derivadas de las variedades de ciclo intermedio se obtuvieron los más altos rendimientos registrados (Cuadro 4), aunque sólo superaron estadísticamente en rendimiento a uno de los testigos. De las familias precoces, sólo el rendimiento promedio para ambas localidades de una de ellas superó numéricamente al testigo T1, pues las medias de este grupo sólo superaron estadísticamente al peor testigo. En promedio, los rendimientos de este grupo fueron los más bajos de los tres estudiados (Cuadro 5).

Se debe aclarar que en los ambientes de prueba de este grupo de familias, las siembras se realizaron antes que en las otras cuatro localidades, cuando en realidad se suelen sembrar hasta el inicio de las lluvias; por ello, las familias precoces aparecen paradójicamente con floraciones más tardías que las de otros dos estratos de precocidad. Sin embargo, el grupo sí conservó su peculiar menor tamaño de planta. Parece que en la primera evaluación sobresalieron las precoces por que la fecha de siembra sólo fue adecuada para ellas, y las intermedias y tardías estuvieron en desventaja.

Discusión

La mayor frecuencia de cultivares criollos de maíz con grano blanco (Cuadro 1) obedece a la preferencia persistente por este color en toda Mesoamérica, lo cual también ha trascendido a los consumidores urbanos. Pero a la vez, se confirma el patrón de variantes subordinadas con otros colores de grano, posiblemente asociadas a razones de variación del gusto, formas especiales de consumo y prevención de irregularidades climáticas en cada ciclo.

La existencia de un patrón varietal con tres niveles de precocidad deja de manifiesto que los agricultores del valle de Puebla han generado y mantienen una diversidad genética cuyos componentes se ajustan a condiciones imprevisibles o específicas dentro de la amplitud ambiental de este nicho ecológico. Es importante señalar la menor frecuencia de genotipos tardíos (Cuadro 2), respecto a la registrada a principios de los años setenta, cuando representaba 43.4% de las variantes regionales (Cervantes y Mejía, 1984). Aunque estas diferencias pueden deberse al método distinto de integrar las muestras de variantes, es probable que los ambientes que favorecen las siembras tempranas en el valle de Puebla se hayan ido reduciendo, como consecuencia del abatimiento de los mantos friáticos, lo que a su vez ha disminuido la humedad residual en el suelo (López, 1993). En otras regiones del país ya se han identificado patrones varietales con este mismo procedimiento (Legaria et al., 1988; Valadez y Muñoz, 1988;

Cuadro 2. Proporción de los grupos de precocidad y rendimiento de grano (t ha^{-1}) en 136 variantes criollas de maíz del valle de Puebla, cultivada durante 1992.

Precocidad	Abundancia Absoluta	Abundancia Relativa	Rendimiento L1	Rendimiento L2	Rendimiento L3	Promedio
Precoces	45	0.33	5.05	3.50	3.35	4.00
Intermedios	66	0.49	4.91	3.40	3.13	3.81
Tardíos	25	0.18	4.62	3.94	3.00	3.41
Total	136	1.00				

L1: Capultitlán, L2: Calpan, y L3: Ocotitlán

Cuadro 3. Rendimiento de grano (t ha^{-1}) y características de floración y altura de planta de variantes tardías sobresalientes, cultivadas durante 1993.

Variante	Rendimiento Tlaltenango	Rendimiento Capultitlán	Rendimiento Promedio	DFM	DFF	ALP
C-3899-3	7.49a	5.33a	6.41a	101	108	273
C-3951-1	6.38a	6.25a	6.31a	102	108	284
C-2801-4	6.21a	5.10a	5.66a	108	114	251
C-3899-4	6.28a	5.01a	5.65a	96	103	263
T1	4.94b	3.41b	4.17b	96	103	263
T2	4.83b	3.07b	3.95b	104	112	270
T3	3.45b	2.79b	3.12b	111	118	264
Promedio general	5.65	3.42	4.53	105	112	279
C.V. (%)	17.2	31.5	26.1	3.3	3.1	5.3

Valores seguidos por la misma letra en columnas son estadísticamente iguales. Prueba DMS (a=0.05), DFM: Días a floración masculina, DFF: Días a floración femenina, ALP: Altura de planta (cm), C.V.: Coeficiente de variación y T: Testigo.

López et al., 1990), los cuales se han usado para orientar los programas de mejoramiento en tales regiones.

De las dos localidades de evaluación de las familias del grupo tardío, en Tlaltenango se obtuvieron los más altos rendimientos (Cuadro 3), ya que en Capultitlán se presentó un ataque severo de rayado fino y achaparramiento, lo cual redujo con ello el rendimiento en este ambiente y en el promedio. A pesar de ello, existieron familias que superaron estadísticamente a los testigos en ambas localidades.

En el ensayo de las familias intermedias, el mejor ambiente fue Huejotzingo, como quedó claramente manifiesto con las mejores familias; sin embargo, el rendimiento medio de las 97 familias en esta localidad sólo superó con poco al de Calpan (Cuadro 4). Fue en este grupo de precocidad intermedia donde se obtuvieron los más altos rendimientos y la máxima altura de la planta; así, además del rendimiento, la selección de este grupo debe orientarse hacia un menor porte. La precocidad de las familias destacadas (Cuadros 3 y 4) se mantuvo muy próxima a los promedios generales de sus grupos de precocidad respectivos.

Entre las familias precoces, los bajos rendimientos obtenidos en ambas localidades de prueba (Cuadro 5) confirman el bajo potencial productivo de estos ambientes, para los cuales la mejor forma de aprovecharlos es precisamente mediante genotipos precoces. En el Cuadro 5 se aprecia claramente que las familias presentaron rendimiento similar en ambas localidades, mientras que en Nenetzintla, en los testigos sufrieron una reducción drástica. Debido a las fechas de siembra más tempranas que se realizaron en estas localidades, el ciclo vegetativo fue más prolongado; sin embargo, bajo ambientes similares estas familias han mostrado ser más precoces que las familias intermedias y tardías

El rendimiento medio global de las familias de ciclo tardío e intermedio superó al rendimiento medio estimado para el valle de Puebla que, según Cervantes y Girón (1993), fue de 3.67 t ha^{-1}, en 1992, lo cual confirma el alto potencial productivo de estos materiales, y particularmente el de las familias sobresalientes.

De acuerdo a los resultados presentados en este escrito se puede concluir que se confirma la importancia de identificar los componentes del patrón varietal para un cultivo dentro de un nicho ecológico, para conformar así la base genética de un programa de mejoramiento *in situ*. Además, este enfoque permite ubicar a cada componente del patrón varietal dentro de ambientes específicos y orientando el mejoramiento de los genotipos a las condiciones donde cada uno de ellos puede expresar su máximo potencial productivo.

Cuadro 4. Rendimiento de grano (t ha^{-1}) y características de floración y altura de planta de familias intermedias sobresalientes, cultivadas durante 1993.

	Rendimiento					
Variante	Huejotzingo	Calpan	Promedio	DFM	DFF	ALP
C-4083-3	7.78a	6.79a	7.29a	101	105	289
C-2826-5	7.65a	6.45b	7.05a	104	110	305
C-2826-1	7.00a	7.09a	7.03a	103	109	287
CSM(2)-6	7.14a	6.62a	6.88a	95	103	276
C-2826-9	7.20a	6.56a	6.88a	104	110	288
T1	6.66a	5.43b	6.05a	99	104	277
T2	6.28a	5.32b	5.88a	98	108	280
T3	5.01b	4.96b	4.98b	101	106	300
Promedio general	5.66	5.52	5.69	100	107	281
C.V. (%)	16.7	22.3	19.8	1.9	2.2	6.3

Valores seguidos por la misma letra en columnas son estadísticamente iguales. Prueba DMS (a=0.05), DFM: Días a floración masculina, DFF: Días a floración femenina, ALP: Altura de planta (cm), C.V.: Coeficiente de variación y T: Testigo.

Cuadro 5. Rendimiento de grano (t ha^{-1}) y características de floración y altura de planta de familias precoces sobresalientes, desarrolladas durante 1993.

	Rendimiento					
Variante	Ocotitlán	Nenetzintla	Promedio	DFM	DFF	ALP
C-3931-9	4.10a	4.42a	4.26a	105	118	203
T1	5.70a	2.45b	4.08a	109	119	182
C-3902-9	3.62a	4.05a	3.84a	99	109	190
C4064-1	3.98a	3.37b	3.68a	105	119	203
C-3931-10	3.74a	3.46b	3.60a	103	114	183
T3	4.69a	1.64b	3.17a	106	123	200
T2	3.45b	2.04b	2.74b	109	123	185
Promedio general	3.52	2.04	2.78	105	117	190
C.V. (%)	30.8	24.8	34.8	2.6	3.3	9.9

Valores seguidos por la misma letra en columnas son estadísticamente iguales. Prueba DMS (a=0.05), DFM: Días a floración masculina, DFF: Días a floración femenina, ALP: Altura de planta (cm), C.V.: Coeficiente de variación y T: Testigo.

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Resultados y Proyecciones del Mejoramiento de Maíz para Tolerancia a Sequía en Ecuador

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Abstract

In 1994, 170,000 ha of flint maize was planted along the Ecuadorian coast, including the valleys of Loja province where rainfall ranges from 400 to 600 mm during the crop cycle. The effect of scarce and irregular rainfall is increased by soil problems (most plots are on steep slopes), resulting in low yields and in some cases total harvest loss. The region is dominated by smallholder farmers for whom maize is both a tradition and a necessity, thereby making it difficult to replace the crop with other species which might be better suited to the area. It is believed that the use of cultivars with drought tolerance – especially in the critical flowering stage – would help reduce the risk of harvest losses and increase productivity. Since 1988 INIAP has worked to develop maize varieties with drought tolerance during flowering and adapted to Ecuadorian ecologies, drawing on the germplasm and technology generated by the International Maize and Wheat Improvement Center (CIMMYT). S_1 *lines were selected under differing moisture conditions and then recombined, forming the improved cultivars INIAP-540 (derived from the CIMMYT Tuxpeño drought selection C6) and INIAP-542 (derived from CIMMYT Pool 26 drought selection* C_1*). The two cultivars have been commercially released and have shown good performance and production stability in low rainfall areas. Currently, through the recombination of various cultivars selected for drought tolerance by CIMMYT, two basic populations have been formed (white and yellow) that will be used to obtain varieties and hybrids.*

Introducción

En 1994 se sembraron alrededor de 170,000 ha de maíz en las provincias de Manabí y Guayas de la costa ecuatoriana y en los valles de la provincia de Loja de la región interandina o sierra. En estas zonas las lluvias constituyen la única fuente de humedad para el cultivo. De acuerdo con los registros pluviométricos de varias décadas de la provincia de Manabí existe una acentuada disminución de las lluvias (Cuadro 1) y específicamente en el período entre 1983-1994, exceptuando 1983 y 1992 cuando la precipitación fue superior a los 1000 mm por la influencia de la corriente del Niño, las precipitaciones oscilaron entre 294 y 687 mm durante la época lluviosa y su distribución fue heterogénea. El cultivo de maíz es afectado por la escasez e irregularidad de las lluvias en estas zonas y se complica aún más por problemas edáficos, ya que la mayor parte de los cultivos se realiza en terrenos con pendiente. Por ello, la producción promedio de maíz en el período 1983-1994 es de 1.28 t/ha y en algunos lugares la cosecha prácticamente fue nula. En los trópicos bajos generalmente ocurren períodos inpredecibles de sequía dentro de cualquier etapa de desarrollo del cultivo, lo que origina caída del rendimiento, especialmente cuando la sequía se produce durante la floración.

Cuadro 1. Promedios de precipitación en Portoviejo, durante siete décadas.

Décadas	Precipitación (mm)	(%)
1930	634	100
1940	589	93
1950	539	85
1960	488	77
1970	476	75
1980	457	72
1990	453	71

Fuente: Instituto Nacional de Recursos Hidráulicos (INERHI) e Instituto Nacional de Meteorología e Hidrología (INAHMI).

En las áreas maiceras ecuatorianas predominan pequeños agricultores, tradicionalmente cultivadores de maíz, para quienes esta gramínea constituye una necesidad, difícil de reemplazar por otras especies que puedan adaptarse mejor a las condiciones climáticas de estas áreas. Así, el uso de cultivares tolerantes a la sequía, especialmente en la etapa de floración, ayudaría a disminuir el riesgo de pérdida del cultivo e incrementaría su productividad. De acuerdo con esta problemática el INIAP ha realizado investigaciones tendientes a la selección de cultivares de maiz tolerantes a la sequía bajo las condiciones de cultivo en Ecuador, mediante trabajos de mejoramiento genético a partir de los cultivares disponibles en el CIMMYT. Actualmente se han liberado comercial dos cultivares de polinización libre, tolerantes a la sequía: INIAP-540 de grano blanco e INIAP-542 de grano amarillo; además, se cuenta con nuevas poblaciones para la obtención de cultivares e híbridos tolerantes a la sequía en floración.

Trabajos realizados

Las investigaciones para la selección de cultivares tolerantes a la sequía se iniciaron en 1988 en la Estación Experimental Portoviejo del INIAP, localizada en el trópico seco del litoral ecuatoriano a 01º12´de latitud S y 80º23´de longitud O, 47 m de altitud, con 26ºC de temperatura media anual y 400 mm de precipitación media anual.

En la época seca se evaluaron por separado las 190 S_1, del Tuxpeño selección sequía C_6 (Tuxpeño C_6) y 250 S1 del Pool 26 selección sequía C_1 (Pool 26C_1), ambas obtenidas en CIMMYT, además se incluyeron seis testigos. La evaluación se realizó en tres condiciones o niveles de humedad: estrés severo, que consistió de dos riegos de germinación-establecimiento, estrés medio, que consistió en la aplicación de cuatro riegos hasta dos semanas antes de la floración, y sin estrés, por la aplicación de siete riegos durante todo el ciclo. Los riegos se aplicaron por surco con un intervalo de 15 días y una lámina de aproximadamente 60 mm en cada uno de ellos (Palacios, 1992).

Se utilizó el diseño latice simple 14 x 14 para el Tuxpeño C_6 y 16 x 16 para el Pool 26C_1 con una densidad poblacional de 40,000 plantas por ha. Las variables evaluadas en ambos casos fueron intervalo de floración o sincronización (días entre 50% de plantas en antesis y 50% de plantas con estigmas visibles) y rendimiento de grano (kg / ha).

En las líneas S_1 del Tuxpeño C_6 las dos primeras condiciones de humedad no modificaron significativamente el intervalo de floración, aunque existió la tendencia a disminuirlo a medida que se redujo el estrés de humedad. Por otro lado, el rendimiento mostró diferencias altamente significativas con el estrés severo y no se afectó con el estrés medio, aunque aumentó en algunas líneas a medida que se redujo el estrés de humedad. En cuanto a los diferenciales de selección todas las S1 seleccionadas con estrés disminuyeron el intervalo de floración (sincronización) en relación con la población total, en promedio 33.7% con estrés severo y 40% con estrés medio. El rendimiento de las S_1 seleccionadas en las dos condiciones de estrés resultó 60 y 34% mayor en comparación con la población total (Cuadro 2).

En las líneas S_1 del Pool 26C_1 existieron diferencias significativas en el intervalo de floración en ambos niveles de estrés, las líneas seleccionadas presentaron menores valores a medida que disminuyó el estrés de humedad (Cuadro 3). El rendimiento presentó diferencias altamente significativas para ambos niveles de estrés y la producción aumentó con la disminución del estrés (Cuadro 3). En relación con los diferenciales de selección ambos niveles de estrés disminuyeron (37.7 y

Cuadro 2. Diferencial de selección para algunas variables de las líneas S_1 provenientes del Tuxpeño selección sequía C_6. Portoviejo, 1988.

Variables	$\overline{X}$ población total (190 S_1)	$\overline{X}$ 10 líneas S_1 seleccionadas por SELINDEX	Diferencial de selección (%)
Días de intervalo de floración (riego germinación-establecimiento)	8.6N.S.	5.7	-33.7
Días de intervalo de floración (riegos dos semanas antes floración)	8.0N.S.	4.8	-40.0
Rendimiento en kg/ha1382** (riego germinación-establecimiento)	2212	+60.0	
Rendimiento en kg/ha (riegos dos semanas antes de floración)	1449N.S.	1943	+34.0
Rendimiento en kg/ha (riego normal)	2639**	2735	+3.6

* , ** y N.S.: diferencias estadísticamente significativas, altamente significativas y no significativas entre las líneas S1

21.2%) el intervalo de floración respecto a la media poblacional; pero, superaron ampliamente el rendimiento medio poblacional con valores de 67.9 y 24.5% en el estrés severo y medio, respectivamente (Cuadro 3).

Después de la selección de líneas se procedió a su recombinación. Al momento de la cosecha se eligieron las mejores mazorcas de cada cruzamiento y el compuesto balanceado obtenido constituyó alrededor de 1 kg de semilla F2 de cada material. Se efectuó la siembra, cultivo, caracterización y cosecha de cada uno. Los resultados de la caracterización de los nuevos cultivares INIAP-540 e INIAP-542 se detalla en el Cuadro 4. Se demostró que ambos cultivares superaron el rendimiento de los tres comerciales cuando hubo escasa e irregular (350 mm y 571 mm) y abundante (1063 mm) precipitación y cuando se presentó un periodo de sequía durante la floración (Cuadro 5).

Con la finalidad de medir la respuesta de los dos cultivares a una amplia gama de ambientes se realizó el análisis de estabilidad del rendimiento de acuerdo con la metodología de Eberhart y Rusell (1966) incluyéndose los datos de 16 localidades, ocho correspondientes a 1992 y ocho a 1994. Después efectuar el análisis estadístico con base en los parámetros que definen la estabilidad del rendimiento, como son el coeficiente de regresión (b_i) y la desviación de la regresión (S_{2di}), se estableció que el cv. INIAP-540 presentó un coeficiente de regresión de 1.033 y una desviación de la regresión de 0.032 e INIAP-542 1.070 y 0.224, respectivamente. Con lo que se concluyó que los dos cultivares presentan buena estabilidad del rendimiento. Además, de acuerdo con los promedios del rendimiento INIAP-540 e INIAP-542 tuvieron un incremento de 21 y 24%, sobre el testigo INIAP-527, respectivamente (Cuadro 6). En trabajos realizados por la Unidad de Validación y Transferencia de Tecnología (UVTT) de la estación experimental

Cuadro 3. Diferencial de selección para algunas variables de las líneas S_1 provenientes del Pool 26 selección sequía C_1. Portoviejo, 1990.

Variables	$\overline{X}$ población total (250 S_1)	$\overline{X}$ 7 líneas S_1 seleccionadas por SELINDEX	Diferencial de selección (%)
Días de intervalo de floración (riego germinación-establecimiento)	5.84**	3.64*	-37.7
Días de intervalo de floración (riegos dos semanas antes floración)	2.74*	2.16*	-21.2
Rendimiento en kg/ ha (riego germinación-establecimiento)	1406**	2361	+67.9
Rendimiento en kg/ha (riegos de dos semanas antes de floración)	3543**	4412	+24.5
Rendimiento en kg/ha (riego normal)	4547**	5379	+18.2

* , ** y N.S.: diferencias estadísticamente significativas, altamente significativas y no significativas entre las líneas S_1

Cuadro 4. Características de los cultivares mejorados de maíz INIAP-540 de grano blanco e INIAP-542 de grano amarillo tolerantes a la sequía en la época de floración.

Características	Variedad INIAP 540 (Tuxpeño Selección Sequía C_6)	Variedad INIAP-542 (Pool 26 Selección Sequía C_1)
Altura de planta	205 cm	241 cm
Altura de mazorca	112 cm	123 cm
Número de nudos y hojas por planta	13	13
Longitud de la hoja de la mazorca	114 cm	103 cm
Ancho de la hoja de la mazorca	10 cm	10 cm
Longitud de la espiga	60 cm	60 cm
Número de ramificaciones de la espiga	20	18
Floración masculina	50 días	52 días
Floración femenina	52 días	54 días
Ciclo vegetativo	115 días	120 días
Longitud de mazorca	17 cm	21 cm
Diámetro de mazorca	5 cm	5 cm
Color de grano	blanco	amarillo
Textura de grano	ligeramente harinoso	ligeramente harinoso

Cuadro 5. Promedios de rendimientos en kg/ ha de dos cultivares mejorados (INIAP-540 e INIAP-542) y tres comerciales durante 1991, 1992 y 1994 en varias localidades de Manabí.

Variedades	Años			$\overline{X}$
	1991 [1]/	1992 [2]/	1993 [3]/	
INIAP-542	3873	5538	4545	4652
INIAP-540	3844	5296	4553	4564
INIAP-541	3284	5165	4597	4349
INIAP-527	3292	4291	3835	3806
INIAP-526	3306	5263	4401	4323
$\overline{X}$	3520	5111	4386	

[1]/ Promedio de dos localidades. Se registraron 350 mm de precipitación en la E.E .Portoviejo.

[2]/ Promedio de ocho localidades. Se registraron 1063 mm de precipitación en la E.E. Portoviejo.

[3]/ Promedio de ocho localidades. Se registraron 571 mm de precipitación en la E.E .Portoviejo.

Portoviejo en zonas secas de 10 localidades ubicadas en Manabí durante 1993 y 1994, los cultivares INIAP-540 e INIAP-542 superaron en rendimiento a los cultivares del agricultor (Cuadro 7).

Con base en todos estos resultados, los dos cultivares fueron liberadas comercialmente en noviembre de 1994 (INIAP, 1994).

Proyecciones

En 1994 se proyectó el desarrollo de cultivares e híbridos tolerantes a la sequía en la etapa de floración. Previo a la formación de las poblaciones básicas se evaluaron en tres localidades semisecas de Manabí los materiales promisorios, blancos y amarillos, de CIMMYT y se contrastaron con algunas variedades comerciales; los resultados más sobresalientes se presentan en el Cuadro 8. Con base en los resultados se seleccionaron los materiales blancos INIAP-540, Ts6 C2F2, TIWD Tol. sequía Co y Pool 16 sequía C2F2 y los amarillos INIAP-542, Pacific 9205, INIAP 526, Pool 26 selección sequía, INIAP-541 y Pool 18 selección sequía, los cuales fueron recombinados en la época seca de 1994, iniciándose la formación de dos poblaciones básicas, una blanca con 72 mazorcas y otra amarilla con 115 mazorcas. En la época lluviosa de 1995 se sembraron en medios hermanos cada grupo, por separado. A la cosecha se seleccionaron 88 y 132 mazorcas de las poblaciones, respectivamente. En los Cuadros 9 y 10 se presentan las características agronómicas de las 25 mejores familias del primer ciclo de selección de medios hermanos de las poblaciones de grano blanco y amarillo, respectivamente.

Cuadro 6. Rendimiento promedio, coeficiente de regresión (b_i), desviaciones de regresión (S_{2di}) y porcentaje de incremento sobre el testigo de los cultivares INIAP-540 e INIAP-542 en 16 localidades de Manabí.

Cultivares	Rendi-miento (kg/ha)	b_i	S_{2di}	Incremento respecto al testigo (%)
INIAP-542	5042	1.070	0.224	24
INIAP-540	4925	1.033	0.032	21
INIAP-526	4832	1.089	0.009	18
INIAP-527 (T)	4063	0.860	0.053	0

Durante la época seca de 1995 se realizó el segundo ciclo de selección de medios hermanos de ambas poblaciones, blanca y amarilla, y las características agronómicas más sobresalientes de las 25 mejores familias de cada población son presentadas en los Cuadros 11 y 12.

Para el desarrollo de híbridos tolerantes a sequía durante la época lluviosa de 1994 se generaron 76 líneas S$_1$ de la población 1 de ciclo vegetativo intermedio y 68 del Pool 18 selección sequía precoz, con tolerancia a sequía en floración. Estas S$_1$ fueron sembradas en la época seca de 1994 obteniéndose en total 190 S$_2$. Los datos de las principales características agronómicas de las mejores 25 S$_1$ seleccionadas con base en el Selindex de la población 1 y del Pool 18 selección sequía se presentan en los Cuadros 13 y 14, respectivamente.

Cuadro 7. Rendimiento promedios (kg/ha) de tres cultivares de maíz en zonas secas de 10 localidades de Manabí, durante 1993 y 1994, UVTT Portoviejo, 1994.

Localidades	Cultivares		
	Agricultor	INIAP-540	INIAP-542
Los Amarillos	1630	3040	2780
El Junco	2327	2671	2422
Danzarín	2696	2707	2640
San Eloy	2057	2955	2673
El Cardón	2190	4522	4524
Tierra bonita	1069	3491	2798
Las Mercedes	3466	4741	4935
Dos Caminos	2108	4104	4453
Pitahaya	2627	3423	4303
San Eloy	2314	2586	2959
$\bar{X}$	2248	3424	3548

Fuente: Archivos UVTT-E.E. Portoviejo

Prosiguiendo con esta actividad durante la época seca de 1994 se evaluaron las S$_1$ por su tolerancia a la sequía sometiéndolas a un estrés de humedad antes de la floración. Tomando como parámetros las variables días a floración femenina, altura de planta y rendimiento, mediante el Selindex se obtuvieron las mejores S$_1$ de la población 1 y del Pool 18 selección sequía, cuyas características agronómicas más importantes se presentan en los Cuadros 15 y 16, respectivamente.

Durante los dos ciclos de 1995 se continuó con el proceso de selección y mejoramiento genético para el desarrollo de los híbridos y se espera tenerlos en 1998.

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Desarrollo y Mejoramiento de Germoplasma de Maíz con Tolerancia a Sequía para las Zonas Tropicales de América Central

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Abstract

Drought is an adverse abiotic factor that further limits the productivity of maize cultivation in marginal environments of Central America and the Caribbean. Drought problems are aggravated when maize is sown on hillside soils with limited water retention capacity or in environments with scarce or erratic rainfall. In these areas, average yield ranges between 0.3 and 0.5 t/ha. Based on this appraisal, the Regional Maize Program (Programa Regional de Maíz, PRM) for Central America and the Caribbean, in conjunction with CIMMYT, is developing a collaborative project for maize genetic improvement. The purpose of this project is to generate and release improved synthetic varieties adapted to limited rainfall conditions and with agronomic performance superior to that of cultivars sown by farmers in marginal areas. The genetic improvement approach used consists of recurrent selection of S_2 *lines of the population Tuxpeño Sequía* C_6 *(TS6) x BS19TS6. Through recurrent selection, we are attempting to accumulate the frequency of favorable genes that determine the cultivars' adaptation to low rainfall conditions and in turn contribute to yield stability in marginal environments. The* S_2 *lines are generated in Honduras. The superior fraction is recombined and experimental synthetics are formed for evaluation in regional trials in multiple environments. Lines are evaluated in Guatemala, El Salvador and Honduras with varying levels of drought. The superior fraction is selected on the basis of an index which includes yield, prolificacy, and anthesis-silking interval. In 1995, the fourth selection cycle was completed, in which the average yield of the experimental variety surpassed the population average by 2.3 t/ha. The outcome of this collaborative project has been the release of synthetic varieties in various countries in the region. Among them is the synthetic B-107, which has up to a 20% greater grain yield than other improved varieties.*

Introducción

La sequía es uno de los factores que más afectan al cultivo de maíz, específicamente en la región del Océano Pacífico en Guatemala, El Salvador y Honduras. Así, las precipitaciones erráticas y en ciertas ocasiones muy escasas, afectan frecuentemente el sur de Honduras, en donde se han registrado precipitaciones de 175 mm en un mismo día y la ausencia de lluvias a lo largo de 45 días, durante el cultivo. Debido a la sequía durante 1994, en Centro América las pérdidas alcanzaron $ 152.4 millones de dólares americanos (Anónimo, 1994).

En las regiones en donde el cultivo de maíz es de temporal, la época de siembra está restringida a un período relativamente corto de 10 a 12 días y un atraso de 8 días puede significar hasta 60% de reducción de la producción.

Tomando en cuenta el serio problema que es la sequía y su efecto en la producción de los pequeños y medianos productores de la región El Programa Regional de Maíz (PRM) con la colaboración del CIMMYT, a finales de la década de los ochenta realizó los primeros trabajos colaborativos sobre el desarrollo de germoplasma con tolerancia a este factor abiótico. Aunque, los países del área previamente ya habían realizado esfuerzos individualmente y se habían obteniendo las variantes de polinización libre como CENTA-Pasaquina en El Salvador, ICTA B-1, y BS-19 en Guatemala y CHOROTEGA B-105 en Honduras (Córdova, 1990).

Las últimas encuestas de las Instituciones de Investigación Agrícola, han demostrado que entre 60% y 70% de la producción de los países del área de Centro América, viene de los pequeños productores y sobre todo de las regiones con laderas, lo que confirma que existe un reto para seleccionar genotipos tolerantes a los ambientes desfavorables.

El objetivo principal de este trabajo es seleccionar germoplasma de maíz de madurez intermedia o precoz con buen comportamiento bajo condiciones de humedad limitada. Aunque también se espera:

1. Mejorar la tolerancia a la sequía en la población Tuxpeño Sequía C_6 x BS-19 mediante selección recurrente en ambientes con diferente nivel de estrés.
2. Evaluar el índice de sequía y hacer progreso genético adecuado a los esquemas de mejoramiento comúnmente usados.
3. Evaluar materiales precoces de grano blanco y amarillo que puedan utilizarse como alternativa en ambientes con humedad limitada.
4. Evaluar la adaptación de acuerdo con la estabilidad del rendimiento en los diferentes ambientes.
5. Generar sintéticos experimentales.
6. Producir suficiente semilla para usar en el PRM.

Por otro lado, en 1987 el PRM puso en marcha diversos trabajos que integran el Proyecto de Sequía, en esta etapa Honduras fue el líder y Guatemala y el Salvador fungieron como colíderes. Para iniciar se seleccionó la población Tuxpeño Selección Sequía, que es uno de los materiales tropicales que el CIMMYT ha mejorado por más de ocho ciclos de selección (Bolaños y Edmeades 1993). Recientemente, Bolaños y Edmeades (1993) identificaron ciertos parámetros que ayudan en la selección de genotipos tolerantes a condiciones de humedad limitada, entre ellas están la sincronía floral, menor número de ramas primarias de la espiga, menor altura de la planta, mayor número de mazorca por planta y el índice de cosecha.

En el proyecto de Sequía del PRM se han utilizado estos parámetros y los primeros resultados indican que la fracción seleccionada redujo la altura de la planta, se mejoró la sincronización floral y aumentó el número de mazorcas por plantas. De acuerdo con Brizuela et al. (1991) los avances del proyecto son notables, estos autores evaluaron una serie de variedades mejoradas (sintéticos) en 11 localidades de Centroamérica, las cuales superaron al testigo del agricultor hasta en 37%. Además, Zea et al. (1989) observaron que entre las líneas del proyecto existen algunas que en condiciones de estrés reducen únicamente 36% su rendimiento respecto a las condiciones óptimas.

Materiales y Métodos

Material genético. Durante 1987, la población que se seleccionó para iniciar los trabajos fue Tuxpeño Selección Sequía C_6 x BS-19 con 400 familias, 200 de cada fracción, la primera se obtuvo del CIMMYT y la segunda del ICTA en Guatemala, en ambos materiales se habían seleccionado genotipos para tolerancia de sequía, por medio del sistema de medios hermanos.

Metodología de mejoramiento. El mejoramiento se ha realizado mediante selección recurrente, en los primeros años se usaron familias que se recombinaban por el sistema de medios hermanos; las evaluaciones se realizaban en las fincas de algunos agricultores y la recombinación de las familias se efectuaba dentro de los predios de la Estación Experimental del PRM, por otro lado se incluyó el manejo con y sin labranza convencional. Para realizar las evaluaciones se utilizó un diseño de latice simple 20 x 20 (400 entradas), con dos repeticiones.

Primera modificación en el sistema. En el segundo ciclo de selección se empezó a usar líneas S1 con las mismas 400 entradas, las evaluaciones únicamente se realizaron en los predios de las Estaciones Experimentales, en tres localidades de Centro América, una en El Salvador, otra en Honduras y dos evaluaciones en Guatemala, en las dos primeras localidades se establecieron los ensayos bajo temporal y en Guatemala uno estuvo bajo estrés y otro en condiciones óptimas de riesgo. Finalmente, en esta la recombinación de la fracción superior y la formación de los sintéticos se realizó en Choluteca, Honduras.

Segunda modificación. En 1993, a partir del tercer ciclo de selección las entradas se redujeron a 225, se trabajó en las mismas localidades, además, se comenzó a utilizar líneas S_2 con el fin de formar sintéticos más uniformes, y se aumentó la densidad de población (85,000 plantas / ha), (15 cm entre planta) para someter a las líneas a condiciones subóptimas. Actualmente, el avance del mejoramiento genético se lleva a cabo a través de las evaluaciones de los sintéticos experimentales desarrollados en el Proyecto de Sequía y se están utilizando como testigos los cultivares locales mejorados.

En el cuarto ciclo de selección, el Programa de Fisiología del CIMMYT colaboró en las evaluaciones de las líneas S_2 en Poza Rica, México; las mejores entradas se llevaron a S_3, de las que se obtuvieron 215 líneas y que son consideradas el material de soporte de la población.

Manejo agronómico. Todas las siembras se realizaron manualmente, depositando 1 o 2 semillas por golpe, posteriormente se raleó a una planta por postura, cada entrada consistió de un surco de 5 m de largo con dos repeticiones. La distancia entre surcos varió entre 0.8 y 0.9 m, para el control de arvenses y la fertilización en el caso de Honduras se utilizó atrazina y pendimentalina en dosis de 2 kg / ha y N-P-K en dosis 80-40-30 kg / ha, respectivamente. La semilla se trató con el insecticida Furatiocarb a razón de 10g / kg de semilla.

Variables registradas. Días a floración masculina y femenina, altura de planta y mazorca, número de plantas con acame de raíz y tallo, mazorcas podridas, mazorcas descubiertas, aspecto de planta y mazorca, humedad, rendimiento de mazorca y de semilla (ajustada a 15% de humedad).

Análisis estadístico. Se efectuó el análisis de varianza por localidad y combinado, el de estabilidad en los sintéticos, comparación de medias por el método de Duncan y se calcularon los índices de selección. El índice de sequía se obtuvo haciendo comparaciones entre el ambiente favorable y el rendimiento del ambiente desfavorable, con calificaciones de escala de 1-5-1 resistente y 5 susceptible.

Resultados y Discusión

Hallauer y Miranda (1981) estiman que la selección basada en progenies endocriadas en S_1, S_2 etc. es teóricamente efectiva para efectuar cambios en la frecuencia de genes con efectos aditivos. Con base en este principio, en el Proyecto de Sequía se han obtenido ciertos avances prácticos en la población Tuxpeño Selección Sequía C_6 x BS-19.

En relación con el rendimiento, el diferencial de selección de la fracción de las 40 familias seleccionadas fue positivo respecto a la media de la población (Cuadro 1). En el análisis combinado el diferencial de selección fue 12.6%; en el Cuadro 2 se describen las características de las mejores 8 familias de la variedad experimental y equivalen a los valores medios de las tres localidades; el diferencial de selección del rendimiento de la variante experimental fue 16%. Durante ese mismo año se evaluó el progreso del sintético regional, mediante la comparación con algunos

Cuadro 1. Ganancia de rendimiento (t/ha) por localidad y combinada de la evaluación de medios hermanos en tres localidades de Centroamérica, 1990. MDS = Mínima diferencia significativa.

Descripción	Localidades Salvador	Guatemala	Honduras	Combinado
Variedad experimental (8 familias)	6.17	6.61	3.87	4.97
Fracción (40 Familias)	5.69	6.05	3.42	4.81
Población	4.84	5.29	2.75	4.27
M D S	1.56	1.33	1.41	1.45
Diferen.de Sel.(%)	17.56	14.36	24.36	12.64
Máximo	6.57	7.01	4.09	5.37
Mínimo	3.13	3.57	1.33	3.38

Cuadro 2. Características promedio de las familias que forman la variedad experimental (VE) cultivadas en tres localidades Centroamericanas 1990-A.

Entrada	Días a floración (d)	Mazorca Altura (cm)	Podridas (%)	Descubiertas (%)	Rendimiento (t/ha)
35	53	86	5.37	9.80	5.23
120	54	87	6.39	6.68	5.03
48	53	92	11.50	9.68	4.98
142	52	85	9.03	12.08	4.96
126	53	90	12.09	10.91	4.92
17	54	85	8.82	6.87	4.90
189	53	86	11.67	6.44	4.87
171	52	90	12.34	10.35	4.86
Media Fracción (VE)	53	88	9.65	9.10	4.97
Fracción (40 familias)	53	90	9.71	10.50	4.81
General	54	90	9.80	11.70	4.27

cultivares que se habían liberado por su tolerancia a la sequía; al respecto, Reyes et al. (1990) observaron que el sintético regional superó al maíz criollo local 38% en rendimiento y que existieron correlaciones altamente significativas en las evaluaciones de los sintéticos y de las familias de medios hermanos entre el rendimiento y el porcentaje de mazorcas podridas (r=0.41 y r=0.34).

De acuerdo con el índice de sequía los dos cultivares sobresalientes en la localidad de Guatemala fueron Lujosa B-106 y sintético regional, pues sus índices fueron 0.904 y 0.709, respectivamente (Cuadro 3).

Durante las dos evaluaciones de las variedades desarrolladas con tolerancia a sequía Cuadro 4, (1990-1991) se conoció su estabilidad mediante la aplicación del modelo de Eberhart y Russell (1966), de acuerdo con ésta el sintético regional, Lujosa B-106, CENTA Pasaquina y BS-19 fueron los que presentaron la mayor estabilidad en todos los ambientes contrastantes de 17 localidades de Centro América, ya que su coeficiente de determinación se aproximó a la unidad (B_i=1)y su desviación de la regresión a cero (S_{di}^2=0). En el Cuadro 5 se presentan resultados de 10 localidades. En 1991, en 6 localidades se pusieron como testigos a variedades mejoradas tropicales, aun así se notó la superioridad de los materiales tolerantes a condiciones de humedad limitada.

Una respuesta positiva del progreso del Proyecto de Sequía, se comprobó con la evaluación de los cultivares de polinización libre realizada por Bolaños (1992) quien documentó la superioridad del sintético sequía, sobre las otras variedades de polinización libre, como resultado del mayor tiempo en el llenado de grano (3 días), por lo tanto esta característica podría tomarse como un criterio adecuado para la selección posterior.

El rendimiento de las líneas que forman la variedad experimental, evaluadas bajo condiciones de estrés en Zacapa, Guatemala, superó con 21% a la media de la población total. Estos resultados coinciden con los de Bolaños y Edmeades (1988), quienes concluyeron que la sequía en el período de floración del maíz, a diferencia de otras etapas, es determinante para el rendimiento del grano. En los resultados de la evaluación de las líneas en 1992, 32% de los materiales no llegaron a la floración femenina y de este 25% no produjo ningún tipo de flor. Esta respuesta es una de las más importantes para seleccionar genotipos con tolerancia a sequía.

En 1994 se evaluaron 225 líneas S_2, las diez más sobresalientes por su rendimiento cuando crecieron con el temporal se presenta en el Cuadro 6. Se observó que el rendimiento del conjunto decayó notablemente con el estrés y en temporal la media de las 10 mejores líneas fue 2.23 t/ha mayor respecto a la media de la población.

El rendimiento medio y el número de mazorcas por planta de la fracción seleccionada incrementó respecto a la media de la población, en las dos localidades de prueba, el ciclo vegetativo no se modificó y hubo ganancia en la sanidad de la mazorca (3.4%) y en el porcentaje de mazorcas descubiertas (2.94) (Cuadro 7).

Durante 1993 se evaluaron los cuatro sintéticos generados en cinco localidades en prueba de validación (Cuadro 8) se observó un pequeño

Cuadro 3. Respuesta al índice de sequía de 8 variedades sintéticas evaluadas en Guatemala, 1990.

Nombre	Origen	Indice sequía
BS-19	Guatemala	0.660
HB-104	Honduras	0.340
Sintético Local	Honduras	0.596
CENTA Pasaquina	El Salvador	0.704
Lujosa B-106	Honduras	0.904
Sintético Reg.	Honduras	0.709
Chorotega B-105	Honduras	0.661
Maicito	Testigo	0.591

Cuadro 4. Medias y parámetros estimados en el análisis para estabilidad del rendimiento de 8 variedades del proyecto de sequía en seis localidades, 1990. Símbolos B_i = Coeficiente de regresión, S_{di} = Desviación de regresión.

Nombre	Rend. t/ha	B_i	S_{di}
BS-19	2.67	0.987	-0.58
HB-104	2.68	0.600	0.68
Sintetico Local	3.08	0.811	0.23
CENTA Pasaquina	2.33	0.909	0.39
Lujosa B-106	2.91	0.883	0.51
Sintético Reg.	3.16	0.914	0.84
Chorotega B-105	3.07	0.955	-0.36
Maicito Testigo Local	2.30	0.916	-0.95

Cuadro 5. Rendimiento medio, coeficiente de regresión (B_i) y desviación de regresión (S_{di}) de siete cultivares del Proyecto Sequía evaluados en diez localidades de Centro América durante 1991.

Tratamiento	Rendimiento t/ha	B_i	S_{di}
Sintético regional	2.64	0.992	0.110
Sintético local	2.57	0.982	-0.110
Chorotega B-105	2.59	0.989	-0.100
Lujosa B-106	2.53	0.993	-0.030
CENTA Pasaquina	2.32	0.946	0.100
BS-19	2.49	0.997	-0.070
Testigo local	2.33	0.989	-0.090

incremento del rendimiento del sintético Omonita 1, superando a los demás.

Con base en los resultados, Brizuela et al. 1989, se recomienda difundir el mejor sintético a nivel de finca para que sea utilizado por los pequeños y medianos agricultores de las zonas marginadas de Centro América y el Caribe.

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Cuadro 6. Características agronómicas de la variedad experimental de las 10 mejores líneas S_2 crecidas en las localidades de Choluteca (Honduras), San Andres (El Salvador)y Jutiapa (Guatemala) durante 1994. RE = Rendimiento con estrés, RT = Rendimiento bajo temporal.

Entrada	RE (t/ha)	RT t/ha	Días a flor	Alt. pta. (cm)	Maz/ desc. (%)	Maz/ pta.
86	1.20	4.23	57	105	11.5	1.19
64	0.95	4.39	58	110	16.3	1.09
68	1.10	4.12	57	110	9.1	1.09
66	0.90	4.65	58	104	0.0	1.14
21	0.98	3.83	57	105	13.6	1.09
173	1.05	4.35	58	98	12.9	1.21
5	0.90	4.01	57	103	15.6	1.27
181	0.70	3.76	57	105	8.4	1.09
163	0.80	3.66	56	95	7.7	1.08
213	0.90	4.11	58	100	0.0	1.10
Media						
Fracción	0.94	4.11	57.3	104	9.5	1.13
Población	0.50	2.72	58.9	105	12.5	1.03
CV(%)	39.4	36.9				

Cuadro 7. Ganancia en la población de sequía para diferentes características utilizado el índice de selección.

Variable	Media de población	Media fracción selección	Diferencia
Rend.(t/ha) Temporal-México	2.72	3.83	1.10
Rend.(t/ha) Choluteca-Hond.	2.39	3.72	1.32
Días a flor (d)	58.9	58.4	-0.26
Altura planta (cm)	104.9	103.4	-1.5
Altura mazorca (cm)	51.7	50.8	-0.9
Mazorcas pod. (%)	10.13	6.69	-3.44
Mazorcas desc. (%)	12.46	9.51	-2.94
Mazorcas/planta	1.03	1.11	0.08

Cuadro 8. Rendimiento medio (t/ha) de cuatro sintéticos tolerantes a la sequía, evaluados en diferentes regiones, durante 1993B.

	Localidades					
Entrada	Choluteca	San Cristóbal	Delic. Chol.	Costa Rica	Choluteca	Promedio
Sint Reg.	0.85	5.75	2.00	2.80	4.09	3.09
Sint Loc.	1.84	5.05	3.10	2.80	5.18	3.59
Omonita 1	2.42	5.93	3.20	3.80	5.19	4.10
Omonita 2	2.00	4.48	3.20	2.70	4.37	3.35
Test Loc.	1.56	4.61	1.80	2.80	4.58	3.07
CV (%)	31.82	9.35	12.8	15.1	13.6	
F(0.05)	NS	NS	*	NS	NS	

Fuente: Informe, Proyecto Nacional de Maíz, Dirección de Ciencia y Tecnología Agropecuaria - Informe Anual 1992. Pp. 33-40.

Mejoramiento de Maíz para Tolerancia a Sequía en el Chaco de Bolivia

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Abstract

In a preliminary evaluation of 254 topcrosses resulting from the combination of S_3 and S_4 lines from a group of CIMMYT hybrids with the open pollinated variety IBO-128 and two local checks, the best 30 lines were selected under conditions of scarce and favorable moisture conditions at Villamontes and Yacuiba, respectively. Three diallels were formed with 10 lines each, and 45 single-cross hybrids were made, denoted as diallel 1 (D_1 = yellow grain), diallel 2 (D_2 - white grain), and diallel 3 (D_3 = drought tolerant). In 1994-95, evaluation trials were established with 134 crosses, planted under two contrasting moisture availability conditions. The experimental plot had 22 plants per row, with 0.75 cm between rows and 0.50 cm between plants. The design was random complete blocks with three replications. The best results were in Yacuiba with yields ranging between 7 and 8 t/ha for the three diallels, whereas in Villamontes yields were from 2 to 3 t/ha due to drought. Anthesis-silking interval was slightly less in Yacuiba than in Villamontes but all three diallels matured six days earlier in Yacuiba, perhaps because they escaped drought stress at the preflowering and grain-filling stages. The best 8-10 lines from each diallel will be used to form hybrids and synthetics for each environment.

El Instituto Boliviano de Tecnología Agropecuaria (IBTA), a través del Programa Maíz, desarrolla trabajos de investigación en el chaco boliviano que forma la mayor área afectada por la sequía. Esta área se extiende por los departamentos de Santa Cruz, Tarija y Chuquisaca donde la superficie afectada, específicamente de las zonas productoras, es de 100,000 ha (36%), las pérdidas alcanzan las 210,000 t y resultan afectados 38,000 productores.

En el Centro de Germoplasma Gran Chaco de Algarrobal (Yacuiba), a partir de 1991, se ha iniciado trabajos de investigación para contrastar el efecto de la sequía, tomando como base líneas avanzadas del grupo de híbridos disponibles en el CIMMYT, el principal aspecto tomado en cuenta fue que el efecto de la sequía en las plantas depende del genotipo, de la intensidad de la sequía y de la etapa del desarrollo en la que ocurre (Rocha et al., 1991).

En la selección de las líneas y la formación de los híbridos, es importante la productividad y la sincronía floral, debido a que por un día de retraso en la emisión de los estigmas con respecto a la liberación del polen el rendimiento se reduce aproximadamente 10%, de manera que con el retraso de 10 días no habría producción de grano (Bolaños y Edmeades, 1993).

Con base en lo anterior, los objetivos de la presente investigación fueron generar y desarrollar híbridos y/o sintéticos que sean tolerantes a condiciones de humedad adecuada y de sequía.

Materiales y Métodos

Prueba de aptitud combinatoria general (ACG)

Durante el periodo 1992-93, se realizó la prueba de ACG de 254 mestizos de la combinación de líneas puras S_3 y S_4, procedentes del grupo de híbridos del CIMMYT, con la variedad de polinización libre IBO-128 que se usó como probador masculino y dos testigos Suwan e IBO-128. Las evaluaciones se realizaron en dos ambientes contrastantes, humedad favorable y sequía. El primero se localizó en Yacuiba, a una altitud de

576 msnm (22° 01' latitud S) y con una precipitación de 950 mm durante el periodo de cultivo el segundo en Villa Montes a 340 msnm (21° 15' latitud S) y con una precipitación de 750 mm, muy irregular, durante el periodo de cultivo. El diseño utilizado fue de latice simple 16 x 16. Las mejores líneas se identificaron reduciendo el intervalo de floración (ASI) bajo sequía.

Prueba de aptitud combinatoria específica (ACE)

Durante el periodo 1993-94 se realizó la prueba de ACE utilizando tres grupos dialélicos, cada uno con 10 líneas; se obtuvieron 45 grupos simples, denominados dialelo 1 (D_1, de grano amarillo), dialelo 2 (D_2, de grano blanco) y dialelo 3 (D_3, con tolerancia a sequía). La siembra se realizó, en el Centro de Germoplasma Gran Chaco Yacuiba, se utilizó el análisis dialélico método 4 de Griffing (1956) para cada localidad y combinando las dos localidades.

Evaluación de híbridos simples

En el periodo 1994/95, se establecieron ensayos de evaluación de los tres grupos dialélicos, en dos localidades de Algarrobal (Yacuiba) y Capirendita (Villa Montes). La siembra en Algarrobal se efectuó el 15 de diciembre de 1994 y en Capirendita el 10 de enero de 1994. La parcela experimental estuvo constituida por 1 surco de 22 plantas cada uno, equivalente a 53,000 plantas por ha.

Las variables evaluadas fueron rendimiento de grano, días a floración masculina, días a floración femenina, intervalo de floración, altura de la planta y aspecto de la mazorca. Para tales caracteres se realizaron los análisis de varianza individual por localidad y combinando las dos localidades.

Resultados y Discusión

Dentro de cada localidad no se observaron diferencias significativas entre los tres grupos dialélicos para ninguno de los caracteres evaluados; sin embargo, entre localidades hubo diferencias altamente significativas.

En la localidad de Algarrobal, bajo condiciones de humedad favorable, los híbridos con tolerancia a sequía (D_3) presentaron los más altos rendimientos 8.20 t/ha con el menor intervalo de floración (1.93 d) en comparación con los híbridos blancos (D_2) y amarillos (D_3), en estos últimos se observó reducción del rendimiento y aumento del intervalo de floración (Cuadro 1); las diferencias anteriores podrían atribuirse al genotipo (Rocha et al., 1991).

En la localidad de Capirendita, donde la humedad fue más limitada, los rendimientos de los híbridos blancos (D_2) disminuyeron considerablemente, hasta 2.62 t/ha, y aumentó ligeramente la diferencia del intervalo de floración a 2.67 d. Asimismo, la diferencia de días a floración masculina y femenina disminuyó 7.7 d (Cuadro 2); dichos resultados se atribuyen al escaso número de días con lluvia, una precipitación fluctuante de 11 a 159 mm, alta temperatura (30.7 °C) y por consiguiente mayor evapotranspiración.

De acuerdo con los resultados en los dos ambientes de evaluación, los híbridos con tolerancia a sequía (D_3) expresaron el mayor potencial de rendimiento, menor altura de planta

Cuadro 1. Comparación de medias de tres grupos dialélicos para rendimiento y otros caracteres agronómicos. Localidad Algarrobal ciclo agrícola 1994-1995.

Híbridos	Rend. (t/ha)	FM (días)	FF (días)	IF (ASI)	AP (cm)	AMZ (1-5)
Tol. Sequía (D3)	8.197	64.40	66.33	1.93	210.2	1.76
Blancos (D2)	7.924	64.97	66.96	1.99	196.4	1.28
Amarillo (D1)	7.381	63.46	64.61	2.19	202.3	1.36

Tol. Seq.: tolerante a sequía, Rend.: rendimiento : FM: Floración Masculina; FF: Floración Femenina;IF: Intervalo de Floración; AP: Altura de planta; y AMZ: altura de mazorca.

Cuadro 2. Comparación de medias de tres grupos dialélicos para rendimiento y otros caracteres agronómicos. Localidad Capirendita ciclo agrícola 1994-1995.

Híbridos	Rend. (t/ha)	FM (días)	FF (días)	IF (ASI)	AP (cm)	AMZ (1-5)
Amarillos (D1)	3.147	56.70	58.72	2.02	202.7	2.22
Tol. Sequía (D3)	2.890	57.80	60.22	2.42	185.2	2.45
Blancos (D2)	2.623	57.77	60.44	2.67	198.3	2.28

Tol. Seq.: tolerante a sequía, Rend.: rendimiento : FM: Floración Masculina; FF: Floración Femenina;IF: Intervalo de Floración; AP: Altura de planta; y AMZ: altura de mazorca.

y mejor aspecto de planta, en comparación con los híbridos de grano blanco (D_2) y amarillo (D_1).

Entre las mejores 10 cruzas simples con mayor tolerancia a sequía (dialelo 3) los rendimientos de los mejores dos híbridos fueron 6.45 y 6.28 t/ha y el ASI de 2.5 y 3.0 d (Cuadro 3); estos resultados permitirán generar híbridos de cruza simple, doble y/o sintéticos.

Cuadro 3. Comparación de las mejores 10 cruzas simples del dialélo 3 bajo humedad limitada.

No. entrada	Cruza	Rend. (t/ha)	FM (dias)	FF (dias)	IF (ASI)	AP (cm)
7	3*10	6.450 a	58.5 ab	61.0 ab	2.5	170
6	3*4	6.275 ab	57.5 ab	60.5 ab	3.0	189
27	3*5	5.930 abc	57.5 ab	60.5 ab	3.0	213
39	10*2	5.540 abcd	56.5 b	59.5 ab	3.0	184
38	10*1	5.190 abcde	57.0 b	59.5 ab	2.9	188
8	4*1	5.050 bcd	56.5 b	59.5 ab	2.5	180
40	10*4	4.475 cde	57.0 b	60.5 ab	3.5	185
30	9*1	4.265 de	56.5 b	59.0 ab	2.9	198
17	6*7	4.010 de	57.0 b	59.0 ab	2.0	167
20	7*3	3.805 e	57.50 ab	60.5 ab	3.0	180

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Maize Breeding for Drought Tolerance in Thailand

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Abstract

Drought stress damages an estimated 3 to 22% of the planted maize area in Thailand every year, resulting in yield losses estimated to be from 129,000 to 858,000 metric tons, worth 10 to 80 million US dollars. The maize breeding program for drought tolerance was established in Thailand in 1982. The maize population KK-DR was developed from six source materials and has been improved for tolerance to drought using an S_1 *recurrent selection scheme. After three cycles of population improvement, three synthetic varieties were developed. These three synthetics, together with seven other open-pollinated varieties and six hybrid varieties, were evaluated in 1991 and 1992 to compare yield potential and other agronomic characters under artificial water stress and non-stress conditions in the summer season.*

The experiments were also conducted in both years under rainfed conditions in the rainy season to compare seasonal effects. In general, hybrids outyielded the open-pollinated varieties under drought, and by an even greater margin under well-watered conditions. The results demonstrated, however, that not all hybrids performed better than the open-pollinated varieties under drought; one of the synthetic varieties showed higher yield potential and more drought tolerance than some hybrids. Maize grown in the summer season under plentiful water showed higher yield potential than in the rainy season.

Maize crop loss caused by environmental stress, particularly drought stress, is observed almost every year in Thailand, and data on the extent and severity of the loss are recorded. According to reports issued by the Office of Agricultural Economics (1985, 1995), maize crop losses varied from 129,000 metric tons in 1988 to 858,000 metric tons in 1982 (Table 1). The estimated value of this loss ranged from 10 to 80 million US dollars per year. Maize area affected varied from 49,000 to 393,000 ha, or from 3 to 22% of the total area sown to maize.

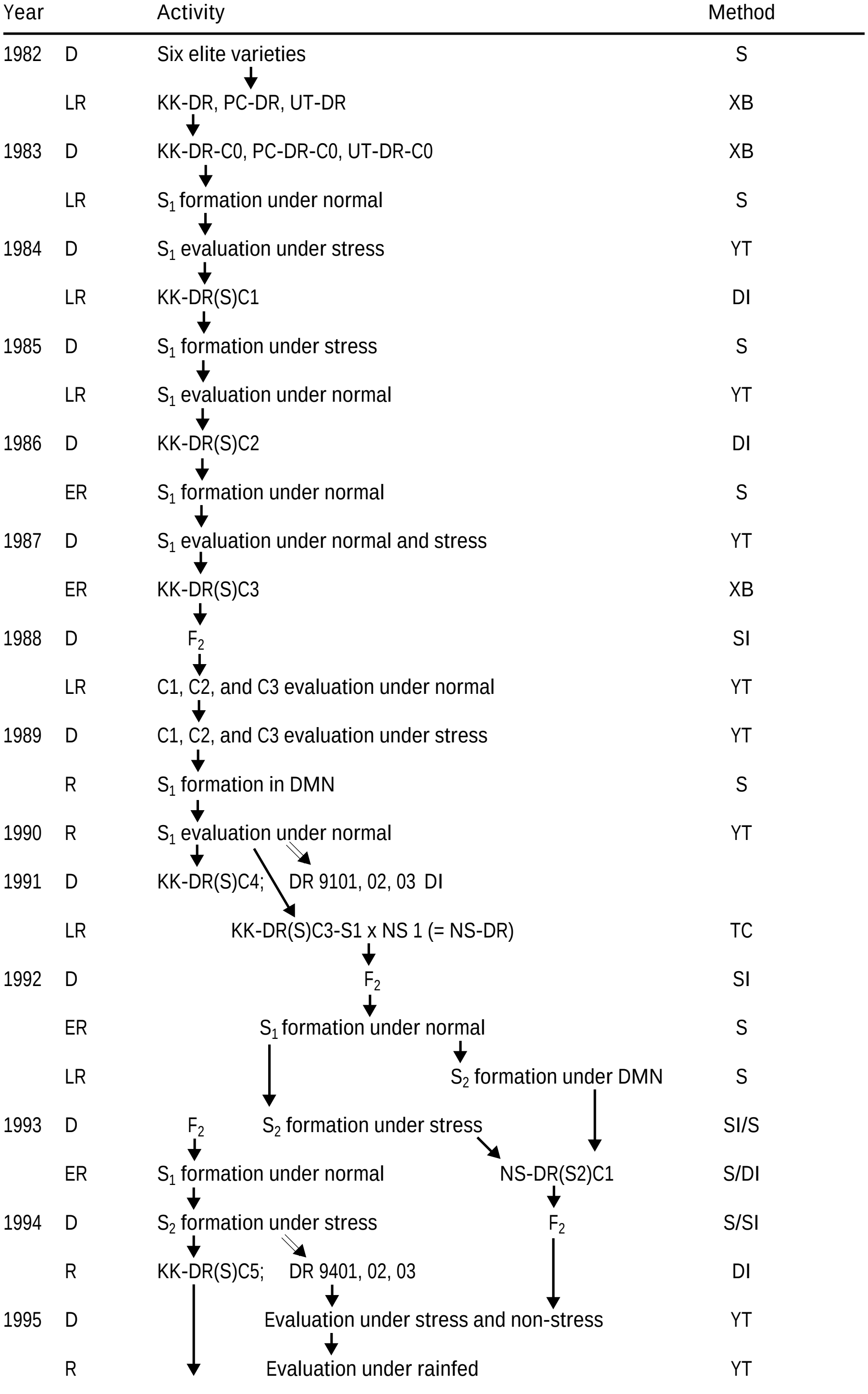
A maize breeding program for tolerance to drought stress was established in Thailand in 1982. Figure 1 shows the development and improvement history of a drought tolerant population, KK-DR. In 1982, six elite varieties were planted under irrigation in the hot summer season at U-Thong Field Crops Research Center. Water stress was applied during the period 35 to 55 days after planting, and irrigation was resumed just before anthesis. Less wilted plants were selected during this water stress period and self pollinated. Selected S_1 lines were random-mated in a half-sib crossing block at three field crops research centers; namely Khon Kean (KK), Pak-Chong (PC), and U-Thong (UT). After this second random mating, families from the KK location showed higher potential than those from other locations. Only this population, KK-DR (Khon Kean Drought Resistance), was carried on and improved using an S_1 recurrent selection scheme (see Fig. 1).

After three cycles of improvement, selected S_1 lines from KK-DR(S)C_3 were topcrossed to Nakhon Sawan 1

Table 1. Estimated maize crop loss caused by drought stress in Thailand from 1975 - 1994.

Crop year	Area damaged ('000 ha)	Area damaged (%)	Crop loss ('000 t)	Estimated value ('000,000 US$)
1975	107	8	253	19
1976	164	13	390	26
1977	229	19	394	26
1978	72	5	153	10
1979	100	7	202	17
1980	88	6	197	19
1981	102	7	241	21
1982	373	22	858	69
1983	122	7	276	27
1984	78	4	190	18
1985	62	3	159	12
1986	136	7	323	21
1987	393	22	806	80
1988	49	3	129	14
1989	76	4	196	23
1990	200	11	482	37
1993	122	9	332	37
1994	61	4	180	21

Figure 1. Drought tolerance population development, improvement, and synthetic formation.



Year		Activity	Method
1982	D	Six elite varieties	S
	LR	KK-DR, PC-DR, UT-DR	XB
1983	D	KK-DR-C0, PC-DR-C0, UT-DR-C0	XB
	LR	S_1 formation under normal	S
1984	D	S_1 evaluation under stress	YT
	LR	KK-DR(S)C1	DI
1985	D	S_1 formation under stress	S
	LR	S_1 evaluation under normal	YT
1986	D	KK-DR(S)C2	DI
	ER	S_1 formation under normal	S
1987	D	S_1 evaluation under normal and stress	YT
	ER	KK-DR(S)C3	XB
1988	D	F_2	SI
	LR	C1, C2, and C3 evaluation under normal	YT
1989	D	C1, C2, and C3 evaluation under stress	YT
	R	S_1 formation in DMN	S
1990	R	S_1 evaluation under normal	YT
1991	D	KK-DR(S)C4; DR 9101, 02, 03 DI	
	LR	KK-DR(S)C3-S1 x NS 1 (= NS-DR)	TC
1992	D	F_2	SI
	ER	S_1 formation under normal	S
	LR	S_2 formation under DMN	S
1993	D	F_2 S_2 formation under stress	SI/S
	ER	S_1 formation under normal NS-DR(S2)C1	S/DI
1994	D	S_2 formation under stress F_2	S/SI
	R	KK-DR(S)C5; DR 9401, 02, 03	DI
1995	D	Evaluation under stress and non-stress	YT
	R	Evaluation under rainfed	YT

Abbreviation and symbol

D = Dry season	ER = Early rainy season	R = Rainy season
LR = Late rainy season	S = Selfing	DI = Diallel
XB = Half sib crossing block	YT = Yield trial	TC = Top cross
SI = Sibbing	⇘ = Out come	↓ = Flow direction
DMN = Downy mildew nursery		

The six elite varieties were: Suwan 1, Pak-chong 1602, Thai DMR #6, Caripeño, Tuxpeño, and TF DMR Composite.

(NS 1), a newly-released high yielding variety. The best performing topcrosses were intermated to form a new population, named Nakhon Sawan Drought Resistance (NS-DR). The hope was that this new population would have improved yield potential as compared to KK-DR. An S_2 recurrent selection scheme was employed to improve this population. Meanwhile, improvement of the KK-DR population was continued. Three synthetic drought tolerant varieties were formed using selected S_1 families of KK-DR(S)C_3 in 1991, namely DR 9101, DR 9102, and DR 9103. These three, together with other cultivars, both open-pollinated (OP) and hybrids (HY), were evaluated under water-stress and well-watered conditions in the dry season, and under rainfed conditions in rainy season, in both 1992 and 1993. The objectives of these experiments were to compare the performance of OP and HY varieties under water-stressed and well-watered conditions in the summer season, and under rainfed conditions in the rainy season. In the same experiments, the selection gains from three cycles of improvement and the performance of the three drought tolerant synthetics were observed. The results are summarized in Tables 2 and 3, which show that the highest yields across sites were obtained from the hybrids DK888 and SX60. The highest yielding OP across sites was DR 9102. Under drought hybrids again outyielded OPs, though the best hybrid, SX 60, did not significantly outyield the best OP, KK-DR(S)C_4.

The drought index (Fischer et al., 1983), which is the ratio of its yield under water stress and well watered conditions, relative to the same ratio for all varieties, indicated that the most drought tolerant entry was the hybrid SX 60, followed by the OP DR 9102 (Table 3). Gains due to selection under drought of around 200 kg/ha/cycle were clear in KK-DR in the droughted environments 92-D1 and 93-D1. DK888, a semiprolific hybrid, showed especially high yields under well-watered conditions, and hence had a high Eberhart-Russell regression coefficient (Table 2).

In 1994, three new synthetic varieties came out from KK-DR (S) C_4. These were DR 9401, DR 9402, and DR 9403. Like the previous experiment, these synthetic varieties, along with another set of OP and HY cultivars, were evaluated in 1995 under water-stressed and well-watered conditions in the dry season and under rainfed conditions. Preliminary results from a single season of data (Table 4) suggest that the hybrids as a group were more drought tolerant, losing 82% of their well-watered yield versus 85% for the OP group. It should be noted that the drought index tends to identify entries with lower yield under well-watered conditions as being drought tolerant, as well as those with a high yield under drought. In addition, differences in maturity can greatly affect yield if drought occurs near flowering (Bolaños and Edmeades, 1992). The anthesis-silking interval (ASI) was also shorter for the hybrids (3.9 d) than for the OPs (6.1 d). For the most drought tolerant hybrid, DK 999, ASI was 0.0 d, whereas for the best OP (DR 9403) it was 3.0 d. The experiment will be repeated in 1996.

Table 2. Average grain yield and stability parameters (Eberhart-Russell) of 16 maize varieties across seasons and years, 1992-1993.

	Grain yield (t/ha)							Regression parameters[a]	
Variety	92-D1	92-D2	92-R	93-D1	93-D2	93-R	Mean	b	SD
Open pollinated varieties									
DR 9101	1.94	5.58	6.86	2.12	5.83	4.93	4.54	0.96	52.6
DR 9102	2.63	6.34	7.64	3.38	6.27	4.74	5.17	0.89	68.8
DR 9103	2.00	6.11	7.29	2.28	5.93	4.44	4.68	1.02	52.1
Pop.49(Y)DMR	2.58	5.27	6.63	1.93	5.18	4.72	4.39	0.84	47.1
KK-DR(S)C1	2.40	5.87	7.32	1.69	6.26	4.18	4.62	1.06	30.2
KK-DR(S)C2	1.80	5.19	7.02	1.67	5.48	4.42	4.26	1.01	33.9
KK-DR(S)C3	2.12	5.60	6.84	2.01	6.16	4.67	4.57	0.98	33.9
KK-DR(S)C4	3.26	5.64	6.84	2.36	6.24	4.77	4.85	0.82*	32.0
Nakhon Sawan 1	2.10	5.60	6.85	1.79	5.87	4.37	4.43	0.99	20.1
Suwan 3	2.07	4.71	6.82	1.51	6.22	5.12	4.41	1.00	83.9
OP mean	2.29	5.59	7.01	2.07	5.94	4.64	4.59		
Hybrid varieties									
NSX 9007	3.65	6.42	8.07	2.45	6.60	4.52	5.28	0.98	66.8
KESX 8901	1.98	5.79	7.29	1.92	5.02	4.34	4.39	0.99	72.9
SX 60	4.13	7.68	8.49	3.53	8.01	5.25	6.18	0.99	77.1
ASVIN THONGCUM	3.74	6.17	8.14	2.49	7.40	5.20	5.52	1.01	57.6
DK 888	3.61	6.28	10.15	2.42	8.46	6.86	6.30	1.33	117.4
SED THEE 633	2.35	5.86	7.60	1.71	6.74	3.50	4.63	1.14	80.7
HY mean	3.24	6.37	8.29	2.42	7.04	4.95	5.38		
Experiment mean	2.66	5.88	7.49	2.20	6.36	4.77	4.89		
CV (%)	25.9	11.8	6.4	25.2	12.9	13.7	13.4		
LSD .05	1.15	1.15	0.80	0.92	1.36	1.09	0.43		

* Significantly different from 1.0 at $P < 0.05$.

[a] b is the regression of individual cultivar means on mean of all cultivars; SD is deviation from regression

D1= water stressed dry season, D2 = non-water-stress dry season, R = rainy season.

Screening Technique

Yield under water stress is compared to yield potential under well-watered conditions to determine yield losses due to drought stress. Water stress should be created during flowering (anthesis and silking), the period when maize is very sensitive to drought stress (Bolaños and Edmeades, 1992; Edmeades et al., 1992; Edmeades et al., 1995), and when stress can cause severe yield loss. Percent yield loss due to water stress for a particular cultivar is a useful measure of the ability of that variety to tolerate drought. A drought index (DI), such as proposed by Fischer et al. (1983), is a measure of yield loss for a variety in relation to the yield losses observed for all varieties in a particular experiment. Both suffer from the defect of identifying genotypes as drought tolerant if they have a low yield under well-watered conditions. A further disadvantage is that the DI of a given variety in a given experiment cannot be compared to that of varieties in other experiments.

Comparisons of percentage yield loss of varieties among experiments is also confounded by differential stress levels among experiments. Comparisons of drought tolerance among varieties or progenies, therefore, should only be made within the same experiment.

Conclusion

From the results of these experiments, we can conclude that:

1. DR 9102 was the highest yielding OP in four of the six testing environments and had the highest average yield among OPs.
2. KK-DR(S)C_4 was the second best OP for yield and showed good stability across testing environments, as seen by the relatively low SD and the b-value significantly less than 1.0.
3. The good performance of DR 9102 and KK-DR(S)C_4 can also be seen in their low percent yield losses due to water-stress and DI values greater than 1.0.
4. The good performance of KK-DR(S)C_4 indicates that our selection has been effective in selecting good performance in both the water-stress and non-stress environments.
5. It is also important to note that some of the OPs were very competitive with the hybrids. Only two of the six hybrids had significantly higher yield (on average) than DR 9102.
6. For the OPs tested in 1995, KK-DR(S)C_4, KK-DR(S)C_5 and DR 9403 appear to be the most drought tolerant. They had the lowest percent yield losses due to water-stress, the largest DI values and relatively short ASIs.

Table 3. Yield loss caused by water stress condition and drought index (DI) of 16 maize varieties at Nakhon Sawan Field Crops Research Center in 1992 and 1993 dry season.

	Yield loss (%)			Drought index[†]		
Variety	1992	1993	Mean	1992	1993	Mean
Open pollinated varieties						
DR 9101	62.9	63.7	63.3	0.82	1.05	0.95
DR 9102	58.5	46.0	52.3	0.92	1.56	1.15
DR 9103	67.2	61.5	64.3	0.73	1.11	0.93
Pop.49(Y)DMR	51.1	62.8	57.0	1.08	1.07	1.06
KK-DR(S)C1	59.0	73.0	66.0	0.91	0.78	0.91
KK-DR(S)C2	65.2	69.6	67.4	0.77	0.88	0.89
KK-DR(S)C3	62.1	67.4	64.7	0.84	0.94	0.93
KK-DR(S)C4	42.1	62.2	52.2	1.28	1.09	1.15
Nakhon Sawan 1	62.6	69.6	66.1	0.83	0.88	0.91
Suwan 3	56.0	75.8	65.9	0.97	0.70	0.91
Mean	58.7	65.2	61.9	0.92	1.01	0.97
Hybrid varieties						
NSX 9007	43.1	63.0	53.0	1.26	1.07	1.13
KESX 8901	65.9	61.8	63.8	0.76	1.10	0.94
SX 60	46.2	56.0	51.1	1.19	1.27	1.18
ASVIN THONGCUM	39.4	66.3	52.8	1.34	0.97	1.14
DK 888	42.5	71.4	56.9	1.27	0.83	1.06
SED THEE 633	59.8	74.7	67.3	0.89	0.73	0.89
Mean	49.5	65.5	57.5	1.12	1.00	1.05
Experiment mean	54.8	65.4	60.1	1.00	1.00	1.00

[†] Drought index (DI) for a variety is the ratio of its yield under water-stress to non-water-stress, relative to the ratio of the mean yield of all varieties under water-stress to non-water-stress; a DI > 1.0 suggests relative drought tolerance, and a DI < 1.0 suggests relative drought susceptibility (Fischer et al., 1983).

Table 4. Yield loss, drought index, and the anthesis-silking interval (ASI) under water stress for 20 maize varieties tested at Nakhon Sawan Field Crops Research Center in 1995.

Variety	Yield loss (%)	Drought index[†]	ASI (d)
Open pollinated varieties			
KK-DR(S)C4	78.9	1.16	6.3
KK-DR(S)C5	79.8	1.11	3.3
DR-Diallel(RC)	88.1	0.65	3.7
NS-DR(S2)C1	84.0	0.88	5.0
DR 9102	86.0	0.78	7.7
DR 9401	84.9	0.84	10.0
DR 9402	83.0	0.94	6.7
DR 9403	79.1	1.15	3.0
Nakhon Sawan 1	91.6	0.46	10.0
Suwan 1	89.2	0.60	5.6
Mean	84.5	0.85	6.1
Hybrid varieties			
SW 3504	85.5	0.80	5.4
SW 3601	68.4	1.75	3.3
NSX 9008	75.1	1.38	3.3
NSX 9210	78.7	1.17	3.0
NSX 9213	83.7	0.90	7.0
DK 999	72.6	1.52	0.0
Tawadar 77	91.2	0.49	7.3
Cargill 922	84.5	0.85	3.0
Pioneer 3011	85.2	0.82	5.0
Convoy 93	76.9	1.28	1.7
Mean	80.2	1.09	3.9
Experiment mean	81.8	1.00	5.00

[†] Drought index (DI) for a variety is the ratio of its yield under water-stress to non-water-stress, relative to the ratio of the mean yield of all varieties under water-stress to non-water-stress; a DI > 1.0 suggests relative drought tolerance, and a DI < 1.0 suggests relative drought susceptibility (Fischer et al., 1983).

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Toward Drought Tolerant Maize in South Africa

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Abstract

The South African maize production area is subject to a rainfall gradient from east to west. As a result, various row spacings are used ranging from 0.9 m in the east, 1.5 m in intermediate areas and 2.0 m in the west. Plant populations range from 40,000 plants/ha in the east to 15,000 plants/ha in the west. Most maize is produced in the relatively dry western regions, whereas five percent of the total maize production is obtained from the Kwazulu-Natal province where rainfall approximates that of First World agriculture. A further complicating factor is the occurrence of a twenty-year rainfall cycle, where a ten-year period of relatively high rainfall is followed by ten years of comparatively low rainfall. Smaller wet and dry cycles occur within the ten year periods. Even during years of adequate rainfall, production is often limited by the effect of midsummer drought during the vulnerable flowering period of maize. Local maize hybrids are characteristically prolific, allowing for both ears to be filled under favourable conditions and at least one ear to be produced under sub-optimal conditions. Prolificacy together with anthesis-silking synchronisation are the two primary characteristics selected to improve drought tolerance in maize genotypes. In the past, a breeding program was followed with the objective of improving maize genotypes for drought tolerance. At present, the breeding program aims to incorporate drought tolerance characteristics from exotic germplasm into local breeding material.

Maize is the staple food of southern Africa, with the agricultural sector playing an important role in the South African economy. White maize is preferred for human consumption, while yellow maize is mainly used in animal feed. Average production of white and yellow maize is about 4 Mt per year. Although it contributes only between 5 to 6 % of the gross domestic product, the total impact of this sector is extensive, due to income and labour multipliers (Erasmus and Hough, 1994).

Lack of water caused by erratic annual rainfall is the most limiting factor in maize production in South Africa. Midsummer drought occurs in nine out of ten years in the western maize producing areas (A.S. du Toit, Grain Crops Institute, unpublished data). This usually has a detrimental effect on maize production as it coincides with the vulnerable flowering period of the crop. The maize production area in South Africa is also affected by the existence of a rainfall gradient from east to west. Most maize is grown in the relatively dry western production areas, with only 5% of total maize production obtained from the Kwazulu-Natal province where rainfall approximates that of First World agriculture. A further complicating factor is the occurrence of a twenty-year rainfall cycle, where a ten-year period of relatively high rainfall is followed by ten years of comparatively low rainfall. Smaller wet and dry cycles occur within the ten year periods (G.P. de Beer, pers. comm.). Due to the occurrence of this East-West rainfall gradient, various row spacings are used, ranging from 0.9 m in the east, 1.5 m in central areas and 2.0 m in the western production areas.

Local maize hybrids are characteristically prolific, allowing for both ears to be filled under favourable conditions and at least one ear to be produced under sub-optimal conditions. Ear prolificacy also allows for the maintenance of ear number per unit area under low plant population density regimes. Ear prolificacy and anthesis-silking synchronisation are the two primary characteristics selected to improve drought tolerance in maize genotypes. Currently, a breeding programme is followed with the primary aim of incorporating drought resistance characteristics into local breeding populations. Past breeding programmes were focused on providing drought-tolerant germplasm to the commercial farming sector, while a wider approach that includes both commercial and small-scale farming sectors is currently being followed. The breeding programme for drought tolerance also incorporates insect and disease resistance characteristics with the long term objective of improving yield stability.

Effect of Drought on Maize Production

Maize is planted on 40% of the cultivated area in South Africa (Mallett and de Jager, 1971). This has remained basically constant since 1961. Agricultural production has almost doubled over the last 20 years. Maize is the major agricultural export product, although grown mainly for domestic consumption (Keegan, 1991). International grain trade is extremely important to South Africa. Since 1956, 23 to 37% of the country's maize has been sold on international markets. South Africa is the largest producer of maize in Africa and is normally a major maize exporter, particularly to other African countries. Throughout the 1980s, world maize production experienced severe fluctuations, mostly as a result of poor weather, and South Africa lost some of its traditional markets to France and China (Clancy, 1992).

Drought reduces maize yield. Mallett and de Jager (1971) found that moisture stress three weeks before silking reduced grain yield by 3.2% per day, whereas after pollination it caused a yield reduction of 4.2% per day. The larger fluctuations in maize production illustrated in Fig. 1 are due to shifts between drought and favourable conditions. During the relatively dry 1965-66 season, total production was only 5.1 Mt, while 1966-67 had favourable rainfall and produced 10.2 Mt of maize (Mallett and de Jager, 1971). More recently, a severe drought during the 1991-92 season reduced maize production by 60% to 3.1 Mt, leading to imports of 5 Mt to meet domestic demand. The 1992-93 season was characterised by a dry period followed by a late wet season (A.S du Toit, unpublished data). Maize yields were threatened by unfavourable hot, dry weather in late December and January. Nevertheless, in January 1993 South Africa predicted a maize crop of 8 to 10 Mt, based on increased planting area and a return to average yields (Sandene, 1993). Also contributing to fluctuations in production has been the replacement of less adaptable lower yielding hybrids with higher yielding, input responsive hybrids.

The Small-scale Farmer

Small-scale farmers are often the people hardest hit by drought and other adverse natural conditions. These people practise mainly subsistence farming, producing very little if any surplus maize for market. In Botswana, only 10 to 15% of those engaged in arable farming regularly produce a surplus and only 30% manage to meet their subsistence needs (Mayende, 1993). Since becoming operational in 1984, the Development Bank of Southern Africa has assisted 23 farmer support programmes reaching 25,000 farmers (Thomas and van Rooyen, 1991). Sustainable agricultural development requires the reduction of drought vulnerability of millions of people living in semi-arid regions, including South Africa, where many in rural areas remain dependant on subsistence agriculture (Weiner and Murphy, 1992) and are especially vulnerable to drought.

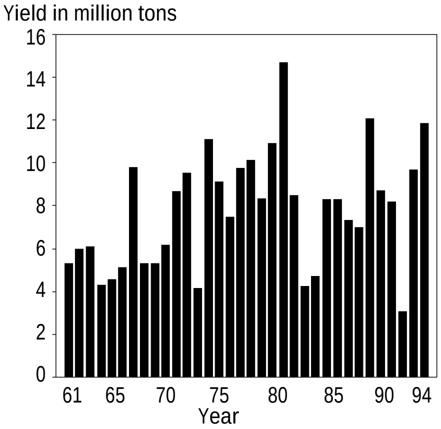

Figure 1. Maize production in South Africa, 1961-94.

The new South African government will have to confront the issue of regular drought conditions as it proceeds with farm policy changes (Missiaen, 1995), and this must necessarily include the small-scale farming community. Specifically, the new Department of Agriculture policy is directed at improving support for the small-scale farming sector and to promote household food security. Research and extension will be reoriented to serve the 95% of farmers utilising small land holdings (Low, 1995). It is thus the aim of both the South African government and the Grain Crops Institute (GCI) to alleviate the constraints on small-scale farmers by providing them with necessary management skills as well as drought tolerant maize genotypes.

The Local Breeding Programme

The overall objectives of the breeding programme are to develop better adapted genotypes able to withstand the effects of drought and other adverse climatic conditions and to improve these genotypes for agronomic performance and for pest and disease resistance. Genotypes so developed are for release to both the commercial and small-scale farming sectors. Population improvement and development, along with line development, receives a high priority in this programme.

In the past, the breeding programme was not focused on breeding for drought tolerance *per se*, but nonetheless selection procedures for other characteristics, and the process of inbreeding, led to an indirect selection for good anthesis-silking synchronisation, both during years of optimal and sub-optimal rainfall. Due to the use of wide row spacings throughout most maize production areas of South Africa and the subsequent low plant densities, ear prolificacy was also an important selection characteristic. This led to most South African breeding populations and hybrids being ear prolific. The justification was that ear prolificacy is a method of overcoming drought conditions by using less plants while still maintaining the same number of ears per unit area. Selection for prolificacy is facilitated by using a reduced stand to enhance the development of more than one ear per plant.

Insect pests and diseases become important factors during periods of sub-optimal rainfall, since they further reduce yield through the damage they cause (J.B.J. van Rensburg, GCI, personal communication). The maize breeding programme thus encompasses an extensive insect and disease resistance programme. A schematic description of the programme as currently followed at the GCI is presented in Fig. 2, and symbols A to E are explained below.

The A-phase comprises the composition and development of breeding populations within heterotic groups. The heterotic groups used by the GCI are defined in Table 1. During this phase, S_2 recurrent selection for combining ability is practised. After crossing to a tester parent, the 20% best-combining S_2 lines are recombined to complete the cycle of selection. These cycles are continued until the desired level of combining ability is reached. In this phase, new germplasm is also incorporated into the breeding programme. Germplasm of unknown heterotic groupings is crossed to tester parents belonging to the various heterotic groups to facilitate intelligent introgression.

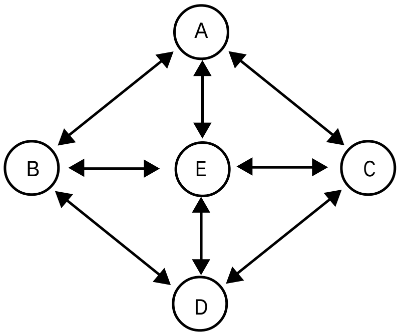

Figure 2. Schematic presentation of the maize breeding programme followed at ARC-Grain Crops Institute, Potchefstroom.

During the **B-phase,** lines identified in phase A are screened for agronomic characteristics, including standability, root strength, prolificacy, drought tolerance, flowering date, anthesis-silking synchronisation, grain quality and utilisation of nutrients. Testcrosses of the lines under the S_2 recurrent selection scheme are also evaluated, and eventually the 20% best performing lines are recombined.

Selection and screening for genotypes exhibiting tolerance to drought stress occurs during this phase. Drought tolerance trials are conducted under two moisture regimes, one under irrigation that acts as a control, and the other under normal dryland conditions. Even during years of adequate rainfall, midsummer drought often occurs during the flowering period of maize, thus facilitating evaluation. Silk extrusion and pollen shedding must be fully synchronised in selected genotypes, and preferably the genotype should produce a profusion of pollen even under adverse conditions. Genotypes with a good physical appearance during periods of drought stress are also selected, as this could indicate a measure of drought tolerance. Plants with a dark, glossy leaf colour are preferred over lighter coloured plants, because the darker plants

Table 1. Heterotic groups used in the ARC-Grain Crops Institute breeding programme.

Yellow germplasm	
A2 — I137TN related	B2 — ‘Corn Belt’ related
A4 — D940Y related	B4 — F2834T related
White germplasm	
A1 — K64R related	B1 — White varieties and I137TN related white lines

seem to withstand drought and heat stress better. Ear prolificacy is also selected during this phase. Du Toit (1991) found that under low plant densities (20,000 plants / ha), secondary ears and ears borne by tillers accounted for 53% of total grain yield. Genotypes experiencing drought stress usually did not fill both ears, bur usually succeeded in filling the primary ear. Ear prolificacy is thus a useful mechanism for providing some yield even under severe drought stress conditions.

The C breeding phase entails recurrent selection for disease and insect resistance. Since drought stress reduces a genotype's ability to resist attacks by insects and diseases, a breeding programme selecting genotypes for drought tolerance should also incorporate at least a degree of resistance to the major disease and insect complexes occurring in the target area (H.C. Kuhn, personal communication). The major insect pests in South Africa include stalk borers, *Busseola fusca* (Lepidoptera: Noctuidae) and *Chilo partellus* (Lepidoptera: Pyralidae). Resistance breeding by means of artificial infestation with larvae has been in progress for a number of years, utilising multiple borer resistant sources from Mississippi and CIMMYT.

Resistance breeding for the following major diseases is conducted at GCI: ear rot caused by *Stenocarpella maydis*, stem rot, boil smut (*Ustilago maydis*), root rot, rust (*Puccinia sorghi*), leaf blight (*E. turcicum*) and maize streak virus transmitted by the maize leaf hopper *Cicadulina mbila* (Homoptera: Cicadellidae). These diseases, except those requiring high moisture conditions, pose a potential threat to maize under drought stress.

The D-phase entails the development of inbred lines, hybrids, synthetics and open-pollinated varieties. All genotypes selected in the previous phases eventually end up in phase D. During this phase inbreeding is continued to S_5. During inbreeding lines are regularly selected for resistance to insects and diseases and for agronomic performance. Selected lines are evaluated in yield trials for general and specific combining ability and the best lines are increased and further characterised. These lines are released to the commercial seed industry, and are also incorporated into synthetics and varieties intended for small-scale farming systems. Lines selected during this stage will be recombined to form new breeding populations.

Phase E encompasses germplasm storage and conservation. All genotypes selected during the previous four phases are stored in GCI's computerised germplasm bank. Lines, populations and synthetics developed at GCI, as well as genotypes imported from foreign sources, are stored in this facility. Most of this germplasm is available to public institutions on request. The total breeding programme, phases A through E, is thus geared to facilitate the needs of both the commercial and the small-scale farming sectors.

Conclusions

Drought has had a serious effect on both the commercial and the small-scale farming sectors of South Africa. To alleviate the constraints faced by the farming community it is necessary to provide maize genotypes able to withstand the detrimental effects of drought, insects, and diseases. The South African government, private plant breeding institutions and the Grain Crops Institute of the Agricultural Research Council are all committed to providing genotypes to both commercial and small-scale farmers to enable them to cope with drought stress. This in turn will lower the country's dependence on imported maize and other food crops during years of drought.

Acknowledgements

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Drought Tolerance at Flowering and Cross-Over Interactions for Yield of Three Maize Populations Grown in Two Agro-ecological Zones of Zimbabwe

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Abstract

*Development of drought tolerant maize cultivars is a high priority in Zimbabwe, where an average of 77% of the arable land is droughty. Two experiments involving random S_1 lines from three maize populations were conducted at three locations in the semi-arid agro-ecological zone Natural Region (NR) IV and one location in the humid zone NR II, to compare grain yield and various secondary traits that might be related to drought tolerance at flowering. Experiment 1 compared 143 lines from ZM601 (selected for drought tolerance for three cycles) with 94 lines from ZM607 (selected for three cycles for high yield under adequate moisture conditions). Experiment 2 compared 162 lines from ZM601 with 154 lines from TSEQ (selected for high yield and drought tolerance for six cycles). Yield responses in experiment 1 showed no advantage for ZM601 over ZM607 in semi-arid, stressed environments. In experiment 2, yield responses were of a cross-over nature; TSEQ out-yielded ZM601 by 33% under stress, while under no stress ZM601 out-yielded TSEQ by 15%. Yield under stress was strongly correlated with anthesis-silking interval (ASI) (r=-0.27** and -0.25** for the two populations) in experiment 1, and for ZM601 in experiment 2 (r=-0.43**), but not for TSEQ (r=-0.13). Days to flowering was negatively correlated with yield, except for TSEQ, indicating that earliness and, hence, drought escape was important for ZM601 and ZM607 but not for TSEQ. Drought tolerance resulted in higher grain yield than drought escape for the experiments in NR IV of Zimbabwe.*

Maize yield in tropical countries is subject to many variables both within and between seasons, but soil fertility and rainfall are probably the most important determinants of yield (Mashingaidze and Manyowa, 1993). According to CIMMYT's estimates, 24 million tons of maize grain are lost annually due to drought worldwide (Edmeades et al., 1995).

In Zimbabwe, an agro-climatological index, incorporating seasonal rainfall, soil productivity, topography and vegetation factors, has been used to classify areas of the country into zones known as 'natural regions' (NRs). Five NRs have been defined, ranging from NRs I and II, which have high production potential and are suitable for intensive farming, to NRs IV and V, which have marginal production potential and are primarily suitable for extensive animal husbandry (Vincent and Thomas, 1961). Seasonal drought and severe dry spells are common in NRs IV and V, but even crops grown in NR II may suffer prolonged periods of limited moisture during the mid-season. There is also a tendency for the less desirable characteristics of weather and soils to reinforce each other, especially in NRs III, IV and V, where drought stress is often compounded by soil infertility. Soils in these areas are generally coarse-textured sands derived from granite, and are generally deficient in nitrogen, phosphorus and sulfur (Grant, 1970). Despite the agro-ecological unsuitability of NRs III, IV and V for intensive crop production, over 75% of Zimbabwe's population live in communal areas, 90% of which are located in these NRs. The majority of people living in these areas depend solely on agriculture for survival, with maize as the staple crop. This highlights the importance of reducing the genetic vulnerability of maize to drought stress.

Drought probably has its most severe effect on maize yield when it occurs during flowering. Drought stress lasting as little as one or two days during flowering may cause as much as a 22% reduction in grain yield (Hall et al., 1981). A characteristic of maize under drought stress is a delay in silking, resulting in an increased anthesis to silking interval (ASI) (Dow et al., 1984). By evaluating maize under moisture-stress during flowering, it is possible to identify genotypes with short ASIs and to use this data in conjunction with grain yield data to select for drought tolerance. This approach has been used by CIMMYT researchers to improve several maize populations including Tuxpeño Sequía (TSEQ) (Bolaños and Edmeades, 1993; Edmeades et al., 1995).

Encouraged by the improvement of TSEQ, CIMMYT has expanded its drought breeding work. ZM601, a maize streak virus (MSV) resistant, high yielding, mid-altitude-adapted population entered the drought improvement S_1 recurrent selection program in 1989, and to date three cycles of selection have been completed. Another population, ZM607, is a high yielding, MSV resistant, mid-altitude-adapted population which has not been selected for drought tolerance. This paper reports on two experiments comparing the drought tolerance and yield performance of S_1 lines from three maize populations, ZM601, ZM607 and TSEQ, grown in two agro-ecological regions (NR II and IV) of Zimbabwe during the 1994-95 season.

Materials and Methods

Germplasm

Tuxpeño Sequía is a lowland tropical, white dent population developed from Tuxpeño Crema I, a lowland tropical population with high and stable yields (Edmeades et al., 1992). Tuxpeño Sequía has undergone eight cycles of full-sib recurrent selection for drought tolerance under managed drought stress in Mexico (Byrne et al., 1995). Cycle six of the population was reselected at CIMMYT-Zimbabwe for resistance to *Exserohilum turcicum* (Northern leaf blight) and *Puccinia sorghi* (common rust), as well as for yield under rainfed stressed and unstressed conditions. Selection for disease resistance did not change its drought tolerance (Short and Edmeades, 1991; Magorokosho and Pixley, 1995). A second improvement cycle in Zimbabwe is near completion.

ZM601 is a late maturing maize population with white, mixed dent and flint kernels, which is adapted to mid-altitude environments. The population was developed from a cross of EV7992 from Tanzania, and an MSV resistant conversion of CIMMYT's Population 43 (Magorokosho and Pixley, 1995). An S_1 *per se* recurrent selection scheme was used. For cycles 1 and 2 of improvement, testing of lines was under three water regimes in Mexico and under rainfed stressed and unstressed conditions in Zimbabwe (Short and Edmeades, 1991). More recent improvement has used evaluations at rainfed stressed and unstressed sites in Zimbabwe only.

ZM607 is a late maturing, high yielding, mid-altitude-adapted population developed at CIMMYT-Zimbabwe. It has not been selected for drought tolerance. It was developed from a cross of EV7992 and an MSV resistant conversion of CIMMYT's Population 44. This population has been improved for three cycles for high grain yield under adequate moisture, but we expect that sufficient variation in drought adaptive traits exists within it, and that with appropriate selection techniques, good drought tolerant lines can be obtained.

Experiments

Experiment 1 compared 143 random S_1 lines derived from ZM601c3F1 with 97 from ZM607c3F1. The lines were evaluated during summer 1994-95 using alpha-lattice designs at three locations in NR IV (Makoholi, Drewton Farm and Matopos) and one location in NR II (Harare). Plant density was 27,000 in NR IV and 53,000 ha^{-1} in NR II. One row plots of 4 m length were used. Data recorded were: days to 50% of plants shedding pollen (AD), days to 50% of plants with silks (SD), plant stand, number of ears with grain, grain yield (GY, t ha^{-1} at 12.5% moisture), leaf rolling score (LROL: 1 = unrolled to 5 = completely rolled), leaf erectness score (LERECT: 1 = upright to 5 = lax), and tassel size score (TSIZE: 1 = small to 5 = large). ASI was calculated as SD-AD, and number of ears per plant (EPP) was calculated as number of harvested ears divided by plant stand.

Experiment 2 compared 162 random S_1 lines derived from ZM601c3F2 with 154 from [TSEQc6]c1F2. Trial sites and season, experimental design, plant density, plot size and data recorded were as in experiment 1. The ZM601 lines were different in experiments 1 and 2.

For both experiments, the data were subjected to lattice analysis of variance for each site before across-location ANOVA and phenotypic correlation analyses were done using SAS (SAS Institute, Inc., 1985). For each experiment, the data were analyzed as two distinct environment sets: NR IV sites, which are drought-prone and with marginal yield potential (Makoholi, Drewton Farm and Matopos), and NR II, which was generally well-watered and with high yield potential (Harare). Phenotypic correlation coefficients were calculated using entry means across sites within environment sets.

Results and Discussion

Responses in grain yield

In experiment 1, grain yield reductions from NR II to NR IV were 65 and 64% for lines from ZM601 and ZM607, respectively (Table 1). ZM607 lines slightly outyielded ZM601 lines under all environments, although the differences were not significant (Table 1). These results suggest that selection for drought tolerance using rainfed stressed conditions in Zimbabwe's NR IV has not resulted in significant yield advantage for ZM601 when compared to ZM607.

In experiment 2, GY responses were of a cross-over nature; lines from TSEQ outyielded ZM601 lines by 33% in NR IV, but in NR II ZM601 lines out yielded those from TSEQ by 15%. The cross-over interaction of populations with environments for yield indicates greater adaptation of ZM601 to favorable Zimbabwean conditions, but superior drought tolerance of TSEQ. Neither of these results is surprising: ZM601 originates from Zimbabwe, whereas TSEQ is from Mexico, and ZM601 has been selected for 3 cycles using rainfed drought stress, whereas TSEQ was improved for 6 cycles using carefully managed moisture-stress regimes.

Responses in flowering behavior

The three populations had similar flowering dates (AD) when evaluated in NR II, without moisture stress. This fact is important to further conclusions because it indicates that the populations are of similar maturity and were at a similar phenological stage whenever moisture stress occurred in NR IV. Differences in performance in NR IV should be due to differences in drought tolerance of the lines.

Table 1. Grain yield, anthesis silking interval, ears per plant and anthesis date for three maize populations evaluated in two experiments at three sites in NR IV and 1 site in NR II, Zimbabwe, 1994-95.

Experiment	Population	NR IV	NR II
Grain yield (t ha^{-1})			
1	ZM601	1.19	3.41
1	ZM607	1.24	3.45
2	ZM601	1.26**	2.48**
2	TSEQ	1.68	2.16
Anthesis-silking interval (ASI, days)			
1	ZM601	2.46*	0.14
1	ZM607	2.79	-0.01
2	ZM601	2.23**	-0.17
2	TSEQ	0.63	-0.16
Ears per plant (EPP)			
1	ZM601	0.99	1.40
1	ZM607	0.93	1.34
Anthesis date (AD, days)			
1	ZM601	80.64**	72.67
1	ZM607	79.64	72.09
2	ZM601	83.35*	72.72
2	TSEQ	79.23	72.05

*, ** Significant differences between populations within an experiment at $P<0.05$ and $P<0.01$, respectively.

In experiment 1, ZM607 lines had significantly larger average ASI than those from ZM601 in NR IV, although this difference was small (Table 1). Frequency distributions of lines for ASI were similar, except that ZM607 had more lines with large ASI than ZM601 (Fig. 1A). In both experiments, ASI in NR II was close to zero days (Table 1), with no significant differences between populations in either experiment. Mean and frequency distributions of lines for ASI were clearly different for the populations in experiment 2; TSEQ had many more lines than ZM601 with short ASI (Fig. 1B).

These results suggest that selection of ZM601 under rainfed moisture-

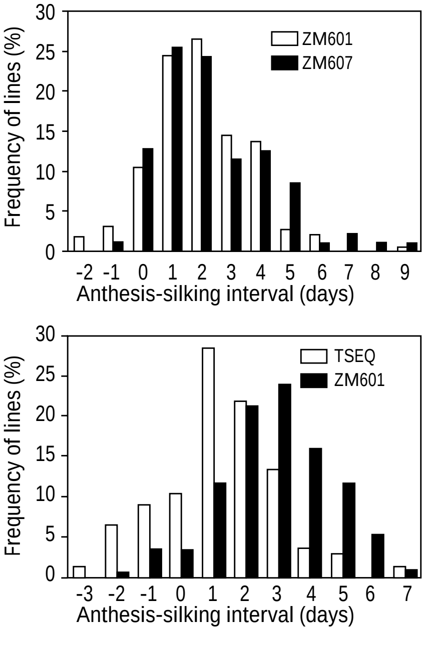

Figure 1. Frequency distributions for anthesis-silking interval of S_1 lines in two experiments evaluated at three sites in NR IV, Zimbabwe, during the 1994-95 season; experiment 1 is presented in diagram A and experiment 2 in B.

stressed conditions may have eliminated the worst fraction of the population for ASI. It is somewhat disappointing, however, that the frequency distributions for ASI do not show greater differences between ZM601 and ZM607; ZM601 had been selected for drought tolerance for 3 cycles and ZM607 had not been selected under moisture-stressed conditions. It is possible that use of rainfed stressed and unstressed sites did not sufficiently stress the germplasm to expose enough variation for ASI and thus enable large selection gains for reduced ASI. Alternatively, one could speculate that the general good performance of ZM607 may partly result from characteristics that include shorter-than-average ASI, even though the population has never been deliberately selected for this trait.

Table 2. Mean scores for leaf rolling, leaf erectness and tassel size score for S_1 lines from three maize populations evaluated in two experiments at three sites in NR IV, Zimbabwe, 1994-95.

Experiment	Population	Score
Leaf rolling score[†] (LROL)		
1	ZM601	2.50
1	ZM607	2.57
2	ZM601	2.86
2	TSEQ	2.88
Leaf erectness score[‡] (LERECT)		
1	ZM601	2.70
1	ZM607	2.71
2	ZM601	1.86**
2	TSEQ	1.76
Tassel size score[§] (TSIZE)		
1	ZM601	2.85
1	ZM607	2.80
2	ZM601	2.81*
2	TSEQ	2.93

[†] Leaf rolling score (1= unrolled to 5= completely rolled); [‡] leaf erectness score (1= upright to 5= lax); [§] tassel size score (1= small to 5= large).

*, ** Significant difference between populations within an experiment at P≤0.05 and P≤0.01, respectively.

Differences in ASI between lines of ZM601 and TSEQ clearly document the superior tolerance of TSEQ to drought at flowering.

For literature concerning the physiological bases of drought-induced changes in ASI for maize, the reader is referred to Edmeades et al. (1995), Dow et al. (1984), Westgate and Bassetti (1990), and Troyer (1983).

Secondary traits

Comparison of the secondary traits leaf rolling, leaf erectness and tassel size revealed few and only small differences among the populations (Table 2). In experiment 2, TSEQ lines had larger tassels and more upright leaves than lines from ZM601. Large tassels are generally considered undesirable because they compete with the ear as a sink for photosynthates. The slightly larger tassel size of TSEQ may be a reflection of its tropical pedigree and/or a manifestation of generally greater vigor relative to ZM601. TSEQ has been selected for upright leaf character because this is believed to optimize leaf-water status under conditions of moisture stress (Blum, 1988).

Correlations of various traits with grain yield under drought stress

Grain yield in NR IV was negatively associated with ASI for lines from both ZM601 and ZM607, but not for TSEQ (Table 3). This result points to the greater drought tolerance of TSEQ relative to the other populations. We hypothesize that ASI of TSEQ lines in this experiment was sufficiently short so as not to constitute an important determinant of yield. A significant number of lines from ZM607 and ZM601, however, had ASI values large enough that yield was adversely affected. Correlations for ASI with GY suggest that yield gains for moisture stressed sites might be achieved for ZM601 and ZM607, but not for TSEQ, by selecting for reduced ASI in rainfed NR IV. Further improvement of grain yield using ASI as an indirect selection trait may be possible for TSEQ if lines are evaluated under more severe moisture stress.

Days to 50% anthesis (AD) was negatively correlated with grain yield for lines from population ZM601 (in both experiments) and those from ZM607(experiment 1), but not for TSEQ (experiment 2). Earliness and, hence, drought escape were

Table 3. Phenotypic correlation coefficients between grain yield under moisture stress and various traits, determined from 94 to 162 S_1 lines from three maize populations, evaluated in two experiments at three sites in NR IV, Zimbabwe, 1994-95.

	Experiment 1		Experiment 2	
Trait	ZM601	ZM607	ZM601	TSEQ
Anthesis silking interval (ASI, days)	-0.27**	-0.25**	-0.43**	-0.13
Ears per plant (EPP)	0.17*	0.14	Not measured	
Anthesis date (AD, days)	-0.31**	-0.22*	-0.18*	0.29**
Leaf rolling score (LROL)	-0.04	-0.21*	-0.26**	-0.11
Leaf erectness score (LERECT)	-0.15	-0.12	0.01	-0.16*
Tassel size score (TSIZE)	0.07	0.06	0.12	0.18*

*, ** = Significant P≤0.05 and P≤0.01, respectively.

important for ZM601 and ZM607, whereas drought tolerance enabled TSEQ lines to achieve greater yield by delaying maturity. The positive correlation of AD with GY for TSEQ in NR IV challenges the widespread perception that escape through earliness is the best solution to maize varietal requirements in drought-prone regions.

High grain yield in NR IV was generally unrelated to leaf rolling, leaf erectness, and tassel size for lines from both ZM601 and ZM607 in experiment 1. In experiment 2, grain yield was associated with leaf rolling for lines from ZM601 but not for lines from TSEQ. Leaf erectness and tassel size scores were weakly correlated with grain yield for lines from TSEQ, but were unrelated to grain yield for lines from ZM601. This contrasts with results of Edmeades et al. (1995), who found that smaller tassels were weakly associated with grain yield under drought stress.

Summary and Conclusion

Grain yield of ZM601 was not different from that of ZM607 in moisture-stressed or unstressed sites. ASI was significantly shorter for ZM601 than for ZM607, but this difference was small. Although this experiment did not include a baseline to allow comparison of progress from selection for these two populations, it is apparent that improvement of ZM601 in rainfed drought-stressed sites has not resulted in a significant yield advantage over ZM607.

Tuxpeño Sequía was clearly more tolerant than ZM601 to drought at flowering. Earliness resulted in drought escape and greatest grain yield for ZM601 and ZM607. By contrast, TSEQ had a positive correlation of anthesis date with grain yield, indicating that drought tolerance enabled it to take advantage of a longer growing season. This result challenges the widespread perception that escape through earliness is the best solution to maize varietal requirements in drought-prone regions.

Cross-over interactions of populations by environments for grain yield highlighted the need for simultaneous selection for moisture-stressed and unstressed conditions if the improved population is expected to yield well in both types of environments.

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Identification and Development of Drought Tolerant Maize Cultivars in Cameroon

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Abstract

In an attempt to form a pair of heterotic drought tolerant populations adapted to the Sudan Savanna of Cameroon, seven varieties introduced from drought-prone areas of West Africa and from CIMMYT were crossed in a partial diallel during the 1991 second growing season. In Evaluations of 31 F_1s obtained at four Sudan Savanna environments in 1992, Tuxpeño Sequía × BDP-SR, MAKA-SR × FBC_6 and MAKA-SR × Tuxpeño Sequía demonstrated 16%, 13% and 12% high parent heterosis, respectively, and 5.1 t/ha average yield. Among the 10 top F_1s, MAKA-SR and Tuxpeño Sequía were involved as parents in four and three crosses, respectively. This suggests that they are good combiners, and the observed heterosis indicates that they belong to opposing heterotic pools. During the 1993 season, six drought tolerant varieties and three drought tolerant inbreds introduced from IITA, in addition to MAKA-SR, Tuxpeño Sequía, Pool 16 DT and P_2 Kollo from Niger, were reciprocally crossed in an incomplete diallel. The resulting crosses were evaluated in three drought-prone sites. Results showed that the general combining ability (GCA) of parents varied with their utilization as male or female. Used as female, MAKA-SR, KU 1414, Tuxpeño Sequía, DR-SR-W_3 and DR SYNT exhibited positive GCA. Used as male MAKA-SR, Tuxpeño Sequía, DR-SR-Y_1, 1787 and Pool 16 DT showed positive GCAs. Early-to intermediate-maturity varieties exhibiting better floral synchronization, good standability at 65,000 plants/ha, and good yield potential were recombined and advanced to F_2 in 1994.

Moisture stress resulting from limited rainfall has been considered as one of the most important maize production constraints in the savanna area of West Africa (Rodriguez, 1985; Lawson and Juo, 1979). Two breeding strategies have been suggested to develop maize varieties suited to these areas: breeding for short duration and breeding for yield under a lower level of moisture supply. The former is often referred to as drought avoidance and the latter as tolerance (Martiniello, 1984). Cameroon's savanna area can be divided into four distinct zones based on average annual rainfall. These include:

1. North Sahel with less than 500 mm per year.
2. South Sahel with 500 to 800 mm per year.
3. Sudan Savanna with 800 to 1100 mm per year.
4. North Guinea Savanna with 1100 to 1400 mm per year of rainfall (Empig et al., 1986).

Maize is grown in all these areas except the North Sahel Savanna zone.

Genetic variability for drought tolerance has been demonstrated in maize by several researchers (Martiniello, 1984). Among the most thoroughly investigated are the 'latente' group of varieties (Castleberry and LeRette, 1979) and the Tuxpeño Sequía population of CIMMYT (Fischer et al., 1983). These two populations have been tested per se in Central Africa along with the SAFGRAD materials, but with limited success (The et al., 1985).

The Cameroon maize program used data from trials conducted by SAFGRAD and IITA from 1986 to 1991 to identify nine varieties with superior performance that trace to drought-prone areas. Those varieties constituted the basic materials being used for the development of drought tolerant maize cultivars in Cameroon.

Specifically, the objectives of the Cameroon maize program were 1) to develop early drought tolerant maize cultivars for the Sudan Savanna and Northern Guinea Savanna, and 2) to develop two mutually heterotic drought-tolerant populations adapted to Cameroon Savanna zones.

Materials and Methods

In 1986 a Cameroonian visiting scientist to IITA screened 120 maize inbreds lines for drought tolerance in a glasshouse under controlled moisture. Leaf rolling and plant wilting were used as major evaluation criteria. Beginning 40 d after planting, maize plants grown in pots (one plant per plot) were subjected to a 21d period during which no moisture was applied. The uniformity of inbred lines enables differences among lines to be easily detected. Selected lines were recombined to form the drought population, DR SYNT. In 1991, nine varieties were crossed in a partial diallel mating design. Seven of these originated from drought-prone areas of West Africa and the other two from CIMMYT. These were MAKA-SR from Mauritania; FBC_6 from Burkina Faso; Tuxpeño Sequía and La Posta Sequía from CIMMYT; BDP-SR from North Côte d'Ivoire; CSP-SR and TZEE-W-SR, all identified from SAFGRAD regional uniform variety trial (RUVT); P_3 Kollo from Niger; and CMS 9015 developed from Kamboinse 88 Pool 16 DT. The F_1 crosses were evaluated in 1992 at four environments using a 7×7 lattice experimental design. During the 1993 growing season, six drought tolerant varieties released from IITA, three drought-tolerant inbred lines identified in the 1986 IITA glasshouse study, and four varieties retained from the 1992 study were crossed in an incomplete diallel mating design. The resulting crosses were evaluated at three drought-prone sites in Sudan and the North Guinea Savanna zone of Cameroon. The drought tolerant varieties from IITA consisted of DR-SYNT, DR-SR-W_3, DR-SR-Y_1, DR-SR-Y_3, DR-SR-Y_2 A and DR-SR-W_2. The inbred lines were 1787, 9848 and Ku 1414-SR, and the varieties retained from the 1992 study were MAKA-SR, Tuxpeño Sequía, Pool 16 DT (CMS 9015) and P_3 Kollo. Varieties selected from this trial were crossed during the 1994 season to form two pools comprising a pair of opposing heterotic populations. Selection of these varieties was made based on high parent heterosis (varieties needed to show at least 10% high parent heterosis), good yield potential, floral synchronization, and standability at 65,000 plants ha^{-1}. Fertilizer was applied at recommended rates, with a side-dressing of fertilizer applied no later than 25 d after planting. An experimental unit for the evaluation of F_1 crosses consisted of a 1 row plot, 5 m long.

Results and Discussion

Drought tolerance ratings of the most tolerant and most susceptible maize lines identified in 1986 in the glasshouse test have been previously reported (IITA, 1986). The most tolerant line was Ku 1414, a downy mildew resistant line developed by the Thailand National Maize Program. Some IITA lines also showed high levels of tolerance. These included 5012, 9499, 1787, and 9848. The most susceptible lines were 5057 and Mo 20W. After the 21 d stress period, Ku 1414 plants showed a 25% decrease in plant height and a 14% decrease in leaf area as compared to unstressed Ku 1414 plants. Plants of the most susceptible line, Mo 20W, were much more affected by stress, and plant height and leaf area were decreased by more than 50%. The transpiration rate of Ku 1414 (0.06 ml/cm^2) was one fourth that of Mo 20W (0.24 ml/cm^2) under unstressed conditions.

Results from the evaluation of the 1992 partial diallel are shown in Table 1. Data obtained for the 31 F_1 crosses evaluated across four environments revealed that the highest yielding crosses were Tuxpeño Sequía × BDP-SR, MAKA-SR × FBC_6 and MAKA-SR × Tuxpeño Sequía. Each yielded 5.1 t ha^{-1}. These crosses exhibited 16%, 13% and 12% high parent heterosis. Among the 10 top F_1s, MAKA-SR was involved in four crosses while Tuxpeño Sequía appeared in three. These findings suggest that MAKA-SR and Tuxpeño Sequía are good general combiners. Their cross also exhibited good specific combining ability (12% high parent heterosis). This suggests that the two varieties belong to opposite sides of a heterotic pattern, and that they could be used as testers to form distinct heterotic groups.

The results from the evaluation of the 1993 incomplete diallel are shown in Table 2. Used as females, MAKA-SR, Ku 1414-SR, Tuxpeño Sequía, DR-SR-W_3 and DR SYNT showed positive general combining abilities (GCAs). The best combiners were DR-SR-W_3, followed by Ku 1414 SR. When used as males, MAKA-SR, Tuxpeño Sequía, DR-SR-Y_1, DR-SR-Y_3, 1787 and Pool 16 DT exhibited positive GCAs. The crosses with the best specific combining ability were DR-SR-Y_1 × Tuxpeño Sequía (6.7 t ha^{-1}), Pool 16 DT × 1787 (6.4 t ha^{-1}) and Pool 16 DT × DR-SR-Y_2 A (6.2 t ha^{-1}). In addition, it was noticed that crosses involving DR-SR-W_3 and Ku 1414-SR as female yielded better than the others on average. The above results suggested that the GCAs of parents involved in these crosses varied with their utilization as male or female.

Table 1. Mean grain yield and high parent heterosis (het.) for selected crosses, 1992.

	Mayo Galké	Sanguere	Soucoundou	Maroua	Means	Het.
	t/ha					(%)
Crosses						
MAKA SR × FBC_6	3.9	5.9	6.4	4.3	5.1	13
MAKA SR × Tuxpeño Sequía	4.0	6.5	5.7	4.4	5.1	12
CSP SR × BDP SR	2.5	5.1	5.5	4.6	4.4	10
FBC_6 × MAKA SR	3.8	6.0	5.8	4.2	4.9	9
FBC_6 × TZEE-W-SR	3.6	5.3	6.1	5.1	5.0	11
FBC_6 × Tuxpeño Sequía	4.2	6.1	6.1	3.5	5.0	11
BDP-SR × MAKA SR	3.4	5.3	5.2	4.7	4.6	10
TZEE-W-SR × MAKA	3.8	5.5	5.4	4.1	4.7	12
Tuxpeño Sequía × BDP SR	4.0	6.5	6.6	3.5	5.1	16
Tuxpeño Sequía × FBC_6	4.0	6.4	6.4	3.5	5.0	11
Parents of crosses						
MAKA SR	2.6	5.2	5.3	3.9	4.2	
FBC_6	3.4	6.1	5.6	3.0	4.5	
Tuxpeño Sequía	3.3	5.5	5.8	3.0	4.4	
BDP SR	2.7	5.2	4.9	3.2	4.0	
TZEE-W-SR	2.9	3.8	4.3	3.9	3.4	
CSP-SR	2.0	3.7	4.7	3.2	3.4	
Checks						
P_3 Kollo	1.6	3.8	4.7	3.6	3.4	
CMS 9015	3.0	4.8	5.5	3.3	4.1	
CMS 8806	4.0	5.0	5.3	4.1	4.6	
SYN E1	3.9	5.3	4.8	3.2	4.3	
SYN E2	3.4	5.0	6.0	3.9	4.6	
Means	3.3	5.4	5.6	3.7	4.5	
CV (%)	21.0	15.1	16.0	26.9	17.2	
LSD $_{(0.05)}$	0.9	1.1	1.2	1.4	1.1	

Based on the 1993 incomplete diallel results, varieties were classified into opposing heterotic pools. Pool I included Tuxpeño Sequía, DR-SR-W_3, Ku 1414, 1787, DR-SR-Y_2A, and Pool 16 DT. Pool II was made up of MAKA-SR, 9848, DR-SR-Y_1, DR-SR-Y_3, DR-SR-W_2. Early- to intermediate-maturity varieties exhibiting better floral synchronization and good standability at 65,000 plants ha^{-1} were recombined and advanced to F_2

Table 2. Grain yield (t/ha) from the drought partial diallel and GCA effects, 1993.

	Male													Array	GCA
Female	1	2	3	4	5	6	7	8	9	10	11	12	13	means	effects
1. Maka SR	4.7		4.1			6.2					5.5	5.0		5.2	+0.3
2. Ku 1414 SR	5.6		4.4		5.1		4.2	5.2	4.1	4.4	4.7	3.7	5.7	4.6	-0.3
3. 9848		5.3												5.3	-
4. Tuxpeño Sequía	4.8	5.6	5.8	4.3			5.0	5.7	5.8	4.5	4.6			4.6	-0.3
5. DR-SR-W_2	4.4	5.3	5.1		4.6	4.8					5.6	4.7	3.8	4.8	-0.1
6. DR-SR-W_3	5.6		4.8	5.0		4.8	4.8				4.1	4.9	4.7	4.7	-0.2
7. DR-SR-Y_1	5.1	5.0	5.5	6.7			5.6	4.1			5.3	5.2		5.4	+0.5
8. DR-SR-Y_2A	5.7	5.6	3.9				3.9	5.0		4.5	4.6	4.9		4.7	-0.2
9. DR-SR-Y_3	4.7	5.7	4.7	4.4		5.4			4.9		4.6	4.3		5.0	0.1
10. DR SYNT		5.6	4.7	5.7	4.3		4.8	5.7		4.7	4.9	3.9	3.6	4.8	-0.1
11. 1787	5.8	5.5	5.5	5.1	5.4		5.1	4.5	5.4					5.3	0.4
12. Pool 16 DT	5.1	5.8	4.8	4.9			5.4	6.2	4.7	5.0	6.4	4.4		5.3	0.4
13. P_3 Kollo		4.3	5.1			6.1					4.8	5.1	2.9	4.7	-0.2
Array means	5.1	5.4	4.9	5.2	4.9	5.5	4.9	5.2	5.0	4.6	5.0	4.6	4.2	4.9	
GCA effects	0.1	0.4	-0.1	0.2	-0.1	0.5	-0.1	0.2	0.0	-0.4	0.0	-0.4	-0.4		

in 1994. Additional work will consist of improving the two pools by reciprocal recurrent selection under controlled moisture and to subdivide the pools by color.

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Progress in Breeding for Drought Tolerance in Tropical Early Maturing Maize for the Semi-Arid Zone of West and Central Africa

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Abstract

Drought constitutes one of the most important factors limiting maize production in the semi-arid zone of West and Central Africa. Using tied and untied ridges to simulate differing moisture conditions, an early maturing maize population, Pool 16 DT, has undergone eight cycles of selection for drought tolerance. Twelve drought-tolerant early-maturing maize varieties have been extracted from this population since 1982 and been made available to national programs in West and Central Africa. To determine progress in breeding for drought tolerance, the varieties extracted from the population were evaluated under non-stress and droughted conditions. The best drought tolerant variety had a yield comparable to the best drought susceptible variety under non-stressed conditions. Correlations between grain yield, anthesis-silking interval (ASI) and ears plant^{-1} *under non-stress conditions were not significant. Under drought stress, however, grain yield and ears plant*$^{-1}$ *were positively correlated (r = 0.67**), and grain yield and ASI were negatively correlated (r = -0.28*). When evaluated under drought stress, differences were detected among varieties for grain yield, ASI, and ears plant*$^{-1}$, *with several drought tolerant varieties from advanced cycles of Pool 16 DT showing superior performance.*

Recurrent drought constitutes one of the major abiotic factors limiting crop production in the semi-arid zone of West and Central Africa. Long-term records show a consistent decrease in total rainfall over time, with alternating dry and wet periods (Farmer and Wigley, 1985). Since 1968, a persistent dry spell has been experienced by all sub-Saharan African countries, particularly in the Sudan savanna zone. Aggravating this is the unreliable and unpredictable year-to-year variability in rainfall that characterizes the semi-arid zone (Eckebil, 1991). It is estimated that drought accounts for yield losses of around 15% annually, though localized losses are likely to be much higher in marginal areas where annual rainfall drops below 500 mm, or where the soils are sandy or shallow (Edmeades et al., 1995). Tolerance to low soil moisture stress is an important trait for increased and stable production in the semi-arid zone of West and Central Africa.

The International Institute of Tropical Agriculture - Semi-Arid Food Grain Research and Development (IITA-SAFGRAD) project initiated a research program in 1979 aimed at developing drought tolerant varieties and moisture conserving agronomic practices, in an effort to meet the challenges posed by drought in the semi-arid zone of West and Central Africa. Agronomic research carried out by IITA-SAFGRAD showed a marked response of maize to tied ridges in the ferruginous tropical soils of the Sudan savanna. Tied-ridges reduce run-off losses and improve water infiltration (Diallo and Rodriguez, 1987).

It was possible to evaluate the performance of maize genotypes under two drought stress conditions by growing them on tied and untied ridges at Kamboinse in the Sudan savanna zone. These conditions simulated two levels of moisture stress, and continue to be used in the population improvement program and for varietal evaluations.

The Sudan savanna zone is characterized by considerable year-to-year variability, in the start and end of the rainy season, in total rainfall and its distribution, and in unpredictable occurrences of 1-3 week dry spells during the rainy season. Consequently, the IITA-SAFGRAD project concentrated its efforts on the development of varieties that combine earliness (82-95 days to maturity) with drought tolerance. In years when the rains start late, however, or when there is a long dry spell of 2-3 weeks after the start of the rainy season, extra-early varieties (less than 82 days to maturity) are preferable to early varieties. So, to reduce the risk of farmers in those years and to widen the area of maize cultivation in the semi-arid zone, development of extra-early varieties was initiated by the IITA-SAFGRAD Project.

Pool 16, a white dent early-tropical maize population developed by CIMMYT, is well adapted to the Guinea and Sudan savanna zones of West and Central Africa. In 1982, Pool 16 was identified as tolerant to drought stress. A recurrent full-sib selection scheme was employed to improve this population for drought tolerance, and the improved version was named Pool 16 DR (Diallo and Rodriguez, 1987). In collaboration with IITA, maize scientists at Ibadan, Pool 16 DR was converted to streak resistance and renamed Pool 16 DT in 1992.

Other sources of drought tolerant varieties used by the IITA-SAFGRAD project are the two populations, DRT-E-W (Early white dent) and DRT-E-Y (Early yellow flint). The two populations were formed in 1988 from landraces that evolved in semi-arid West African countries and some improved varieties that showed good performance under drought stress. Conversion of the two populations to streak resistance was initiated using artificial infestation of viruliferous leafhoppers. Presently, each population has a good level of resistance to maize streak virus.

Traits such as number of ears plant^{-1} (reduced barrenness), anthesis and silking dates and the anthesis-silking interval (ASI) are influenced by drought stress and have proved useful when selecting for drought tolerance in maize (Herrero and Johnson, 1981; Struck et al., 1986; Bolaños and Edmeades, 1988; Edmeades and Bolaños, 1989; Edmeades et al., 1995). Since 1982, Pool 16 DT has undergone eight cycles of improvement for drought tolerance using full-sib recurrent selection for reduced ASI, increased ears plant^{-1} and increased grain yield, while maintaining maturity in order to prevent the selection of escapes. Tied and untied ridges (at Kamboinse, Burkina Faso), as well as high plant density (at Farako-Ba, Burkina Faso in the Guinea savanna zone), have been used to induce different moisture levels and stressed conditions for selection. Using these strategies, several drought tolerant varieties have been extracted and released by national programs in West and Central Africa. The purpose of this study was to:

1. Compare the performance of drought tolerant varieties extracted from Pool 16 DT and other sources under stressed and non-stressed environments.
2. Quantify the progress made after eight cycles of full-sib selection Pool 16 DT.

Materials and Methods

The performance of 15 drought-tolerant and two susceptible open-pollinated early maturing maize varieties (Table 1) was evaluated

Table 1. Description of early maturing maize cultivars evaluated in two water-stressed and three well-watered environments in West Africa.

Cultivar	Origin	Drought stress reaction
Across 86 Pool 16 DT	IITA-SAFGRAD/CIMMYT	tolerant
FBA 86 Pool 16 DT	IITA-SAFGRAD/CIMMYT	tolerant
Across 87 Pool 16 DT	IITA-SAFGRAD/CIMMYT	tolerant
Across 88 Pool 16 DT	IITA-SAFGRAD/CIMMYT	tolerant
FBA 88 Pool 16 DT	IITA-SAFGRAD/CIMMYT	tolerant
FBA 88 Pool 16 DT (HD)	IITA-SAFGRAD/CIMMYT	tolerant
Across 90 Pool 16 DT	IITA-SAFGRAD/CIMMYT	tolerant
FBA 90 Pool 16 DT (HD)	IITA-SAFGRAD/CIMMYT	tolerant
Maroua 90 Pool 16 DT	IITA-SAFGRAD/Cameroon/CIMMYT	tolerant
Pool 16 Sequia	CIMMYT	tolerant
Kamb 88 Pool 16 DT	IITA-SAFGRAD/CIMMYT	tolerant
DR-Y Pool SR BC_2F_2	WECAMAN/IITA	tolerant
DR-W Pool SR BC_2F_2	WECAMAN/IITA	tolerant
EV DT 94 C_3	WECAMAN/IITA	tolerant
DRT-E-Y	WECAMAN	tolerant
DRT-E-W	WECAMAN	tolerant
TZE Comp 4 C_1	IITA	susceptible
Safita-2	IITA-SAFGRAD/CIMMYT	susceptible

under rainfed conditions during the regular planting season and in dry-season nursery conditions. Five trial sets were evaluated. The first was planted on 21 July, 1995 at Sinematiali, Cote d'Ivoire (latitude 9^o 37'N, 305 masl). Rainfall during the test period was 517 mm, which was below the average annual rainfall of 944 mm. The second set was planted on 19 July at Ferkessedougou, Cote d'Ivoire (latitude 9^o 35'N, 325 masl), which had a below average rainfall of 594 mm. The third set was planted on 27 July, 1995 at Kamboinse, Burkina Faso, in the Sudan savanna zone (latitude 12 ^{o} 28'N, 296 masl), which had a rainfall of 491 mm, slightly below the average of 600 mm recorded for this zone. Planting was timed so that flowering and grain filling occurred during the drought period. The fourth and fifth sets were planted in 1995-96 dry-season nursery (November - March) at Ferkessedougou. The fourth was the irrigated control, while the fifth had no irrigation from about two weeks before flowering until the end of the season. The experimental design was a randomized complete block with four replications for the trials planted during the growing season and three replications for those in the dry-season nursery. Each plot consisted of two 5 m rows, with row and hill spacings of 0.75 and 0.40 m, respectively. Three seeds were planted hill^{-1} and later thinned to two, giving a plant density of 66,700 ha^{-1}. Fertilizer was applied at 75:75:75 kg N:P_2O_5:K_2O ha^{-1} at sowing as compound fertilizer. An additional 69 kg N ha^{-1} was topdressed four weeks later. Sprinkler irrigation was used to apply 12 mm of water per week over all treatments in the dry-season nursery at Ferkessedougou until about two weeks before flowering. The irrigation was continued only in the control treatments during the remainder of the growing season.

Thirty bordered plants were randomly chosen in each plot for collecting the flowering data (days to 50% anthesis and silking). Anthesis-silking interval was calculated as the difference between 50% anthesis and 50% silking. Ears plant^{-1} was determined by dividing the total number of ears harvested by the number of plants harvested, and grain yield (at 15% grain moisture) was obtained from shelled grain (trials conducted under drought stress) or by assuming a shelling percentage of 80% (trials conducted under well-watered conditions). Varieties developed from cycles 0, 1, 2, 4 and 8 of selection were among the 15 drought-tolerant entries. Mean grain yield of the varieties from each cycle was regressed on the selection cycles to obtain estimates of gain per cycle. The estimates were obtained for the stressed, non-stressed and combined environments.

Results

Grain yield, days to 50% silking, ASI and ears plant^{-1} of early-maturing maize cultivars evaluated in three well-watered and two water-stressed environments are presented in Table 2. EV DT 94 C_3, TZE Comp 4 C_1, FBA 90 Pool 16 DT (HD), Kamb 88 Pool 16 DT and Across 88 Pool 16 DT were the five top yielding varieties in well-watered environments. Of these varieties, only TZE Comp 4 C_1 is known to be drought susceptible. The lowest yielding group of entries comprised DR-W-Pool SR BC_2F_2, Pool 16 Sequia, Maroua 90 Pool 16 DT and Safita-2. The remaining varieties could be classified as intermediate for grain yield. In the water-stressed environment, the drought tolerant variety, DRT-E-Y and FBA 88 Pool 16 DT (HD), which in well-watered environments were among the intermediate and lowest yielding entries, recorded the highest grain yields. The variety TZE Comp 4, one of the latest to flower, was among the highest yielding entries in well watered environments but was one of the lowest yielding entries under drought stress. Safita-2, a variety extracted from Pool 16 but not intentionally selected for drought tolerance, and Pool 16 Sequia, a drought tolerant version of Pool 16 selected mainly in Mexico, were the lowest yielding entries in well-watered environments, but showed high yield under water-stress. The varieties EV DT 94 C_3, Across 88 Pool 16 DT, FBA 88 Pool 16 DT(HD), DRT-E-Y and DR-Y Pool SR BC_2F_2 yielded well in both stressed and non-stressed environments. A non-significant rank correlation (r = -0.18) was obtained between yield performance under stress and under well-watered conditions. The results revealed that days to silking of the varieties were prolonged under water stress. Similarly, water-stressed conditions increased ASI and reduced ears plant^{-1}. Grain yield was strongly correlated with ears plant^{-1} ($r = 0.67^{**}$) and showed a weak negative correlation with ASI ($r = -0.28^{*}$) under stressed conditions, though not under well-watered conditions (Table 3). There was no significant interaction between ASI and ears plant^{-1} in either the well-watered or the water-stressed environments.

Grain yields of the drought tolerant cultivars extracted from different improvement cycles of Pool 16 DT under water-stressed and non-stressed environments, as well as across the two water regimes, are shown in Table 4. Under well-watered conditions, drought tolerant selections from the advanced cycles of Pool 16 DT were superior to selections made in earlier cycles. Under drought conditions, however, the 1988 selections from Pool 16 DT tended to be superior to both earlier and more recent selections, EV DT 94 C4, the 1994 drought tolerant selection from Pool 16 DT, and outyielded the 1986 selection Across 86 Pool 16 DT by 6%. The 1988 selections, Across 88 Pool 16 DT and FBA 88 Pool 16 DT (HD), outyielded Across 86 Pool 16 DT by 18% and 25%, respectively. There was little or no gain in yield when the varieties from the different selection cycles were evaluated under stress conditions; only about 0.02 t/ha or 2% per cycle (Fig. 1). On the contrary, estimated gain/cycle was 0.11 t/ha (or 10% per cycle; a total gain of 0.9 t/ha in eight cycles) and 0.06 t/ha (5% per cycle; a total of about 0.5 t/ha), when selections were evaluated under non-stress and combined environments, respectively.

Discussion

The first drought tolerant cultivar from Pool 16 DT was selected in 1984. Since then, Pool 16 DT has been taken through eight improvement cycles for drought tolerance using tied and untied ridges to simulate different moisture levels and selecting for increased grain yield and ears plant^{-1}, and shorter ASI. The earlier maturing varieties appeared to have had clear advantage over the later maturing varieties. However, within the same maturity group there existed differences in grain yield among varieties, indicating that the high performance of some under drought stress was not only due to escape but also to drought tolerance.

Table 2. Grain yield, days to silk and anthesis-to-silking interval (ASI) of early maturing maize cultivars grown in three well-watered and two water stressed environments in West Africa.

	Grain yield (kg/ha)		Days to silking		ASI (d)		Ears/plant	
Maize cultivars[†]	Well-watered	Water stressed*	Well-watered	Water stressed	Well-watered	Water stressed	Well-watered	Water stressed
EV DT 94 C$_3$	6357	1191 (7)	54	56	0.4	0.9	1.0	0.7
TZE Comp 4 C$_1$	6171	1091 (13)	56	58	1.2	0.9	0.9	0.7
FBA 90 Pool 16 DT (HD)	6142	1095 (12)	54	55	0.7	0.7	1.0	0.7
Kamb 88 Pool 16 DT	5915	1010 (15)	55	57	1.6	1.6	0.9	0.7
Across 88 Pool 16 DT	5861	1366 (3)	54	55	0.7	1.0	0.9	0.8
DRT-E-Y	5775	1567 (1)	53	55	1.5	1.9	1.0	0.9
DRT-E-W	5759	1147 (9)	54	55	1.6	1.0	1.0	0.7
Across 90 Pool 16 DT	5751	1089 (14)	53	55	1.0	0.9	1.0	0.7
Across 87 Pool 16 DT	5723	935 (17)	54	57	1.4	1.1	0.9	0.8
FBA 86 Pool 16 DT	5561	1097 (11)	54	55	0.6	1.1	1.0	0.7
Across 86 Pool 16 DT	5414	1124 (10)	54	55	1.6	1.0	1.0	0.8
DR-Y Pool SR BC$_2$F$_2$	5374	1357 (4)	54	57	1.2	1.7	0.9	0.8
FBA 88 Pool 16 DT (HD)	5368	1502 (2)	54	55	0.6	1.0	1.0	0.8
DR-W-Pool SR BC$_2$F$_2$	5202	982 (16)	54	56	1.0	1.3	1.0	0.7
Pool 16 Sequia	5191	1337 (5)	54	56	0.6	1.0	0.9	0.8
Maroua 90 Pool 16 DT	5153	1208 (6)	54	56	1.0	0.6	0.9	0.8
Safita-2	5022	1167 (8)	55	55	1.0	1.4	0.9	0.8
Mean	5632	1192	54	56	1.0	1.2	1.0	0.8
LSD ($P<0.05$)	517	476	0.9	1.6	0.7	0.8	NS	NS
CV (%)	11	38	2	2	79	66	8	16

[†] Entries sorted in descending order according to grain yield in well-watered environment.

* Rank for grain yield in parentheses.

Pool 16 Sequia was among the lowest yielding entries under well-watered conditions, but it performed very well under drought stress. The fact that the varieties Kamb 88 Pool 16 DT, TZE Comp 4 and Across 90 Pool 16 DT were among the top yielding entries in well-watered environments but performed poorly under drought stress supports the findings of Badu-Apraku et al. (1995), who reported that these varieties are adapted to high-yield environments. It is interesting to note that drought tolerant varieties, EV DT 94 C_3, Across 88 Pool 16 DT, FBA 88 Pool 16 DT (HD), DRT-E-Y and DR-Y Pool SR BC_2F_2 yielded well in both stressed and non-stressed environments. The ideal maize cultivar for ensuring stable yields in the semi-arid zone should yield well both under drought and well-watered conditions. The performance of these varieties indicate that significant progress has been made in breeding for drought tolerance and yield stability, and that these varieties should therefore be promoted for adoption.

The drought tolerant selections from advanced cycles of Pool 16 DT were superior to the earlier selections under well watered conditions. Under drought stress however, selections from 1988 were superior to the selections from both earlier and later cycles. In effect, no significant progress was made for yield under drought in this population after 1988, suggesting that variation for the traits under selection might have been exhausted, or that selection sites did not discriminate among progenies. This observation was not surprising, since Pool 16 DT has been handled as a closed pool since 1982 with no introgression of drought tolerant germplasm into it. It was therefore expected that there may be little or no genetic variability for the drought adaptive traits, ASI and ears plant^{-1}. In addition, the trials reported herein were evaluated under

Table 3. Correlations between grain yield, anthesis-silking interval (ASI) and ears plant^{-1} of early-maturing maize genotypes evaluated under three well-watered and two water-stressed environments in West Africa.

Characters	Correlation coefficients Well watered	 Water stressed
Ears plant^{-1} versus yield	0.15	0.67**
ASI versus yield	-0.12	-0.28*
ASI versus ears plant^{-1}	0.03	-0.11

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

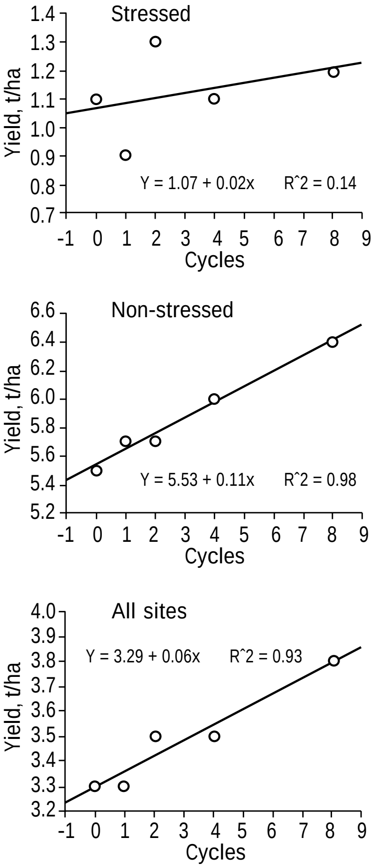

Figure 1. Response of grain yield in Pool 16 DT to eight cycles of full-sib selection for drought tolerance evaluated under moisture stress, non-stress and combined environments.

Table 4. Evaluation of the progress made in developing drought tolerant varieties from cycles of selection in Pool 16 DT.

		Grain yield (t/ha)						
		Well-watered		Water-stressed		Across sites		% grain yield of check under water stress
Maize variety	Cycle of selection	Varieties from cycles	X of cycle	Varieties from cycles	X of cycle	Varieties from cycles	X of cycle	
EV DT 94 C_3	8	6.4	6.4	1.2	1.2	3.8	3.8	106
FBA 90 Pool 16 DT (HD)	4	6.1	6.0	1.1	1.1	3.6	3.5	97
Across 90 Pool 16 DT	4	5.8		1.1		3.4		97
Across 88 Pool 16 DT	2		5.9	1.4		3.6		118
Kamb 88 Pool 16 DT	2	5.9	5.7	1.0	1.3	3.5	3.5	89
FBA 88 Pool 16 DT (HD)	2	5.4		1.5		3.4		125
Across 87 Pool 16 DT	1	5.7	5.7	0.9	0.9	3.3	3.3	80
FBA 86 Pool 16 DT	0	5.6	5.5	1.1	1.1	3.3	3.3	97
Across 86 Pool 16 DT (check)	0	5.4		1.1		3.3		100

irrigation conditions and water was withheld completely in the stressed environments from the period of rapid elongation of reproductive structures until maturity. This situation is rare during the normal growing season in the semi-arid zone of West and Central Africa and the selections may never have been subjected to such conditions. Further studies and a more comprehensive analysis of the data accumulated over the years in this selection program are needed to confirm or refute our results. The results clearly show, however, that varieties selected for drought tolerance perform well under normal season conditions but not vice versa.

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Alleviating the Effects of Drought on Maize Production in the Moisture Stress Areas of Kenya Through Escape and Tolerance

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Abstract

The effects of drought on production of maize, the staple food crop, are of considerable concern in Kenya, where over 70% of land area is arid or semi-arid. Maize germplasm improvement has relied on open-pollinated cultivars selected for earliness to fit the short growing seasons in the semi-arid areas, though hybrids are widely used elsewhere. Semi-arid eastern Kenya receives 500-800 mm rainfall per annum; relatively low, of uncertain distribution, and bimodally distributed. Inter- and intra-population improvement procedures have been used to develop 'Katumani Composite B' (KCB) and 'Makueni Composite', both early-maturing with 61 and 55 days to 50% pollen shed, respectively, at Katuman. KCB is widely grown in eastern Africa, and has an average yield of 4 t/ha under well-watered conditions. Genotype evaluations have indicated that further improvement based on earliness beyond that of KCB will be limited. Development of drought tolerant germplasm with the maturity of KCB has been initiated. The approach taken involves incorporation of drought tolerant materials developed at CIMMYT into the locally adapted populations. Advances made, reflections on methodology, and approaches to germplasm development and improvement progra are reviewed. Non-genetic strategies are also obviously necessary to maximize production of these early maturing, drought escaping and drought tolerant cultivars.

Maize is an important crop in Kenya, as reflected by the large area devoted to its production (80% of total cereal area), high human consumption levels (93% of total maize production), and its large share of the national food market. Annual production of maize is 2.7 million tons from an estimated 1.3 million hectares (KARI, 1994). At times production is less than consumption, and imports become necessary.

Table 1. Characteristics of the major maize agro-ecological zones in Kenya.

	Highland late maturity	Mid-altitude late maturity	Mid-altitude intermed. maturity	Mid-altitude early maturity	Lowland humid coastal
Elevation (masl)	>1800	1400-1800	1400-1800	900-1800	<900
Annual rainfall (mm)	>1800	1000-1800	800-1200	400-800	400-1400
Growing season (days)	120	180	170	120	120
National maize area (%)	30	42	16	8	4
National production (%)	35	25	25	10	5
Potential yield (t/ha)	6.7	5.2	3.7	2.7	3.3
Farmer yield (t/ha)	2.0	0.7	1.1	0.5	1.0
Yield gap (t/ha)	4.7	4.5	2.6	2.2	2.3

Adapted from KARI, 1994

Maize production zones in Kenya include the highland late maturity; mid-altitude late, intermediate and early maturity; and lowland humid coastal zones. These are delineated by elevation, amount of rainfall, and length of growing season (Table 1). Insect pests, lack of inputs, drought stress, low soil fertility, low yield stability among cultivars, and limited adoption of improved crop husbandry practices are the main factors limiting maize production in Kenya (KARI, 1994).

Semi-arid areas of Kenya

Most Kenya receives relief type rainfall from monsoon winds off the Indian Ocean. Highland areas in central Kenya and parts of the Rift valley and Mt. Elgon areas are considered moist. Some convectional rainfall is received around Lake Victoria and in the coastal lowlands. Less moisture is deposited in the mid-altitude areas and leeward sides of the highlands. Semi-arid areas are spread throughout Kenya, but the bulk are in the Eastern province and lower altitudes of the Rift Valley, Western, Central, Coast and Nyanza provinces. The semi-arid areas of eastern Kenya comprise the districts of Machakos, Kitui, Kajiado, Makueni, Mwingi, Tharaka-Nithi, Mbeere, Lower Kirinyaga, and Muranga. The mid-altitude early-maturity maize improvement program, based at the National Dryland Farming Research Center (NDFRC), Katumani, a center of the Kenya Agricultural Research Institute (KARI), also operates testing at selected sites outside the eastern Kenya region (Table 2).

Arid and semi-arid areas that traditionally experience moisture deficits comprise over 70% of Kenya's land area and carry over 20% of the human population. Increasing population pressure in the highlands has resulted in a forced migration of people to the semi-arid areas. These areas have an elevation of 900-1800 m and receive 400-800 mm rainfall per annum. This is distributed bimodally (long rains from March to June, short rains from October to January), with erratic distribution and rain showers often of short duration. Large fluctuations in seasonal rainfall (Keating et al., 1992) have caused recurring famine.

Maize is grown on small farm units averaging 4 ha, this land being shared with other crops and livestock (Mugo et al., 1996). These authors found that 74% of maize is produced as intercrops and only 26% in pure stands. Maize production is dependent on family labor, using ox-drawn plows and hand tools. Crop rotation with both legumes and non-legumes is practiced by 40% of the farmers. There is little use of fertilizer, but various types and forms of manure are used by 60% of the farmers. Purchased maize seed is grown by 44% and local cultivars by 67% of the farmers. Maize production is low, averaging 0.5 t/ha, and farmers perceive the major constraints to maize production to be drought, stem borers, weeds, and lack of capital for purchased inputs. Maize streak virus is not a problem in the region, in part due to resistant germplasm and the length of the cropping season; plus distinct cropping seasons with dry spells are believed to disrupt vector population dynamics (Mugo et al., 1996). Drought occurs both in the long and short rainy seasons.

Various management strategies have been proposed to minimize the effects of drought stress on maize in semi-arid Kenya. These include suitable water management, irrigation, alternative crops, and response farming techniques, where input levels are adjusted according to early season rainfall events. These technologies serve best when used in conjunction with drought-tolerant cultivars.

Table 2. Testing sites for the mid-altitude early-maturity maize improvement program.

Site	Cooperator[†]	Season	Elevation (masl)	Mean annual rainfall (mm)
Katumani	NDFRC, Katumani	Long rains, Short rains	1600	711
Kitui	NDFRC, Katumani	Long rains, Short rains	1097	766
Kampi-Ya-Mawe	NDFRC, Katumani	Long rains, Short rains	1120	698
Kiboko[‡]	NDFRC, Katumani	Long rains, Short rains	975	595
Mwea-Tebere	RRC, Embu	Short rains	1189	890
Marimanti	RRC, Embu	Long rains	900	650
Homa-Bay	RRC, Kisii	Short rains	1134	800
Pekerra	RRC, Perkera	Long rains, Short rains	1000	600
Alupe	RRC, Kakamega	Short rains	1189	1775
Mbita point	ICIPE	Long rains, Short rains	1137	850

[†] NDFRC = National Dryland Farming Research Center, ICIPE = International Center for Insect Physiology and Ecology, and RRC = Regional Research Center.

[‡] Irrigated site

Drought Escape and Tolerance in Maize

Drought escape

Drought-escaping cultivars flower early and complete the sensitive silking period while there is moisture available (Dowker, 1971). The crop completes its grain filling period utilizing residual moisture stored in the soil. However, a short growth period dictates lower biomass and grain yields under well-watered conditions, due to the reduced period for photosynthesis. Drought escape is a logical approach in an environment with inherently short rainy seasons and where seasonal rainfall amounts are regular and distribution is relatively certain.

Drought tolerance

Drought escaping cultivars vary in production with available rainfall where this is low and variable, as in eastern Kenya (Dowker, 1971, Njoroge, 1985, Keating et al., 1992, Mugo et al., 1996). Dowker (1971) demonstrated this effect by comparing an early and a late maturing cultivar, Taboran and Machakos Local White. Either resulted in superior performance, depending on the amount and distribution of the rainfall. Dowker (1971) noted that growing early-maturing maize cultivars would increase the reliability of maize yields in low rainfall areas but would decrease yields in high rainfall seasons. Thus, drought tolerant genotypes that are slightly later to flower could increase production in highly variable environments like eastern Kenya by boosting yields in both dry and well-watered seasons.

Germplasm Improvement for Drought Escape

Katumani Composite B

Development of drought escaping germplasm started with the development of two populations: Katumani synthetic series 1, based on the landrace ‘Machakos Local White’; and Katumani synthetic series 2, based on ‘Taboran’, an exotic variety (Njoroge, 1985). Each series was subjected to intra- and inter-population selection procedures for cycles. The local germplasm series included Katumani synthetics I, III, V, and VII, while the exotic germplasm series included Katumani synthetics II, IV, VI, and VIII (Fig. 1). The ear-to-row half-sib family selection procedure, described by Darrah and Mukuru (1977), was a major component in the improvement of the synthetic series. Selection was for early-maturity, grain yield, grain type, and disease resistance (*Exserohilum turcicum*, *Bipolaris maydis*, and *Puccinia sorghi*) (Dowker, 1964). Improvement involved introgression of exotic materials at various stages, especially for the development of synthetics VII and VIII, the two latest synthetics. The synthetics are not reconstituted regularly, some contain more than the 5-7 lines, and they are maintained by half-sib pollination procedures.

Various Katumani materials were evaluated at Katumani and Maruba sites in the long rainy season of 1983 (Njoroge, 1985). Katumani represented a drought stressed environment, whereas Maruba received some irrigation water and represented a more favorable environment. Days to 50% silking in the Katumani synthetic series 1, in which improvement emphasized earliness, was reduced by 1.4 d per cycle (Table 3). There was no significant change in earliness in Katumani synthetic series 2, which had early maturity derived from Taboran. Here emphasis was placed on increasing grain yield and altering expression of other characters.

Selection increased the yield of Katumani synthetic series 1, with a higher rate of increase in the unfavorable environment where the late-maturing Machakos Local White and Katumani synthetic I had very low yields (Table 3). The yield of Katumani synthetic series 2 was not significantly increased by selection, probably because selection was mainly to eliminate the yellow grain color introduced from from Taboran (Dowker, 1964). Katumani synthetics III and IV showed the highest grain yield, indicating that a combination of mass and S_1 selection for earliness and grain yield was adequate for population improvement. The good performance of Katumani synthetics III and IV has led to their utilization for the development of drought tolerant germplasm (Table 4). The reduction in performance of Katumani synthetics VII and VIII may represent the effect of the introgression of exotic germplasm (Fig. 1). However, Njoroge (1989) extracted lines from each with acceptable earliness, high grain yield and good seedling vigor. These lines have produced some hybrids with good performance in the region.

Intra-population improvement methods were used to improve the crosses between the synthetic series in order to develop composite varieties (Fig. 1). The two prominent varieties of this type are ‘Katumani composite A’ (KCA) from Katumani Synthetics III x IV; and Katumani composite B (KCB) from Katumani Synthetics V x VI. KCA was released quickly, but replaced shortly after with KCB, which was improved mainly by ear-to-row half-sib family selection up to Cycle 12 . Early records are not available, but the emphasis was on earliness, uniformity, and high grain yield (Njoroge, 1985). Katumani composites A and B were outstanding in grain yield for both the poor Katumani and favorable Maruba environments (Table 3). These series have continued to produce useful lines for early maturity and other favorable characters (Njoroge, 1989). Additionally, one cycle of S_1 recurrent selection for earliness in Katumani composite gave an earlier and higher yielding synthetic cultivar (Katumani Mpya) that is being considered for release in the Makueni composite growing region. Adoption of KCB is good, with 30-40% of Kenyan farmers reported to be growing the variety (Muhammed and Parton, 1992; Mugo et al., 1996). KCB is finding use in several other eastern African countries as well.

Makueni Composite

Makueni composite (MC) was developed and promoted for its earliness; on average it was eight days earlier than KCB (Table 3), the earliest of all the Katumani synthetic series. It is an advanced generation of a cross between the French accession ‘Early Progeny’ and Taboran (Fig. 1) (Njoroge, 1985), where Taboran contributed earliness and high grain yield. The cross was subjected to four cycles of ear-to-row half-sib family selection for early-maturity, high yield, white kernels and disease resistance, and has been improved subsequently solely through intra-population improvement. MC had significantly lower grain yields than KCB in the well watered Maruba environment, but the two cultivars had similar grain yields in the dry Katumani environment (Table 3). This may explain why many farmers still prefer to grow KCB even in the drier areas of eastern Kenya. From a survey (Mugo et al., 1996), only about 2% of farmers reported growing MC, and these were in Kitui District, an area classified as excessively dry and a target area for MC. The low adoption rate was in part attributed to unavailability of seed. However, it is considered likely that MC will be utilized as source germplasm for earliness.

Table 3. Grain yield and days to silking for Katumani synthetic series 1 and 2 evaluated at Katumani and Maruba* during the 1983 long rains season.

	Yield (t/ha)		Days to silking	
	Katumani	Maruba	Katumani	Maruba
Katumani Synthetic Series 1				
Machakos Local White	0.06	2.98	72.0	71.8
Katumani Synthetic I	0.84	2.30	68.0	66.0
Katumani Synthetic III	1.71	2.96	67.0	64.5
Katumani Synthetic V	1.56	2.84	68.0	65.3
Katumani Synthetic VII	1.15	2.02	65.0	67.0
Katumani Synthetic Series II				
Taboran	1.52	2.39	63.5	63.5
Katumani Synthetic II	1.13	2.98	65.5	66.8
Katumani Synthetic IV	1.33	3.22	63.3	63.8
Katumani Synthetic VI	0.84	2.02	65.8	66.3
Katumani Synthetic VIII	1.25	2.84	63.0	64.8
Composites Cultivars				
Katumani Composite A	1.56	3.34	67.3	69.0
Katumani Composite B	1.79	3.46	67.8	67.5
Makueni Composite	1.68	2.06	59.0	59.3
Mean	1.27	2.78	65.8	65.8
LSD ($P<0.05$)	0.35	1.09	4.6	4.1
CV	33	24	4	5

* Katumani site received 208 mm rainfall, while the Maruba site received supplemented irrigation.

Table 4. Germplasm used to develop drought tolerant source populations.

Source material	Brief description of source material
Drought tolerant source population I (Flints, DTSPI*)	
KAAP4	Ex-CIMMYT (PR 8530) with two cycles of selection for earliness.
Napples	An early maturing genotype held at Katumani.
SPE C_5 F_2	White grain early tropical CIMMYT genotype selected for prolificacy.
DLC III	Early maturing flint population developed at Katumani.
Makueni composite	Early maturing cultivar released in 1989 (Fig. 1).
Katumani syn. IV	Katumani synthetic series 2 cycle 2 (Fig. 1).
Pool 15-22	Selected line from Pool 15 of CIMMYT.
Drought tolerant source population II (Dents, DTSPII*)	
Source material	Brief description of source material
Katumani syn. III	Katumani synthetic series 1 cycle 2 (Figure 1).
Pool 16 Seq. C_2 F_2	Drought tolerant white grain tropical early maturity CIMMYT pop.
Pool 16 SR	CIMMYT Pool 16 selection with maize streak disease resistance.
DLC II	Early maturing dent population developed at Katumani.
Kat SYN C1	Synthetic developed with lines from the Katumani population.
EV 7992	An ex-CIMMYT genotype obtained through Harare.

* DTSPI = Drought Tolerant Population I; DTSPII - Drought Tolerant Population II

Development of Drought Tolerant Germplasm

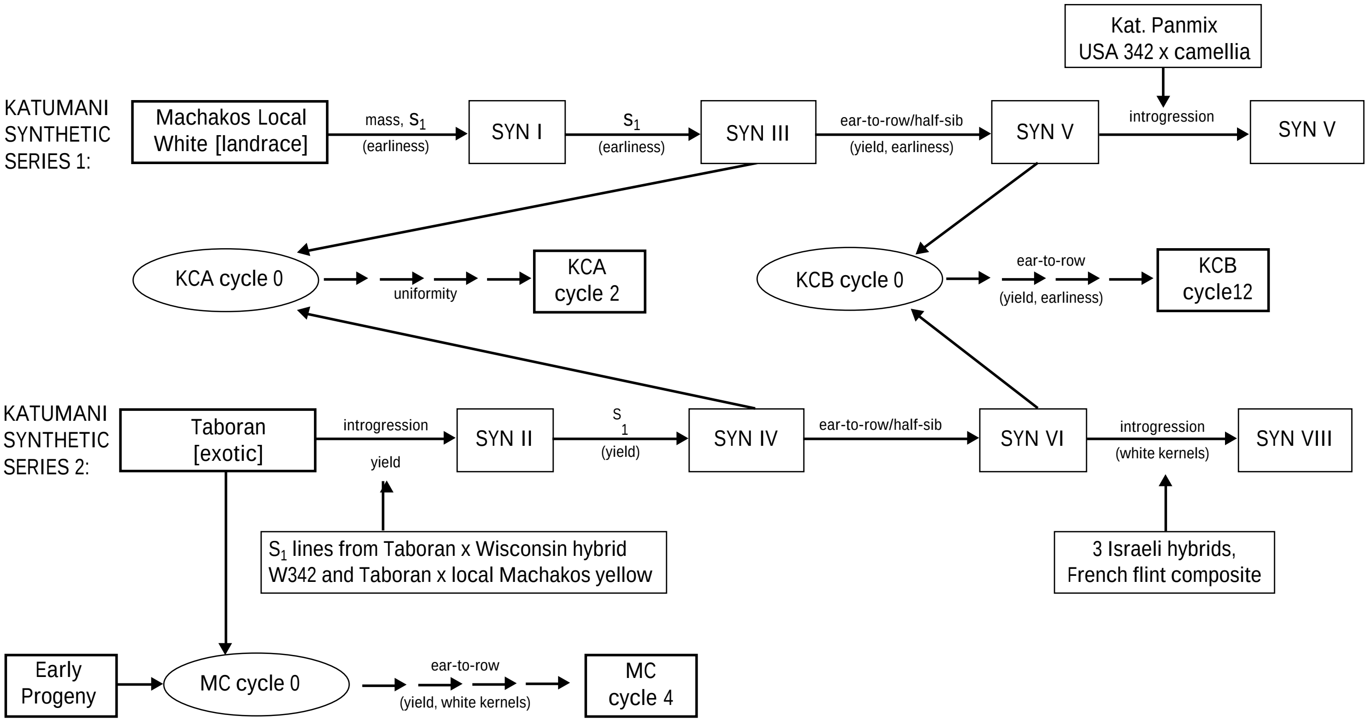
Drought tolerant populations are currently being developed through introgression and intra-population improvement methods. Sources were Katumani and Makueni populations and drought tolerant germplasm developed by CIMMYT. Drought tolerant germplasm from CIMMYT is later maturing than Katumani and lacks adaptation. Katumani and Makueni populations were combined with the CIMMYT drought tolerant germplasm to develop two parallel populations based on grain type. Makueni formed the basis for the flint type, and Katumani the basis of the dent type (Table 4). These populations are targeted to fall within the KCB maturity range.

A bulk half-sib method was utilized for making the initial crosses in April 1994 (Fehr, 1988). This was followed by three seasons of random mating within the two populations with mass selection for maturity and grain type. The random mating was expected to be adequate to break up linkage blocks and to stabilize the populations. This will be followed by S_1 recurrent selection of drought tolerant lines in a managed drought nursery at the Kiboko site, where irrigation and isolation are available. Selected lines should show good performance under both well-watered and water-stressed conditions. Lines will be evaluated for drought tolerance at both the seedling and flowering growth stages, within the same maturity group. Selection parameters will include 63-66 d to pollen shed, high seedling vigor, good emergence from drying soil, reduced leaf rolling, reduced leaf senescence, reduced ASI, large seed weight per ear, high prolificacy, and high yield to grain moisture ratio under water-stressed conditions (Ngure, 1995).

Non-Genetic Strategies

Germplasm improvement is just one technology for improving agricultural production in semi-arid areas. Soil and water management techniques and practices are a primary focus of technology development at NDFRC, Katumani. Climatic risk management through tactical response farming techniques is an approach where farmers adjust the planting dates,

Figure 1. A schematic outline of germplasm improvement of the mid-altitude early maturing maize improvement program. Selection practices are indicated above arrows, and selection emphasis below.



cultivar choice, fertilizer levels, and planting density depending on seasonal characteristics detected from rainfall amount, distribution, and onset dates at the beginning of every season (Wafula et al., 1992). While genetic approaches have sought to stabilize production across seasons through increased reliability of maize production, the farming approaches seek to maximize the potential of individual seasons. Irrigation is limited by short supply and availability of capital for setting up irrigation systems in subsistence farming communities. Alternative and possibly better suited cereal crops like sorghum and millet are under improvement for production and processing of alternative food forms from their products. Finally, the benefits of any of these strategies will only be maximized under suitable crop management practices such as timeliness in planting, weeding, and pest management.

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Breeding Drought Tolerant Maize in the mid-Atlantic Region of the USA

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Abstract

Drought is a major abiotic factor limiting maize yields in the mid-Atlantic region of the USA. A major objective of the Delaware maize breeding program is to identify drought tolerant germplasm and utilize it to develop adapted drought tolerant genotypes for the seed industry. Potential sources of germplasm (public inbreds and populations, commercial hybrids, and GEM accessions) and breeding populations derived from these sources are evaluated per se in screening nurseries at both moderate and high plant densities. Genotypes with reduced anthesis-silking interval (ASI), good ear development and agronomic performance, and pest resistance are used as source materials to develop breeding populations. Testcross hybrids of S_2 selections are evaluated at two irrigated and one dryland location to identify genotypes with adequate yield potential and agronomic performance. The second year of yield testing involves evaluation at two to three irrigated and two to three dryland locations, including at least one location on the sandy soils of the Delmarva Peninsula. Genotypes with high yield and good agronomic performance are advanced for more extensive testing in subsequent years at multiple locations. These procedures appear to have potential for developing adapted drought-tolerant germplasm with levels of pest resistance and agronomic performance adequate for the mid-Atlantic region.

Maize is important in the mid-Atlantic region for its feed value, for use as a rotational crop with soybeans, small grains, and vegetables, and as the major crop capable of utilizing the large quantities of manure produced by the expanding poultry and livestock industries in the region (Hawk and Smith, 1993).

Drought is the major abiotic factor limiting maize yields on the Delmarva peninsula and contributes to the instability of the local feed supply for the broiler industry. Drought conditions may occur as often as three years out of five, resulting in large annual yield fluctuations. Delaware average maize yields set a state record of 7.8 t ha^{-1} in 1994, but were only 4.4 and 5.3 t ha^{-1} due to severe droughts in 1988 and 1993, respectively. Irrigation would provide the best assurance of maintaining high yields, but over 80% of Delmarva maize acreage is still under dryland production.

Yield reductions of 50% or more are recorded when drought occurs during the sensitive flowering stage (Claassen and Shaw, 1970). Silk delay and an increase in the anthesis-silking interval (ASI) can occur under moisture deficits, and selection for reduced ASI has resulted in more stable grain yields in lowland tropical maize populations (Edmeades et al., 1992). A major effect of drought is embryo abortion, which is related to the inhibition of photosynthesis and the subsequent reduction in assimilates available to developing kernels (Schussler and Westgate, 1991; Westgate and Boyer, 1985). Silk delay is more likely a symptom of reduced assimilate flux than the direct cause of barrenness (Edmeades et al., 1992). Stem infusion of high levels of sucrose (Zinselmeier et al., 1995b) can partially restore seed set in drought-stressed plants, but other studies indicate that young embryos are unable to utilize stem reserves due to direct effects on ovary water status and / or insufficient sink demand (Schussler and Westgate, 1994; Zinselmeier et al., 1995a).

Selection for drought tolerance in lowland tropical maize significantly increased ear biomass at 50% anthesis and reduced tassel biomass, indicating that selection can increase partitioning to the developing ear (Bolaños and Edmeades, 1993). These results and experiences with breeding for drought tolerance in the US Corn Belt (Troyer, 1983) suggest that selection for reduced ASI and early ear development, either under drought stress or at high plant densities, may be an effective strategy for identifying genotypes capable of sustaining kernel growth under stress conditions.

Climatic factors and agronomic practices such as reduced tillage can also increase the incidence and severity of many maize diseases (anthracnose stalk rot, gray leaf spot, Stewart's bacterial wilt, etc.) and insect pests such as European corn borer, which are endemic to the region. Drought tolerant hybrids must also possess adequate levels of pest resistance, agronomic performance, and yield to be useful in the mid-Atlantic area. Extensive yield trial evaluations have been useful for identifying high yielding hybrids with stable performance related to drought tolerance in US maize (Jensen and Cavalieri, 1983). We describe here breeding and evaluation strategies which utilize both *per se* and topcross or hybrid testing schemes to develop high yielding, drought tolerant inbreds and hybrids with adequate levels of pest resistance and good agronomic performance.

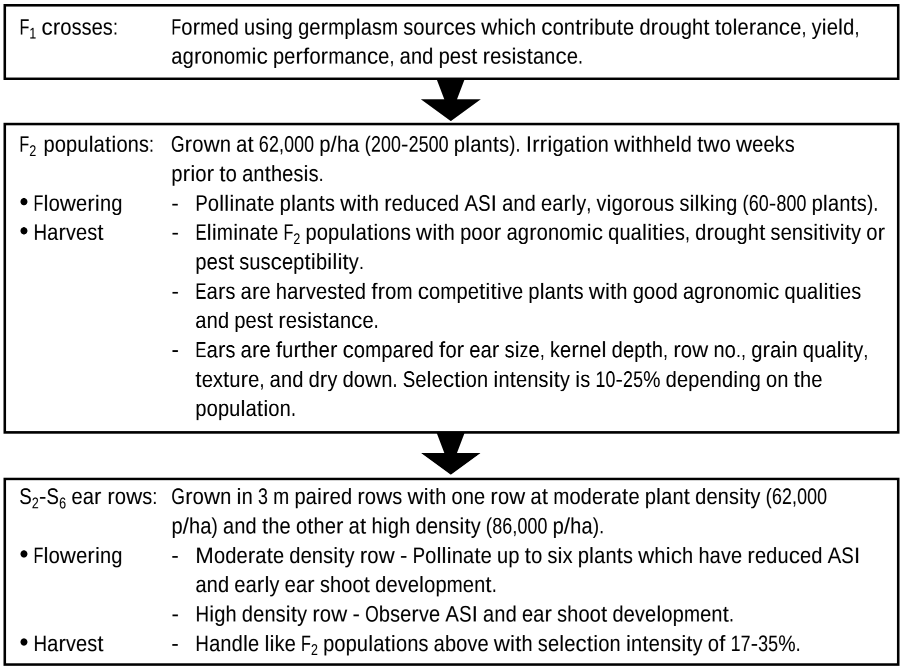
Materials and Methods

Germplasm sources for drought tolerance include public inbreds and populations, GEM (USDA Germplasm Enhancement of Maize Project) accessions and commercial hybrids. Drought tolerant genotypes are included as parents to produce breeding populations which are primarily advanced by the pedigree method, although recurrent selection procedures are compatible with our drought tolerance evaluation program. The University of Delaware drought tolerance breeding procedures consist of a *per se* evaluation for drought tolerant traits during the inbreeding phase (Fig. 1), coupled with a multi-stage yield testing program (Fig. 2) which first identifies hybrids with high yield potential, followed by more extensive testing in a wide range of environments.

Per se evaluations

The Delaware nursery is planted on a Matapeake silt loam soil. There are large annual differences in level of drought stress on this soil type, and we currently do not have any means to exclude rainfall. Overhead irrigation is available on part of our nursery which allows us to moderate the stress level. Irrigation is withheld about two weeks prior to anthesis to promote drought stress during the flowering period. F_2 populations and S_2 to S_6 ear rows are grown at 62,000 plants ha^{-1} in 6 m rows. Beginning in 1996, we plan on modifying our evaluation strategy of S_2 to S_6 ear rows to provide observation of ear selections at both moderate and high plant densities. The S_2 to S_6 ear rows will be planted in 3 m paired rows with one row at 62,000 plants ha^{-1} and the other at 86,000 plants ha^{-1}. More advanced selections may be replicated to provide a more thorough assessment of pest

Figure 1. *Per se* evaluation for drought tolerance, agronomic performance, and pest resistance during the inbreeding phase at Newark, DE.



F_1 crosses: Formed using germplasm sources which contribute drought tolerance, yield, agronomic performance, and pest resistance.

F_2 populations: Grown at 62,000 p/ha (200-2500 plants). Irrigation withheld two weeks prior to anthesis.
- Flowering
  - Pollinate plants with reduced ASI and early, vigorous silking (60-800 plants).
- Harvest
  - Eliminate F_2 populations with poor agronomic qualities, drought sensitivity or pest susceptibility.
  - Ears are harvested from competitive plants with good agronomic qualities and pest resistance.
  - Ears are further compared for ear size, kernel depth, row no., grain quality, texture, and dry down. Selection intensity is 10-25% depending on the population.

S_2-S_6 ear rows: Grown in 3 m paired rows with one row at moderate plant density (62,000 p/ha) and the other at high density (86,000 p/ha).
- Flowering
  - Moderate density row - Pollinate up to six plants which have reduced ASI and early ear shoot development.
  - High density row - Observe ASI and ear shoot development.
- Harvest
  - Handle like F_2 populations above with selection intensity of 17-35%.

resistance, agronomic and drought performance. This modified planting pattern also assures that neighboring rows in adjacent plots are always at the same plant density. We plan on pollinating the moderate density row and utilizing the high density row for assessing agronomic (stalk and root lodging, plant and ear height, etc.) and drought tolerant traits (ASI, early ear shoot development, staygreen). Superior families may be regrown to provide more adequate sampling of the within-family genetic variance. Winter nurseries are also used to advance superior families, but drought evaluation is more limited in those nurseries.

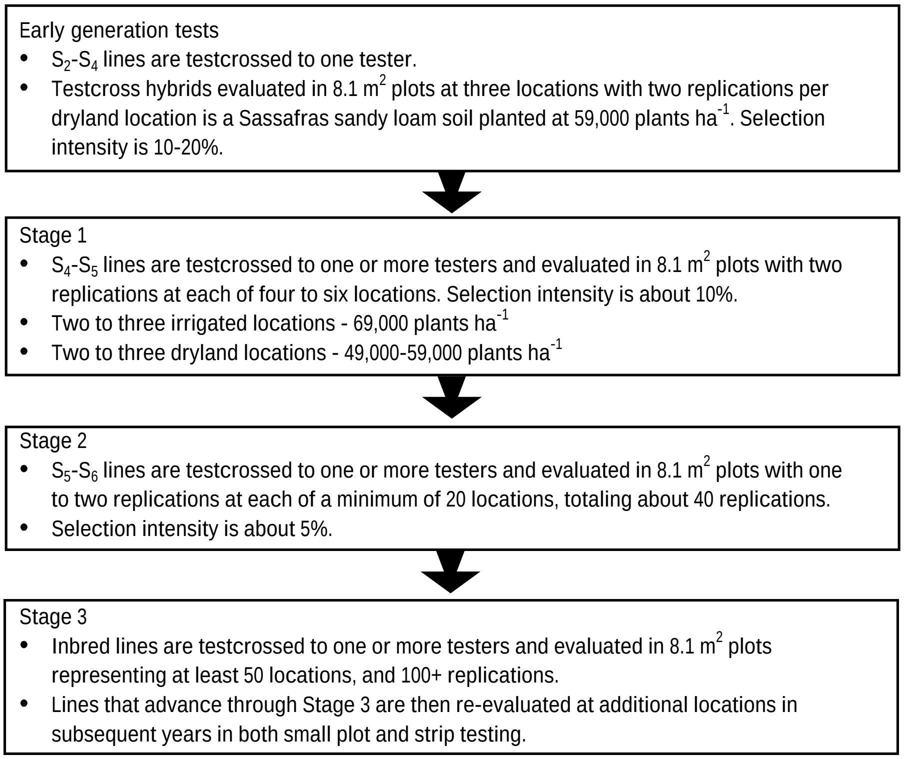
Yield trial evaluations

Yield testing is initiated on S_2 to S_4 lines, with the inbred stage for testing (S_2, S_3 or S_4) determined by the specific population and its performance *per se*. Early generation tests utilize one tester, and additional testers added as lines are promoted to more advanced testing stages. Advanced testing stages use an increasing number of locations to assess stability of performance across a range of environments. All advanced lines are also evaluated *per se* in the nursery in 3 m paired rows at moderate and high plant densities.

Commercial hybrid evaluations for drought tolerance

Two Pioneer hybrids of similar maturity, P3525 and P3527, were chosen for a study evaluating their relative yield performance and drought tolerance. One (P3527), a popular hybrid, has been reported to have less drought tolerance than the newer hybrid, P3525. These two hybrids were evaluated at five locations (three dryland and two irrigated) in 1993 with four replications per location. Plot size was four 6 m rows with 76 cm between rows. The center two rows were harvested for yield. Data on ASI were collected at one dryland location in 1993. Due to limited data, the ASI data were again collected in 1994 at a dryland location, Middletown, DE.

Figure 2. Yield trial evaluations for drought tolerance, agronomic performance, and pest resistance.



Early generation tests
- S_2-S_4 lines are testcrossed to one tester.
- Testcross hybrids evaluated in 8.1 m^2 plots at three locations with two replications per dryland location is a Sassafras sandy loam soil planted at 59,000 plants ha^{-1}. Selection intensity is 10-20%.

Stage 1
- S_4-S_5 lines are testcrossed to one or more testers and evaluated in 8.1 m^2 plots with two replications at each of four to six locations. Selection intensity is about 10%.
- Two to three irrigated locations - 69,000 plants ha^{-1}
- Two to three dryland locations - 49,000-59,000 plants ha^{-1}

Stage 2
- S_5-S_6 lines are testcrossed to one or more testers and evaluated in 8.1 m^2 plots with one to two replications at each of a minimum of 20 locations, totaling about 40 replications.
- Selection intensity is about 5%.

Stage 3
- Inbred lines are testcrossed to one or more testers and evaluated in 8.1 m^2 plots representing at least 50 locations, and 100+ replications.
- Lines that advance through Stage 3 are then re-evaluated at additional locations in subsequent years in both small plot and strip testing.

Results and Discussion

The sporadic nature of droughts on the Delmarva peninsula limits progress in identifying drought tolerant inbreds and hybrids. However, as indicated by results of the 1995 stage-three yield tests, a few DE inbreds produced hybrids which performed well at both high yielding and water-stressed locations. These same inbreds had excellent ear development in our 1995 nursery, which experienced poor seed set on many inbreds because of heat and drought stress. More extensive testing will be necessary to determine whether these inbreds are indeed drought tolerant. We are confident that the utilization of both irrigation and moderate to high plant densities will enable us to better regulate stress levels in our nurseries and accelerate breeding progress for both drought tolerance and agronomic performance.

The yield comparison between the two Pioneer hybrids revealed consistent yield differences across all five locations, with P3525 outyielding P3527 (Fig. 3). Yield levels ranged from 2.2 to 15.7 t ha^{-1}. Percent nubbin ears at the three dryland locations was at least two times greater for P3527 than for P3525 (Fig. 4), indicating that P3527 aborted more kernels than P3525 under drought stress conditions. Anthesis-silking (% plants) data revealed more synchronous flowering for P3525 than P3527 (Fig. 5). Hybrid P3525 initiated silking ahead of anthesis, whereas silking lagged anthesis by several days in P3527. These results suggest that P3525 is more capable of maintaining ear growth and development under drought stress. Drought tolerant hybrids will be most beneficial to dryland farmers on the Delmarva peninsula, many of whom suffered complete yield losses during the 1993 drought.

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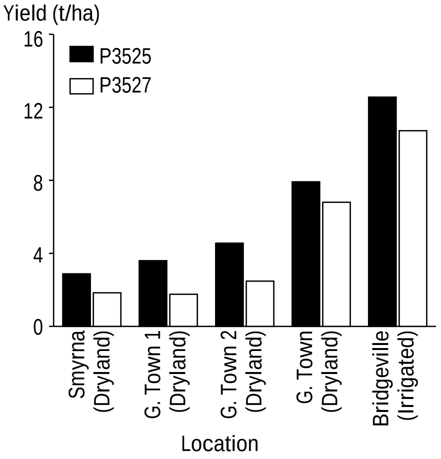

Figure 3. Yield comparisons of P3525 vs. P3527 hybrids at dryland and irrigated locations, 1993.

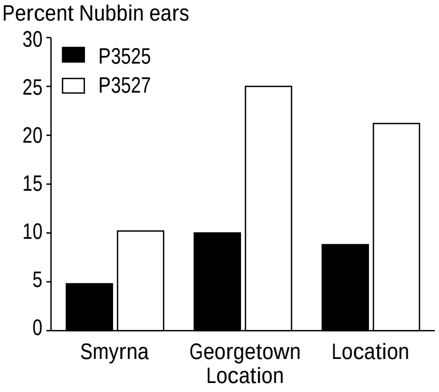

Figure 4. Percent nubbin ears of P3525 vs. P3527 hybrids at dryland locations, 1993.

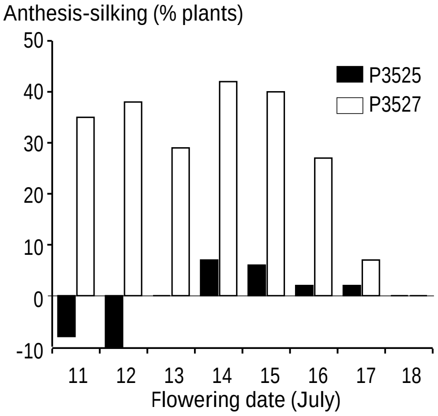

Figure 5. Anthesis-silking (% plants) for P3525 vs. P3527 hybrids at Middletown, DE, 1994 (50% anthesis date: P3525, July 13; P3527, July 12).

Maize Population Improvement for Low Soil N: Selection Gains and the Identification of Secondary Traits

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Abstract

Tropical maize is frequently grown under sub-optimal levels of soil N. Cultivars with improved tolerance to low N can be developed by simultaneously selecting for greater grain yield under stress and for secondary traits expected to confer an advantage under stress. Several traits were combined for ideotype selection in the tropical maize population Across 8328 BN. Gains over five cycles of full-sib recurrent selection averaged 84 kg grain/ha/year (4.5% per year) at low N and 120 kg grain/ha/year (2.3% per year) at high N. Selection under low N using this ideotype was associated with increased vegetative biomass, increased movement of N from vegetative parts to the grain, delayed senescence, decreased floret number, and an increase in the length of the lag phase of grain growth. Another approach to improving yield under low N is the use of controlled drought as a surrogate stress. Four tropical maize populations were selected for tolerance to drought at flowering and during grain filling. Gains over two to eight selection cycles averaged 100 kg grain/ha/year (3.4% per year) at low N and 75 kg grain/ha/year (1.2% per year) at high N. Two possible mechanistic explanations for improved performance under low N of populations selected for drought tolerance are reduced ear abortion and delayed leaf senescence.

After drought, low soil nitrogen is the most important abiotic factor limiting maize yields in the tropics. Approaches to developing improved cultivars for low N environments include selection for improved yield potential, selection for yield under N stress, and selection for specific mechanisms which are expected to confer tolerance. Ideotype selection emphasizes yield in addition to other secondary traits. Most of CIMMYT's work on tolerance to low N and drought has used selection indices to combine data on grain yield under stress and non-stress conditions with information on secondary traits. In this paper we review different selection approaches and their impacts on maize yields under low soil N. We report the changes that have occurred under low N with ideotype selection for low N and for mid-season drought stress at CIMMYT, and discuss the adaptive value of various secondary traits under low N.

Selection for Yield with High Soil Nitrogen

Maize breeding nurseries are usually supplied with adequate levels of nitrogen fertilizer. This practice increases the genetic variance and thus the heritability for grain yield, and maximizes yield gains for high-yielding conditions. It has been argued that crop improvement under high N will have a spillover effect such that yields in N-limited environments will increase as well. A comparison of unimproved tropical maize landraces with improved populations under high and low N levels supports this conclusion (Lafitte et al., 1997a). In that study, we compared 38 accessions from the CIMMYT maize germplasm bank with 26 improved maize populations. Grain yield of the improved group was superior to the landrace group at both high and low N levels, and this was due to increases in both biomass production and harvest index with improvement (Table 1). However, although grain yields increased under both high and low N, conventional breeding resulted in this group of germplasm producing larger absolute and relative gains under high (1.62 t ha^{-1}, 79%) *vs.* low N (0.56 t ha^{-1}, 51%). Castleberry et al. (1984) also found that selection under well-fertilized conditions increased grain yields more under high than low N conditions. Calculations based on broad-sense heritabilities and genetic correlations between grain yields under low and high N show that, in spite of lower heritabilities under low N, selection gains under low N are predicted to increase if selection is conducted under *both* low and high N (Bänziger and Lafitte, 1997b).

Results of Selection for Yield with Low Soil Nitrogen

Results from selection for grain yield under low soil N were reported by Muruli and Paulsen (1981). In that study, a single cycle of selection among half-sib families of a tropical maize population resulted in greater yields under low N, but a yield reduction was observed at high N. At CIMMYT, we have developed two source populations comprising unimproved accessions from the germplasm bank, and these have been improved for grain yield and plant type exclusively under low N. Yields of these populations under low N have improved significantly with only a few cycles of recurrent selection (Lafitte et al., 1997b). However, it is not possible to directly evaluate the impact of the low N selection environment using these data, because the base population was very heterogeneous and large initial gains are to be expected.

The absence of reports from low N breeding nurseries confirms that few breeders are willing to accept low N fields as their sole selection environment. This reflects not only the difficulties of working in low N nurseries but also the perception that farmers are not willing to sacrifice yield potential in the cultivars they use. In environments where lower yield targets are expected, farmers generally accept cultivars that are less responsive to applied N, but good yields at moderate N levels are still required. In addition, nurseries with high-to-moderate N are useful for carrying out selection for plant type, lodging, and disease resistance. In CIMMYT's work on ideotype selection for drought and low N, we have used both stressed and non-stressed nurseries to preserve yield potential while improving stress tolerance.

Table 1. Mean performance of landrace and improved maize germplasm groups when grown under high and low levels of soil N at Poza Rica during the 1987 winter season. Differences between the landrace group and the improved group are statistically significant at $P<0.05$, unless indicated as not significant (ns) (Lafitte et al., 1997a).

	Low nitrogen		High nitrogen	
	Landrace	Improved	Landrace	Improved
Early genotypes				
Grain (t/ha)	1.10	1.66	2.06	3.68
Biomass (t/ha)	2.64	3.75	5.16	8.33
Total N (kg/ha)	30.5	36.0 ns	82.2	98.7
Harvest index	0.42	0.46	0.41	0.48
Number of entries	19	12	19	12
Late genotypes				
Grain (t/ha)	1.09	1.61	2.65	3.78
Biomass (t/ha)	4.34	4.82 ns	8.51	9.78
Total N (kg/ha)	39.2	44.4 ns	104.4	116.3 ns
Harvest index	0.20	0.32 ns	0.34	0.39
Number of entries	19	14	19	14

Results of Selection for Components of N Metabolism

The problem of low heritability of yield under low N could be avoided if a specific mechanism for tolerance to low N could be identified, allowing selection of superior families in a controlled environment. Teyker et al. (1989) selected seedlings from a temperate maize population on the basis of high or low rates of seedling nitrate uptake. After one cycle of divergent selection the resulting populations differed significantly in nitrate uptake, and these differences were associated with plant size. Yield and N use characteristics in the field were not influenced by selection.

Seedling nitrate reductase activity measured *in vitro* was correlated with N uptake in the field for a set of 12 tropical and 12 temperate maize cultivars (Feil et al., 1993). In a recurrent selection study, Eichelberger et al. (1989) reported the results of selecting for high or low levels of leaf nitrate reductase activity (NRA). While selection was effective in altering NRA, increases in that trait were not associated with improved plant performance under either high or low levels of N supply.

Root characteristics are another trait which could affect performance under low N conditions. After only three cycles of ideotype selection for low N with no selection for root traits, root mass increased significantly in the lowland tropical cultivar Across 8328BN (Lafitte and Edmeades, 1994c). This indicates the importance of root mass for maize growing in low N conditions. Most measurements of root characteristics are impractical for breeding nurseries, though electrical capacitance measurements provide a rapid indication of rooting volume (Chloupek, 1977). Preliminary results on maize showed differences in capacitance readings among genetic materials though there was no apparent relationship with N use efficiency (van Beem, pers. comm., 1995; Smith et al., 1994). We are now selecting divergently among maize full-sib families for root capacitance meter readings, in order to evaluate possible benefits under low N and in other environments.

Selection of Stress-tolerant Ideotypes

Selection for low N environments

In 1986 CIMMYT began recurrent selection for improved performance under low N in the experimental variety Across 8328. Results from the first three cycles of selection are reported more fully elsewhere (Lafitte and Edmeades, 1994 a, 1994b), and are summarized here. Data are included from evaluations conducted after five cycles of selection. Key conclusions have also been drawn from a broader analysis of genetic gains under low N, based on additional information from other studies (Bänziger et al. 1997a, Bänziger and Lafitte, 1997a).

Our initial ideotype for low N environments had vigorous vegetative growth to capture available N before it was lost to weeds or to the environment, good flowering synchrony to allow establishment of the grain sink, and delayed senescence to allow continued N absorption during grain filling. Families were simultaneously evaluated in high N nurseries to maintain or improve yield potential and to maintain plant height and maturity. We began selection among full-sib families of Across 8328 because it had produced superior yields at both high and low levels of soil N in a preliminary study. We identified secondary traits consistent with our ideotype, and examined their relationships with grain yield. Several traits were correlated with yield at low N, and these were included in a selection index (Table 2).

Divergent selection experiments indicated that realized heritabilities of the secondary traits were relatively high for ear leaf area and plant height, but were low for green leaf number and ear leaf chlorophyll concentration. No measurement was made of the heritability of the anthesis-silking interval, though it is known to be quite high for maize grown under drought stress (Bolaños and Edmeades, 1993). Later studies based on the genetic analysis of many more experiments indicate that the broad-sense heritability of green leaf number is greater than the heritability of yield under low N, while the heritability of chlorophyll concentration is lower (Bänziger and Lafitte,1997b). In addition, anthesis-silking interval and the number of ears per plant under low N have similar heritabilities to yield, and are highly correlated with yield under low N.

After three cycles of selection using the index shown in Table 2, we found that grain yield had increased by 75 kg/ha/cycle under low N, and by 137 kg/ha/cycle under high N. Selection also resulted in significant increases across N levels in grains per ear, plant height, maturity, and aboveground

Table 2. Traits used in selecting superior full-sib families of Across 8328BN, C_0-C_3. +N and -N indicate high and low N, respectively (Lafitte and Edmeades, 1994a, b).

Trait	Indicator for:	Genetic correlation with yield -N[a]	Genetic correlation with indicated trait[a]	Relative selection pressure
Grain yield -N	Yield -N	1.00	1.00	1.00
Plant height -N	N uptake	0.55	0.90	0.50
Ear leaf area -N	N uptake	0.46	0.56	0.25
Chlorophyll, ear leaf, -N	N uptake, senescence	ns	0.78 (with N uptake)	0.50
Green leaf number, -N	N uptake, senescence	0.46	1.00 (with N uptake)	0.50
Anthesis-silking interval, -N	Sink formation, partitioning	-0.30	-0.62 (with harvest index)	-0.25 (1 cycle)
Grain yield +N	Yield +N	0.51	-	1.00
Plant height +N	Plant type	0.67	-	as needed[b]
Anthesis date +N	Maturity	ns	-	as needed[b]

[a] Genotypic correlation measured in C_0.

[b] Selection pressure applied as necessary to maintain trait constant in the selected fraction.

biomass. The rate of senescence declined with selection, and the amount of N mobilized from the vegetative parts to the grain increased. The number of florets per ear declined significantly. Selection for increased plant height at low N resulted in greater height at high N as well, with increased risk of lodging. Vigorous vegetative growth at low N was associated with poor performance in some environments. These results indicated that gains could be made with selection, but that the ideotype required some modification. In C_4 and C_5 the selection index was modified to reduce the emphasis on plant height, ear leaf area, and chlorophyll at low N, and to return the population to its original height and maturity. Slight selection pressure was directed towards reducing tassel size and maintaining green husks during grain filling (as an indicator of grain filling duration).

After five cycles of selection, C_0 and C_5 were evaluated in three low N environments, five high N environments, and four environments where radiation availability was altered by shading or by the removal of alternate plants. The yield increase was 84 kg/ha/cycle (4.5% per year) under low N, and 120 kg/ha/cycle (2.2% per year) with high N (Table 3). Plant height was still greater in C_5, but the maturity of the two cycles was similar. As we found in the earlier evaluation of C_3, the primary yield component that changed with selection was the number of grains per ear. The gains under low N may also include specific adaptation to the low N selection environment that was used for evaluations as well. Across 8328BN has been released in several countries. We think that it may also make an important contribution as a source of useful traits for low N environments. Both population bulks and lines are available from this population.

Table 3. Characteristics of C_0 and C_5 of Across 8328BN measured in different environments. Asterisks indicate a significant difference between C_0 and C_5.

	Low N		High N		All environments	
Trait	C_0	C_5	C_0	C_5	C_0	C_5
Grain yield (t/ha)	1.66	2.08 *	4.93	5.53 *	3.66	4.02 *
Ears/plant	0.94	0.99	1.07	1.14	1.08	1.13
Grains/ear	167	201 *	349	368	285	308 *
Plant height (cm)	161	181 *	211	226 *	195	214 *
Days to anthesis	64.3	64.2	65.0	65.1	63.3	63.2

Selection for drought tolerance

We conducted a study to compare ear growth dynamics in C_0 and C_3 of Across 8328BN, and in C_0 and C_8 of the cultivar Tuxpeño Sequìa, which had been selected for drought (Lafitte and Edmeades, 1995). The number of florets per ear decreased with selection in both populations. In both populations, the rate of ear or floret abortion was less after improvement, so the final number of ears per plant or grains per ear increased. The length of the lag phase between fertilization and the onset of the linear phase of grain growth tended to be greater in the selected cycles. We hypothesized that there might be common responses to selection for drought stress and for low N.

As a consequence, we evaluated original and advanced selections of four lowland tropical maize populations that had undergone recurrent selection for tolerance to mid-season drought stress in five experiments differing in N supply (Bänziger et al., 1997b). The populations had been improved using full-sib or S_1 recurrent selection for two to eight selection cycles each. In the five experiments N accumulated in aboveground biomass at maturity averaged 52, 63, 105, 151, and 163 kg N/ha, and grain yields of 3.0, 2.9, 5.2, 6.0, and 6.5 t/ha were correspondingly obtained. Selection for tolerance to mid-season drought stress increased grain yields by an average of 86 kg/ha/year, with slightly larger gains under severe N stress (100 kg/ha/year; Table 4). Drought tolerant selection cycles consistently had a shorter anthesis-

Table 4. Characteristics of original and drought-tolerant cycles of four lowland tropical populations improved for an average of six years under drought and well-watered conditions, when evaluated in five experiments differing in N supply. Results are averaged across experiments.

	Original cycle	Drought-tolerant cycle	Significance
Grain yield (t/ha)	4.44	4.96	***
ASI (d)	2.1	0.6	*
Ears per plants	0.95	1.02	*
Kernels per ear	330	331	ns
Kernel weight (mg)	264	273	*
Biomass (t/ha)	9.2	9.7	+
N accumulation (kg/ha)	105	109	*
Harvest index	0.48	0.51	**
Green leaf no. below ear	3.5	4.1	***

silking interval (ASI), more ears per plant, a larger kernel weight, delayed leaf senescence (green leaf number below the ear during grain filling), larger biomass, and an increased N accumulation at maturity. Changes with selection in ASI, biomass and N accumulation were larger under severe N stress than under well-fertilized conditions. These results indicated that selection under mid-season drought stress leads to reduced ear abortion and a more efficient use of leaf N for intercepting radiation, traits which are of adaptive value under N stress. No similar spill-over effect from selection under low N to drought-stressed environments was observed, perhaps because the vigorous early growth exhausted the soil moisture supply more rapidly (unpublished data).

Conclusions

Ideotype selection that includes high and low N selection environments or drought has proven to be an efficient approach to increase grain yields under low and high N. Selection under low and high N using grain yield and secondary traits increased grain yields in one lowland tropical population by 84 and 120 kg/ha per cycle under low and high N, respectively. Selection under drought stress and well-watered conditions using grain yield and secondary traits increased grain yields in four lowland tropical populations by 100 and 75 kg/ha/cycle under low and high N, respectively. In both selection programs a shortened anthesis-silking interval, reduced barreness and delayed leaf senescence, measured under low N or drought, have been shown to be useful indicators for low N tolerance, when included with grain yield in a cultivar improvement program.

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Potential for Developing Nitrogen Use Efficient Maize for Low Input Agricultural Systems in the Moist Savannas of Africa

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Abstract

The moist savannas of Africa have considerable potential for maize production, but soils are generally low in available N. Improved N use efficiency is a key to economically and ecologically sustainable maize production. Studies have been conducted at IITA to determine the potential for breeding maize with greater N use efficiency (grain yield per unit available soil N) and to identify mechanisms of N stress tolerance. Elite populations and hybrids were found to differ in N uptake, utilization and grain yield, but genotype by N interactions (GxN) frequently were not significant. Phenological traits including grain-filling duration and anthesis-silking interval have shown GxN in some environments. GxN interactions for yield and ears plant^{-1} *were detected among* S_1 *families from the TZPB-SR population, indicating the potential for using population improvement methods to develop varieties with specific adaptation to N stress. Combining ability of elite inbred lines was evaluated under low and high N. Crosses involving TZi lines 25, 34, and 35 performed well under low N. TZi 3 was the best parent under high N. Crosses with TZi 15 were susceptible to N stress. Precise selection criteria related to the mechanisms of N stress tolerance are needed to achieve more rapid progress through breeding. Studies were undertaken to investigate relationships between root morphology and N uptake efficiency and to develop screening techniques for root characteristics. The temporal movement of mineralized N through the soil profile was measured to see if rapid early root growth could increase N uptake. Results suggest that maximum rooting depth may be more critical in the savannas, because substantial quantities of N move out of the root zone around flowering time. Visual scores of root size at 5 weeks after sowing showed some correspondence with grain yield, but some stress tolerant inbreds had below average combining ability for root size. On-farm trials comparing an N-efficient hybrid (8644-27) and an N-inefficient open-pollinated variety (TZB-SR) demonstrated the need for an integrated approach that includes stress-tolerant cultivars and rotations with legumes to improve soil fertility and maize productivity in the African savannas.*

The moist savannas of West Africa have great potential for maize production. Higher radiation levels, lower night temperatures and reduced incidence of disease and insect pests increase yield potential in comparison to the traditional area for maize cultivation in the forest zone (Kassam et al., 1975). In the northern Guinea savanna, maize varieties which mature in four months can be planted after the first rains and harvested at the end of the season when the grain can be readily dried and stored. In the past two decades maize has spread rapidly into the savannas, replacing traditional cereal crops like sorghum and millet, particularly in areas with good access to fertilizer inputs and markets (CIMMYT, 1990; Smith et al., 1994).

Soils in the savannas are mainly kaolinitic alfisols, which are generally low in organic matter and cation exchange capacity (Jones and Wild, 1975). Traditional farming systems relied on shifting cultivation and prolonged bush fallows to restore fertility. As land-use intensifies, fallow periods are reduced, resulting in serious land degradation in some areas. A complex of problems develops including soil erosion and compaction, low soil organic matter, poor water holding capacity, and an increase in persistent weeds such as *Imperata cylindrica* (in the more humid areas) and parasitic plants (*Striga* spp.) (Berner et al., 1995; Weber et al., 1996).

Average rates of fertilizer use in Nigeria are about 12 kg nutrients ha^{-1} of arable land, and figures for other West African countries are lower (FAO, 1992). Farmers in the savanna zone often apply greater amounts of N fertilizer and organic manures to maize because they recognize that it has higher nutrient requirements than their traditional crops. However, due to poor transportation and marketing infrastructure, fertilizer is often not available at the right time. Furthermore, fertilizer is expensive in Africa and the ratio of farm-level N fertilizer price to maize grain price is relatively high in most countries (CIMMYT, 1990; López-Pereira and Filippelo, 1994). Overuse of fertilizers can also be detrimental. Nitrate is readily leached in savanna soils, which may lead to contamination of ground waters, and use of certain N fertilizer formulations has resulted in acidification of some soils (Juo et al., 1995). Technologies developed for maize based cropping systems in the savannas should therefore aim to improve soil fertility and crop productivity through the combined use of crop rotations, organic manures, and judicious inputs of inorganic fertilizers.

One strategy for improving productivity of maize under suboptimal N fertility is to select for nitrogen use efficiency, which is defined here as grain yield per unit available soil N (Moll et al., 1982). Variation in the capacity of maize genotypes to take up N from the soil and to utilize plant N for grain production has been widely reported (Chevalier and Schrader, 1977; Moll et al., 1982; Pollmer et al., 1979). Where suboptimal N fertility is a common feature of the target environments of a breeding program, greatest gains from selection for that environment can be achieved by selecting under N stress (Lafitte and Edmeades, 1994a).

In the early phases of the hybrid industry in the United States, double-crosses were shown to have greater stability across years and locations than single-crosses (Sprague and Federer, 1951). In temperate germplasm, prolificacy (having more than one ear per plant) has been associated with high grain yield under low N fertility, and often imparts greater yield stability over a range of environmental conditions (Moll et al., 1987; Motto and Moll, 1983). On-farm trials in the northern Guinea savanna of Nigeria showed that farmers would be interested in growing prolific varieties, particularly for intercropping with short-statured legumes (G. Weber, unpublished data, 1992).

Farmers in the savannas plant maize immediately following the onset of the rains, despite the risk of drought and the potential need to replant, because they anticipate greater yields with early planting. After the rains begin there is typically a flush of mineralized N that is released which can readily be lost due to leaching. Surveys of farmers' fields in the northern Guinea savanna of Nigeria showed that available nitrate-N was the only soil-related characteristic correlated with maize yield (Weber et al., 1995). Maize cultivars with high N uptake capacity and high root length densities in the subsoil have been shown to improve the utilization of soil nitrate supply in temperate environments (Weisler and Horst, 1994). Studies have been conducted at IITA to:

1. Determine the potential for breeding maize with greater N use efficiency (grain yield per unit available soil N).
2. Characterize the N response of elite populations, inbred lines and hybrids.
3. Identify mechanisms of N stress tolerance.
4. Develop effective breeding strategies and screening techniques for N use efficiency.

This paper summarizes some of the major findings from this research and discusses future strategies for improving N use efficiency in maize.

Materials and Methods

N use efficiency of populations

In 1989, nine open-pollinated cultivars and one commercial hybrid developed at IITA were compared during the first and second rainy seasons at Ikenne (6°54′N), Mokwa (9°18′N) and Samaru (11°11′N), Nigeria, representing the lowland forest zone, southern and northern Guinea savannas, respectively. Cultivars were chosen to reflect a range of improved breeding populations which are well adapted to the region. Treatments were arranged in a split-plot design with N rates of 0, 60, and 120 kg N ha^{-1} as main plots and genotypes as subplots, with four replications. N was applied as calcium ammonium nitrate in a split application at zero and four weeks after planting. Adequate levels of phosphorus and potassium were applied on the basis of soil test results. Plots consisted of 4 rows, 5m in length, with 75 cm between rows and 25 cm intra-row spacing. The first and fourth rows were used for destructive plant sampling at silking and the two central rows were used for measuring agronomic characteristics and grain yield. At silking, four plants were harvested, dried, and weighed to measure biomass. At harvest, stover biomass was determined from four plants after removing the ears. Chlorophyll concentrations were estimated from the ear leaf of ten plants per plot at two weeks after silking using a portable photometer (Hardacre et al., 1984). Yield components were estimated from ten ears per plot. Representative subsamples of plant and grain samples were ground in a Wiley mill for N analysis using the micro Kjeldahl method. N harvest index is defined as the proportion of the total above-ground plant N found in the grain. N utilization efficiency is the grain weight produced per unit of N in the plant above ground at harvest.

Selection for prolificacy

Selection had been carried out for prolificacy in the TZPB population at IITA in the late 1970s (IITA, 1980). A selection program was initiated in 1989 to quantify the magnitude of genetic variation and genotype by nitrogen interaction for ear number in this population, and to determine if prolificacy is beneficial under N stress. In 1989, 58 S_1 families which showed some degree of prolificacy were selected from TZPB-SR C_1 and recombined to form TZPB-SR prolific C_0. In 1990 250 S_1 families from this population were evaluated at 0 and 120 kg N ha^{-1} in Mokwa, Nigeria, using single, 5m-row plots with two replications. Stay-green ratings were assigned to each plot to indicate the proportion of leaves below the ear which remained green at four weeks after silking. The best 102 S_1 families were sib-increased for further evaluation at the same site in 1991. N treatments and plot size were the same as in the previous year, but number of replications was increased to four.

Performance of inbred lines under N stress

Twenty-nine tropical inbred lines were crossed to six testers to determine their relative combining ability at low and high N. Open-pollinated testers TZB-SR and EV88 Suwan 1-SR and single-cross TZi 15 x TZi 17 were chosen to represent the Caribbean flint heterotic group, whereas the open-pollinated testers EV 8443-DMRSR and Maracay 7921-SR and single cross TZi 3 x TZi 4 represented the Tuxpeño heterotic group. The resulting 174 crosses were grown in Ikenne in a split-split plot design with N levels of 0 and 120 kg N ha^{-1} as main plots, testers as subplots and inbred lines as sub-subplots. Plot size was a single 5m row, with four replications.

In 1995 14 tropical inbred lines were chosen as parents for a diallel experiment to determine general and specific combining ability (GCA and SCA) at low and high N in Mokwa. One cross was not available so there were a total of 90 hybrids for evaluation. These were planted in a lattice design with three replications (randomized complete blocks) and adjusted means were used in calculating combining ability. Each plot was planted in strips of 0 and 120 kg applied N ha^{-1}, which were arranged on opposite sides of a 2 m alley, to give more precise estimates of percent yield loss due to N stress. Griffing's Model I, Method 4 (Griffing, 1956) was used in calculating GCA and SCA.

Effect of heterosis and type of hybrid on N use efficiency

The IITA inbred lines 1368, 5012, 9071, and KU1414-SR are known to combine well with each other (S.K. Kim, pers. comm., 1995). These were crossed to generate the six possible single-crosses and three double-crosses. The double crosses were intermated to produce an open-pollinated synthetic with some degree of inbreeding (F=1/4) due to the small number of parental lines involved. Trials were conducted in the forest zone, southern and northern Guinea savannas of Nigeria in 1991 and 1992 using N treatments of 0, 70, 140, and 210 kg N ha^{-1} (Akintoye, 1995). The objectives of this study were to see if the genetic heterogeneity of the double-cross hybrid would provide some stability under N stress in comparison to the single-cross and to determine the effects of hybrid vigor or genetic heterozygosity on N use efficiency among genotypes with the same gene frequencies.

Root morphology in relation to NUE

Studies were conducted in collaboration with the University of Hannover, Germany, with support from GTZ, to investigate possible relationships between root growth parameters and N use efficiency (Heuberger et al., 1995; Oikeh, 1996; Oikeh et al., 1996). Our initial hypotheses were that:

1. Rapid, early root growth would enable the maize plant to catch the N flush that occurs early in the growing season.
2. Deep root systems with high root length densities would promote greater N uptake.
3. Vigorous root growth would permit better penetration of compacted layers.

A series of field experiments were conducted in Ikenne, Mokwa and Samaru, Nigeria, to compare nitrogen use efficiencies of maize cultivars and to investigate potential relationships with root growth characteristics. Root length densities (RLD) were determined at 15 cm increments down to the maximum root depth at 28 DAP and at silking using the core method (Tennant, 1975). Two Ph.D. dissertations describing these experiments are currently in preparation, so only general conclusions will be discussed in this paper.

The same set of 90 hybrids generated from diallel crosses among 14 tropical inbred lines described earlier were sown in two replicates in Ibadan, Nigeria (7°26′N), in 1995 without any addition of fertilizer. At 5 weeks after sowing, a uniform volume of soil was excavated around 5 plants plot^{-1} (measured as one spade width from the base of the plant), and the soil was carefully shaken from the roots. Visual ratings on a scale from one to five were assigned to each plot to measure root size (1=big, 5=small).

A seedling screening technique was developed using PVC tubes of varying height (20 and 90 cm), with and without wax layers to provide an impediment to root growth. Ranges in soil bulk densities and nitrate supply were also investigated. Measurements were taken on the number of roots penetrating the wax layer, rate of appearance of roots at the bottom of the tubes, and root length densities above and below the wax layers. Greatest differentiation among varieties in root growth parameters was obtained using small PVC tubes (filled to 16 cm height, 5.7 cm diameter), and a relatively high bulk density of 1.55 g cm^{-3} to simulate deeper soil layers, without wax layers. These conditions were employed to screen four replicates (pots) of the hybrids from the 14-parent diallel described above. Two pre-germinated seeds were planted in each pot. Levels of N were controlled to provide 60 mg available nitrate-N pot^{-1} and adequate quantities of P, K, Mg, Mn, Cu, and Zn were supplied in a nutrient solution. Soil moisture content was maintained at 13.3% by watering twice daily with distilled water.

Availability of soil nitrate during the cropping season

Movement and depletion of soil N throughout the root zone were monitored in the field experiments investigating relationships between NUE and root characteristics mentioned above. Additionally, an experiment was carried out in 1994 and 1995 in Mokwa to measure the release of mineralized nitrogen following the onset of the rains, and the rate of NO_3 leaching through the soil profile during the cropping season. The objectives were to provide information on temporal availability of mineralized N and to assess the potential contribution of early N uptake and root growth characteristics on N use efficiency.

Results

N use efficiency of populations

Nitrogen treatments had a significant effect on grain yield and most other parameters at all sites, but severity of stress increased from the southern to northern latitudes. Yield reduction under 0 kg N ha^{-1} in comparison to the 120 kg N ha^{-1} treatment ranged from 21% in Ikenne (first season) to 67% in Samaru. Cultivars differed in average grain yield at all sites, but because of large genotype by location interactions, differences across sites were not significant (Table 1). Differences among cultivars were observed for N uptake, N concentration in the grain, N harvest index, and N utilization efficiency. Genotype by N interactions were not significant for any traits across sites. TZB-SR, TZSR-W-1, and Tuxpeño populations (EV 87 TZPB-SR, EV 8443-DMRSR, and EV 7921-SR) produced the greatest average biomass across N levels and environments (Table 2). TZSR-W-1 and the Tuxpeño populations had high N uptake and grain yield, whereas TZB-SR had average N uptake and the lowest harvest index among all the cultivars evaluated. Concentration of N in the grain was greatest in TZSR-W-1 at all sites. EV 8428-SR, hybrid 8321-18, and EV 7921-SR had high harvest indices. Averaged across sites, EV 8428-SR had the highest shelling percentage, harvest indices (N and dry matter), and N utilization efficiency, but the lowest biomass and total N uptake of all cultivars. N uptake and partitioning for each cultivar and N level at the savanna site, Samaru, is shown in Figure 1. Grain N under 0 kg N ha^{-1} was lowest for TZB-SR, a widely grown cultivar in the Nigerian savanna. The hybrid had the highest grain yield but a much lower grain N than TZSR-W-1 at 0 kg N ha^{-1}. Although GxN interactions were not significant for yield or grain N at Samaru, the greatest advantage of the hybrid for these traits was observed at 60 kg N ha^{-1}, primarily because it was able to resist barrenness under moderate N fertility.

GxN interactions were observed at some locations for some phenological traits, including grain filling duration and anthesis-silking interval. Figure 2 shows the length of grain filling at Ikenne, second season, at each N level. Cultivars are arranged in order of decreasing yield under low N.

Table 1. Analysis of variance comparing ten maize cultivars grown at three N levels across four ecologies in Nigeria, 1989.

Source	Grain yield	Stover dry matter	Total dry matter	Harvest index	Kernel number	300-kernel weight	Ears plant^{-1}	Shelling (%)	Grain N (g kg^{-1})	Total plant N	N harvest index	N utilization efficiency
Location	**	**	**	**	ns	**	**	*	**	**	**	**
Nitrogen	**	*	**	ns	**	ns	*	ns	**	**	ns	ns
L x N	**	ns	*	**	*	**	**	**	ns	**	**	**
Genotype	ns	**	**	*	*	**	ns	**	**	**	*	*
G x L	**	ns	*	**	**	ns	*	ns	ns	ns	ns	ns
G x N	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
G x L x N	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

*, **Significant at the 0.05 and 0.01 probability levels, respectively; ns = not significant

Table 2. Means of ten maize cultivars grown at three N levels averaged across four ecologies in Nigeria, 1989.

Variety	Grain yield (Mg ha^{-1})	Stover dry matter (Mg ha^{-1})	Total dry matter (Mg ha^{-1})	Harvest index (%)	No. kernels plant^{-1}	300 kernel wt. (g)	Ears plant^{-1}	Shelling (%)	Grain N (g kg^{-1})	Total plant N (kg ha^{-1})	N harvest index (%)	N utilization efficiency
N level kg ha^{-1}												
0	2.14	2.60	4.74	45.0	334	68.3	0.79	78.9	1.42	49.6	61.2	43.4
60	3.16	3.15	6.32	50.6	394	70.6	0.90	81.6	1.46	69.5	66.8	46.2
120	3.81	3.27	7.08	54.0	428	73.5	0.94	81.8	1.52	84.9	68.0	45.1
LSD (0.05)	0.86	0.47	0.89	ns	33	ns	0.11	ns	0.04	11.3	ns	ns
Cultivar												
TZB-SR	2.87	3.36	6.24	45.6	399	65.2	0.85	79.9	1.44	67.8	60.8	42.5
EV 87 TZPB-SR	3.24	3.50	6.73	47.3	363	74.6	0.85	79.4	1.47	75.2	62.4	42.7
EV 85 TZSR-W-1	3.17	3.22	6.39	48.7	402	68.5	0.89	80.4	1.53	73.8	65.0	43.1
DMR-LSRW	2.91	2.91	5.82	49.5	371	70.9	0.88	80.4	1.48	64.4	66.2	45.0
EV 8443-DMRSR	3.28	3.12	6.40	50.6	365	75.8	0.88	82.7	1.50	73.4	66.3	44.6
EV 8428-SR	2.93	2.64	5.57	53.1	384	72.2	0.91	84.8	1.44	62.3	68.7	48.2
EV 7921-SR	3.13	3.00	6.13	51.0	380	72.5	0.88	82.6	1.45	68.3	66.5	46.1
EV 86 TZUTSR-W	2.88	2.77	5.65	50.6	410	66.2	0.84	81.4	1.44	64.3	64.3	44.9
EV 88 Suwan 1-SR	2.89	2.78	5.67	50.7	370	71.0	0.88	77.4	1.44	64.0	66.0	46.2
8321-18 (hybrid)	3.09	2.76	5.85	51.7	408	71.2	0.89	78.7	1.48	66.9	67.2	45.7
LSD (0.05)	ns	0.32	0.54	4.0	30	3.3	ns	3.0	0.05	6.6	4.4	3.0

ns = F test for main effect not significant at the 0.05 probability level

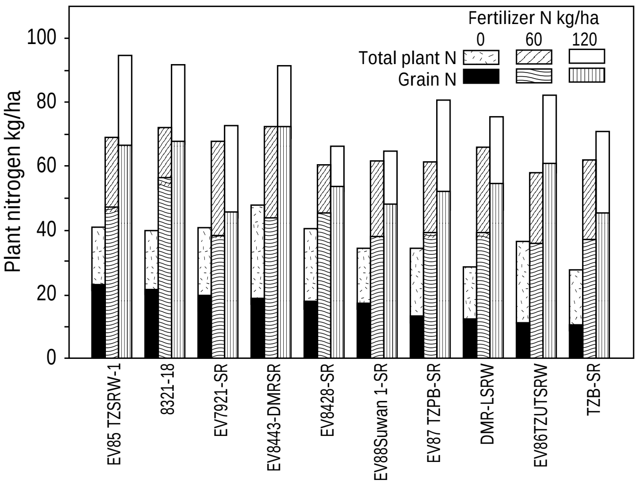

Figure 1. Nitrogen content of ten cultivars at three N levels in Samaru, 1989.

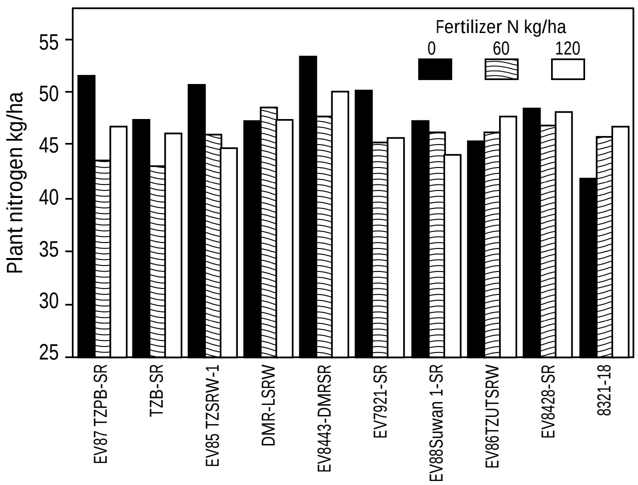

Figure 2. Length of grain filling period of ten cultivars at three N levels in Ikenne, second season, 1989. Error bar represents standard error of the difference between any two treatment means.

TZSR-W-1 and the Tuxpeño populations increased the duration of grain filling at 0 kg N ha^{-1} and were relatively stress tolerant. One possible explanation could be that these cultivars grew deeper root systems in response to N stress, and hence maintained N uptake and photosynthesis longer. The same cultivars also showed high N uptake after silking in Mokwa (data not shown). The hybrid did not perform well in the forest zone. It is relatively susceptible to *Bipolaris maydis* and *Curvularia lunata*, which resulted in early senescence of leaf tissue and compounded the effects of N stress.

Correlations of traits measured at each site with yield at 0 kg N ha^{-1} are shown in Table 3. Changes in correlations across sites may reflect differences in the intensity of N stress at each site, but also suggest that different strategies for N stress tolerance were employed in different environments. Number of ears plant^{-1} was significantly correlated with yield under low N at three out of four sites. Yield and kernel number plant^{-1} were correlated only under the more extreme N stress conditions which occurred at the savanna sites. N uptake during grain filling was highly associated with yield at Mokwa, but not at Samaru.

Selection for prolificacy

Results from the study characterizing N use efficiency of populations in 1989 showed that existing elite populations adapted to the region were strongly single-eared. Average

Table 3. Correlations between yield and other traits at low N (0 kg N ha^{-1}) based on genotype means at four locations in Nigeria, 1989.

Variable	Ikenne A[a]	Ikenne B[a]	Mokwa	Samaru
Anthesis-silking interval	-0.65*	-0.17	-0.36	0.48
Grain filling duration		0.70*		
No. expanded leaves (3 WAP)	0.68*			
Chlorophyll concentration	0.73*	0.08	0.31	
% green leaves below ear	0.74*			
Plant dry matter (silking)		0.66*	0.59	0.28
Stover dry matter (harvest)	-0.25	0.77**	0.59	0.39
Total dry matter (harvest)[b]	0.51	0.93**	0.91**	0.78**
Harvest index[b]	0.69*	0.24	0.37	0.85**
Ears plant^{-1}	0.79**	0.78**	0.05	0.70*
Kernel number plant^{-1}	0.21	0.36	0.73*	0.82**
300-kernel weight	0.48	0.43	0.76*	0.25
Shelling percentage	-0.01	0.17	0.25	0.48
Plant N concentration (silking)			0.15	0.84**
Stover N concentration (harvest)	0.04	0.13	0.26	-0.04
Grain N g kg^{-1}	0.10	0.07	0.36	0.49
Plant N content (silking)			0.60	0.56
Stover N content (harvest)	-0.08	0.55	0.55	0.11
Grain N content[b]	0.95**	0.97**	0.98**	0.99**
Total plant N[b]	0.61	0.86**	0.95**	0.77**
N harvest index[b]	0.46	0.13	0.30	0.81**
N uptake during grain filling[b]			0.98**	-0.04

[a] A, B = first and second rainy seasons, respectively

[b] autocorrelated with yield

values for ears plant^{-1} for 250 S_1 families from TZPB-SR prolific C_0 at 0 and 120 kg N ha^{-1} were 1.10 and 1.26, respectively, indicating that some progress had been achieved in selecting for prolificacy. Analysis of variance showed highly significant differences among families for grain yield, ears plant^{-1}, stay-green rating, and anthesis-silking interval (ASI), but only ASI showed significant GxN interaction (data not shown). However, when the best 102 families were rescreened the following year with four replicates, GxN interactions were detected for yield and ears plant^{-1}. Families with higher average ear number across the four replications generally had higher yields under low N (r=0.59**). The 19 best prolific families were recombined to form TZPB-SR prolific C_1 and the 13 families with greatest tolerance to N stress were recombined to form TZPB-SR LN C_0.

Table 4. Analysis of variance for 29 inbreds in crosses with six non-inbred testers at two nitrogen levels in Ikenne, Nigeria, 1990.

Source	df	Grain yield (t ha^{-1})	Ears plant^{-1}	ASI[1] (days)
		Mean Squares		
Replication	3	12.2	0.027	7.2
Nitrogen	1	510.8**	0.140 ns	1104.6**
Error a	3	7.6	0.026	6.9
Testers	5	20.8**	0.207**	4.3 ns
N x testers	5	1.0 ns	0.028 ns	11.5 ns
Error b	30	2.5	0.045	6.9
Inbred	28	4.2**	0.078**	6.3**
N x inbred	28	0.9**	0.038 ns	5.5**
Tester x inbred	140	1.1**	0.042*	3.1 ns
N x T x I	140	0.4 ns	0.040*	2.9 ns
Residual	1008	0.4	0.032	3.0

[1] ASI = anthesis-silking interval

*, **Significant at the 0.05 and 0.01 probability levels, respectively

ns = not significant

Table 5. Testcross performance of inbred lines at two N levels in Ikenne, Nigeria, 1990.

TZi #	Name	Origin	Grain Color[a]	Grain yield 0 kg N ha^{-1}	Grain yield 120 kg N ha^{-1}
TZi 35	KU1414	KU1414 (Thailand)	Y	3.07	4.55
TZi 34	7268	Comm. hybrid x SR	Y	3.05	4.63
TZi 20	4013	Across 7635 x TZSR	Y	2.94	4.22
TZi 32	9485			2.76	4.14
TZi 18	4001	Sete Lagoas 7728 x TZSR	Y	2.76	3.50
TZi 3	1368	Across 7721 x TZSR	W	2.69	3.90
TZi 8	2097	TZB x TZSR	W	2.62	4.20
TZi 10	5057	Tlatt. 7844 x TZSR	W	2.62	3.91
	HI 26[b]	CI21E(=K577C x Hy) BC2	Y	2.54	3.70
	ICAL210[c]	Cuban flint LC	Y	2.53	3.69
	CM 103[d]	Colombia 1 x 38-11	Y	2.51	3.13
TZi 30	9848	Hi29 BC_1 x RppSR	Y	2.48	3.63
TZi 5	1394	Guana Caste 7729 x TZSR	W	2.47	3.94
TZi 25	9450	B73 BC3 x RppSR	Y	2.47	3.28
TZi 2	1201	Across 7622 x TZSR	W	2.46	4.19
TZi 6	1787	TZPB EPS	W	2.45	3.61
TZi 7	2096	TZB x TZSR	W	2.43	3.96
TZi 14	9043	Rpp TZSR-Y x N28	W	2.43	3.56
TZi 11	9006	Mo17 x TZSR	W	2.43	3.39
TZi 24	9432	1195 x RppSR	Y	2.38	3.28
	ICAL 27[c]	ETO x 2053-11	W	2.37	3.85
TZi 28	9499	F44 x RppSR	Y	2.37	3.34
TZi 12	9030	N28 x TZSR	Cr	2.35	3.81
TZi 27	9490	F44 x RppSR	Y	2.31	3.30
TZi 4	1393	Guana Caste 7729 x TZSR	W	2.30	3.54
	CM 116[d]	Puerto Rico Gr.1	Y	2.29	3.70
TZi 9	5012	Sids 7734 x TZSR	W	2.24	3.15
TZi 15	9071	N28 x TZSR	W	2.22	3.22
TZi 17	9091	RppSR (TZ)	W	2.13	3.48

[a] W, Y, Cr = white, yellow, creamy white grain color

[b] From Hawaii

[c] From Colombia

[d] From India

Performance of inbred lines under N stress

Analysis of variance for the crosses of 29 inbreds with 6 non-inbred testers is shown in Table 4. Significant differences were observed in average testcross performance of inbred lines for grain yield, ears plant^{-1}, and anthesis-silking interval (ASI). N x inbred interactions were observed for grain yield and ASI. Significant tester x inbred interactions were observed for grain yield and ears plant^{-1}, indicating the presence of specific combining ability for those traits. Lack of N x tester x inbred interactions for grain yield and ASI suggests that heterotic patterns were similar across N levels. Crosses with inbred lines 7268 and KU1414-SR had the highest grain yields under low and high N (Table 5). Inbreds 1201 and 2097 were identified as N stress susceptible, because they performed well in crosses at high N, but had only average yields under low N. Specific combining ability for these four inbreds at each N level is shown in Figure 3. The N stress tolerant inbreds (7268 and KU1414-SR) performed well in crosses with all non-inbred testers, regardless of heterotic group. Inbred 1201 showed good combining ability with TZB-SR and EV 88 Suwan 1-SR, but not with the Caribbean flint hybrid tester (TZi 15 x TZi 17) nor with any of the Tuxpeño testers. Inbred 2097 showed poor combining ability with both hybrid testers under low N, and with TZi 15 x TZi 17 under high N. In summary, some crosses clearly showed greater heterosis than others, and those crosses were frequently superior at both N levels. Inbred lines did not, however, conform with the anticipated heterotic patterns. Because this experiment was conducted in the forest zone (Ikenne), it is possible that heterotic potential was not fully expressed, and some inbred lines may have performed poorly under both low and high N due to lack of resistance to foliar diseases or other constraints in the forest environment.

In the diallel experiment conducted in Mokwa in 1995, there was significant GCA for grain yield under both N treatments, but SCA was only significant under high N (data not shown). For ears per plant, GCA was significant under low N and SCA was significant under high N. GCA for yield loss due to N stress was also significant, indicating the presence of GxN interactions. Average grain yields of the inbred parents in diallel crosses are shown in Figure 4. All of these inbreds were included in the testcross trial described above (Table 5), so results can be compared across the two experiments. Crosses with 9450 (TZi 25), 7268 (TZi 34), and KU1414-SR (Tzi 35) were consistently high yielding under low and high N fertility in both trials. Inbred 1368 (TZi 3) had the highest general combining ability for grain yield under high N in Mokwa, but GCA for grain yield under low N was only slightly above average. Inbred 9499 (TZi 28) was a good combiner for grain yield at both N levels in Mokwa, but performed poorly in Ikenne. This inbred is known to be highly susceptible to *Sesamia calamistis* stem borers, which are prevalent in the forest zone. Inbred 9071 (TZi 15) was susceptible to N stress in both experiments.

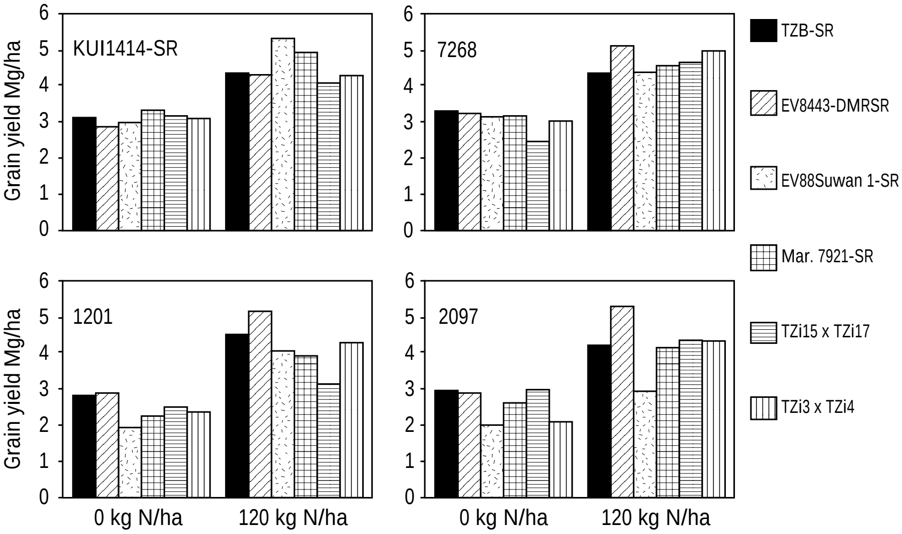

Figure 3. Grain yield of two N-stress tolerant inbreds (KU1414-SR and 7268) and two N-stress susceptible inbreds (1201 and 2097) in crosses with six testers under low and high N fertility in Ikenne, Nigeria, 1990.

Effect of heterosis and type of hybrid on N use efficiency

Means of single and double crosses and the synthetic across five environments are shown in Figure 5. At some sites the highest yielding genotype was a double cross, while at others a single cross was superior. There was no evidence that double crosses were more tolerant of N stress. In contrast to the hybrids, the synthetic was not able to respond to additions of fertilizer above 70 kg N ha^{-1}. At 0 kg N ha^{-1}, the relative ranking of inbred parents for average grain yield in single crosses was 1368>KU1414-SR>5012>9071. Averaged across locations, the best single cross was 1368 x KU1414-SR. Crosses with 5012 did not respond to additions of fertilizer above 140 kg N ha^{-1}.

Root morphology in relation to N use efficiency

RLD estimates had large experimental errors and relationships with grain yield under N stress were quite variable from one trial to another (data not shown). In the southern Guinea savanna, SPL, a semi-prolific population from

CIMMYT, performed consistently well under low N and had a high harvest index and N utilization efficiency (Heuberger, unpublished, 1995). In experiments in the northern Guinea savanna, TZPB-SR had consistently high RLD, N uptake and grain yield under N stress (Oikeh, 1996). Hybrid 8644-27 showed good NUE across sites in the savanna and had a high harvest index and N utilization efficiency. Hybrid 8321-18 had below average RLD. TZB-SR had poor root growth and a low harvest index, and was relatively susceptible to low N stress.

Although differences could be observed among hybrids for shoot and root growth parameters of seedlings in PVC tubes, the technique was not precise enough to differentiate segregating families in a population (data not shown). Although the lack of precision may have been due to the limited number of plants sampled per genotype, increasing the number of replicates would make the technique impractical as a rapid screening method. There were some indications of relationships between root characteristics in the tubes and root growth, N uptake and grain yield in the field, but results were not consistent. It can be concluded that the seedling screening method was a poor predictor of field performance under low N.

Correlations between the root growth parameters of 14 inbred lines in diallel crosses (data not shown) and their yield in crosses (Fig. 4) were not significant, but were in the expected direction. Inbred 1368 (TZi 3) ranked first for both the visual rating of root size in Ibadan and appearance of root tips in PVC tubes, and was the highest yielding parent under high N fertility. Among the inbreds that performed well under low N, 9450 ranked second for visual ratings of root size and third for appearance of root tips in PVC tubes, whereas KU1414-SR and 7268 were not outstanding for either root characteristic. Inbred 9071 (TZi 15) was susceptible to N stress, and ranked llth out of the 14 inbreds for root size rating and 14th for appearance of root tips in PVC tubes.

Availability of soil nitrate during the cropping season

Studies conducted to monitor soil nitrate movement in the root zone at experimental sites in the savannas showed that NO_3-N was released through mineralization well into the cropping season (data not shown). Substantial amounts of nitrate had reached the 90 cm soil depth by silking time, which represented the maximum rooting depth in most experiments. Apparent leaching of nitrate out of the root zone continued through the grain filling period.

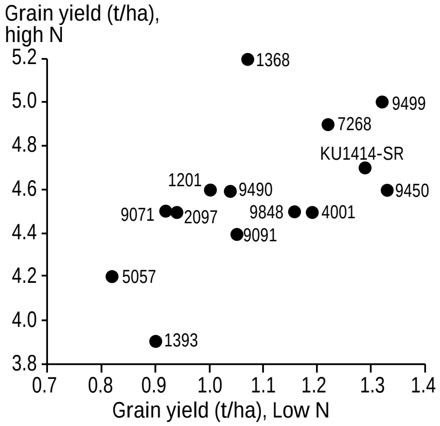

Figure 4. Average grain yield of inbred lines in diallel crosses under low and high N fertility in Mokwa, 1995.

Discussion

Lack of pronounced GxN interactions in these experiments implies that for routine breeding activities, preliminary evaluation of genotypes can be carried out at a single, moderate N fertility level, provided that advanced materials are screened under N stress prior to release. Progress from selection at one N level should also be expressed to some extent at other N levels. However, the presence of significant GxN among families within the TZPB-SR prolific C_0 population indicates that there is scope for improving the specific adaptation of maize to low N fertility conditions, if appropriate selection criteria are utilized. Although progress was achieved in selecting for prolificacy, further research is needed to determine if prolific genotypes have an advantage under low N fertility. In the trials conducted to investigate root characteristics, a semi-prolific cultivar from CIMMYT, SPL, performed consistently well under N stress. Further selection for prolificacy will be carried out at IITA to meet potential demands for prolific cultivars in the savannas.

General combining ability of inbred lines for grain yield under low N was significant in two experiments (Table 4; Fig. 4), and relative performance across sites was quite consistent. These results also indicate that progress can be achieved in developing NUE populations, synthetics and hybrids when genotypes are screened under uniform, N-deficient conditions.

Due to their high yield potential, hybrids may require more N to attain maximum yields than open-pollinated varieties. There was no evidence from this work that hybrids are inherently susceptible to low fertility, and in fact their greatest advantage over open-pollinated varieties may be realized at moderate N levels (Oikeh et al., 1996; Smith et al., 1997). Results suggest that hybrid breeding programs in the region should place greatest emphasis on development of high yielding, NUE single crosses, because there is no apparent advantage of double-cross hybrids under N stress (Fig. 5). On the other hand, since the single-cross hybrids currently available in the region are not greatly superior to double crosses, seed companies may prefer to market three way and double crosses because they are easier and less costly to produce.

The hypothesis that rapid, early root growth would enable the maize plant to catch the N flush that occurs early in the growing season and have better N use efficiency was not substantiated by these experiments.

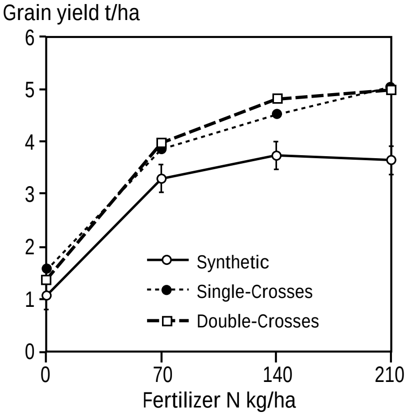

Figure 5. Average grain yield of the synthetic, single-crosses, and double-crosses at four N levels across five locations in Nigeria. Vertical bars represent standard errors for genotype means.

Rates of root growth observed in small tubes at the seedling stage and measurements of RLD in the field at 4 WAP did not correspond well with grain yield under N stress. Roots occupy a relatively small proportion of the soil volume at the early growth stages, which increases sampling variation and reduces precision of RLD estimates. Furthermore, differences in initial biomass and N uptake may have little impact on N use efficiency because the greatest amounts of N are taken up later in the season when plants are undergoing rapid vegetative growth. Finally, there was little evidence that the N flush following the onset of the rains is immediately lost from the root zone through leaching. N mineralization and movement of nitrate to lower soil depths occurred more gradually than expected, with substantial amounts of N being lost from the root zone around silking time. Maximum rooting depth may therefore be more critical than rapid early root growth in determining NUE.

Attempts to determine mechanisms of N stress tolerance have led to varying conclusions. In several experiments we conducted in the southern Guinea savanna, N uptake was closely correlated with grain yield under low N. Other studies have shown that varietal differences in N utilization efficiency are more closely associated with yield performance under low N (Lafitte and Edmeades, 1994b; Moll et al., 1982). Changes in correlations across sites suggest that different mechanisms contribute to N stress tolerance in different environments (Table 3; Lafitte and Edmeades, 1994c). In our experiments some genotypes exhibited high N uptake efficiency while others showed high N utilization efficiency. Despite the inherent variability in measuring root parameters, root morphology appeared to provide an explanation for performance of some genotypes under N stress. Lafitte and Edmeades (1994c) observed that selection for N stress tolerance increased root growth, providing additional evidence that ability to extract N from the soil, perhaps from greater depths, plays a role in determining NUE. We are presently combining various populations and inbred lines that have shown either high N uptake efficiency or high N utilization efficiency into a common pool for further selection for N stress tolerance.

There is still a need to find reliable, rapid screening techniques for root growth parameters. In 1996 we will initiate screening for root pulling strength, to see if this characteristic can be used as a selection criterion for N stress tolerance as well as root lodging resistance. Increased root size may also improve drought tolerance. Although a larger root system may compete for photosynthates and reduce maximum yield potential, we feel that reduced losses due to N stress, drought and lodging will provide a net benefit in the lowland tropical environments of Africa, where maize yields average only about 1 Mg ha^{-1}. Ultimately we see the need to incorporate resistance to *Striga* spp. into our N stress tolerant cultivars, because these parasites are ubiquitous in the savannas and often cause greatest damage under poor fertility conditions (Berner et al., 1995).

Although low N fertility is clearly one of the most important constraints for maize production in the savannas, farmers are not likely to adopt a variety simply because it is tolerant to N stress. TZB is relatively susceptible to N stress, yet it spread rapidly through the savannas of Nigeria following its release. It is appreciated for its high yield potential and small, flinty kernels, which are suitable for traditional processing methods. Thus, processing and storage characteristics may be as important as N stress tolerance in determining the acceptability of improved cultivars. Although there is clear justification for continued research to develop NUE cultivars, breeding alone cannot solve the problem of low crop productivity due to poor soil fertility. Greater root growth is observed at moderate N fertility than at low or high N levels (Eghball and Maranville, 1993; Oikeh, 1996). In some experiments, N utilization efficiency was also greatest under moderate N fertility. Maize can contribute most to the overall efficiency of the farming system if moderate levels of N fertility are maintained. On-farm trials showed that an N-efficient hybrid (8644-27) outyielded an N-inefficient open-pollinated variety (TZB-SR) by 7.2% when following a previous maize crop. Use of the efficient variety following a soybean rotation resulted in a 31.1% increase in maize yields, illustrating the need for an integrated approach to improve soil fertility and maize productivity in the African savannas (Oikeh, 1996).

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Selection for Response to Low Nitrogen in the La Posta Maize Population

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Abstract

Improved maize cultivars that require low levels of nitrogen fertilization to produce high grain yields would be highly desirable for areas practicing low input agriculture. We conducted two studies in a lowland tropical maize population to 1) estimate the effectiveness of recurrent selection for improved agronomic performance in the population under low levels of applied N, and 2) determine the effects of six cycles of recurrent selection on the N response of the population. In one study, 100 randomly chosen full-sib families from La Posta maize population were evaluated at 40 (low N) and 160 (high N) kg N ha^{-1} *applied as ammonium sulfate at two locations in 1985 and 1986 in Ghana, West Africa. Expected genetic gain per cycle of full-sib selection for grain yield, mid-silk, plant height and grain moisture were 4.6, 2.4, 2.8, 8.4% at low N and 5.0, 1.9, 1.4, 5.4% at high N, respectively. In the other study, cycles 0, 2, 4, and 6 of La Posta were evaluated at 0, 80, and 160 kg N ha*$^{-1}$ *at six locations in 1986. Between* C_0 *and* C_6*, yields increased by 0.26, 0.50 and 0.63 t ha*$^{-1}$ *at 0, 80 and 160 kg ha*$^{-1}$ *of N applied, respectively. It was concluded from the two studies that recurrent selection would be effective in improving the population under low and high N, although absolute gains are lower under low N.*

Maize is an important crop under rain-fed agriculture in the lowland tropics. Most cultivated soils in these regions, particularly the savanna soils, are deficient in N (Djokoto and Stephens, 1961; Ahn, 1970; Sanchez, 1976). Because the available N is limited in these soils, inorganic N fertilizers are usually recommended when maize is grown. However, due to high fertilizer costs, resource-poor small-scale farmers are unable to adopt fertilizer recommendations. For example, maize producers in Ghana mostly rely on soil residual N to grow the crop. As a result maize yields are low, averaging approximately 1.3 t ha^{-1}. Therefore, maize cultivars that are productive under these conditions are highly desirable.

Nitrogen utilization (N uptake and translocation to developing kernels) in maize is under polygenic control (Harvey, 1939; Pollmer et al., 1979) and variation exists among maize genotypes for N utilization (Harvey, 1939; Chevalier and Schrader, 1977; Pollmer et al., 1979). Genotypic variation for N utilization has permitted selection for this trait (Muruli and Paulsen, 1981; Moll et al., 1987). Maize breeding programs traditionally develop maize varieties under high levels of N fertilization. This practice seeks to eliminate N as a variable to facilitate selection (Balko and Russell, 1980; Muruli and Paulsen, 1981). Since genotypic variation for N utilization exists in maize, the N response of the original population is altered in successive cycles through recurrent selection for improved agronomic performance (Allan and Darrah, 1978; Muruli and Paulsen, 1981; Kamprath et al., 1982). We conducted two separate experiments to:

1. Determine the effectiveness of recurrent selection for improved agronomic performance at low levels of N fertilization in a lowland tropical maize population.
2. Determine changes in response to N fertilizer in a lowland tropical maize population following six cycles of conventional recurrent selection.

Materials and Methods

Experiment 1

One hundred full-sib families chosen at random from La Posta maize population were evaluated at 40 kg N ha^{-1}(low N) and 160 kg N ha^{-1}(high N). Each N level was considered a separate field trial planted adjacent to each other at Fumesua and Damongo in 1985 and at Nyankpala and Kwadaso in 1986. The experimental design was a RCB with blocks-in-replications and restriction on randomization for each N level. The 100 full-sibs were randomly grouped into 10 sets of 10 families, which were randomly assigned to 10 blocks within a complete replication. The 10 families were then randomized in the 10 plots in each block. A plot consisted of a single row of each family at 50,000 plants ha^{-1} density. Nitrogen was applied at 40 and 160 kg N ha^{-1} as ammonium sulfate in equally split applications during the first and fourth weeks after emergence. Phosphorus was applied at 60 kg P_20_5 ha^{-1} to all plots as triple superphosphate prior to planting.

The traits considered were grain yield, days to mid-silk, plant height, grain moisture, ears per plant, lodging and ear and N stress ratings. Nitrogen stress was visually rated prior to flowering based on the number of chlorotic maize leaves and the extent of lower leaf chlorosis on a 1-5 scale (1 = no N stress, and 5 = extreme N stress). Analyses of variance were computed for each environment (year-location) and combined over environments for each trait and N level, assuming all effects were random (Steel and Torrie, 1980). The pooled (over sets) genotypic variance among full-sib families, genotype x environment interaction, and error variances were estimated along with estimates of variances on these variance components following the procedure suggested by Comstock and Moll (1963). Mean performance of the full-sibs under each level of N was estimated for each trait by averaging the performance of the families in each environment and across environments. Heritabilities and expected genetic gain from one cycle of full-sib family selection were computed for the traits under each N regime.

Experiment 2

The N response of cycles 0, 2, 4 and 6 of La Posta maize population was studied in Ghana, West Africa. La Posta or CIMMYT Population 43 is a white dent, late maturing Tuxpeño-related synthetic which produces tall, vigorous-growing plants and is well adapted to the lowland tropics (Pandey et al., 1986; CIMMYT, 1987). Cycles 1 and 2 were developed using full-sib selection in which only among-family selection was done. Cycles 3 through 6 were developed using modified full-sib selection in which both among- and within-family selection was practiced. Both selection schemes were based on an international progeny testing program with one test location at CIMMYT, Mexico, and other test locations in three to five other countries in the lowland tropics (Pandey et al., 1986). The cycles were grown in 1986 at Nyankpala (Guinea savanna, fine sandy-loam Alfisol), Damongo (woodland savanna, fine sandy-loam Alfisol), Pokuase (coastal savanna, fine sandy-loam Dystrochrept), Ejura and Kpeve (forest-savanna transition, fine to coarse sandy-loam, Oxisol), and Kwadaso (forest, coarse sandy-loam Paleustult). The previous crop was cowpea (*Vigna unguiculata* L. Walp.) at Kpeve, Damongo and Ejura. The fields at Nyankpala, Kwadaso and Pokuase were under grass fallow since the previous maize crop in 1983.

The experimental design was a randomized complete block in a split plot arrangement with four replications at each site. Nitrogen rates were assigned to main plots and selection cycles were the sub-plots. Sub-plots consisted of two 5 m rows at 50,000 plants ha^{-1} density. All trials were rainfed except at Kwadaso where supplemental irrigation was applied. Nitrogen rates of 0, 80, and 160 kg N ha^{-1} were applied as ammonium sulfate in a split dose; half of each rate was applied at one week and the remainder at four weeks after emergence. Phosphorus was applied at 60 kg P_20_5 ha^{-1} to all plots as triple superphosphate prior to planting. No K was applied because of the consistent lack of response of maize to K fertilization in Ghana (Ahn, 1970; Dennis, 1983). The traits measured were grain yield, days to mid-silk, plant height, grain moisture, ears per plant and lodging and ear ratings.

Cycles of selection and N levels were considered fixed effects and environments were considered random effects. Analyses of variance were computed in each environment (location) and combined over environments for all traits (Steel and Torrie, 1980).

Results and Discussion

Experiment 1

Mean square estimates for each N level (data not presented) showed that all traits were significantly ($P \leq 0.01$) affected by environment. Effects due to genotype were significant for grain yield, mid-silk, plant height and grain moisture at both low and high N. No significant genotype effect was detected for lodging, ears per plant, N stress and ear acceptability ratings. Genotype x environment interaction (GxE) effects also were significant for nearly all traits at both N levels.

Mean performance of the full-sibs at each N level in the four environments is presented in Table 1. Mean grain yield at low N was 9% lower than the yield at high N. Mean days to mid-silk, grain moisture at harvest, plant height, number of ears per plant and ear rating were similar at both low and high N. Lodging was more severe at high N and N stress scores were higher at low N.

Estimates of variance components showed genotypic, GxE, and error variances were significant at both low and high N (Table 2). Genotypic variances for mid-silk, grain moisture and plant height were greater at low N, but the variance for grain yield was greater at high N. GxE variance estimates were more important than genotypic variances for grain yield and grain moisture at both low and high N, and for plant height at high N, but were less important than genotypic variances for mid-silk at both N levels and for plant height at low N. Error variances were far greater than either genotypic or genotype x environment interaction variances. The use of larger plots and/or more than two replications per environment would be needed to reduce the contribution of residual variance to phenotypic variation.

Heritabilities calculated on a family mean basis and expected gain from recurrent full-sib family selection at each N level followed the same general pattern as genotypic variances (Table 2). Estimates of heritability for grain yield, mid-silk, plant height and grain moisture in the population were in close agreement with those reported in the literature (Hallauer and Miranda, 1981). The magnitude of heritability of a trait depends on whether its mode of inheritance is simple or complex and generally ranges below 0.3 for grain yield and between 0.5 and 0.7 for days to flower, plant height and grain moisture. Selection for increased grain yield and for reduced days to mid-silk, grain moisture and plant height would be effective at both high and low N.

Experiment 2

The combined-over-environments analyses of variance for five traits measured (data not presented) showed that environments, N, and cycles were significant sources of variation in all traits. N x environment interaction effects were significant for days to mid-silk, lodging and ear acceptability, whereas cycle x environment

Table 1. Mean response of 100 full-sib families to low and high N fertilizer application in four environments in Ghana, West Africa.

Environment	Grain yield ($t\ ha^{-1}$)	Mid-silk (d)	Grain moisture ($g\ kg^{-1}$)	Plant height (cm)	Lodging[†] (score)	Ears $plant^{-1}$ (no.)	N-stress rating[‡] (score)	Ear acceptability[§] (score)
Low N fertilizer application								
Fumesua 1985	4.72	62	233	214	2.0	0.89	2.0	2.8
Damongo 1985	5.09	63	234	200	3.1	0.97	-	2.6
Nyankpala 1986	3.91	59	299	164	2.6	1.02	3.1	3.5
Kwadaso 1986	7.07	57	240	208	1.1	0.97	2.3	2.4
Mean	5.20	60	251	197	2.2	0.96	2.5	2.8
SE	0.26	0.3	4	3	0.1	0.01	0.1	0.1
High N fertilizer application								
Fumesua 1985	5.17	61	228	210	2.0	0.93	2.0	2.7
Damongo 1985	5.45	63	244	196	3.5	0.99	-	2.8
Nyankpala 1986	4.67	59	320	164	3.7	1.02	2.6	2.7
Kwadaso 1986	7.83	57	236	208	1.3	0.99	1.3	2.2
Mean	5.78	60	257	195	2.6	0.98	1.9	2.6
SE	0.26	0.3	4	6	0.1	0.01	0.1	0.1

[†] 1 to 5 score, 1 = all plants erect, 5 = extremely lodged.

[‡] 1 to 5 score, 1 = no N stress, 5 = extreme N stress.

[§] 1 to 5 score, 1 = good ear, 5 = poor ear.

interaction effects were significant for grain yield, mid-silk, and plant height. These significant interactions were due to differences in magnitude rather than rank order of values for the traits in the different environments. No significant N x cycle interaction effects were detected for any trait, indicating that the relative performance of the cycles did not change under the different N regimes.

Since the N x cycle interaction effects were not significant, the nature of the N and cycle responses can be explained entirely by their main effects (Table 3). Mean grain yield at zero applied N was approximately 37% and 43% lower than grain yield at 80 and 160 kg N ha^{-1}, respectively. Grain yield at 160 kg N ha^{-1} was approximately 10% higher than yield at 80 kg N ha^{-1}.

The significant N x location interactions for grain yield suggest that yield response to N differed among locations. Though data are not shown, substantial yield increases were observed from 0 to 80 kg N ha^{-1} in all environments. These yield increases ranged from 31% in the coastal savanna to 107% in the Guinea savanna. Yield increases of 11%, 15%, 21% and 40% were observed from 80 to 160 kg N ha^{-1} at Nyankpala, Kwadaso, Pokuase and Ejura, respectively. No further yield increase was detected at Damongo and Kpeve beyond the 80 kg N ha^{-1} rate. The lowest grain yield (1.5 t ha^{-1}) was observed under zero applied N in the Guinea savanna and the highest (4.4 t ha^{-1}) was observed in

Table 2. Estimates of genotypic (σ^2_G), genotype x environment (σ^2_{GE}) and error (σ^2_e) variances, heritability (h^2) and expected gain from one cycle of full-sib family selection (GFS) at low and high nitrogen in La Posta maize population.

Trait and N level	σ^2_G	σ^2_{GE}	σ^2_e	h^2	GFS†
Grain yield (t ha^{-1})					
Low N	0.058 ±0.030	0.080 ±0.055	0.885 ±0.066	0.309 ±0.159	0.24
High N	0.074 ±0.030	0.105 ±0.055	0.843 ±0.063	0.360 ±0.146	0.29
Mid-silk (d)					
Low	0.913 ±0.181	0.260 ±0.120	1.800 ±0.134	0.759 ±0.150	1.46
High	0.598 ±0.136	0.115 ±0.131	2.160 ±0.161	0.667 ±0.152	1.11
Grain moisture (g kg^{-1})					
Low	26.35 ±8.90	47.70 ±11.93	150.0 ±11.2	0.463 ±0.156	7.07
High	13.15 ±6.27	43.00 ±10.09	122.9 ± 9.2	0.334 ±0.161	3.67
Plant height (cm)					
Low	62.40 ±13.46	48.44 ±10.11	115.7 ± 8.6	0.701 ±0.151	16.60
High	55.63 ±13.25	72.11 ±11.53	107.1 ± 8.0	0.639 ±0.152	10.46

† Standardized selection intensity, K = 1.755.

Table 3. Mean response of six cycles of selection in La Posta maize population to N fertilization in Ghana, 1986.

Nitrogen applied	Population cycle	Grain yield (t ha^{-1})	Mid-silk (d)	Grain moisture (g kg^{-1})	Plant height (cm)	Ears plant^{-1} (no.)	Lodging† (score)	Ear acceptability‡ (score)
0 kg ha^{-1}								
	C_0	2.89	58.1	248	192	0.90	1.9	3.5
	C_2	2.93	57.3	242	181	0.90	1.9	3.6
	C_4	2.86	56.6	239	178	0.93	1.9	3.5
	C_6	3.15	56.0	247	174	0.91	1.8	3.3
	Mean	2.96	57.0	244	181	0.91	1.9	3.5
80 kg ha^{-1}								
	C_0	4.56	56.7	251	203	0.92	2.3	2.9
	C_2	4.42	56.1	247	198	0.95	2.3	2.9
	C_4	4.75	54.7	243	186	0.95	2.0	2.8
	C_6	5.06	54.3	242	187	0.95	1.9	2.6
	Mean	4.70	55.4	246	193	0.94	2.1	2.8
160 kg ha^{-1}								
	C_0	5.00	56.6	250	201	0.92	2.5	2.9
	C_2	5.07	55.8	244	196	0.94	2.6	2.8
	C_4	5.09	55.3	249	182	0.96	2.2	2.9
	C_6	5.63	54.0	244	187	0.93	2.2	2.7
	Mean	5.20	54.8	247	192	0.93	2.4	2.8
Overall								
	C_0	4.15	57.1	250	198	0.91	2.2	3.1
	C_2	4.14	56.4	244	198	0.93	2.3	3.1
	C_4	4.23	55.5	244	182	0.94	2.0	3.1
	C_6	4.62	54.8	245	183	0.93	1.9	2.8
	Mean	4.29	56.0	246	189	0.93	2.1	3.0
				Standard errors				
Nitrogen means		0.25	0.3	*NS*	5	*NS*	0.1	0.1
Cycle means		0.10	0.2	*NS*	2	*NS*	0.1	0.1
Cycle means at same Nitrogen level		0.17	0.2	*NS*	3	*NS*	0.2	0.2
Nitrogen means for same or different cycles		0.29	0.4	*NS*	5	*NS*	0.2	0.2

† 1 to 5 score, 1 = all plants erect, 5 = extremely lodged.

‡ 1 to 5 score, 1 = good ear, 5 = poor ear.

the forest zone. The relatively high yield under unfertilized conditions at some locations indicated high soil residual N from nitrogen contributions of preceding legume crops through N fixation and mineralization of organic residues.

Nitrogen treatment means for the other agronomic traits showed the response of these traits to N fertilization was similar at 80 and 160 kg N ha^{-1} (Table 2). There was a significant delay in silk emergence, a significant reduction in plant height and lodging, but grain moisture and number of ears per plant did not change when N fertilizer was not applied. Ears from plants grown without N fertilizer were rated less acceptable than ears from plants which received fertilizer. Though silk was delayed by two days when fertilizer N was not applied, no significant differences were observed among N treatments for grain moisture content at harvest. This suggests that grain filling was curtailed at low N and, as a result, grain moisture was similar for all treatments.

Individual cycle response of grain yield to N fertilization is illustrated in Figure 1. Grain yield of all cycles increased as fertilizer N supply was increased. In all cycles, the response of grain yield to applied N was much greater for the first rather than the second increment of 80 kg N ha^{-1}. For example, the yield difference between the unfertilized treatment and 80 kg N ha^{-1} was 1.9 Mg ha^{-1} compared with 0.6 Mg ha^{-1} between 80 and 160 kg N ha^{-1} for the sixth cycle of selection. Yield responses were very similar for cycles 0 through 4, but tended to be greater for cycle 6 (Fig. 1).

Though the various cycles were developed under mainly high N conditions at CIMMYT-Mexico and at other experiment stations in the lowland tropics, grain yield of the improved cycles increased across N levels. These observations do not support the notion that conventional breeding results in varieties which are productive only under the conditions in which they were bred, even though yield gains in absolute terms tended to be smaller under zero applied N (0.26 t ha^{-1} between C_0 and C_6) than when N was applied (0.50 and 0.63 t ha^{-1} between C_0 and C_6 at 80 and 160 kg ha^{-1} of N applied, respectively).

The effects of N fertilization on days to mid-silk, plant height, lodging and ear acceptability followed the same general trends for all cycles (Table 3). Days to mid-silk decreased and plant height, lodging and ear acceptability increased as N supply was increased. Grain moisture and number of ears per plant were not significantly influenced by fertilizer N application.

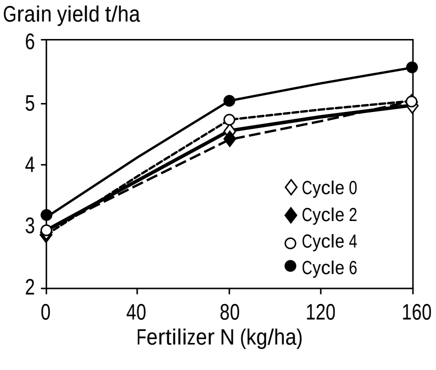

Figure 1. Relationship between applied fertilizer N level and grain yield of La Posta selection cycles 0 to 6; data from six Ghanaian locations.

Changes in grain yield between C_0 and C_6 went along with earlier mid-silk, shorter plant height, less lodging and ears which were rated more acceptable.

Results from the six cycles studied suggest that recurrent selection for improved agronomic performance altered grain yields under low and high N supply, with gains tending to be higher under high versus low N.

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Improvement of the Maize Population "Elite Synthetic NT" for Soils with Low Nitrogen Content

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Abstract

The maize population 'Elite Synthetic NT' has been selected with the objective of improving its yield potential in soils with low nitrogen (N) availability. During the 1994/95 season, 144 half-sib families showing good male-female flowering synchrony were evaluated with and without N fertilizer at Sete Lagoas, MG. The experimental design utilized was a 12 x 12 lattice, with 5 m plots. The open-pollinated variety 'BR 106', selected in soils with high fertility, was used as a between block check. Mean ear weight for the selected families in N+ and N- environments averaged 4,511 kg/ha and 3,327 kg/ha, respectively. Yield reduction between environments averaged 27.14% for the selected families and 65.8% for BR 106. The results indicate that selection in N- environments is an efficient approach for developing genotypes with better performance in soils with low nitrogen content.

Nitrogen (N) availability is estimated to be the principal limiting factor in more than 20% of arable land (Lafitte and Edmeades, 1988). Nitrogen fertilizer application can overcome this limitation in many tropical regions, but the high risk resulting from high cost and uncertain economic return frequently deters farmers from using it. This has brought about an intensified search for technologies which can increase the efficiency of N use by plants (Furlani et al., 1985). For small-scale farmers in Brazil, improved N use efficiency is particularly important because there are no government fertilizer subsidies.

Increasing the N use efficiency of maize germplasm may reduce the effects of soil N deficiency on maize production. Superior genotypes may either be more efficient at N uptake or N utilization, or both. Traditional breeding programs commonly do not select under low N conditions because higher environmental variation reduces the heritability of grain yield (Blum, 1988). It is not clear whether selection in N limited environments is a better strategy to improve N use efficiency (Clark and Duncan, 1991).

Genetic variability for N use efficiency under low N was found for inbred lines (Balko and Russell, 1980) and tropical cultivars (Thiraporn et al., 1987; Lafitte and Edmeades, 1994a,b). Moll et al. (1987) observed in temperate maize germplasm that materials selected for N use efficiency had good yields at high N levels, but they could not be distinguished from unselected materials at low N levels. It has been suggested that selection efficiency can be increased in environments with low N levels by selecting for secondary characteristics, provided they are correlated with grain yield and less affected by the environment. For a breeding program, utilization of secondary characteristics is frequently limited due to the difficulty in measuring them with precision and rapidity (Beauchamp et al., 1976; Clark, 1982).

This study evaluates ear yield of half-sib families from Synthetic Elite NT under high and low N conditions and compares their performance with a commercial check entry. Synthetic Elite NT has been selected under low N conditions, whereas the check entry was developed in high fertility environments.

Material and Methods

Maize population Synthetic Elite NT was formed in 1987 from the 10 best inbred lines belonging to the breeding program of the National Center for Maize and Sorghum

Research (CNPMS). All possible crosses among lines were made and a balanced bulk of F_1 seed from each cross was recombined. In 1989 and 1990, a second and third recombination was carried out by planting a balanced bulk of seed from selected ears in isolation. During the third recombination, several plants were selfed and 400 S_1 ears were selected. Two cycles of recurrent selection were completed under high N conditions and the best 10% of the lines were recombined each time. A third cycle of selection was planted at a population density of 100,000 plants/ha and under low N conditions in 1993. A mixture of pollen from 50 tassels was taken each day and used to pollinate plants with good flowering synchrony (i.e., short anthesis-silking interval, or ASI).

The resulting 144 half-sib families were evaluated in two environments: on fertile soil (N+) and poor soil (N-) at Sete Lagoas-MG, Brazil (19° 28' S, 44° 15' W). The soil is classified as latosoil dark red, dystrophic and of clay texture. The field trials were planted during the rainy season using a 12 x 12 simple lattice experimental design. An intercalate check entry, BR 106, was planted in each block. In the N+ environment, 400 kg/ha of 4-14-8 (NPK) fertilizer was applied at planting and 60 kg/ha of N was side-dressed later in the season. No fertilizer was applied in the N- environment. Plots consisted of one 5 m row spaced 0.90 m between rows and 0.20 m between plants within rows. Water stress occurred during the 10 days around the flowering period. Ears were weighed from each plot. Percent moisture was measured and used to correct the weights to 14.5% moisture. Data for ear weight from both trials were analyzed using the procedures given by Cochran and Cox (1957).

Results and Discussion

Soils were analyzed for major nutrients (Table 1). The soil in the N- environment contained medium levels of Ca and P, a low level of K and a high level of Mg (based on recommended levels from Comissão, 1989). The level of organic matter suggested that N levels resulting from N mineralization might be high. However, only 25 kg/ha of N was available as NO_3 and NH_4 in the top 40 cm of the N- soil (data not shown). The N+ environment had adequate levels of all elements based on soil analyses and applied fertilizer.

Analysis of variance for ear weight showed highly significant (P£0.01) differences among half-sib families in both environments. Values for the coefficient of variation (CV, Table 2) were relatively high and similar for both environments; typical of trials grown under stress conditions (Blum, 1988; Parentoni et al., 1992; Machado et al., 1992; Gama et al., 1994). A lower coefficient of variation would normally be expected under unstressed, N+ conditions, so drought stress during flowering may have affected both environments and

Table 1. Chemical composition of the soils in environments with and without nitrogen. Sete Lagoas - MG, Brazil, 1994/95.

Soil depth	pH	Ca (eq.mg/100 cc)	Mg	K (ppm)	P (ppm)	O.M. (%)	NH_4 (ppm)	NO_3 (ppm)
Without nitrogen (N-)								
0-20 cm	6.2	3.69	1.04	34	7.5	3.18	1.72	3.26
20-40 cm	6.4	3.95	1.15	45	10.0	3.19	2.45	3.08
With nitrogen (N+)								
0-20 cm	6.4	6.65	0.63	194	42	2.56	-	-
20-40 cm	6.4	5.40	0.54	122	15	2.19	-	-

Table 2. Mean ear weight for the best 20% selected families and tester BR 106 in two environments; i.e., with (N+) and without (N-) nitrogen. Sete Lagoas - MG, Brazil, 1994/95.

Treatment	N+ (kg/ha)	Treatment	N- (kg/ha)
58	9000	58	5447
55	6812	91	5320
116	6749	141	5102
19	6697	31	5092
59	6661	16	4887
110	6649	55	4863
94	6566	71	4853
90	6418	47	4800
88	6405	50	4726
9	6396	90	4615
20	6328	99	4612
92	6195	129	4604
44	6154	125	4603
34	6114	77	4592
131	6051	144	4524
48	6018	21	4514
107	5967	116	4511
108	5933	88	4478
137	5908	9	4464
3	5898	20	4427
141	5884	62	4368
73	5880	34	4345
50	5847	142	4303
144	5688	97	4282
37	5673	114	4266
51	5659	69	4212
17	5648	87	4171
87	5602	48	4114
BR 106 (Tester)	5585	BR 106 (Tester)	1910
Selected Mean	4511	Selected Mean	3287
CV (%)	22.3	CV (%)	23.43
LSD (0.05)	183	LSD (0.05)	138

may have resulted in high and similar CVs in both environments.

Grain yield ranged from 2,380 to 9,000 kg/ha for the N+ environment and from 1,764 to 5,447 kg/ha for the N- environment. Yields of the 20% (28) best families in each environment are presented in Table 2. Thirteen families were selected in both environments. The mean performance of the selected families was very encouraging, considering their contrasting performance to check entry BR 106. Mean grain yield of the selected families in the N- environment (3,287 kg/ha) was 27% less than in the N+ environment (4,511 kg/ha), whereas the check entry reduced its yield by 66% from 5585 kg/ha under N+ conditions to 1910 kg/ha under N- conditions. All selections leading to BR 106 were conducted under N+ conditions (Santos et al., 1994), and this may be the reason for its poor performance under N- conditions.

The lower production costs associated with omitting fertilizer application probably compensated for the yield disadvantage of 1,224 kg/ha under N-, with the net benefit of N use efficient families presumably larger in the N- environment. Thus, sowing N use efficient germplasm like Synthetic Elite NT may be a viable production strategy for regions with predominantly small, low income, self-sufficient farms, especially when combined with minimal organic fertilizer application. Areas like the northeast region of Brazil, where yields range from 500 to 1,000 kg/ha at present, could profit from such germplasm. The results of this study confirm the existence of genetic variability for N use efficiency in maize, and are in agreement with the results presented by Balko and Russell (1980), Thiraporn et al. (1987), and Lafitte and Edmeades (1994a,b).

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Selection for Low N Tolerance in the Thai Maize Breeding Program

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Abstract

One of the most important factors limiting maize yields in Asia is low soil fertility, especially low N. Inorganic fertilizer use, however, is very limited among farmers because of its high cost. Genetic variation in response to N supply found in many studies suggests it is possible to breed varieties or hybrids with tolerance to low N. Nakhon Sawan Field Crops Research Center (NSFCRC) of the Department of Agriculture of Thailand was invited by the CIMMYT Asian Regional Maize Program (ARMP) to be the key Asian country in selecting for low N tolerance. Collaboration between ARMP's member countries working on this project will be strengthened. Selection for low N tolerance in NSFCRC maize breeding program was initiated in 1995. Two successive crops of maize were planted with no fertilizer in 1995ER and 1995LR to lower the level of soil nitrogen in a field of approximately 0.7 ha. This is considered a N-limited environment and will be used for screening germplasm for tolerance to low N. Germplasm will include inbred lines, varieties and populations from NSFCRC, CIMMYT and ARMP. The features of an ideotype adapted to low N environments will be high grain yield under both -N and +N (non-limited N). The germplasm will be tested for grain yield and other important agronomic characters such as plant height, synchrony of male and female flowering, number of ears per plant and time of senescence and maturity under both N-limited and non-limited environments. Tolerance to low N can be selected for using the combined data from both environments. After 3-4 cycles of selection, the amount of progress will be evaluated and selected lines and improved populations can then be distributed to breeding programs in Asia.

One of the most important factors limiting maize yields in Asia is low soil fertility, especially low N. The high cost of inorganic fertilizer dramatically limits its use by farmers. Genetic variation in response to N supply of inbred lines (Balko and Russell, 1980) and maize populations (Lafitte and Edmeades, 1994) has been observed, and it appears possible to breed varieties or hybrids with tolerance to low N. Lafitte and Edmeades (1994) observed no negative association between selection for grain yield under low and high N conditions. This suggests that, to obtain high grain yield at low N with at least a modest increase in grain yield under high N, selection should be conducted simultaneously under both conditions.

Nakhon Sawan Field Crops Research Center (NSFCRC), Department of Agronomy, Thailand is a key center of CIMMYT's Asian Regional Maize Program (ARMP) for selection for low N tolerance. The objectives of this project are to develop populations, varieties, and hybrids tolerant to low N and to facilitate collaboration between ARMP member countries in the exchange and distribution of germplasm. Evaluation trials under both low and high N conditions will be started in the middle of April 1996. This presentation documents the breeding materials, screening technique, selection criteria and breeding scheme which will be used.

Materials and Methods

The breeding materials include populations, varieties, hybrids and lines which can be classed according to source as either exotic or Thai germplasm:

1. Exotic germplasm from CIMMYT, ARMP and others.
2. Thai germplasm from NSFCRC, Kasetsart University (KU) and private companies

Experimental conditions

The project was initiated in 1995 during the late-rainy season at NSFCRC, Thailand (15 °N, 100 °E and 86.8 m elevation). The experimental field was divided into low-N and high-N blocks. The low-N block comprises an area of 0.7 ha, which was previously depleted of N by growing two maize crops in the 1995 late-rainy, and dry seasons and removing all above-ground biomass. This block will receive 62.5 kg P ha^{-1} as triple-super-phosphate broadcast prior to planting in each crop season, but no N will be applied. The high-N block will receive 150 kg N ha^{-1} each season. 62.5 kg ha^{-1} of N and 62.5 kg ha^{-1} of P_2O_5 will be broadcast prior to sowing and the remaining N will be sidedressed at about 35 days after sowing. Maize will be oversown in 5 m rows with the spacing between and within rows, 25 and 75 cm, respectively, and thinned to a final density of 53,000 plants ha^{-1}.

Experimental design

The breeding materials will be sown in two-row plots with two or three replications at each N level. Materials will be grouped in two types of experiments. The first includes populations, varieties and hybrids; the second only includes inbred lines. A randomized complete block or simple lattice experimental design will be used. Plots will be separated with a single check row of the NSFCRC variety NS 1. To control the effects of soil variation, the mean yield of the two check rows bordering a plot will be used as a covariate for that experimental plot in the analyses.

Data collection

The following data will be collected under both N levels:

- Grain yield.
- Plant and ear height.
- Anthesis-silking interval.
- Number of ears plant^{-1}.
- Number of aborted ears.
- Number of green leaves below the top ear at 4 weeks after silking (for further details on measuring leaf senescence rate, see Binford and Blackmer, 1993).
- Nitrate reductase activity (NRA) of leaf lamina at 10 and 20 days post-anthesis (the measurement is based on the method described by Jaworski, 1971). Athough lower nitrate levels occur post-anthesis than at earlier stages of development, the plant still needs N for grain development; thus, a plant exhibiting higher NRA at this stage should develop more grains. In support of this, Deckard et al. (1973) found total leaf canopy NRA was positively correlated with both grain yield and total grain protein production for six maize hybrids, and Hageman et al. (1976) observed a low but significant positive correlation between NRA and grain yield.
- Nitrogen concentration of stem and leaf at anthesis and physiological maturity, so that the relationship between nitrogen content in plant tissue and grain yield under high and low nitrogen conditions can be determined.

The data collected on these secondary traits will be used as selection criteria. Genotypes selected should have an anthesis-silking interval of less than 5 days under low N conditions, at least one ear per plant, a low number of aborted ears and a low level of leaf senescence. The correlation between grain yield and these secondary traits, under low and high N conditions, will also be determined.

Selection index

The selection index described by Fischer et al. (1983) will be used to aid selection.

$$\text{Low N index}_a = \frac{\text{Yield}_a\,(-N)}{\text{Yield}_a\,(+N)} \times \frac{\text{Site mean yield }(-N)}{\text{Site mean yield }(+N)} \qquad (1)$$

Where:

Yield_a (-N) = mean grain yield of genotype A under low N

Yield_a (+N) = mean grain yield of genotype A under high N

Site mean yield (-N) = mean grain yield of all genotypes under low N

Site mean yield (+N) = mean grain yield of all genotypes under high N

Selection for high grain yield under high or low nitrogen conditions may lead to genotypes adapted to those specific conditions. Hence, simultaneous selection under both conditions should be made using this selection index. A low N index > 1.0 indicates relatively low N tolerance, whereas an index < 1.0 indicates a relatively low N susceptibility.

Collaborative research

The established facilities will be used for collaborative research in the region. Maize germplasm including populations, varieties, hybrids and inbred lines from ARMP's member countries will be tested here under low and high N conditions, and conversely, low N tolerant inbred lines and populations developed at NSFCRC will be sent to other member countries for testing in their low N environments. By this process, adapted genotypes will be selected and used as source breeding materials for low N tolerance in the various breeding programs, or evaluated in multi-location field trials prior to release.

Conclusions

Selection for low N tolerance has just started in the Thai maize breeding program. Nursery development started in 1995. The expectation is that this will facilitate collaborative work on low N tolerance between ARMP's member countries, and that ultimately this will benefit not only member countries but all tropical maize growing areas.

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Simulation Models and Statistical Methods to Assist in Targeting and Breeding for Drought Tolerance

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Abstract

Simulation models can be used in combination with spatial (geographic information systems) and historical data to determine how different sites and seasons (the target population of environments - TPE) provide different challenges to plant cultivars. Examples for maize in Central America and southern Africa and for sorghum in northern Australia are used to demonstrate aspects of the nature of these three TPEs. Models can be used to simulate the value of different traits over a range of environments from the TPE. For such 'specific-adaptation' cultivars, models might also be used to determine where the cultivars would be best deployed. Further, if models are used to determine the 'types' of abiotic challenges that exist in the TPE, we can ensure that the combination of test environments sampled in the multi-environment trials matches the frequency of challenges in the TPE. It is argued that, in smaller, more-targeted multi-environment trials, it should be feasible to identify the same superior genotypes that would have been selected in more extensive and costly random testing in the production environment. The paper also illustrates how pattern analysis of multi-environment trials can elucidate different aspects of the interaction of genotypes with dryland environments. For maize, this analysis demonstrates the necessity of testing in both dry and irrigated environments to facilitate drought tolerance gains in a diverse TPE. In the case of sorghum, the same statistical techniques demonstrate differences among locations within a geographically large TPE. These results correlate with independent measures of the environment (simulation model output). The linkage between real data and simulation output allows breeders to weight selection decisions by location and season, depending on how representative the sampled environments are of the real TPE.

No breeding program can pursue all avenues of improvement within its mandated region. However, a program can improve its efficiency by setting objectives that directly reflect the importance of challenges faced. We begin with a discussion of the broad parameters in a breeding program - describing environments and selecting for 'broad' or 'specific' adaptation. The rest of the paper is essentially a review of methods that we have used to attempt to set breeding objectives in dry environments and methods of achieving them. In the past, it has been difficult to quantify the incidence of abiotic stresses in time and space, other than through empirical guesses. New methods exist to assist this process. The major objective of this paper is to illustrate the combined use of two types of tools — simulation models and pattern analysis — in targeting (setting objectives) and breeding for drought tolerance in tropical cereals. We draw together examples from previous papers for two breeding programs, one with a worldwide mandate for maize, the other for sorghum in northeastern Australia.

Defining the Mandate of a Breeding Program

Geographic mandate regions and genotype by environment interaction

A program's objectives are determined by the geographic extent of the mandate region and the diversity of environments they contain. In a physical sense, this includes a range of soil types (and differences within soil types), topography and climate, and climatic variability. Other attributes of growing environments are the extent and intensity of biotic stresses (diseases, insects and weeds) and management and history of the cropping system. Together, all of these factors and their interactions with each other ensure that each season on each field provides a different challenge to any cultivar. Even though yield or profit outcomes from a single crop may be similar in different seasons, they will have resulted from different combinations of these factors.

Comstock (1977) describes all of these possible combinations of production factors as a 'target population of environments (TPE)'; i.e., the set of challenges that a crop can potentially encounter. For pests and climate this could include challenges projected to be a problem in the future. For example, a disease with potential to devastate a crop may not be present in a geographic area, but its potential for yield losses may demand that resources are invested to incorporate resistance into all new germplasm. Some consider global warming as part of the potential TPE and have argued for investment of resources to breed for elevated temperatures.

The flow of germplasm and production of cultivars by a program like that of CIMMYT's maize program might be viewed as in Figure 1. The central box denotes the TPE and contains several different sub-divisions of the TPE (for this example consider them as geographic regions, except for E), their importance being denoted by their size; A is less important than C. However, sub-TPE E (a disease) is important because it occurs across all of the others except A. The cultivars illustrate how the concepts of broad and specific adaptation are dependent on the definition of TPEs. Cultivar 1 (e.g., a CIMMYT 'Across site' cultivar) has broad adaptation to all sub-divisions of the TPE, including that for the disease (E). Cultivar 3 (e.g., a CIMMYT ear rot resistant cultivar) has been developed in sub-TPE B, but also has specific 'stress' adaptation for the disease sub-TPE E. This might become source germplasm that can be passed to a local breeding program working in sub-TPE D to produce a cultivar that may also be said to have 'broad adaptation', although only to the mandate region for that program. Cultivar 4 (e.g., a CIMMYT 'best at site' cultivar) is a direct selection from testing in sub-TPE C and has specific 'geographic' adaptation. This single figure is an idealization of how germplasm is developed and tested, but obviously to develop cultivars with specific or broad adaptation consideration must be given to the appropriate sampling of the sub-TPEs where cultivars are to be grown.

Cultivars (genotypes) do not always perform the same relative to each other in the different seasons and locations of a TPE. This genotype by environment interaction (GxE) complicates the selection of superior genotypes. If all seasons and locations resulted in the same ranking of genotypes, then breeding programs could operate at one location, knowing that improved germplasm would be suited to anywhere else in their mandate region. However, for almost all plant-breeding objectives, this is the exception rather than the norm. In practical terms, if we can sub-divide the TPE based on an understanding of the important GxE interactions, then we can stratify sampling and use the data more effectively.

Figure 2 illustrates the yield distribution in a theoretical TPE for sorghum in seven locations over more than 70 years in northern Australia. The locations are samples from an area of about 200,000 km^2. The yield data were obtained using a sorghum crop simulation model to 'grow' crops each summer, given

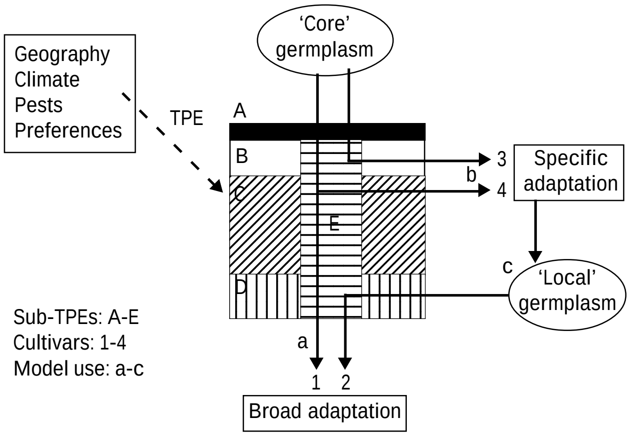

Figure 1. Flow of different adaptation types of cultivars (1 to 4) in a two-stage breeding program and points of intervention (a to c) for simulation models in improving breeding efficiency. The boxes A-E represent sub-components of the target population of environments (TPE), which might be defined as different geographic regions, soil types, season types or stresses that occur discretely (A) or across (E) different sub-TPEs. See text for further discussion.

sufficient planting rain (Hammer and Muchow, 1994). The TPE is described by the distribution of different yields across seasons and locations. In this case, the TPE is bi-modal across seasons within sites. The southern sites, which have deeper soils (Bongeen, Condamine, Bowenville, Dalby) generally yield above 2.0 t/ha, although the range of yields is still quite wide. Not shown in the figure is the 10% or so of seasons when no crop was planted in the simulation, because no planting rain was received.

The resources for sorghum breeding in Australia are insufficient to breed specific genotypes for each location. A better option is to develop broadly adapted genotypes for the overall TPE or for a few sub-divisions of the TPE. In selecting for broad adaptation, one might be tempted to concentrate testing at high yielding sites with few tests at low yielding sites. The question of how else one might sub-divide this TPE and choose and weight testing locations is addressed later in this paper.

The nature of challenges in the TPE

All challenges experienced by a crop might be considered to act at different intensities. For example, it may be difficult (i.e., uneconomic) to breed a maize cultivar with tolerance to extreme levels of rarely occurring soil toxins or catastrophic weather (hurricanes) or pest events (plagues). While genetic variation may exist in response to some of these events, more profitable areas of emphasis are often where the effect of the challenge on yield is low to moderate, rather than extreme. Even high input levels can be considered a challenge to the crop to exhibit maximum yield without lodging. Further, apart from yield, the breeder must consider how the quality of the harvestable product is challenged by stresses experienced.

Challenges associated with the ‘within-season’ climate tend to cause large GxE interactions partly because they generate a much greater variety of environments across locations or seasons. One response to this type of large variation is to breed for specific adaptation. This approach was adopted successfully by CIMMYT in breeding for drought tolerance in tropical maize (Fischer et al., 1989; Bolaños and Edmeades, 1993). The method was the abiotic equivalent of using infestation or special screening sites to select for pest or disease resistance and is described in detail elsewhere in this book.

Obviously it is quite valid to divide a TPE into sub-divisions for different types of stress; e.g., tolerance to a specific pest, as for sub-TPE E in Figure 1. A more difficult task is sub-dividing the TPE when the stress is not always present, is difficult to quantify, and contributes to substantial GxE interaction. Drought and other abiotic stresses fall into this category. Models can assist in sub-dividing the ‘abiotic’ (as opposed to geographic) TPE and help identify ways of dealing with the sub-TPEs. Selection options that are realized when viewing the sub-TPE include the use of traits to deal with stresses.

Uses of Simulation Models in Breeding Programs

Crop simulation models are a combination of mathematical functions describing growth and yield of crops based on weather records and descriptions of site, soil, crop and cultivar characteristics. Their major advantage over experimentation is that, given available input data, many seasons can be simulated at different locations under different management practices. The disadvantage of most current models is that they are not sufficiently sensitive to reliably simulate differences among cultivars. Attempts are being made to remedy this by targeted physiological research (Hammer et al., 1996b).

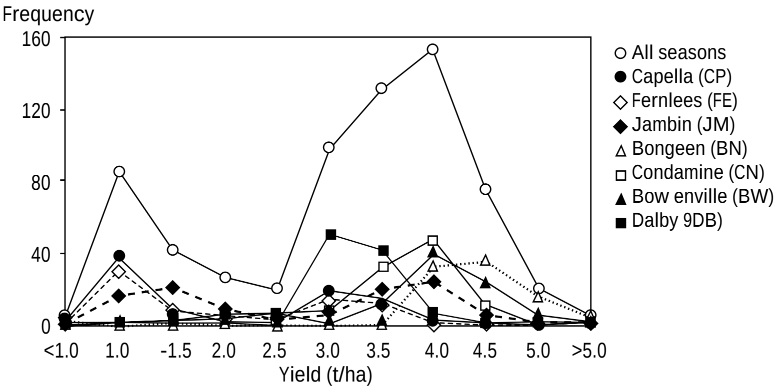

Figure 2. Frequency distribution of simulated sorghum yields over >70 years in Queensland grouped by location for 7 locations. The simulation assumed that sorghum was planted each summer in a continuous rotation, providing that planting rain was sufficient.

Potential uses in breeding programs of simulation models that we are investigating are to:

- Interpret production and yield gap survey figures to define TPEs.
- Define areas suitable for cultivars with specific adaptation.
- Sub-divide a TPE.
- Identify and evaluate the potential worth and appropriateness of traits for a TPE.
- Improve selection and the characterization of genotype performance.

Yield potential, yield gap and variability

Simulation models can be combined with survey information to help identify the size of the gap between actual and potential (climate-limited) yields. For example, Park and Sinclair (1993) recently analyzed maize yields for 30 years in the USA and determined that they were closing on the climatic limit to yield as determined by simulation models.

Yield records are often incomplete, so inter-seasonal variability is not revealed. If more complete weather records are available, then a simulation model can give a better representation of the true variability at a location. In Figure 3, it can be seen that simulated sorghum yields for a major site in Australia vary greatly year-to-year (as does real production, data not shown). In such sites, even 10 continuous years of production data may not represent the long-term influence of climate on production. In 1996, for example, the average actual sorghum yields in Australia were 2 to 4 times greater than the averages of the previous four years, due to a more favorable quantity and distribution of rainfall. Given the life expectancy of a new cultivar, the question to be faced is: what is the reliability of predicting the relative performance of genotypes for the next ten years, based on the run of years sampled during a cycle of a breeding program?

The purpose of simulation models in the context of yield-gap analysis is mainly to try to break the TPE into sub-populations that result from factors that can be accounted for by models.

Definition of geographic regions for specifically adapted germplasm

Given CIMMYT's main task of supplying source germplasm with particular attributes, one use of models is in defining the extent of suitability of the germplasm; that is, given specifically adapted germplasm, where are the potential areas for its deployment (the dotted line of germplasm transfer and model use 'c' in Fig. 1)? Chapman and Barreto (1996) conducted a preliminary analysis of this issue using two attributes that CIMMYT addresses: maturity and drought tolerance. Different maturities are required so that farmers can fit cultivars into their cropping system, given the limitations of both climate and management. Similarly, where in the world is drought-tolerant germplasm likely to be most useful? They linked a simulation model to a geographic information systems (GIS) database of world climate (mean monthly temperature and rainfall). For Central America, they considered two questions:

1. What is the variation in flowering date across locations for a cultivar of a particular maturity type?
2. Given a restriction to season length, where might different maturity types 'fit'?

Figure 4 shows the results for question 1. Large variations in temperature with latitude and elevation in Central America cause substantial differences in flowering date. A useful observation from this map can also be made from the locations of the CIMMYT testing stations. A cultivar of this maturity type in Poza Rica would be expected to flower in about the same amount of time in much of the Yucatán

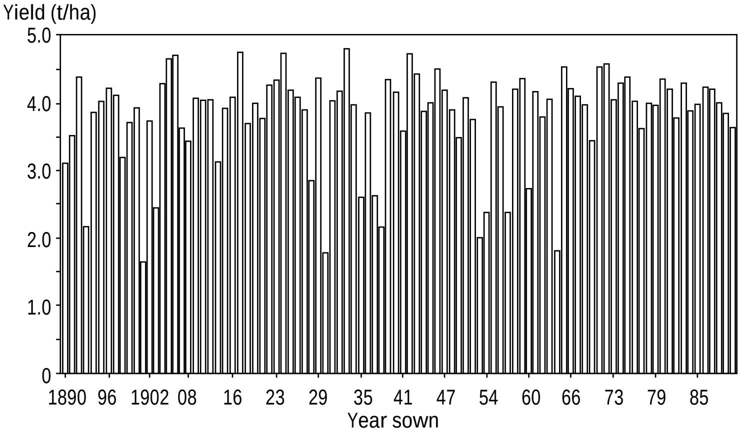

Figure 3. Simulated sorghum yields (from Fig. 2) for each of 91 years at the Condamine Plains location in Queensland.

Peninsula and of coastal Central America. They also determined how much thermal time would be accumulated in 70 days from the same planting date (Fig. 5). The figure shows the locations where different maturity types would meet this criterion for season length. Thus, the figure defines the potential geographic extent of the TPE (based on maturity) for each of the cultivar maturity types shown. While this simulation was done using the same planting date for all parts of the region, it is possible to define the size of the cropping window at each location and identify which germplasm fits best into the system.

Chapman and Barreto (1996) also constructed a map of flowering dates for southern Africa for a particular cultivar. Using this map and historic rainfall data, they calculated the average amount of rainfall that would occur in the four weeks around flowering, given a planting date of January 1 (Fig. 6). This produced a map showing where drought tolerant germplasm is likely to be of most use. The zone where rainfall in the four weeks bracketing flowering is less than 100 mm might be considered suitable for sorghum while areas where rainfall is greater than 200 mm are suitable for most maize cultivars. The area in between these is the geographic region of the TPE for drought-tolerant maize. These types of analyses can also be used in the interpretation of testing program results: one can stratify results to evaluate the performance of cultivars in locations where drought stress is expected to occur.

The definition of a specific geographic region encompassing the TPE is reasonably reliable for an attribute such as maturity, given that temperature tends to vary more across locations than it does across seasons. However, inter-seasonal variation in rainfall is substantial for

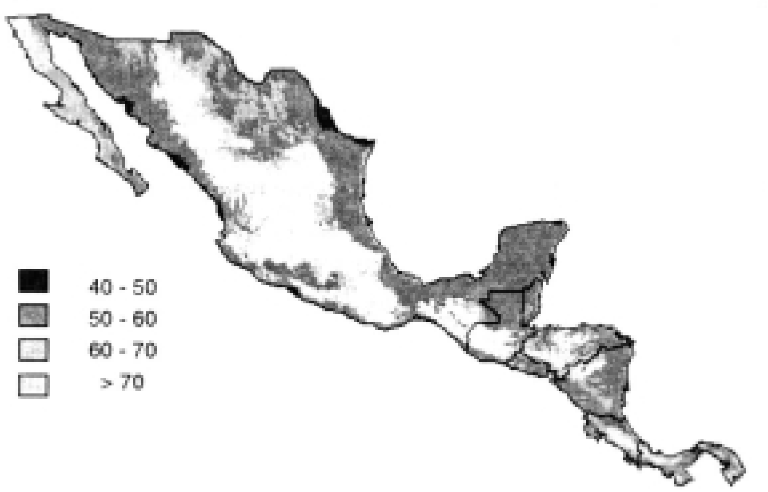

Figure 4. Latin America North: Predicted anthesis date (days after sowing) from interpolated weather data for a 20-leaf maize cultivar planted on June 1 (after Chapman et al., 1996).

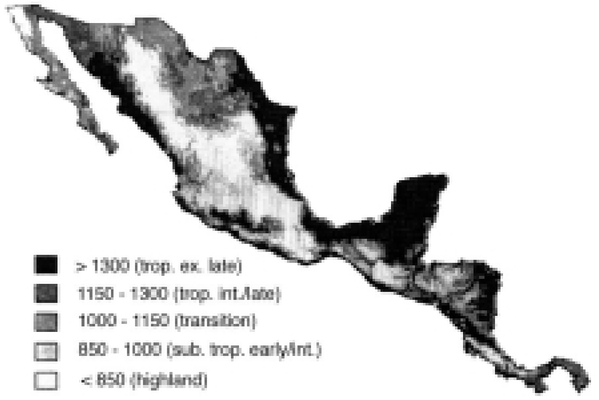

Figure 5. Latin America North: Accumulated thermal time (°Cd) calculated from interpolated data surfaces for 70 days from June 1. The climate is suitable for either tropical early or subtropical intermediate to late germplasm in the 1000 to 1150 °Cd area (after Chapman et al., 1996).

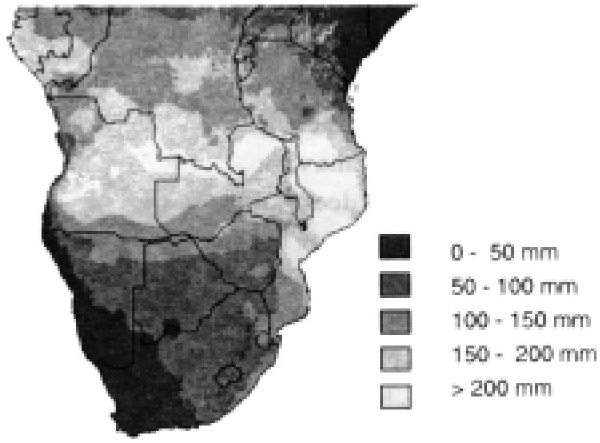

Figure 6. Southern Africa: Average amount of rainfall estimated between anthesis minus 3 weeks and anthesis plus 1 week for a simulated 18-leaf cultivar sown on January 1 (after Chapman et al., 1996).

many areas of the world, and consequently the geographic extent of the TPE for drought-tolerant maize would vary year-to-year. Below we describe a strategy that can be used to sub-divide the TPE season-to-season.

Subdividing the TPE over seasons and locations

TPEs can be subdivided in various ways. In defining crop targeting “mega-environments”, the CIMMYT Maize Program uses elevation as one criterion, although this is related as much to disease complexes as germplasm adaptation. Pollak and Corbett (1993) subdivided the TPE for maize in Central America into different climate types based on mean monthly variables. However, these methods are limited in that they do not really interpret the environment as it directly affects the crop, and do not include season-to-season variation. Outputs from simulation models can help characterize TPEs in this way.

Using the model runs described for Figure 2, Cooper and Chapman (1996) analyzed the patterns of stress that would be experienced by sorghum crops in each location and season, following the method of Muchow et al. (1996). Each day the model calculates the relative transpiration of the crop (ratio of potential to actual transpiration). This can be used as an index of the degree of stress experienced with the ratio approaching zero as stress becomes severe. Using pattern analysis, the vector of average values of the index each week during the crop cycle was used to separate the 660 simulated seasons into groups. This grouping procedure revealed five different season types (Fig. 7a). One season type, occurring in 35% of seasons, had little or no stress throughout the season. Another two types were stresses beginning in mid-season; in the remaining two types, stress began later. Of the mid-season stress types, one (mid-season terminal) continued until harvest while the other was relieved before harvest. Similarly, severe and mild versions of the late-season stress were identified. The frequency of occurrence of these stresses varied among locations (Fig. 7b). Locations in the northern part of the region (Fernlees, Capella, Jambin) have shallower soils and a greater probability of encountering water deficit, particularly that beginning mid-season. There were differences among locations in frequencies of the different types of water deficit experienced.

The season types can be used to resolve the TPE for yield into sub-groups. Figure 8 shows the distributions of simulated yields grouped by season type rather than by location (Fig. 2). The ‘no stress’ season type accounts for most yields greater than 3 t/ha, while the mid-season droughts account for most of the yields below 2 t/ha. The ‘late-season’ severe drought results in yields of 0 to 2.5 t/ha. The TPE could then be sub-divided into ‘no stress’, ‘mid-season’ and ‘late-season severe’ season types to be targeted separately in the breeding program. The yields in different years of a ‘late-season’ mild drought vary from 1.5 to 4.5 t/ha and would be difficult to target directly. This figure clearly shows

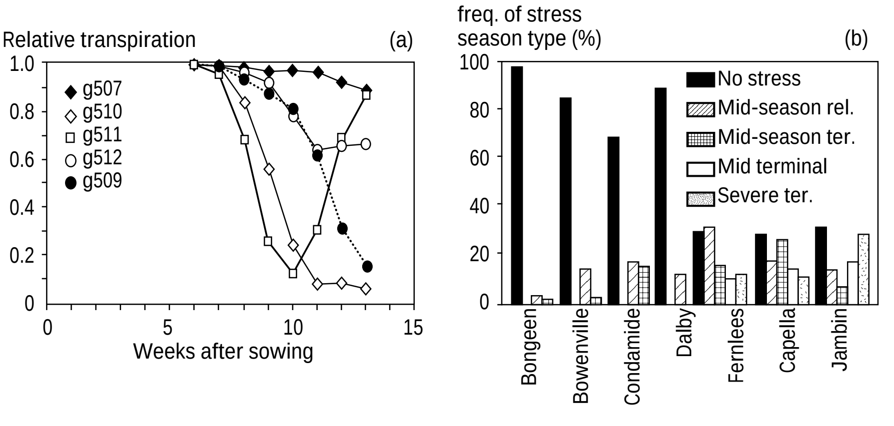

Figure 7. (a) Five major patterns of water deficit observed during 660 simulated seasons across 7 locations in Queensland sorghum areas (overall frequencies were 35%, 10%, 16%, 22% and 17% for the groups as listed) and (b) frequency of water deficit season types within each of the seven locations (after Cooper and Chapman, 1996).

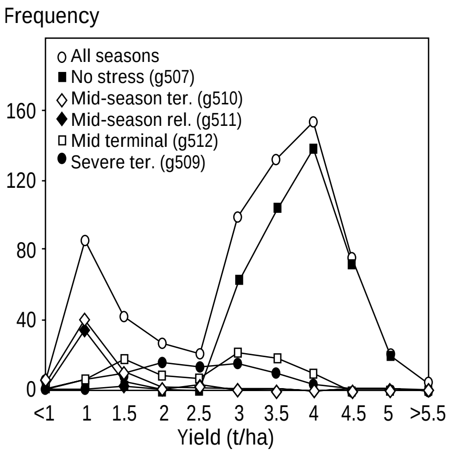

Figure 8. Frequency distribution of simulated sorghum yields over >70 years and seven locations in Queensland, grouped by stress season type (Fig. 7), cf. grouping by location (Fig. 2).

how the bimodal pattern of yields over the region arises from the different patterns of drought experienced.

These different types of water deficit and their importance in the crop's response to drought have been alluded to for at least 35 years (e.g., Denmead and Shaw, 1960); however, no one has directly quantified the frequency of occurrence of the stresses. Fischer et al. (1989) recognized their importance by using both types of stresses in their selection program to successfully improve drought tolerance of tropical maize (Bolaños and Edmeades, 1993; Chapman et al., 1996). Ludlow and Muchow (1990) discussed different genotypic traits that are likely to be valuable when dealing with different patterns of stress. A valid strategy is to breed cultivars with specific drought tolerance to these stresses, and models might be used to improve the deployment of the new cultivars. One might further ask, what is the scope for breeding cultivars with adaptation across different types of stresses?

Trait identification and evaluation

For many years, physiologists have argued the value of secondary traits to select for tolerance or resistance to environmental challenges, particularly drought (Ludlow and Muchow, 1990). While genetic variability for some traits appears to sufficient to warrant exploratory research, the value of the traits themselves has always been difficult to prove. Muchow et al. (1992) evaluated several traits using a simulation model for sorghum. More recently, Hammer et al. (1996a) simulated an entire multi-environment trial for sorghum by introducing genetic variation for phenology, tillering, stay-green, and transpiration efficiency into the sorghum model of Hammer and Muchow (1994). They simulated ten years of experiments at each of three locations for 24 theoretical genotypes; each genotype had different combinations of the following traits:

- Three rates of development generating early, medium, and late maturing phenology types,
- Two levels of stay-green (95% or 50% of leaf dead by maturity),
- Two levels of transpiration efficiency (9 Pa or 9.9 Pa), and
- Two levels of tillering (present or absent).

All other effects were depended on feedback from these changes into other aspects of the model, which depended on interactions with the environment during the crop life cycle. Briefly, their results were as follows:

- On average, late maturing types yielded more than early or medium maturing types, although this was associated with significant advantage in the few high-yielding years, rather than superior performance in the majority of years. In low-yielding environments, the early maturing type was often superior.
- The stay-green trait caused a slight increase in average yield in each maturity type. The improved yield occurred in both low- and high-yielding environments, but the magnitude of the effect was small and less than that found for the other traits.
- Averaged across environments, enhanced transpiration efficiency caused higher yield for each maturity type. Yields were substantially improved in the mid-yielding environments, with little effect in low-yielding environments and a substantial yield cost in high-yielding environments.
- The absence of tillering reduced average yield in each maturity type, largely due to an inability of the non-tillering type to take advantage of high-yielding environments.

These differences in performance come about mostly from changes in the cultivar's usage of water during the season; all traits except transpiration efficiency affect the seasonal distribution of green leaf area and therefore transpiration. Hammer et al. (1996a) concluded that there was no reason why trait consequences cannot be simulated, if:

1. The trait's physiological mode of action is understood and quantified.
2. The crop model is sufficiently detailed to simulate the interactions with growth and development generated by expression of the trait in any particular environment.

The use of models provides focus in the design of experimentation to estimate the value of various traits in the improvement of crop adaptation. In Australia, this is being conducted for several traits in sorghum: stay-green, osmotic adjustment, and nitrogen use efficiency (see papers in the Proceedings of the 3rd Australian

Sorghum Conference, referred to in Hammer et al. 1996b).

We can evaluate how often a trait is likely to be valuable by combining an adequate simulation model with historical weather data. If we have further classified the seasons into different types (as Cooper and Chapman did above), then we can see in which types of seasons traits are likely to work best. Beyond this, in a farm decision-making mode, we can even use season predictors such as the Southern Oscillation Index (see Chapman and Stone, 1977) to determine the type of season that lies ahead and choose our cultivar appropriately.

Improving the selection process

There are several further uses of simulation models in plant breeding. They can help to monitor the development of trials, to 'benchmark' yield potential, and to calculate derived variables for selection. Chapman (1995) describes a set of programs developed at CIMMYT to manage weather data during the season. One use of the programs is to plan planting dates for genotypes (lines) with different thermal time requirements for flowering, so that their flowering is synchronous and crosses between them can be made. Additionally, daily updates of thermal time accumulation can be compared with requirements of various germplasm to predict peak flowering times.

Saulescu and Kronstad (1995) have run a crop simulation model at each location in their wheat MET trials. The model gives them a 'benchmark' yield for the season. While this is a useful application, the same benchmark can be arrived at via many different pathways. Characterizing the season in terms of the type of water deficit rather than yield may be a more useful approach for predicting genotype performance at many locations. Application of either technique could be extended by using simulated genotypes that detected different environmental characteristics.

A further use of simple simulation models was made by Chapman and Edmeades (1996) to determine the radiation use efficiency of families of a drought-tolerant maize population. With a large number of genotypes, it is not possible to continuously monitor changes in light interception. Hence, using about five measurements of light interception, they fitted appropriate statistical models to estimate the integral of radiation intercepted through the season for each of 100 genotypes. Using a simple physiological model (when other factors are not limiting), they used this total radiation and harvested biomass to estimate the radiation use efficiency for each genotype, so that they could then be selected on this criteria.

Pattern Analysis of GxE Interactions

So far this paper has dealt entirely with 'simulated' data. Analysis of MET datasets can help dissect the causes of GxE interaction and indicate when it is necessary to split TPEs into sub-divisions to achieve genetic gains. Chapman et al. (1996) analyzed the results of evaluation trials that were designed to determine the effectiveness of selection for drought tolerance in several CIMMYT maize populations. The populations had been improved by simultaneous selection under drought and irrigated conditions (Fischer et al., 1989; Bolaños and Edmeades, 1993).

Substantial GxE interaction for yield was found in 10 trials. Chapman et al. (1996) applied pattern analysis (see Cooper and Hammer, 1996, for papers on the application of this method in plant breeding) to determine the environmental characteristics associated with the genetic gains. Figure 9 shows the principal components of the 10 environments plotted as vectors and the genotypes plotted as points. The components for drought environments (open triangles 1 to 5) are generally at right angles to those for the irrigated environments (closed triangles 6 to 10). Hence, genotypes plotted near the top of the figure have good adaptation to irrigated conditions, while those at the bottom have poor adaptation. Genotypes on the left are poorly adapted to drought while those on the right have the best adaptation to drought. Good adaptation to both irrigated and drought conditions is indicated in genotypes near the top right.

The arrows in Figure 9 join successive cycles of recurrent selections within each of three populations. They indicate that adaptation to both drought and irrigated conditions was achieved by selection, since all three populations progressed from the left toward the top right of the figure (see Chapman et al., 1996 for details). More critically, the degree of independence between the vectors for irrigated and drought environments indicates that it would not be possible to select in irrigated environments and expect to achieve gains in drought-prone environments. Note that the selection process of using both irrigated and stressed environments effectively assumed an equal weighting between them, regardless of their distribution in the TPE. In practice, this weighting varied year-to-year and was applied as an index of traits, rather than to yield alone.

Another application of pattern analysis to genotypic trial data was made using the Australian sorghum testing trials (Cooper and Chapman, 1996). GxE interactions for yield in two testing programs was large with substantial re-ranking of genotype performance, and indicated that the TPE was complex. A variant of a retrospective analysis method (DeLacy et al., 1994) was used to classify testing locations on the basis of the way in which they discriminate among genotypes over 17 years of testing. This pattern analysis identified two major groups of locations, one in the drier northern part of the cropping zone, and another with locations mainly on deeper soils in the southern part of the cropping zone. When they combined this information with that obtained by simulation, they found a high correlation between one PCA axis and the frequency of simulated seasons that had stress (from Fig. 7). This combination of statistical analysis and modeling supports the hypothesis that differences in genotype performance among locations were associated with the presence or absence of drought stress. Given the findings in the maize analysis described previously (orthogonality of irrigated and droughted selection environments, Fig. 9), it would seem important to ensure adequate testing in both drought and high-rainfall seasons to improve the broad adaptation of sorghum in the Australian TPE.

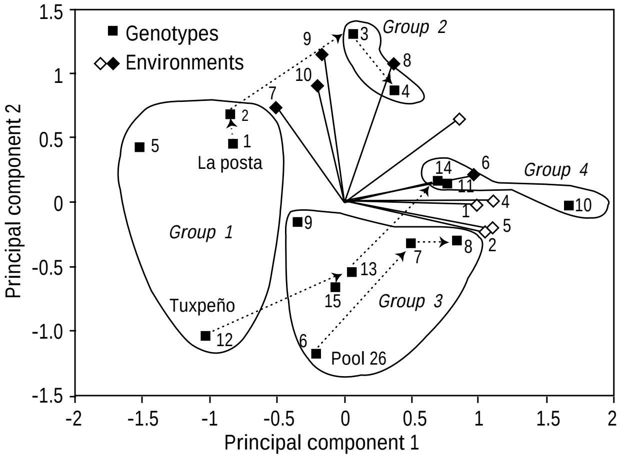

Figure 9. Two-way principal component analysis of 15 genotypes (plotted as points) in ten environments (plotted as vectors). PCA axis 1 appears to be associated with drought tolerance while PCA2 with yield potential. Genotypes having similar response patterns are enclosed by loops.

Opportunistic Breeding for Drought Tolerance?

We have reviewed some methods of both defining and subdividing the ‘geographic’ TPE in terms of frequency of drought occurrences. While producing source germplasm with ‘specific’ adaptation may be appropriate for CIMMYT, resources in smaller mandate regions will not always allow breeders to conduct this type of program. An alternative approach would be to take advantage of seasons / locations when drought occurs and select for broad adaptation to dryland environments. When a sorghum multi-environment trial is conducted, we can classify the season type at each location and weight the data according to the long-term frequency of occurrence of the season type in our TPE. The main aim of this process is to efficiently stratify sampling of the overall TPE. The process attempts to take account of temporal and spatial variation in environment, rather than assuming that the ‘average’ environment at any particular location is always appropriate for testing. Potentially, there are many variations on this concept which could contribute to the improvement of broad adaptation to variable climates. We are currently evaluating several in sorghum and wheat breeding programs in Australia.

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Experimental Designs and the Analysis of Multilocation Trials of Maize Grown Under Drought Stress

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Abstract

Data from multilocation trials are important in agriculture because they can be used to: 1) estimate and predict yield differences among genotypes, 2) assess genotype x site interaction and yield stability, and 3) select superior genotypes for planting in future years and at new sites. Data from multilocation trials is imprecise, complex and noisy. To increase the accuracy of genotypic yield estimates and their contrasts, one can therefore: 1) partition the error variance by using incomplete block designs in the form of lattice or row-column designs, 2) partition the genotypic variation by using spatial models of the form of nearest neighbor analysis, and 3) partition the genotype x site interaction variation by using statistical models that will remove noise from the source of variation. Since these strategies are applied to orthogonal sources of variation, they can be used independently. In this study we discuss practical concepts related to increasing the precision of the comparison between genotypic means through improved experimental designs (replicated or unreplicated). Data from the CIMMYT Early Drought Experimental Variety Trial (EDEVT), which included eight drought tolerant maize genotypes, two CIMMYT long-term reference checks and two different local checks, were used. The experimental design used in each of the 21 sites was an alpha (0,1) lattice. The efficiency of the lattice design was compared with the conventional randomized complete block design in each site. Changes in the significance of some genotypic mean contrasts when using adjusted vs unadjusted means were assessed. Genotype x site interaction analysis using the AMMI model, and the grouping of sites without genotypic rank changes using the SHMM model, were performed on the adjusted genotype means.

Multilocation trials are important in plant breeding and agronomic research because data from such trials can be used to:

1. Estimate and predict yield differences between genotypes.
2. Study genotype x environment interaction patterns and genotypic stability across sites.
3. Select superior genotypes or agronomic treatments for planting in future years and at new sites (Crossa, 1990).

The three principles of experimental designs are replication, randomization, and local control (Fisher, 1931) and the choice of experimental design has three components:

1. Treatment design.
2. Error-control design.
3. Sampling and observation design (Hinkelmann and Kempthorne, 1994).

The treatment design considers which and how many treatments should be included in the study, as well as the structure (if any) of treatments. Breeders compare unstructured sets of alternative treatments, such as genotypes (varieties, hybrids, etc.) and each treatment (genotype) has the same importance. In this case, the unstructured set of genotypes might include one or more “control” genotypes. Agronomists usually compare treatments that represent a complete factorial structure, including each combination of levels of the factors in the experiment, such as fertilizer levels, plant density, and herbicide. Agronomists usually choose particular levels of a quantitative factor, such as levels of nitrogen, not for their direct interest but rather as representatives of a range of interesting levels of the quantitative factor in order to study the shape of the response surface.

Within-site considerations

The error-control design consists of the arrangement of treatments among experimental units using specific rules. Examples are the complete randomized design, complete (or incomplete) block design, latin square design, etc. These designs control local variation (random experimental variance) differently. For example, the calculated mean of the ith genotype ($\bar{y}_{i.}$) or the difference between the mean of two genotypes (say genotypes ith and i'th) ($\bar{y}_{i.}$-$\bar{y}_{i'.}$), at a given site, are only estimates of the true (unknown) population mean (μ_i) or their difference (μ_i-$\mu_{i'}$), respectively. The precision by which these values (estimators) estimate the parameters is represented by the standard error of the mean ($\sigma/\sqrt{n}$) or the standard error of the difference between two means [$\sigma\sqrt{(2/n}$]. Sigma squared (σ^2) is the within-site experimental error variance that is estimated, in each site, by the mean squared error ($\hat{\sigma}^2$). This error measures several factors that affect the variable's response in each plot, such as differences in soil fertility, moisture, shading and competition from one plot to another; n is the number of observations (replicates) per treatment. If the observed difference between genotypic means is to be significant, we need to make $\hat{\sigma}\sqrt{(2/n)}$ sufficiently smaller than $\bar{y}_{i.}$-$\bar{y}_{i'.}$. The estimate of the standard error of the difference between two means can be made smaller by increasing the number of replicates (n) per treatment (expensive and perhaps unaffordable) or by decreasing the random experimental error variance by using an improved design or ancillary observations as covariables, and by spatial analysis (e.g., nearest neighbor analysis).

The third component of the experimental design is the sampling and observation design, which determines whether the observational units are the same as the experimental units or whether there is a need to subsample experimental units.

Multilocation trial considerations

Data from multilocation variety trials are imprecise, complex, and noisy and, as pointed out by Crossa et al. (1991), there are three error control strategies for increasing the accuracy of genotypic yield estimates and their contrasts:

1. Partition the error variance by using incomplete block designs such as lattices (Yates, 1936) and / or using covariables.
2. Partition the genotypic variation by using spatial methods (neighbor analysis) (Besag and Kempton, 1986).
3. Partition genotype x site interaction variation by using statistical models that will remove residual variation (noise) from that source of variation.

Since these three error control strategies are applied to orthogonal sources of variation, they can be used independently or simultaneously. However, it is expected that the most accurate genotypic yield estimates and contrasts would be obtained by integrating these three approaches.

Consider a trial in which g genotypes are evaluated at s sites. After removing the replicate effect, the variability among the observations can be subdivided as

$$\mathbf{y_{ij} = \mu + g_i + s_j + gs_{ij} + e_{ij}}$$

where μ, g_i, s_j, gs_{ij}, e_{ij} represent the effects of the general mean, genotype, site, genotype x site (or GE) and a random error, respectively. The presence of gs_{ij} in the model implies that the expected value of y_{ij} depends not only on the effects of the genotypes and the sites but also on the particular combination of the levels of g and s. Statistical significance of each of these source of variations and genotypic mean comparisons can be found through the analysis of variance (ANOVA).

The presence of a significant gs_{ij} is, most of the time, a fact of life in multilocation trials. It complicates the interpretation of results and the identification and recommendation of suitable genotypes (usually the high yielders) to a wide range of sites. However, the ANOVA only detects the significance of gs_{ij}; when this term is significant; it indicates that further exploration and investigation on the patterns of genotypic response across sites is justified.

Many statistical models have been developed to assess GE, to study genotypic stability and to examine the genotypic pattern of response across environments (Crossa, 1990). In general, the methods can be classified as:

1. Univariate parametric methods, such as regression (Finlay and Wilkinson, 1963; Eberhart and

Russell, 1966), ecovalance (Wricke, 1962), stability variance (Shukla, 1972), and the superiority measure (Lin and Binns, 1988).
2. Univariate non-parametric methods, such as those including ranking techniques (Huehn, 1990).
3. Multivariate descriptive methods, such as pattern analysis (classification and ordination) (Byth et al., 1976).
4. Multivariate parametric methods, such as additive main effects and multiplicative interaction analysis (AMMI) (Gauch, 1988), and shifted multiplicative model cluster analysis (SHMM) (Cornelius et al., 1992; Crossa et al., 1993).

Each method has a different purpose and examines different aspects of the information contained in the two-way table of genotypes and environments. Some of them estimate stability parameters, others are basically used for grouping environments or genotypes into homogeneous subsets, and others examine and quantify that part of the GE which is due to crossover interaction.

In this study, we briefly describe the practical principles of complete and incomplete block designs and how they relate to the concept of precision for comparing two genotypic means. We also comment on the needs, use, and precision of unreplicated trials. Data from a maize multilocation variety trial in droughty and normal environments are used to show how precision between treatment contrasts can sometimes be improved by the use of better designs. The AMMI biplot and the SHMM clustering method were used in the same maize multilocation variety data for investigating:

1. Genotypic patterns of stability.
2. Positive interactions among subsets of sites and genotypes.
3. Sub-groups of sites without significant crossover interactions.

Experimental Designs

Randomized complete block designs

The notion of blocking refers to specific groupings (arrangement) of the experimental units in which subsets of homogeneous units are identified (Lentner and Bishop, 1993). A block is a group of experimental units which provides a homogeneous effect on a response variable. For t treatments, a complete block has t experimental units (although there is no reason why a block cannot have 2t or 3t treatments, in which case each treatment would appear twice or three times, respectively, in each complete block).

The randomized complete block design (RCBD) is the simplest of block designs. It uses only one grouping or blocking system, usually to eliminate soil heterogeneity in one direction. In the RCBD, each treatment (genotype) occurs once in each block, therefore the treatments and blocks are said to be “orthogonal” to each other. If two factors are orthogonal their contributions are independent parts of the total sum of squares. Because the RCBD is balanced, all treatment comparisons (contrasts) are free of block effects.

The RCBD should be constructed so that experimental units of different complete blocks are as heterogeneous as possible. In the field, complete blocks with perfect within-block homogeneity are never attained. If we use b complete blocks we loose b-1 degrees of freedom from the error variance, compared with a completely randomized design. Because of this, complete blocks in the field should be as homogeneous as possible within-block, with as much heterogeneity as possible among blocks, so that there will be enough reduction in the error variance to compensate for the loss in degrees of freedom. On the other hand, if we block when all the experimental units are homogeneous, we increase the error variance (because the error has b-1 less degrees of freedom) and obtain less precision than with a complete randomized design. A similar conclusion can be reached when comparing incomplete block designs to the RCBD.

Incomplete block designs

Given that the number of treatments (genotypes) increases in an orthogonal design, the size of blocking units must also increase until they become too large to effectively control soil variability in the field. One way to overcome this problem is to use incomplete block designs, in which blocking units do not include all the treatments, hence the design is non-orthogonal. Blocking units can be kept small to provide better control of field variation. The disadvantage of this is that, the smaller the size of blocking units relative to the number of treatments, the less the information that can be obtained on treatment comparisons within blocking units.

In an incomplete block design, information on differences between treatments can be obtained from comparisons within blocks (intra-block information) and between blocks (inter-block information). Intra-block and inter-block estimates can be calculated and combined to form each adjusted treatment mean. In incomplete block designs, we hope to reduce the random variance (estimated by the error mean square), against some loss of information because we cannot compare with the same precision (the same standard error of the difference between two genotypes) each genotype with every other genotype in each block. Although we do not know in advance the gain in efficiency achieved through this reduction in the experimental error, we can indirectly assess the loss of information when comparing treatments occurring in different blocks. Suppose that treatment 1 occurs in sub-block 1 and treatment 2 in sub-block 2. If treatments 3, 4, and 5 occur in both sub-blocks, then treatments 1 and 2 can be compared by comparing each with the average of treatments 3, 4, and 5 (Mead, 1990). This reduces by 33% the precision with which the difference between treatments 1 and 2 is estimated (Mead, 1990).

For large numbers of treatments, incomplete blocks designs generally reduce the error variance very efficiently. A rough guide of the precision of an incomplete block design was derived by Mead (1990) by considering the minimum (MINVAR), maximum (MAXVAR), and average (VAR) variance between two treatment means. For t = number of treatments, r = replications per treatment, and k = average number of times that treatment pairs occur together in a block, MINVAR = $\sigma^2(2/r)$ and MAXVAR = $\sigma^2(2/k)$. A good approximation of the average variance per treatment pair difference is VAR = MINVAR+(MAXVAR-MINVAR)/t. For an incomplete block design with 12 treatments, 3 replicates, 2 sub-blocks per replicate, and each with 6 treatments, the number of total pair-wise comparisons in each sub-block is (6x5)/2 = 15 and over the set of 6 sub-blocks, 6x15 = 90. There are (12x11)/2 = 66 treatment pair-wise comparisons in total. Therefore, $k = (90/66) = 1.3636$, MINVAR = $\sigma^2(2/3) = 0.667s^2$, MAXVAR = $\sigma^2(2/1.3636) = 1.467s^2$ and VAR = $0.667\sigma^2 + \sigma^2 (1.567-0.667)/12 = 0.733\sigma^2$ giving a standard error of 0.856σ. Therefore, only a reduction of 10% or more in the magnitude of σ^2 will increase the precision of the comparisons $[(0.733)(0.91)\sigma^2 = 0.667\sigma^2]$, so this must be a goal when using incomplete block designs.

Lattices, alpha-lattices and row-column designs

Lattice designs, such as square and rectangular, are incomplete blocks designs termed “resolvable designs”, because the sub-blocking units are arranged in complete replicates. They can never be less efficient than the ordinary RCBD. However, the use of square and rectangular lattices cannot be suitable for all situations. The number of treatments in any given trial is not always a perfect square or a multiple of incomplete block number and plots per block, demanded by the square or rectangular lattice.

In 1976, a new kind of resolvable incomplete block design called the alpha-lattice, generalized lattice, or simple alpha-design was developed by Patterson and Williams (1976). These can be thought of as a generalization of the square lattice of Yates, and their main advantage is flexibility; they are suitable whenever the number of treatments is a multiple of the block size and they can be easily adapted even when it is not. When plots are long and narrow the alpha-designs can remove variation down columns of plots in the field (Patterson and Hunter, 1983). Alpha-lattices, as well as Yate’s simple and triple lattices, are not balanced; that is, every pair of treatments does not appear together in the same block the same number of times. A pair of treatments concurring twice would be compared more precisely (with smaller standard error) than two which concur just once, and these in turn more precisely (with less standard error) than two which do not concur at all. An alpha (0,1)-lattice is a design in which for any two treatments the number of concurrences is either zero or one. An alpha (0,1,2)-lattice is a design in which for any two treatments the number of concurrences is either zero, one or two. Given the choice, an alpha (0,1) would be preferable to an alpha (0,1,2); however if an alpha (0,1,2) design has to be used, one with as few pairs of treatments as possible concurring twice would be preferred. A safe rule of thumb for choosing the block size of an alpha-design is to make the block size equal to or slightly smaller than the square root of the number of treatments.

With prior knowledge about the nature of soil variation in a given field, once can reduce block size accordingly.

During analysis, the “relative efficiency” for a particular lattice design is defined as the ratio of the average variance of treatment differences in the RCBD to the average variance of such differences in the incomplete block design (including recovery of inter-block information). If the blocking has been effective in removing field variability, the reduction in the error mean square more than compensates for the effect of confounding caused by the incomplete blocks and the relative efficiency will be greater than one. Note that a gain in efficiency does not simply mean reducing the size of the standard error of the difference between two treatment means, but also results in obtaining a ranking of adjusted means which is closer to the true ranking.

Incomplete block designs are effective when plots are long and narrow. They provide a good sample of the experimental area in one direction and the blocking deals with variation in a second direction at right angles to the first (Patterson and Hunter, 1983). When plots are small, an incomplete block design controls variation in only one direction. The common solution to this problem is to use Yate’s (1937) lattice squares with two blocking systems to eliminate soil variability in two directions. However, the number of treatments must be a perfect square and the number of replicates required for balance is often more than can be accommodated when seed supplies and land or labor resources are limited. Row-column designs (Patterson and Robinson, 1989) follows the tradition of Yate’s lattice squares but place fewer restrictions on the number of treatments and replicates. Row-column designs control variation in two directions and are appropriate when plots are more square in shape. Although row-column designs are not balanced, when it is natural to arrange the treatments in a rectangular array, such designs can be advantageous. They are more economical and widely used than the lattice squares.

Experimental layout in the field is often such that replicates are contiguous and columns (blocks) of each replicate form long columns running across all the replicates. If an experiment has this characteristic, it is called a ‘latinized’ design and can be used with either alpha or row-column designs (Williams, 1986). In the latinized designs, a treatment should occur only once in the long column running across the replicates.

The generation of alpha lattices and row-column designs, as well as their latinized designs, can be achieved by using the ALPHA+ software. Statistical analyses of results from these designs can be performed using computer packages such as SAS, GENSTAT, REML, and purpose-designed programs such as ALPHANAL (see Barreto et al., 1997).

Design of unreplicated trials

For the last 50 years the development of experimental designs has aimed to provide:

1. Estimates of treatment comparisons with a minimum standard error of a difference between treatment means.
2. A valid estimate of the error variance.

Kempton (1984) has questioned the importance of these objectives in a plant breeding program, and suggested that within-site replication of test lines may not always be necessary. The author based his conclusions on the following arguments. First, the main objective of a breeder when testing and selecting genotypes (lines, families, etc.) is to maximize the genetic gain, that is, the breeders wants to have a broad (rather than a precise) assessment of the population. This can be better achieved by screening many (perhaps 1,000-1,500) families from a population, if there are few resources available or specialized labor and land are required. More precision (replicates, etc.) is needed later in the program when fewer families are evaluated. Second, to conduct a field experiment for so many genotypes is difficult, because soil heterogeneity in the field cannot easily be accounted for, and seed supplies may be insufficient. Finally, when genotypes are evaluated at many sites, one loses precision in the comparison between genotypic means within a site, due to the potentially large genotype x site interaction variance.

The main question when designing unreplicated trials is how to control soil variability in the field. Briefly, we will describe three methods for controlling soil variability as suggested by Kempton (1984).

Method 1 uses repeated check plots; Method 2 uses blocking test plots; and Method 3 uses sites as replications.

Method 1 - Method 1 consists of distributing replicated plots of check genotypes (for which seed is plentiful) over the trial area in a standard design. The main advantage of this method is that the test genotypes can be arranged systematically on the field. Since no randomization is required genotypes under test can be arranged by parentage. Control of soil variability will be effective if, and only if, the yield of the check genotypes shows the same pattern of response to soil fertility as the test genotypes; at least two check genotypes with a genetic background similar to that of the test genotypes should be used. In fact, if an inappropriate check is used, the adjustment of test plot yields based on check plot yields will *increase* the error. For example, when screening inbred lines it would be inappropriate to use a full-vigor hybrid cultivar as a check genotype, given the differences of its response to moisture and nutrient stress from that of lines and the inter-genotypic competition that would result from its tallness and intense use of resources.

A couple of questions need to be addressed in applying Method 1. How should the check genotype(s) be distributed in the field? What should the frequency of checks be? Concerning the first, Federer (1956) proposed a class of designs called the "augmented design", where each repetition of the check genotype is in a complete or incomplete block and the test genotypes are assigned to plots that are not allocated to check genotypes, so estimates of block effects and error are with respect to test genotypes. In these designs the check genotypes are allocated at random to the plots in a block; this nonsystematic arrangement has the advantage of giving unbiased error estimates; its disadvantage, compared with a systematic allocation of check genotypes to plots, is an irregular distribution pattern over the experimental area. Lin and Poushinsky (1983) pointed out that, in this type of design, unbiased error estimation is less important than an effective yield adjustment of the test genotypes. Later, Federer et al. (1975) proposed a series of "augmented row-column designs" in which check genotypes cover diagonal bands of the field such that each test genotype is more or less equidistant from either two, three, or four check genotypes. This arrangement allows for adjustment of test plots by row and column, and is flexible with respect to the number of test and check plots.

The issue of how the check genotypes should be arranged in the field is not a problem if the number of test genotypes is small. However, if the number of test genotypes is large, the number of check plots cannot be large for practical reasons and a large number of plots within a block will be required. This becomes important, because the main assumption is that plots within a block are homogeneous. Lin and Poushinsky (1983) proposed a modified augmented design with a split-plot structure, where whole plots can be laid out in a standard design, but sub-plots are always in a 3 x 3 arrangement, with the center point used as a check and with a shape as square as possible. Check genotypes are assigned to check plots according to the design used for whole plots, and test genotypes are assigned randomly to non-check plots.

Concerning the frequency of check plots, generally when the frequency of check plots increases, better local control and greater genetic gains (at a constant selection intensity) are achieved. However, if the total number of experimental plots must remain constant, fewer test plots can be used, and selection intensity is therefore reduced. Kempton (1984) recommended not to use a frequency of check plots greater than one in five, unless the trial size can be increased proportionately.

Method 2 - Method 2 consists of randomizing all test genotypes across the field and of allocating them to blocks which are approximately square; no check genotypes are used. Here, the test genotypes within blocks are compared, rather than being compared with an independent check. Selection is then performed within blocks by choosing the highest yielding genotypes per block. This is similar to the "grid" mass selection method of Gardner (1961), where each grid is a small block from which the best plants are selected.

Method 3 - Method 3 consists of planting one replicate at each site, rather than multiple replicates at one site. A strategy suggested by Kempton (1984) is to arrange one replicate of a lattice design at each site, so that individual sub-block effects can be estimated for each site (replicate) and test genotypes can be adjusted for the blocks in which they lie. However, the sub-block effects are confounded with the genotype x site (replicate) interaction and the effectiveness of blocking will depend on the size of genotype x site variance compared with plot variance. Cornelius and Byars (1976) showed how part of the replicate (site) x genotype interaction may be associated with differences in linear response to a single covariable and how this component of the replicate (site) x genotype interaction can be separated in the analysis, so that estimates of sub-block effects can be improved. In general, it is expected that the efficiency of an incomplete block analysis with replicates that are not adjacent, such as in this case, will be lower than when replicates are contiguous.

The Use of RCBD and Alpha-Lattices: An Example

Experimental data

The dataset used is from an Early Drought Experimental Variety Trial (EDEVT), consisting of 12 genotypes arranged in a 4x3 alpha (0,1) lattice with 4 replicates at each of 21 international sites (Table 1). Two entries (Local check 1 and Local check 2) differed between sites and another two are long-term CIMMYT reference checks (Santa Rosa 8330 and Across 8331). Further details on the EDEVT can be found in Edmeades et al. (1995). At each site an RCBD analysis and a lattice analysis with recovery of inter-block information were performed to calculate the efficiency of the lattice and to examine the precision and significance of treatment contrasts. Later, AMMI and SHMM methods were used for studying genotype x environment interaction and examining yield stability. Another dataset analyzed but mentioned only briefly throughout the paper is the Late Drought Experimental Variety Trial (LDEVT), where 20 genotypes arranged in an alpha (0,1) 5´4 lattice were evaluated at 19 international sites.

Results of RCBD and alpha (0,1) lattice analyses

The adjusted yield means of 10 genotypes in 21 sites (S) are given in Table 2. The site yield ranged from 0.42 t/ha under severe drought stress in Godhra, India, to 6.00 t/ha in Bogor, Indonesia. Minimum, maximum, and average standard errors of the difference between pairs of genotypes for the alpha (0,1) lattice designs in each of the sites are shown in Table 3. Also shown is the standard error of the difference between pairs of genotypes for the RCBD and the corresponding minimum, maximum, and average efficiencies calculated using the various standard errors. The sites Makaholi in Zimbabwe (S9) and Jipijapa (Ecuador, S4) had the largest gains in efficiency, 24% and 23%, respectively. On the other hand, Tak-Fa (Thailand, S13), Rampur (Nepal, S15), Jutiapa (Guatemala, S18), and Llano de Cruz (Panamá, S19) showed no improvement of the alpha lattice over the complete block design. Two of the six sites with the lowest yield due to severe drought stress had gains in efficiency of 11% (S2) and 23% (S4). Three sites (S3, S9, S12) with intermediate yield production levels also had high gains in efficiency (22%, 24%, and 18%, respectively). The least significant difference (LSD, P£0.05) for the average standard error of pair-wise comparisons averaged across sites

Table 1. Site, genotype and country names and site and genotype codes of 21 sites and 10 genotypes included in trial EDEVT.

Site name	Country name	Site code
Tlaltizapán intermediate drought stress (IS)	México	S1
Tlaltizapán severe drought stress (SS)	México	S2
Tlaltizapán well-watered (WW)	México	S3
Jipijapa	Ecuador	S4
Portoviejo	Ecuador	S5
Chiclayo	Perú	S6
St. Cruz	Bolivia	S7
Charagua	Bolivia	S8
Makaholi Station	Zimbabwe	S9
Chitala	Malawi	S10
Kutamani	Kenya	S11
Awassa Res. Station	Ethiopia	S12
Tak-Fa	Thailand	S13
Godhra	India	S14
Rampur	Nepal	S15
Bogor	Indonesia	S16
St. Cristobal	Nicaragua	S17
Jutiapa	Guatemala	S18
Llano de la Cruz	Panamá	S19
Cd. Obregón	México	S20
New Delhi	India	S21

Genotype name	Genotype code
Local check	G1
Local check	G2
Santa Rosa 8330 RE[†]	G3
Across 8331 RE[†]	G4
Pool 18 Sequía C_3 F_2	G5
Pool 18 Sequía C_2 best ASI F_2	G6
Pool 18 Sequía C_2 smallest tassels F_2	G7
TEWF Drought Tol. Syn.2 F_2	G8
TEYF Drought Tol. Syn.2 F_2	G9
Pool 16 C_{20} Syn.1 F_2	G10
TIWD Drought Tol. Population C_0	G11
DTP1 C_5 Early Selection F_2	G12

[†] RE= Reference checks.

from the alpha lattice design (SE=0.36 t / ha, Table 3) with 21 degrees of freedom is 0.76 t / ha. The LSD(0.05) from the RCBD (0.39 t / ha, Table 3) with 33 degrees of freedom is 0.79 t / ha.

The range of minimum, maximum, and average efficiencies were 30.6, 19.1, and 23.6, respectively (Table 3), with standard deviations of 10.0, 6.5, and 8.0. These results contrast with those obtained in the Late Drought Experimental Variety Trial (LDEVT), where the range of minimum, maximum, and average efficiencies are 40.0, 36.3, and 38.6, respectively, with standard deviations of 10.5, 9.4, and 10.1. Maximum gain in average efficiency obtained in a site was 40%. These results indicate, as expected, that for a larger number of treatments (12 in EDEVT vs. 20 in LDEVT), there were gains in efficiency using the alpha lattice over the RCBD.

Another point of interest is the change in significance of some pair-wise comparisons, when using adjusted means obtained with inter-block analysis of the alpha lattice versus the unadjusted means obtained from the RCBD. The significances of all (12x11) / 2 = 66 pair-wise comparisons using the adjusted vs. unadjusted means were examined for the site with the largest gain in efficiency, Makaholi, Zimbabwe (S9). Nine of the comparisons (14% of the total pair-wise contrasts) that were non-significant in the RCBD were significant when using the adjusted

Table 2. Adjusted alpha-lattice yield means of 10 genotypes and 21 sites included in trial EDEVT.

Site	Genotype										
	G3	G4	G5	G6	G7	G8	G9	G10	G11	G12	Mean
1	1.56	1.57	2.81	2.43	2.41	2.50	2.62	2.79	1.83	2.15	2.27
2	0.58	0.34	0.83	0.53	1.08	0.83	0.68	1.26	0.13	0.26	0.65
3	3.12	3.10	3.18	3.29	3.71	3.36	3.17	3.66	3.00	3.39	3.30
4	0.78	0.59	1.62	1.15	1.14	0.98	1.14	1.31	0.39	0.68	0.98
5	4.19	3.93	4.00	3.63	3.85	4.04	3.21	4.26	4.89	4.30	4.03
6	2.09	0.98	0.33	0.33	0.72	0.62	0.45	0.33	1.66	1.88	0.94
7	0.89	1.05	1.23	1.32	1.21	0.99	1.20	1.70	0.69	0.94	1.12
8	2.49	0.82	2.82	1.93	1.81	2.60	3.33	2.53	2.19	3.17	2.37
9	3.60	2.80	2.86	3.59	3.23	3.38	3.16	2.89	3.79	3.97	3.33
10	1.74	2.05	2.72	2.25	2.92	2.55	2.46	2.70	2.53	2.26	2.42
11	0.28	0.11	0.40	0.37	0.28	0.30	0.30	0.33	0.22	0.12	0.27
12	2.63	2.34	3.43	2.94	2.65	2.97	2.87	3.03	3.05	3.75	2.97
13	2.15	2.38	1.89	1.47	2.09	1.29	1.85	1.82	1.28	1.67	1.79
14	0.24	0.33	0.62	0.39	0.33	0.48	0.40	0.46	0.29	0.65	0.42
15	3.50	4.36	4.62	3.53	3.25	3.10	3.61	3.37	3.16	4.31	3.68
16	6.01	6.03	5.94	5.97	5.80	5.58	5.12	6.17	6.46	6.84	5.99
17	4.66	4.53	4.02	3.98	4.66	3.91	3.65	3.92	4.53	4.97	4.29
18	1.87	2.72	2.88	2.69	3.26	2.50	2.15	2.11	2.74	3.38	2.63
19	2.68	2.28	2.85	2.75	2.32	2.10	2.44	2.31	2.74	2.42	2.49
20	1.37	1.46	2.51	2.40	1.94	1.52	2.46	2.19	1.82	2.12	1.98
21	1.67	2.37	1.59	2.52	2.04	1.99	2.21	2.74	3.19	2.05	2.24
Mean	2.29	2.20	2.53	2.35	2.41	2.27	2.31	2.47	2.41	2.63	2.62

Table 3. Minimum (LMIN), maximum (LMAX), and average (LAVER) standard errors of the difference (SE) between two adjusted genotypic means obtained from an alpha-lattice design, the standard error of the difference between two unadjusted means obtained from an RCBD (BAVER), and minimum (EMIN), maximum (EMAX) and average (EAVER) efficiencies for 21 sites included in trial EDEVT.

Site	Alpha lattice SE			RCBD SE	Relative efficiencies		
	LMIN	LMAX	LAVER	BAVER	EMIN	EMAX	EAVER
S1	0.14	0.15	0.15	0.15	7.12	2.85	5.16
S2	0.21	0.22	0.22	0.24	13.76	7.89	11.05
S3	0.34	0.36	0.35	0.42	25.69	17.40	21.82
S4	0.19	0.21	0.21	0.25	30.35	18.43	23.13
S5	0.51	0.51	0.51	0.53	4.38	4.38	4.38
S6	0.30	0.31	0.31	0.31	4.67	0.69	2.20
S7	0.23	0.24	0.24	0.25	7.94	2.19	4.40
S8	0.76	0.76	0.76	0.76	0.30	0.30	0.30
S9	0.47	0.52	0.50	0.62	30.63	18.96	23.56
S10	0.43	0.46	0.45	0.45	5.46	0.02	1.56
S11	0.09	0.09	0.09	0.10	13.55	8.23	10.26
S12	0.46	0.48	0.47	0.55	20.61	14.00	17.55
S13	0.38	0.38	0.38	0.38	0.00	0.00	0.00
S14	0.10	0.10	0.10	0.11	12.33	5.14	7.93
S15	0.75	0.75	0.75	0.75	0.00	0.00	0.00
S16	0.37	0.39	0.38	0.41	10.08	3.47	6.02
S17	0.33	0.34	0.34	0.34	2.24	-0.12	0.76
S18	0.46	0.46	0.46	0.46	0.00	0.00	0.00
S19	0.27	0.27	0.27	0.27	0.00	0.00	0.00
S20	0.23	0.25	0.25	0.27	15.94	5.48	8.65
S21	0.49	0.51	0.50	0.51	3.48	0.19	1.43
Average	0.36	0.37	0.36	0.39	9.93	5.21	7.15

means (Table 4). Six out of 9 of these comparisons involved local checks G1 and G2. Furthermore, one comparison (G2 vs G10) that was significant using unadjusted means (RCBD) turned out to be highly significant when using adjusted means. For the larger trial (LDEVT) at the site with the largest gain in efficiency (40%), 15 comparisons that were non-significant when unadjusted means from RCBD analysis were compared turned out to be significant when adjusted means were compared, and 4 pair-wise comparisons changed from significant under RCBD analysis to highly significant. Furthermore, three significant or highly significant comparisons under RCBD analysis turned out to be non-significant when adjusted means were compared.

These results indicate the importance of lattice adjustment in sites where incomplete blocks have shown high gains in efficiency. These adjustments will increase the precision of some genotypic contrasts and therefore will help the researcher select superior genotypes and compare the genotypes to locally adapted checks. It is clear in this study that the use of alpha-lattice designs has improved the efficiency compared with the RCBD. Furthermore, the use of improved designs (such as the row-column design), ancillary observations as covariables, and spatial analyses may further increase the precision of comparisons between genotypic means.

Table 4. Standard error (Std. Error) and probability (Prob.) of pair-wise comparisons of genotypes included in trial EDEVT that changed their significance when unadjusted means from RCBD were used instead of adjusted means from the alpha lattice.

	RCBD		Alpha lattice	
Contrast	Std. Error	Prob.	Std Error	Prob.
G1[†] -G9	0.61374	0.159	0.4914	0.050
G1 -G10	0.61374	0.110	0.4934	0.017
G2 -G7	0.61374	0.090	0.4914	0.017
G2 -G8	0.61374	0.068	0.4914	0.041
G2 -G9	0.61374	0.069	0.4914	0.013
G2 -G10	0.61374	0.046	0.4934	0.004
G4 -G11	0.61374	0.148	0.4914	0.050
G4 -G12	0.61374	0.204	0.4914	0.027
G5 -G12	0.61374	0.136	0.4914	0.035
G10 -G12	0.61374	0.551	0.4914	0.040

[†] G1 and G2 are local checks

Assessing Genotype x Environment Interaction

This part of the paper deals with two methods, AMMI and SHMM, that may help the researcher to interpret the patterns of genotype responses across environments; i.e. genotype x environment interaction and yield stability.

The AMMI model

The factor analytic model (FANOVA) was introduced by Gollob (1968) and Mandel (1969, 1971) for studying interaction in complete two-way layouts. Gauch (1988) renamed it as the Additive Main Effects and Multiplicative Interaction (AMMI) model and used it in multilocation variety trials. The AMMI model integrates additive main effects and multiplicative interaction components in a single analysis by extracting first the additive main effects and then using principal component analysis to investigate the multiplicative genotype x environment interaction part of the model. The general AMMI model can be represented as

$$\bar{y}_{ij.} = \mu + g_i + s_j + \Sigma_k^t \lambda_k \alpha_{ik} \gamma_{jk} + \bar{\varepsilon}_{ij.}$$

where $\bar{y}_{ij.}$ and $\bar{}_{ij.}$ denote the means of the genotype and residual error on the i^th^ genotype at the j^th^ site; μ is the grand mean; g_i and s_j are the genotype and site deviations from the grand mean, respectively; λ_k is the square root of the eigenvalue corresponding to axis k; α_{ik} and γ_{jk} are the genotype and site scores for axis k.

The genotype x environment interaction in the AMMI model is represented by the string of multiplicative terms ($\Sigma_k^t \lambda_k \alpha_{ik} \gamma_{jk}$) such that, when the interaction can be represented by only one term, the AMMI model takes the form $\bar{y}_{ij.} = \mu + g_i + s_j + \lambda_1 \alpha_{i1} \gamma_{j1} + \bar{\varepsilon}_{ij.}$. This is called the AMMI$_1$ model and is useful only when much of the variability (sum of squares) due to genotype x environment interaction can be explained by $\lambda_1 \alpha_{i1} \gamma_{j1}$. In this case, the rest of the multiplicative terms are considered noise or nonsystematic components of the genotype x site interaction. This reduces the accuracy of yield estimates and thus should be considered residual variation and discarded, even though the axes involved are statistically significant (Crossa et al., 1991).

One important feature of AMMI$_1$ analysis is its graphical representation, showing main effect means of genotypes and environments on the abscissa, and scores for the first axis of the genotypes (α_{i1}) and sites (γ_{j1}) as ordinates. This graphical display, in fact, represents the variability due to main effects of genotypes and sites plus that due to genotype x site interaction which is explained by the first multiplicative component of $AMMI_1$. Genotypes with the same score on the x-axis have similar means and those with the same y-score have similar interaction. Genotypes and sites with large (positive or negative) scores have large interactions and those near zero have small interaction. Genotypes with positive scores and sites with negative score have a negative interaction as well as genotypes with negative scores and sites with positive scores. Genotypes and sites with scores of the same sign (either positive or negative) have a positive interaction.

The SHMM model

In plant breeding and crop production, the most critical genotype x environment interaction involves significant reversal of genotypic rank across sites. This interaction is called crossover interaction (COI), as opposed to scale change or non-crossover interaction (non-COI) (Baker, 1990). Statistical tests for identifying and quantifying COI in medical trials have been proposed by Azzalini and Cox (1984) and Gail and Simon (1985). However, most statistical methods for studying genotype x environment interaction in the context of multilocation trials, including AMMI, fail to distinguish between COI and non-COI.

The shifted multiplicative model (SHMM) developed by Seyedsadr and Cornelius (1992) for analyzing non-additivity in a two-way table in the context of genotype x environment interaction and supplemented by other statistical tools (Cornelius et al, 1992; Crossa et al., 1993; Cornelius et al., 1993) provides an analytical tool for finding subsets of sites (or genotypes) with negligible genotypic rank change. This method is called the “SHMM clustering method” and can be used for clustering genotypes into subsets without significant genotypic rank change interaction.

The SHMM model (Seyedsadr and Cornelius, 1992) is

$$\bar{y}_{ij.} = \beta + \Sigma_k^t \lambda_k \alpha_{ik} \gamma_{jk} + \bar{\varepsilon}_{ij.}$$

where $\bar{y}_{ij.}$ and $\bar{\varepsilon}_{ij.}$ denote the means of the genotype and the residual error on the i^th^ genotype at the j^th^ site; β is the shift parameter; λ_k is the square root of the eigenvalue corresponding to axis k; α_{i1} and γ_{j1} are the “primary effects” of genotype and site, α_{i2} and γ_{j2} are the “secondary effects” of genotype and site, etc. The $SHMM_1$ model has only one multiplicative component and is represented by $\bar{y}_{ij.} = \beta + \lambda_1 \alpha_{i1} \gamma_{j1} + \bar{\varepsilon}_{ij.}$.

The main principle in SHMM cluster methodology is that variation owing to secondary and higher effects (tertiary, quaternary, etc.) that exist in the entire dataset will be recovered as primary effects in smaller clusters or differences among clusters. This is carried achieved by using a distance measure between paired sites that is the residual sum of squares of $SHMM_1$, when fitted to those pairs of sites. This concept of distance allows two sites with negligible genotypic rank changes to be close together and two sites with large genotypic rank changes to be far apart. Once the distances for all pairs of sites have been obtained, a cluster analysis for combining subsets is utilized. From the dendrogram produced by the cluster analysis, sub-groups of sites can be identified to which $SHMM_1$ gives an adequate fit. The dendrogram for the SHMM clustering method for grouping sites without COI can be performed easily using a SAS program that appeared in the appendix of Crossa et al., (1993). A similar SAS program for the SHMM clustering method for clustering genotypes into groups without COI can be obtained from the first author.

The shift parameter has an important role in determining if data has a significant genotypic rank change. When the $SHMM_1$ are plotted against primary effects of environments, the diagram shows a set of concurrent regression lines that may intercept at one point. The expected value of y at that point of concurrence is the shift parameter. Then, if $SHMM_1$ is an adequate model to fit the data and all the primary effects of the environments are of equal sign, the regression lines do not cross over.

Illustration of the use of the AMMI and SHMM models

In this part of the paper we demonstrate the use of AMMI and SHMM analyses on the EDEVT data using the adjusted means of 10 genotypes (local checks are excluded) from each of the 21 sites.

Results of AMMI analysis

The AMMI analysis of variance indicates that 40% of the sum of squares due to genotype x environment interaction can be explained by the first component (axis). Therefore, it is appropriate to display the relationships between the mean of the genotypes and environments and their first principal component scores (PC1).

Genotypes show much more variability in interaction than in main effects (Fig. 1), whereas sites show a lot of variability in both main effects and interaction. From the AMMI_1 graphical representation depicted in Figure 1, it is possible to compute the expected yield for any genotype x site combination. The additive part is computed by adding the mean of the genotype plus the mean of the site minus the grand mean. The interaction part is simply the genotype score times the site score. These two parts add to produce the expected value of the AMMI_1 model (Crossa et al., 1991).

According to the mean yield (abscissa) and interaction (PC1, ordinate) we can place the sites in three groups. Those from low yielding sites (S2, S4, S6, S7, S11 and S14) had positive first components (PC1s), except for S6 with a high negative PC1. These sites were characterized by low average rainfall or irrigation supply during the season (358 mm) (Edmeades et al., 1995). All were distinguished by extremely dry conditions at the end of the grain filling period. At site S6, on the other hand, plants were severely stressed at flowering, and rain that came at mid-flowering favored the later flowering genotypes. The three highest yielding sites (S5, S16 and S17) had negative PC1s, and were characterized by an average seasonal rainfall of 976 mm, with virtually no drought stress at any stage of the season. These sites favored the later maturing genotypes, such as G11 and G12. The rest of the sites showed intermediate yield and intermediate to low interactions.

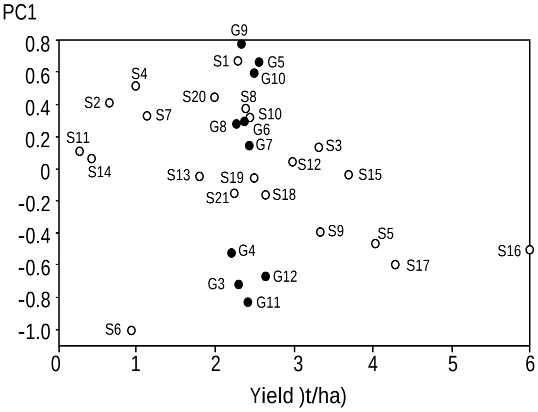
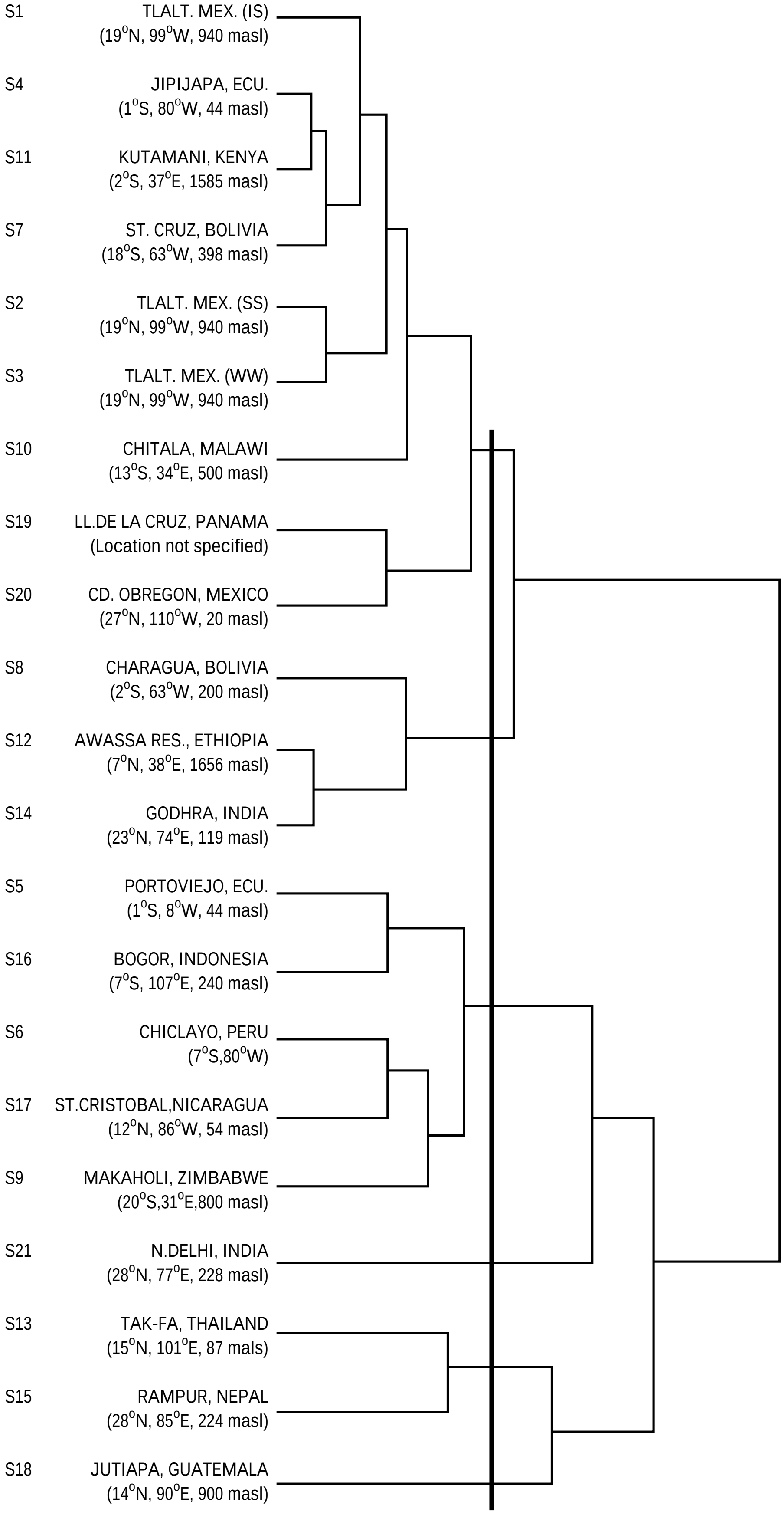


Figure 1. AMMI display of the mean yield and the first principal components scores of 10 maize genotypes and 21 sites included in EDEVT.

Analysis also indicated three groups of genotypes. Group 1 (G5, G9 and G10) was the earliest to flower (mean anthesis date was 54.1 days), had a low superiority index (low is best) of 67.2 (Lin and Binns, 1988), and had high positive PC1s. Two of these genotypes (G5 and G10) had a long history of selection for mid-season drought tolerance. Group 2 (G6, G7 and G8) was slightly later flowering (55.4 days) and contained two selections of Pool 18 Sequía C_2, which might be expected to perform similarly across locations. This group had intermediate-low PC1 values. Their mean superiority index was 72.9, suggesting they were less stable than Group 1. Group 3 (G3, G4, G11 and G12), with high negative PC1s, was later flowering than the other two groups (59 days), and had a mean superiority index of 84, suggesting relatively erratic yield across locations. The exception was G12 (DTP1 C5 early selection), a drought-tolerant population which had the lowest superiority index (53.1) of all genotypes tested. This analysis confirms that stable and relatively high yield in this set of environments is associated with earliness and drought tolerance, and that later maturing genotypes, while higher yielding in unstressed environments, are less stable in yield. The performance of G12 suggests that selection for drought tolerance can combine stability with the high yield potential of the later maturing genotypes. Genotype G7 (Pool 18 Sequía small tassel selection) must also be considered stable, since it had the lowest PC1 score (0.15).

Genotypes in Groups 1 and 2 interacted in a positive direction with low yield sites (except S6) and negatively with high yield sites. Genotypes in Group 3, on the other hand, interacted positively with high yield sites and negatively with low yield sites, again with the exception of S6. Time to flower of Groups 1 and 2 (54 and 55 days) versus that of group 3 (59 days) is likely the main reason for these interactions. Early maturing genotypes tend to escape the consequences of terminal drought, while late flowering types more frequently encounter terminal drought stress in these short-season, marginal rainfall environments.

Figure 2. Dendrogram from SHMM cluster analysis of 21 sites included in trial EDEVT. The vertical line marks the cutting point.



Results of SHMM analysis

Cluster analysis based on the residual sum of squares after fitting the $SHMM_1$ model produced the dendrogram depicted in Figure 2. A reasonable cutting point of the dendrogram is shown as a vertical line where four sub-groups of sites are formed:

1. Sites S1, S4, S11, S7, S2, S3, S10, S19, and S20.
2. Sites S8, S12, and S14.
3. Sites S5, S16, S6, S17, and S9.
4. Sites S13 and S15.

Sites S21 and S18 are left unclustered. The number of genotypic rank changes (COI) within these sub-groups should be less than among sub-groups, and we expect the response of the 10 genotypes in each of these four sub-groups of sites to be parallel or nearly parallel.

In general, the sub-groups of sites were not associated with site productivity. For example, high yield sites S5, S16 and S17 were included in the same group as one of the low yield sites (S6). If these groupings emerge as consistent patterns over several seasons, a breeder seeking to increase the cost effectiveness of a testing network could identify a subset of “key” testing sites within each sub-group and thus reduce the cost of testing without sacrificing important information on adaptation and performance of genotypes.

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Addressing Soil Variability in Low Nitrogen Breeding Programs

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Abstract

When crop improvement is conducted under conditions of low soil nitrogen supply, the relative magnitude of experimental variability tends to increase, and this can mask differences among genotypes. Some recommendations for managing low-N nurseries emerged during the course of a recurrent selection program to improve the yield of tropical maize grown with limited soil N. This program was conducted on a site with alluvial soils, which are characterized by considerable spatial variation in soil texture and N-supplying capacity within each experimental area. Incomplete block designs were very effective in improving experimental efficiency for evaluations of progeny grown at low N. Covariate adjustments based on check yields in previous seasons were effective for yield testing of experimental cultivars. The mean chlorophyll concentration of adjacent rows in the same season was also highly correlated with yield, and served as an effective covariate. The soil parameters examined (nitrate level of air-dried soil prior to planting, organic matter content, and penetrometer resistance) were less effective covariates than were historical yields of check entries, provided those check yields had been collected after the field had reached a low N level. Yearly collection of variability data is not required at this location.

This presentation addresses practical aspects of conducting maize improvement for conditions of low soil N. It describes the development of low-N fields and important features of low-N nurseries, and evaluates some statistical tools and management approaches to address spatial variation in N availability.

Methods and Materials

Data presented here were collected in a number of trials planted in low-N fields over a period of several years. All experiments were conducted at CIMMYT's experiment station near Poza Rica, Puebla, México (21 °N, 60 m elevation). The site was formerly part of a riverbed, and the soil is characterized as a sandy loam (Tropofluvent), but varies from a loam to a sandy loam across the station. Maize is sown in both winter and summer seasons in Poza Rica. Irrigation is applied as necessary to prevent moisture stress. The standard station fertilization regime is 200 kg N ha^{-1} and 18 kg P ha^{-1}. In the low N (-N) fields, no N is applied. Weeds and insects are controlled chemically. In the studies described here, fungicide was applied during the winter season to minimize the severity of foliar diseases. Plots were overplanted and thinned to a density of 40,000-53,000 plants ha^{-1}, depending on the maturity and level of improvement of the population under evaluation. Details of representative experiments are described more fully in Lafitte and Edmeades (1994).

Developing low-nitrogen experimental areas

Three fields were prepared for low-N experiments by planting several maize crops with no applied fertilizer and then removing all aboveground biomass, as described in Table 1. After about six seasons of continuous maize cultivation, the fields were sown for one season with a green manure crop of mucuna or beans. This management approach combines with climatic variation to result in variation in the observed yield reduction from season to season (Fig. 1).

Results and Discussion

What is different about low-N nurseries?

As N stress increases, progeny yields decrease, but the experimental error does not decrease as rapidly (Table 2). The coefficient of variation increases, and it becomes more difficult for breeders to see genetic differences among families. When the effect of soil variation is reduced by using a lattice design (see below), the error variance is similar for high and low-N nurseries. The genotypic variance is less under low N, so the broad-sense heritability for grain yield is less in the low-N environment (Bänziger et al., 1997).

Can soil properties reveal spatial variation?

The observed variation in yields under low N must be related to soil properties that affect N supply. Nitrogen is often applied in the irrigation water as well, but growth trends in the field are not consistent with variation in N supply from irrigation. Soil NO_3 level in the upper 0.15 m of the profile (measured in field D3 near flowering during the 1986 winter season) was only weakly related to the average grain yield of the eight full-sib families which occupied that area of the nursery during the following season (correlation coefficient 0.37*, n=42). Soil organic matter in the top 0.6 m of the profile (measured in field G1 for bulked samples collected from plots measuring 5.5 m by 1.5 m during the winter of 1992) was not related to grain yield of check rows grown in the summer of 1992 (correlation coefficient 0.38 (ns), n=24). We measured soil resistance to a depth of 0.45 m with a cone penetrometer system (Rimik Model CP-10, Remik Pty. Ltd., Toowoomba, Australia). While this rapid, integrated measure of soil physical properties might be more feasible for routine use in a breeding program than measures of chemical properties, high variability in the penetrometer readings resulted in a correlation that was too weak to serve as an effective covariate (r=0.40** between full-sib family yields and total resistance in the upper 0.45 m). We conclude, therefore, that the available methods of measuring soil properties do not provide practical indicators of soil variability that can be used routinely in a breeding program.

Can historical yields predict spatial variation?

Field G1 - Baseline uniformity levels in the study portion of G1 were established by planting a check hybrid every 7 rows in the winter of 1987. These check yields were well correlated with progeny yields both in the subsequent season and in experiments several years later (Table 3).

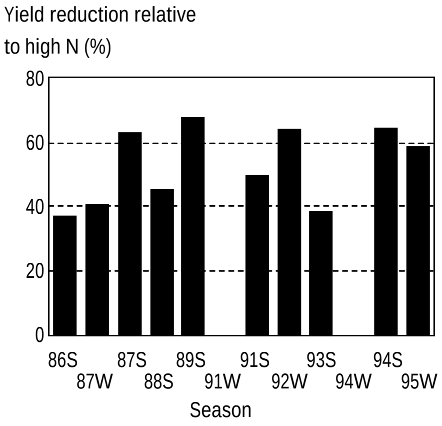

Figure 1. Yield reduction in field G1 over time. Mucuna was planted in 91W and soybean was planted in 94W.

Table 1. Steps in the development of low-N experimental areas.

Field	No. green maize crops removed before expts. started	Seasons of biomass removed from expts.	Yield reduction Initial	Yield reduction Current	Current status
D3	3	1	37%	-	Abandoned
G1	3	2	40%	60%	In use since 1987
C1	2	2	20%	60%	In use since 1989

Table 2. Mean yield and standard error of the mean (SE) (t ha^{-1}), and coefficient of variation (CV) for full-sib families of the cultivar Across 8328BN for high and low levels of N in two seasons.

	High N			Low N			
Field and year	Mean	SE	CV	Mean	SE	CV	Season
D3, 1986	5.93	0.53	13%	3.74	0.68	26%	86B
G1, 1987	7.15	0.70	10%	2.77	1.08	39%	87B

Table 3. Correlation between baseline yields and yields measured in subsequent seasons for fields G1 and C1.

Field	Baseline measurement	Subsequent season	Correlation
G1	winter,1987	summer,1987	0.58**(progeny)
G1	winter,1987	winter,1990	0.68**(check rows)
G1	winter,1987	summer,1992	0.61**(progeny)
C1	summer,1989	summer,1991	0.36**(check rows)

***Field C1* -** The uniformity of C1 was measured by planting a check hybrid every 10 rows in the summer of 1989. The maximum yield reduction in the poorest section of the field was 50% in that season, but the average yield reduction was only about 20%. These check yields were only weakly correlated with check yields measured in the same field two years later (Table 3). We conclude that historical check yields can be useful, but that the baseline studies must be conducted after a sufficient level of N stress is achieved. Other studies indicate that a yield reduction of 40% or more is appropriate for low-N nurseries (Bänziger et al., 1997), and it seems that this same level of stress should be used for establishing baseline yields as well.

What statistical method to use?

Incomplete block designs are often used in breeding programs to reduce the effect of spatial variability. Another common system is the use of a covariate based on grain yield of check rows, but this approach requires additional land and labor. We compared the efficiency of a simple alpha (0,1) lattice design, a covariate based on check yields (current or historical), and a covariate based on the ear leaf chlorophyll content of adjacent families. We used data from progenies in low-N breeding nurseries and from evaluations of experimental varieties (for details, see Lafitte and Edmeades, 1994). Progenies were planted in single rows, and ear leaf chlorophyll concentration was measured with a hand-held photometer for 5 plants in each family. Variety trials were planted using 4-row plots. In the winter season of 1990 (90A), a check row was sown alongside each plot, and yields from those rows were used for covariate adjustments.

The covariate generated from check yields with low N in 1987 was applied to data from subsequent trials in the same field. Use of the covariate significantly reduced the error variance for progeny trials (230-252 full-sib families of a late lowland tropical population) conducted in the summer seasons of 1987 and 1992 (Table 4). The covariate from 1987 resulted in a standard error of the difference among means for the 1992 evaluation which was similar to that obtained using the average ear leaf chlorophyll concentration of adjacent rows measured in 1992 (Figs. 2 and 3).

Despite the stability of the covariate with time, a simple lattice design resulted in a higher efficiency than the covariate based on check yields for the progeny trials conducted in both 1987 and 1992 (Table 4). In the variety trials, which were characterized by larger plots and fewer entries, the covariate analysis

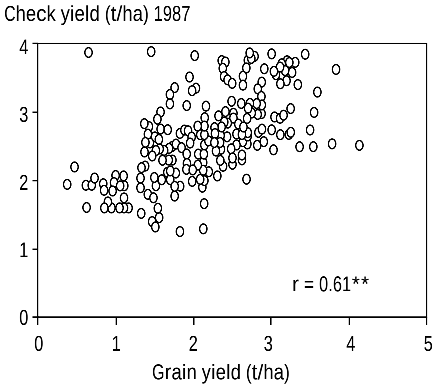

Figure 2. Check yields in 1987 vs. progeny yields in 1992.

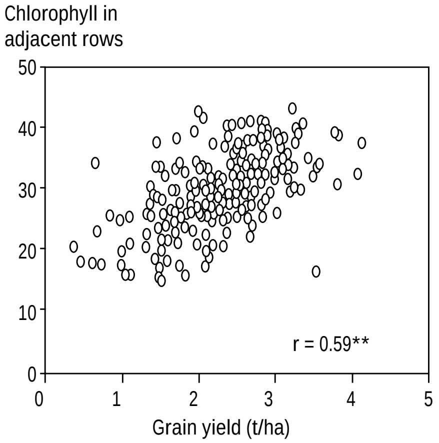

Figure 3. Mean chlorophyll content in adjacent rows vs. grain yield of progeny, 1992.

Table 4. Standard errors of differences among means (S_d) and percent efficiencies relative to a randomized complete block design (RCBD) (in parentheses) of different designs for various experiments conducted at Poza Rica, México, from 1987-1992. NA indicates data are not available.

Experiment	Entries	Reps.	SED (efficiency)		
			RCBD	Lattice	Yield covariate
Progeny (check data collected in same season)					
S_1 x S_1 1987A, -N	140	3	96	NA	63(234)
S_1 x S_1 1987A, +N	140	2	62	NA	62(100)
Progeny (check data collected in previous season)					
Full-sibs 1987B, -N	230	2	108	52(213)	85(160)
Full-sibs 1992B, -N	230	2	67	45(224)	53(163)
Varieties (check data collected in same season)					
1990A, -N	25	4	39	22(203)	20(369)
Varieties (check data collected in previous season)					
1991B, -N	12	4	30	34(80)	25(143)

resulted in superior efficiency. Plot size in these highly variable fields is particularly important, since it affects the physical size of each incomplete block and the potential of the lattice design to reduce experimental error. Even though there is some interaction among progenies growing in single-row plots, we found that benefits from using multiple-row plots were offset by the need to increase the area of each incomplete block (Bänziger et al., 1995). We conclude that a lattice design with a small block size is effective for low-N nurseries. For experiments with multiple-row plots, it would be better to use a covariate adjustment at the Poza Rica station.

Managing N supply by intersowing

Another approach to managing variability is to intersow a crop with the maize which will absorb soil N as it becomes available. We planted wheat in the row alongside maize during the winter cropping cycle, and allowed the wheat to grow until about 2 weeks before flowering (Trt.1) or until maturity (Trt.2). The control yield of 1.6 t ha^{-1} was already quite low due to N stress. Trt. 1 reduced yield by 40% relative to the control, and Trt. 2 resulted in a 58% yield reduction. These results have led us to use intersown “catch crops” of wheat (winter) or sorghum (summer) to increase N stress in low-N nurseries.

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Model 2 to Select for Drought Tolerance

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Abstract

A model is developed to differentiate between ontogenetic and phylogenetic drought tolerance (DT) and their interaction in annual plants. The relationship among these components and observed variation in ontogenetic profiles of DT are explained. Confusion among these components and other mechanisms of DT within groups of varieties with similar days to flowering are discussed. The use of the model helps avoid misinterpretation of DT responses and may facilitate more efficient selection under drought.

In selecting for drought tolerance (DT) in annual plants, several genotypes can be evaluated and they can come from one or several species. A complicating factor is that their vegetative cycles usually differ in length; a difference often manifest as differences in the number of days to flowering. When comparing genotypes for DT, observed differences in response can be because the genotypes are at different ontogenetic stages, come from different species (phylogeny) with associated differences in ability to tolerate drought, or differ in their expression of various genetically controlled DT mechanisms. Confusion regarding the basis of response differences can result.

In this paper, use of Model 2, a ontogenetic and phylogenetic tolerance model, is described for the analysis of variation in response to drought. Relationships are established with regard to ontogenetic DT profiles for several varieties differing in the length of their vegetative cycles.

Development of the Model

Statistical model

Let us consider an experiment under drought to compare *v* varieties of *s* species at *o* ontogenetic stages. A split plot design can be used for such comparisons with *b* randomized blocks. Where ontogenetic stages are assigned to main plots, species to subplots, and varieties to sub-subplots, the linear model would be:

$$y_{ijkl}=\mu+b_l+o_i+e_a+s_j+(o{*}s)_{ij}+e_b+v_k(s_j)+(o{*}v(s))_{ijk}+e_c \qquad (1)$$

where y_{ijkl} is the observation of variety *k* of species *j* at ontogenetic stage *i* in the block *l*; μ is the general mean, b_l is the block effect, o_i is the effect of the ontogenetic stage, s_j is the species effect, $v_k(s_j)$ is the variety within species effect, $(o{*}s)_{ij}$ is the ontogenetic stage x species interaction effect, $(o{*}v(s))_{ijk}$ is the ontogenetic stage x variety within species interaction effect; and e_a, e_b and e_c are random elements of error associated with main plots, subplots and sub-subplots, respectively. Other theoretical considerations are found in Kempthorne (1979), Martínez (1972) and Méndez (1976).

The statistical model taking in account the mean squares of the analysis of variance would be as follows:

$$Y=B+O+E_a+S+O{*}S+E_b+V(S)+O{*}V(S)+E_c \qquad (2)$$

where Y is the total variance and the other variances match their corresponding terms in Equation 1.

Mathematical model

Let us consider a particular situation in which the environmental conditions are uniform and measurement is without error. In such a case, phenotypic variation corresponds to genotypic variation (Márquez, 1971) and the error variance terms can be ignored, so that

$$Y=O+S+O{*}S+V(S)+O{*}V(S) \qquad (3)$$

S and V(S) determine the variation among phylogenetic groups and they can be represented as P; accordingly the interactions O*S and O*V(S) can be represented by O*P. Thus, the following simplified mathematical model is obtained:

$$Y=O+P+O*P \qquad (4)$$

Model of Ontogenetic and Phylogenetic Drought Tolerance

Let us suppose a variable can be defined that can integrate all DT effects. One possibility is the ‘energy’ accumulated by a plant against drought conditions (Muñoz and Rodriguez, 1988). This would include the plant’s water and dry matter resources and the DT mechanisms described by May and Milthorpe (1962). If we call this variable *r* and its associated variance R, the model can be written as:

$$R = R_o + R_p + R_o*R_p \qquad (5)$$

This expression means that when we evaluate the drought tolerance of several varieties from different phylogenetic groups, R can be divided in three components: R_o, the ontogenetic DT; R_p, the phylogenetic DT; and R_o*R_p, the interaction of R_o and R_p, as indicated previously by Muñoz and Rodríguez (1988).

Discussion

Figure 1 is a representation of the ontogenetic DT profiles for *n* varieties, in terms of *r* (‘energy’) or other variables associated with drought tolerance; e.g., fresh weight and yield. R_o represents variation across ontogenetic stages. If we obtain averages of all values for each ontogenetic profile (each variety), then R_p represents the variation from to , the variance for drought tolerance among species. Deviations from a parallel condition among profiles represents the interaction R_o*R_p.

When we consider the life cycle of an annual plant, the seed represents the highest level of DT. The onset of susceptibility to drought comes with germination. DT increases as the plant’s root system develops and at the same time the plant is adding leaves. A reduction in DT occurs again as the plant switches from vegetative to reproductive phases, and this results from changes in various genetically controlled systems at the onset of gametogenesis. Flowering time and the two weeks following represent a second period of great susceptibility because of the effects of drought on seed set and grain filling. DT increases during the period of grain filling until it reaches its highest level when the seed is physiologically mature. The curves in the two diagrams in Figure 1 represent variation in DT versus development stage from species 1 to species n. Several studies that include many observations have been carried out to document ontogenetic profiles (Quezada and Muñoz, 1985; Santacruz and Muñoz, 1990; Pedroza and Muñoz, 1993).

When varieties of the same species are compared under drought and they have different numbers of days to flowering, ontogenetic tolerance (or escape) and tolerance derived from other mechanisms may be confused. Comparisons within groups of varieties with similar days to flowering helps avoid this confusion. When varieties from different species are compared, there is opportunity for confusion among

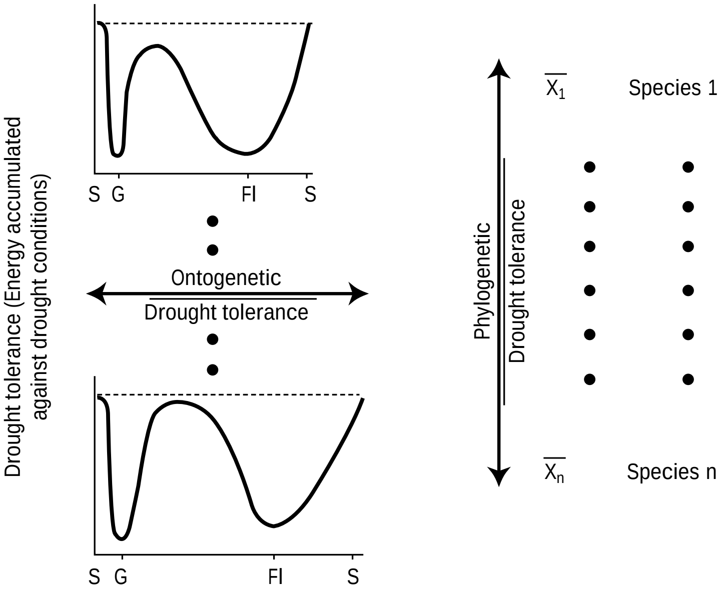

Figure 1. Ontogenetic and phylogenetic drought tolerance. G, Fl and S refer to germination, flowering and mature seed formation, respectively.

R_o, R_p and mechanisms among varieties within species for DT. The above model may provide an approach to help solve this problem, remedy many misinterpretations, and facilitate more efficient selection under drought.

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The Alpha Lattice Design in Plant Breeding and Agronomy: Generation and Analysis

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Abstract

The use of incomplete block designs has gained wider acceptability among researchers in developing countries as a tool to control random variation, particularly for evaluation trials of many genotypes. In the CIMMYT Maize Program, alpha (0,1) lattice designs have been used since 1986 for evaluating groups of more than 200 genotypes, generally planted in single row plots. Relative efficiencies of 1.0-2.0 have been observed, but the use of the alpha-lattice designs has thus far been restricted mainly to genotype evaluation trials. There is little information on the use of these designs in agronomic experiments, although they could be useful where there is no factorial type relationship among treatments, where the number of treatments is relatively large (e.g., > 16), and where soil heterogeneity at the test site is high. Among the most important constraints to the use of these designs are: the lack of an appropriate language-independent software interface for entering and transforming data files, the difficulty of handling information in a common format, and the lack of integration with other analytical tools (graphing applications, selection algorithms, regression, etc.). A software module in English and Spanish that facilitates and integrates the use of the ALPHANAL and LATANOVA programs (Scottish Agricultural Statistics Service, Edinburgh) for the design and analysis of alpha (0,1) lattices is described. The software also allows for the processing of lattice-adjusted means using selection software developed by the CIMMYT Maize Program. This type of easy-to-use software offers an additional resource for improving the efficiency of agricultural research in national agricultural programs in developing countries.

The traditional design for evaluating agricultural experiments is one in which the experimental units are grouped in complete blocks that individually contain all the treatments. This type of design assumes that variation between units of a block is less than that between units of different blocks, so that experimental precision is increased by virtue of error control (Steel and Torrie, 1980). Also, in this type of design each treatment occurs with the same frequency in each block; we say that blocks and treatments are orthogonal, a property that facilitates the mathematical calculations needed to produce an analysis of variance. Table 1 shows a general classification of the experimental designs that are most commonly used in agriculture. However, when the number of treatments is large, the randomized block and the latin square designs are generally unsuitable, because the size of the block and (as a result) soil heterogeneity increase. This may cause the variation within blocks to be larger than the variation between blocks, which would tend to increase the experimental error and diminish the researcher's ability to observe statistical differences among treatments.

In an incomplete block design (e.g., lattices), the number of plots per block is smaller than the total number of treatments (e.g., genotypes). An

Table 1. Main types of square and rectangular lattices.

Name	No. genotypes	No. reps multiple of	No. blocks multiple of
Simple lattice	k^2	2	2k
Triple lattice	k^2	3	3k
Simple rectangular lattice	k(k+1)	2	2(k+1)
Triple rectangular lattice	k(k+1)	3	3(k+1)

N.B. number of plots per block is k in all cases
Source: González (1989).

incomplete block design is considered resolvable if the blocking units are arranged in complete replicates (a complete set of treatments is obtained by putting together the blocks of one replicate). In the field, an incomplete block design is indistinguishable from a randomized complete block design. However, practical considerations dictate that all designs used for agricultural trials be resolvable. Because they are resolvable, lattices can never be less efficient than a complete block design.

The quality of an incomplete block design is judged by the harmonic-mean efficiency factor (HMEF), which is the ratio of the average variance with which a complete block design would estimate treatment differences and the average variance with which the incomplete block design would estimate these differences, if the error mean square were the same in both cases. The value of HMEF is always greater than 0 and less than 1. The difference simply measures the confounding between treatments caused by using incomplete blocks. However, when laying out the trial in the field, we should try to achieve maximum homogeneity possible within each incomplete block depending on soil conditions, fertility gradients, moisture, slope, etc. The rule of thumb for selecting the size of an incomplete block (*k*) is to take a value that is the same or smaller than the square root of the number of treatments, *v*, (i.e., $k <= \sqrt{v}$).

To judge whether the incomplete block arrangement was more effective than the complete block design, we have to wait for the experiment to be completed and compare the corresponding experimental errors. The relative efficiency (RE) of a lattice design is defined as the ratio between the average variance of the differences between treatments (ignoring the use of incomplete blocks and assuming that the replicates were complete blocks), and the average variance of the differences between treatments in the incomplete block design (including recovery of inter-block information). The RE is analogous to the definition of the HMEF, but the former uses observed estimates of the experimental error. If blocking has successfully removed variation (i.e., if the reduction in the error mean square compensates for the effect of confounding caused by incomplete blocks), then the relative efficiency will be greater than 1. As mentioned above, the fact that lattices can revert to complete blocks if the efficiency is less than 1 ensures that lattices can never be less efficient than a complete block design. Table 2 summarizes the principal types of square and rectangular lattices.

Some historical events that were important in the development of experimental designs, including alpha designs devised by Patterson and Williams (1976), are shown in Table 3. These are type (0,1) incomplete block designs. The term in parentheses indicates the type of restriction the combination of paired entries has with respect to incomplete blocks. In the case of an alpha lattice (0,1), every treatments in each pair never appear together (0) or are together in only one

Table 2. Classification of main designs.

Complete block	Block design randomized blocks	Row-column designs latin square
Resolvable incomplete block designs	Square lattices * simple * triple	lattice square
	rectangular lattice * simple * triple	
	alpha designs	row-column alpha designs

Source: González (1989).

Table 3. Some important events in the history of experimental design.

Year	Event
1910	The concept of replication is introduced in agricultural research
1920s	R.A. Fisher introduces the randomization concept and the complete block designs (variation control in one direction) and latin square (variation control in two direction perpendicular among each other)
1936	Frank Yates introduces square lattices
1940	Frank Yates introduces lattice square designs
1949	Harshbarger introduces rectangular lattices designs
1976	Patterson, and Williams introduce alpha designs
1978	Patterson, Williams, and Hunter produce a catalog of alpha designs for experiments in the range of 20-100 treatments and up to 4 replications
1984	Paterson and Patterson developed an algorithm that automatically generates alpha lattice designs. In 1987 this algorithm is made available for use in microcomputers

Source: González (1989).

experimental block (1). Many alpha-lattice designs exist for a given number (v) of treatments, block size (k) and (r) number of replicates; however, only some have an HMEF that is high enough to be acceptable. The best alpha-lattice design for a specific combination of replicates, blocks, and treatments is obtained based on an algorithm developed by Paterson and Patterson (1984) that forms the basis of the ALPHAGEN program.

In the CIMMYT Maize Program, alpha-lattice designs have been used since 1986, particularly in the physiology-agronomy unit for evaluating trials with more than 200 genotypes, generally in single row plots 2.5 - 5.0 m long. Relative efficiencies of 1.0-2.0 have been observed, but their use has been restricted to genotype evaluation trials. There is no information on the use of alpha-lattices in agronomic experiments at CIMMYT, although they could be useful when there is no factorial-type relationship among treatments, the number of treatments is large (e.g., > 16), and soil heterogeneity at the test site is high. In these cases, the use of incomplete blocks is recommended to improve the control of random variation through the efficient use of experimental design tools.

Despite the fact that software programs for designing and analyzing alpha-lattices are available to researchers in national agricultural research programs in developing countries, little use has been made of them. Among the most important reasons are the absence of a software interface for entering and generating data files, the difficulty of handling information in a common format, and the lack of integration with other analytical tools (those for graphing, selection algorithms, regression, etc.).

This paper introduces a software module that facilitates and integrates the use of the ALPHAGEN and LATANOVA programs (Scottish Agricultural Statistics Service, Edinburgh), for the design and analysis of alpha (0,1) lattices and for processing the output with the Selection Assistant software developed by Barreto et al. (1991), as part of the genotype evaluation and selection process in a maize improvement program.

Software Description

At this time, CIMMYT is using ALPHAGEN.EXE for generating randomized designs and LATANOVA.EXE for doing analyses of variance of alpha (0,1) lattices. Both programs were developed originally by the Scottish Agricultural Statistics Service, Edinburgh, in FORTRAN computer language and were brought to CIMMYT to be used on the VAX mainframe computer. Later ALPHAGEN.FOR was modified to produce output in the form of field books and was adapted for use on IBM-compatible micro computers. Also, ALPHANAL.EXE was modified to incorporate statistics from randomized complete blocks, and its name was changed to LATANOVA.EXE. Both programs were further modified especially to improve the output format. Some general characteristics of both programs as currently implemented for use on IBM-compatible micro computers are:

ALPHAGEN.EXE

This generates randomization and field layouts for alpha (0,1) lattice designs. Its present limitations are: maximum number of replications = 6; maximum number of entries = 300. The program obtains input from users and displays the randomization plan on screen or stores it in a disk file. Output includes field layouts, replication, block, and entry codes, and the HMEF value. Processing this information further on a word processor has been a prerequisite for using the analysis program.

LATANOVA.EXE

This performs the analysis of variance and generates the lattice-adjusted means. The adjusted means can later be used in further analyses. This program has strict requirements in terms of input file characteristics (three different files), which to a certain degree have made it hard to use. The CIMMYT Maize Program developed data conversion software to facilitate the use of both programs. They were later integrated into a software system (ALPHA, developed in Turbo Pascal language © v 7.0 by Borland International 1992) which assumes that all information is centralized in MSTAT (Michigan State University) files. This step has made information easier to handle, since MSTAT is currently being used in many national programs for entering data and analyzing test results.

Structure of the Integrated System

To start the system, the programs are loaded from the distribution diskette onto a subdirectory of the hard disk. The word ALPHA is then keyed in on the operating system. Figure 1 illustrates the options menu available for analyzing alpha-lattice experiments designed at CIMMYT. The desired option is selected with the cursor or by simply pressing the letter describing that option. Options on the main menu include:

1. Produce a new randomization.
2. Analysis of variance and means adjusted for lattice.
3. Selection assistant.
4. Editing and transforming data files.

Each option has a specific subprogram to enter the information needed to carry out the desired option. Questions for the option of generating new randomization (1) and analysis of variance (2) are shown in Figures 1 and 2, respectively. The description of the Selection Assistant option is not presented in this document because there is a separate instruction manual on how to use it (Barreto et al., 1991). The option for editing and transforming data files (4) is illustrated in Figure 3. For using the latter, the program follows the software conventions described in the MST Data Assistant program (Barreto and Raun, 1988). The following sections present a detailed description of the questions included in Options 1 and 2 for generating and analyzing alpha-lattices, respectively.

Figure 1. Main menu with options for generation and analysis of alpha-lattice designs.

```
Generation and Analysis of Alpha-Lattice
                Designs
```

```
N  NEW RANDOMIZATION
A  ANOVA ALPHA-LATTICE
S  SELECTION ASSISTANT
V  VIEW/EDIT DATA FILE
T  TERMINATE
```

```
 Generate Randomization Alpha-Lattice (0,1)
Number of replications in design            2
Number of treatments (e.g. genotypes)       4
Number of plots per block                   2
Randomize first replication (Y,N)?          Y
Number of check treatments                  0
Output file name                        TEMPO
```

Option 1: Generating new randomization

***Number of replications in the design* -** Number of replications per treatment.

***Number of entries (genotypes)* -** Total number of entries or treatments (including checks).

Figure 2. Questions required for creating a new randomization for an alpha-lattice design.

```
Analysis of Variance with LATANOVA

MST File name containing data
Variable containing replicate number       1
Variable containing block number           2
Variable containing plot number            3
Variable containing entry number           4
Variables to be used in analysis           1
First case to be included                  1
Last case to be included                   1
MSTAT filename for adjusted means
Harmonic mean efficiency factor       0.9999
Job title
```

Figure 3. Screen for using a MSTAT master file and executing LATANOVA.

```
Create / Read MST data files

File name       |            |
```

***Number of entries per block* -** This question defines the size of the block. The current software version only allows a block size that is an integer multiple of the total number of entries. For example, if the total number of entries is 33, possible block sizes can only be 11 or 3.

***Randomize the first replication (Y,N)?* -** The user can request that the first replication not be randomized but ranked by entry order (which is generally not advisable). It should be noted that using this option does not alter the lattice structure, but there is a sequential rearrangement of the entry numbers in the first replicate.

***Number of checks* -** If a certain number of cultivars is to be included as checks, ALPHAGEN attempts to place each check in a different block. In the subsequent randomization the checks use entry numbers from 1 to the specified number of checks.

***Name of the MSTAT output file* -** This is the master file (MSTAT format) generated by Option 1 in the program, which should be used for entering data of the variables to be analyzed and for using the analysis program (Option 2). However, the program under Option 1 generates intermediate files in ASCII format having the same name but different extensions and which contain all the ALPHAGEN output. These files are: Extension .FDS contains all output information including HMEF. Extension .DSN contains the field books in ASCII format (Rep, Block, Plot, and Entry, in that order). It should be noted that design information in MSTAT format is stored in files having the extensions .TXT and .DAT.

Option 2: Analysis of variance on alpha-lattices

***File containing data* -** This the MSTAT file generated by the design software (Option 1), to which have been added variables with data to be analyzed (e.g., yield, flowering date, ASI, etc.).

***Variable with replication number* -** The number of the column in the MSTAT file that contains the replication code for the alpha-lattice generated by ALPHAGEN.

***Variable with block number* -** The number of the column in the MSTAT file that contains the block code for the alpha-lattice generated by ALPHAGEN.

***Variable with plot number* -** The number of the column in the MSTAT file that contains the plot code for the alpha-lattice generated by ALPHAGEN.

***Variable with entry number* -** The number of the column in the MSTAT file that contains the entry or treatment code for the alpha-lattice generated by ALPHAGEN.

***Variable(s) to be analyzed* -** Numbers of the columns in the MSTAT file that contains variables to be used in the analysis of variance. The software can analyze a maximum of 10 variables at the same time. These are specified by their corresponding column number, separated by spaces (e.g., 3 4 5) or using a dash (e.g., 3-5).

***First case to be included* -** The first case of the MSTAT file to be included in the analysis.

***Last case to be included* -** The last case of the MSTAT file to be included in the analysis.

***MSTAT file for adjusted means* -** Name of file supplied by user to be used for storing adjusted means per lattice to be used later with the Selection Assistant. The name should be different from that of the master file containing the original data.

***Efficiency of the alpha-lattice design* -** This is the HMEF value and it is requested by LATANOVA. ALPHAGEN generates this value and it is recorded in a file with an .FDS extension and in the MSTAT file created through Option 1 as part of the file descriptor.

***Title of work* -** This is simply an alternative descriptor defined by the user to identify the work in the analysis program. It appears as a title at the top of each analysis of variance.

Hardware Requirements

To be used in an integrated manner, the software system requires an IBM compatible computer (8086, 286, 386, or 486, with or without a mathematical coprocessor), equipped with a minimum of 640 KB RAM, a hard disk with at least 2 MB available space on a MSDOS Version 3.3 operating system or higher. However, on a 8086 or 286 without a coprocessor, it takes considerably more time to run an analysis of variance. The amount of available memory for the program after loading the operating system should be at least 590 KB to run ALPHAGEN. The other options require less memory (512 KB). The amount of memory available can be ascertained by executing the CHKDSK or MEM command (only on DOS version 5.0 or higher).

Types of Output Files

Option 1: Generate new randomization

As indicated before, Option 1 produces a series of files in ASCII and binary format that contain the randomization and additional information on alpha-lattice designs. These files have the same name (defined by the user), but have different extensions. Depending on their extensions, files contain the following:

***ALPHAGEN.IN files* -** This file contains information needed to run the ALPHAGEN.EXE program using entry redirection or piping (e.g., ALPHAGEN <ALPHAGEN.IN). This step is clear to the user because ALPHAGEN is run directly from Option 1. The file is in ASCII format and contains the answers to questions in ALPHAGEN.EXE, one answer per line, including random seeds used to generate randomization (these are automatically provided by the program in Option 1). Since the name of this file is always the same (and is regenerated every time Option 1 is used), the file on the disk is always the same as the last randomization done.

***Files with an .FDS extension* -** Output information (ASCII format) that includes FEMA, the number of reps, blocks, and entries (including checks), and the field book with randomization ranked by plots and with headers for every column (Tables 4 and 5).

Files with a .DSN extension - Contain the field book in ASCII format (rep, block, plot and entry, in that order), but with no heads. These files may be used to generate field books using a word processor.

Files with .TXT and .DAT extensions - MSTAT binary files containing field layouts ranked by plot numbers. These files are ready to be edited by the user at the end of each Option 1 session. The user should enter the variables of interest using the data editor to add variables (columns) and do transformations between variables using the conventions described in the MST Data Assistant (Barreto and Raun, 1988).

Option 2: Analysis of variance of alpha-lattices

Option 2 does the analysis of variance of alpha-lattice designs by running the LATANOVA.EXE program. A prerequisite for using this option is that the data to be analyzed be in MSTAT format. During the analysis, Option 2 does a number of file conversions to make it easy for the user to utilize LATANOVA.EXE. Among those conversions are the creation of new ASCII files with the field layout of the design, the data to be analyzed and storage of the lattice-adjusted means in a binary MSTAT file. As in the previous option, the output files have the same name as defined by the entry file but different extensions.

Table 4. Example of a file generated by ALPHAGEN.EXE for an experiment with 2 replicates, 24 entries and 4 incomplete blocks of 6 plots each.

The Complete Design File (.FDS)

```
DESIGN 1                              SECTION A
   2   24    4    6.780439
   1
                                      SECTION B
   8    7   20   12   16   21
  17    9   15   10    1    4
  19   11    5   23   14    2
   6   24   22   18   13    3

  12   19    2    4   18   24
  22    5   17   21    3    1
   9   11   16   14   20    6
  15   13    7    8   10   23
                                      SECTION C
REPLICATE 1
   1    2    3    4    5    6
   7    8    9   10   11   12
  13   14   15   16   17   18
  19   20   21   22   23   24

REPLICATE 2
   4   13   18   12   22   20
  21   15    7    6   24   11
   8   14    5   17    3   19
   9   23    2    1   10   16
   1                                  SECTION D
REP BLOCKPLOTRANDOMIZED 1ST REP
   1    1    1    8
   1    1    2    7
   1    1    3   20
   1    1    4   12
   1    1    5   16
   1    1    6   21
   1    2    7   17
   1    2    8    9
   1    2    9   15
   1    2   10   10
   2    1   26   19
   .    .    .    .
   .    .    .    .
   2    3   38   11
   2    3   39   16
   2    3   40   14
   2    3   41   20
   2    3   42    6
   2    4   43   15
   2    4   44   13
   2    4   45    7
   2    4   46    8
   2    4   47   10
   2    4   48   23
*END*
```

Table 5. Explanation of an output file generated by ALPHAGEN.EXE for an experiment with 2 replicates, 24 entries and 4 incomplete blocks of 6 plots each.

This is a text file with four sections but only sections A and D are important.

Section A
Characteristics of selected design

DESIGN 1 *TYPE OF DESIGN*
2 24 4 6 .780439

NO. REPS/TRTS/BLKS/BLK SIZE/Efficiency Factor of Harmonic Mean
1

Section B
Field layout with plot 1 on the upper left corner in block 1.

8	7	20	12	16	21	*BLOCK 1*
17	9	15	10	1	4	*BLOCK 2*
19	11	5	23	14	2	*BLOCK 3*
6	24	22	18	13	3	*BLOCK 4*

Section C
Entries in each rep. and block. The entries in first rep. are always presented in sequence and the numbers have been correspondingly swapped in the other reps.

Section D
This is the most important section as it includes the randomization in a format that can be utilized for preparation of field books of imported into MST.

Depending on its extension, each output file contains:

LATANOVA.IN file - These files contain information needed to run the LATANOVA.EXE program using entry redirection or piping (e.g., LATANOVA <LATANOVA.IN). This step is clear to the user because LATANOVA is run directly from Option 2. The file is in ASCII format and contains the answers to the questions in LATANOVA.EXE, one answer per line. Since the name is the same (and is regenerated each time the option is used), the file on disk is always the same as the last analysis done using Option 2.

Files with a .DSN extension - Contain the field book in ASCII format (rep, block, plot and entry, in that order), but without headers. This file can be used to generate field books using a word processor.

Files with a .LAD extension - Data to be analyzed (ASCII format) which include plot number and data variables separated by spaces with heads for each column.

Files with a .VAR extension - A FORTRAN reading format for each variable and names of variables to be analyzed.

Files with an .AOV extension - A LATANOVA.EXE output file in ASCII format that contains the analysis of variance tables for each variable analyzed and the means with and without lattice adjustment (Table 6).

Table 6. Example of output file from LATANOVA (.AOV) with ANOVA tables and unadjusted and adjusted means.

```
#PLOTS = 450 #REPS = 2 # VARS = 225 # BLOCKS/REP = 15                         Code for design
EFFY = .8889 CRIT = .00 MISS. VAL. CODE = -99.                              HMEF (first value)

ANOVA of Trial 1603M

ANALYSIS OF VARIANCE FOR VARIABLE AD                                        Variable analyzed

LATTICE ADJUSTED ANALYSIS                                                   ANOVA for lattice

SOURCE        DF      MS

REPS           1     .0200
BLK(ADJ)      28     3.9279
TRT          224    10.7597
TRT(ADJ)     224    10.3873
RESID        196     2.6914

TOTAL        449     6.7877

F (REPS) = .007 (1, 196 DF)
F (TRTS) = 3.859 (224, 196 DF)

AV. SE = 1.1922     LSD (0.05) = 3.3247     F SIG = 1.0     DF = 196     CV = 2.2

RCBD ANALYSIS                                                               ANOVA for RCBD

SOURCE       D.F.   SUMS OF SQUARES   MEAN SQUARES   F VALUES

REPS           1      .25000000        .25000000       .088
ENTRIES      224   2410.25000000     10.76005000      3.783
ERROR        224    637.16460000      2.84448500
TOTAL        449   3047.66500000

REP MEANS                                                                   Replicate means
    1  74.102
    2  74.116

S.E. (DIFF) = 1.68656 (224) D.F.                              Standard error of difference
COEFF. OF VARIATION = 2.28     OVERALL MEAN = 74.1089                  CV and overall mean

RELATIVE EFFICIENCY RCBD/LATT ADJ:
CALCULATED AS (SED(RCBD)**2/SED(LATT.ADJ)**2) = 1.0007                  Relative efficiency

1
1  UNADJUSTED MEANS                                                  Unadjusted means RCBD
  ENT    |AD     |ASI    |GY    |EPP    |GPE    |100KW   |LODG%  |LROLSC|

   1    75.00    1.00    .81    .83   166.05   11.05    16.66    2.16
   2    74.00    2.00   1.19    .65   287.72   12.85    18.06    3.00
   3    72.50   -1.00   1.55    .94   212.12   14.55    11.11    2.50
   .      .       .      .      .       .        .        .       .
   .      .       .      .      .       .        .        .       .
 225    68.50    -.50   1.71   1.00   264.05   12.30    11.11    3.50

1   ADJUSTED MEANS                                                  Lattice adjusted means
  ENT    |AD     |ASI    |GY    |EPP    |GPE    |100KW   |LODG%  |LROLSC|

   1    74.88    1.20    .71    .82   165.69   10.55    23.31    2.42
   2    74.00    1.99   1.19    .67   287.33   13.13    20.00    3.03
   3    72.48   -1.09   1.56    .97   211.99   14.52    12.28    2.47
   .      .       .      .      .       .        .        .       .
   .      .       .      .      .       .        .        .       .
 225    68.58    -.41   1.70    .99   264.33   12.18     6.45    3.43
 MEAN   74.11     .40   1.03    .86   198.62   11.74    17.01    2.95     Descriptive
                                                                     statistics means
 LSD     3.32    2.61    .58    .30    74.69    2.73    30.44     .96
 CV     2.213    18.9  27.36  16.67    19.02   11.36    87.57   15.76
```

Adjusted means files with .TXT and .DAT extensions - Files in binary MSTAT format that contain the lattice-adjusted means for the variables of analysis selected in Option 2. The file always contains the first variable with the entry number (treatment) and the last variable called INDICE. This makes it easy to use this file with the Selection Assistant (Barreto et al., 1991). This file can be modified using the MST Data Assistant editor (Barreto and Raun, 1988).

Examples of Output Files

Option 1: Generate new randomization

Table 4 shows an example of randomization for a file having 24 entries in incomplete blocks of size 6 and two reps. The file presented is an .FDS extension file (complete design). Table 4 shows notes in the right margin describing the important parts of this output file. Table 5 briefly describes each of the sections of the output file having the .FDS extension.

Option 2: Analysis of variance of an alpha-lattice

Table 6 gives an example of an output file (extension .AOV) generated by LATANOVA. In the right margin are the descriptions of each of the statistical parameters and elements for analysis.

References

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Developing Drought and Low-Nitrogen Tolerant Maize: An Overview

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Timothy Reeves set forth clearly the challenges that agriculture and CIMMYT face in the coming century. How can large increases in food supply be obtained in a sustainable way, with little increase in land area devoted to production, and with the least impact on environment? This workshop addresses those issues for marginal lands — lands where drought is frequent and nutrients sparse, lands that are home to many of the world's poor. The progress and continuing efforts outlined by the overview presentations and posters and evidence of extensive international cooperation in such efforts bode well towards meeting Reeve's challenges. Let me summarize my thoughts about several aspects of these efforts.

Importance of marginal environments

A strong case was made that serious problems exist for maize in areas of Latin America, Africa and Asia subject to drought and nutrient limitations. In many cases, the small and highly variable yields of such marginal lands are the basis of subsistence farming, with little in the way of surplus to support urban populations. An equal concern is that such "traditional" agriculture (Schulze, 1964; Loomis, 1984) is linked inevitably with poverty for its practitioners. A clear message of this meeting is that traditional agriculture is alive, still unwell in many areas of the world, and little affected or improved by advances in science and technology during this century.

To a fair extent, water and nutrient deficiencies are problems of different areas or, as is more difficult for farmers, of different seasons. Identification of problem areas is a very difficult task. It was done here by mapping climate data and through assessment of crop losses. While these reports are convincing about the extent of problems, they are much less convincing about the degree and causes. A series of experts from pathology to soils might give seemingly reasonable independent estimates of 30% loss to disease, 50% to moisture stress, 30% to weeds, 40% to nitrogen deficiency, 10% to nematodes, 15% to acid, and so on. The sum of those estimates, however, is not believable. Those who fund research have learned to disregard such claims, relying instead, and unfortunately, on hearsay and guesswork in setting priorities.

The databases and logic of assessments of crop losses need to be explained clearly. M.X. Santos set a good example in examining the situation in Brazil. Improvements in simulation models and geographical information databases will assist in the future. More attention to soil is also required. Crops at many tropical sites suffer moisture stress not because of a shortage of rain but because soil profile characteristics limit water-holding capacity and the extent of rooting. As a result, amounts of stored moisture are simply too small to carry crops through modest periods without rain.

Progress through breeding and in training

The evolution and domestication of most crop plants took place under marginal conditions and one might well wonder about expectations that selection and breeding might somehow now improve yield and stability (i.e., a small interannual variation). Yet CIMMYT's group has demonstrated splendid progress on both points. Their various selections are clearly superior to the indigenous populations from which they derive, when faced with moisture stress or nitrogen deficiency. Outstanding points in the research include the control gained over a principal indicator of barrenness (a variable anthesis-to-silking interval, ASI) and greatly improved understanding of maize physiology in the face of nutrient and water deficits. Integration of this understanding into the selection programs is truly exemplary of the approach that will be increasingly needed in the future.

The continued success of the CIMMYT Maize Program in training is also impressive. The quality of young scientists who have assisted in this work is indeed remarkable and their impact will be felt throughout the balance of their careers. That the same is true for outreach training is evident from the high quality of national reports presented at this meeting.

Yield gaps, and gaps in understanding

The low yield levels (1-2 t grain ha^{-1}) of maize in many marginal environments are in shocking contrast to record yields of maize (near 22 t ha^{-1}) obtained under good conditions at higher latitudes. The true “yield gap” is much smaller, however, as indicated by attainment of only 6 to 9 t ha^{-1} in tropical areas with adequate water and nutrients, and diseases and weeds controlled. The real issue, then, is not why stressed crops in the tropics yield only 20% of that obtainable nearby, but why the gap between attainable yields of tropical and temperate zones is so large. I am convinced again that differences in temperature and radiation patterns are the root of these yield differences. Further progress will require understanding of the mechanisms controlling developmental advance (phenology) and maintenance respiration. Daily integrals of radiation for tropical and temperate zones are generally similar but peak radiation levels during the day are often greater in the tropics. Peak levels cause problems in photosynthesis (light saturation accompanied by down-regulation, photoinhibition, and photo-damage) that strongly limit biomass production and yield. Sufficient knowledge of mechanisms now exists for assessment of these issues in tropical maize.

International cooperation

Marginal agriculture is widespread in the tropics and a network for exchange of people, information and germplasm is extremely important. The international cooperation evident in this meeting is indeed impressive. It is clear that an effective network exists and that it functions well. The challenge now is to sustain its vigor.

A concern

Throughout history, traditional agriculture has been associated with farm families that include numerous children (Loomis, 1983). This arises in part from the labor-intensive nature of such systems and, in many cases, from lack of alternative security for farmers in old age. While marginal agriculture does poorly in producing food surpluses that might support urban populations, it has been far too effective in producing during each generation a surplus of people who must migrate to cities and towns.

All involved in the improvement of traditional agriculture must be sensitive to two dangers. One is that even slight improvements in yield will simply lead to further subdivision of existing lands given to subsistence farming. The other is that such improvements will extend subsistence farming to even more marginal lands. Either way, one consequence is an increased flow of surplus people from farms to cities. This population issue places agronomists in a quandary — because our basic mission is to insure the food supply. Guidance is absent as policy makers continue to ignore the problem or fail to understand it. We should consider whether efforts to improve yields from marginal lands must be accompanied by research aimed at reducing the dependence on labor. While remaining skeptical that farming of marginal lands will solve many of the world’s food problems, I come from this meeting convinced of the importance of efforts to improve agriculture there.

References

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Review of the Symposium on Developing Drought and Low N Tolerant Maize

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The first day of the symposium was spent in establishing the need for the symposium and describing the extent of drought and low nitrogen growing conditions throughout the developing world. It was agreed that maize is often grown in regions or fields that are characterized by adverse soil and climatic (especially precipitation) conditions. Thus, one can expect that farmers in developing countries, especially smallholders, need maize varieties that can tolerate limited water and nitrogen availability, the dominant growth limiting factors. Varieties intended for use by these farmers must therefore have a high degree of tolerance to drought and to low levels of soil nitrogen.

To address this issue, scientists from 41 countries have met for a further 4 days, sharing findings and insights by means of 101 oral and poster presentations, informal conversations and small group meetings**.** Their goal was to share findings and insights in order to improve maize production in developing countries in general, and in adverse environments on small-holder farms specifically.

Participants have been teaching each other to “talk” to the maize plant, and to listen to it when it “talks” to us. However, the maize plant still carries many secrets, and modern technology does not yet give as much conversational help as we have hoped it would, although we believe that some tools, such as molecular marker technology, will give us at least a little more information and power to make desired changes.

The symposium concentrated on two approaches. Physiology tries to understand principles of growth and production and tries to use this knowledge to increase the efficiency of plant breeding. Breeding tries to develop improved cultivars in any manner that will work. For the former group, the phrase, “theory that gives results” seems to apply, whereas for the latter more empirical and intuitive group, the most descriptive phrase is “results that lead to theory”. The symposium has brought these two approaches together in a productive interaction of styles and knowledge. Three facts of life constrict our possible courses of action:

- Hybrids are replacing many of the open-pollinated varieties (OPVs) in developing countries.
- Research funding is dropping drastically due to massive public disinterest in agricultural research, especially research on production agriculture.
- We have finally realized that agricultural production is an integral part of, and is affected and controlled by, socioeconomic forces, aspirations, and changes.

Breeding for drought and low nitrogen tolerance

Breeding for drought and low nitrogen tolerance works everywhere these conditions occur. However, the efficiency of the breeding process can be enhanced by selecting for key traits that aid us in identifying drought or low N tolerant germplasm. In the case of drought, the length of the anthesis-silking interval (ASI) is one of the most important traits, and we have learned several ways to increase speed and accuracy of breeding for short ASI and its consequent trait, resistance to barrenness. We also can manipulate the environment to help us identify tolerant genotypes more accurately, for instance through managed irrigation regimes. Fortunately, we can identify genotypes that combine drought or low N tolerance with high yield potential. It appears that, in some cases, cultivars with tolerance to drought also will be tolerant to low N. Unfortunately, this does not seem to work the other way around. There was no agreement, however, about how far we should go in that direction. Should we select for genotypes able to make at least some grain under absolutely disastrous levels of drought or exceedingly low levels of soil N? And if we do this, should we then be satisfied with varieties with relatively low yield potential in good conditions? Or, for such very adverse conditions, should some other crop such as sorghum or millet replace maize?

Planting at high densities and / or inbreeding can help to identify genotypes with long ASI and barrenness under dry growing conditions (i.e., genotypes with poor drought tolerance). High plant densities and / or inbreeding may also increase the opportunity to select for tolerance to low N. There seemed to be disagreement about the utility of breeding at high densities — would it answer all needs or only part of them?

Technology transfer

In developing countries, agricultural research programs and small seed companies need more knowledge about the best field-oriented technologies that are appropriate and affordable to use when selecting for drought and / or low N tolerance. National program scientists admire the CIMMYT equipment and facilities but cannot duplicate them at every breeding site. A personal thought from a pragmatic plant breeder who has seen many unhappy surprises when hybrids that had been carefully tested on-station were released to farmers: more consideration should be given to on-farm testing in developing countries, as a way of proving stability of new cultivars, including their reaction to drought and low N, and their interactions with on-farm cultural conditions. Precise approximations of on-farm environments are always only approximations, no matter how carefully they have been carried out.

Socioeconomic issues and cultural practices

There is a need for further definition of the types of farmers and growing conditions that maize hybrids and OPVs are targeted towards, because this relates to the level of stress tolerance that needs to be incorporated in the respective types of germplasm. It is often suggested, for example, that hybrids most likely will be grown on good soils and OPVs on poor soils, but is this really true? One analysis (Waddington and Heisey, 1997) indicated that more can be gained by adapting better cultural practices than by breeding for drought and low N tolerance. Have we thought about this, or do we even want to think about it? It is quite likely that, as cultural practices change, genotypes will need to change also. Will we produce a marvelously successful solution to today’s problems only to find that our solution is no longer needed, or needs updating even before it is released? Or will a new genotype lead farmers into using a new type of management which in turn gives breeders opportunity for still newer genotypes even better suited to that type of management?

The role of women in agricultural systems should be considered more carefully in the development of new germplasm. For example, when women (rather than machines and herbicides) do the planting, weeding, and harvesting, will specially adapted plant types and different plant densities be needed? Have we taken the time to learn all we should know about the role of women in maize agriculture?

Collaboration

The need for collaboration and cooperation to make the best use of limited funds and resources as well as to improve the precision and speed of plant breeding to improve stress tolerance has been discussed. Regional grouping of institutions in neighboring countries seems essential, and it seems clear that CIMMYT can play an important role in making these collaborations work. CIMMYT’s role should be as a neutral facilitator, not a self-appointed director. Also, some globally centralized research functions will be needed. CIMMYT may be the right organization to do this, in partnership with and in response to requests from national programs or other organizations in developing countries. Much more planning and thought, however, needs to be given to the concept of regional collaborative networks. The concept is attractive, but details with regard to responsibilities of national programs, private industry, NGOs, and CIMMYT are lacking, as well as a timetable, sources of funds, and mechanism of operation.

Finally……

An unexpected bonus of this meeting may be that it will serve to advertise the worldwide importance of drought and low-N conditions in developing countries, the real consequences of ignoring this problem (which daily gets worse), and the benefits to humanity (especially the poor) that can come from funding breeding and research intended to increase the tolerance of cultivars to drought and to low N. It has now been shown that improvements can be made through breeding. Efforts are sure to pay off, if they are supported with funds and facilities.

Reference

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Conclusions:

What Have We Learned and Where Do We Go?

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The Symposium

Goals of the meeting were to bring together researchers having an active role in investigating and improving drought and low N-tolerance of maize, and to share their insights on: distribution, timing and intensity of these stresses; traits related to tolerance to drought and low N; selection methodologies and results from selection experiments; field techniques that improve efficiency of selection; sources of tolerant germplasm; crop management techniques complementing tolerant germplasm; and mechanisms for more effective NARS-CIMMYT collaboration in abiotic stress tolerance.

The 4.5 day-long meeting was attended by 121 participants, categorized as: national program invitees: 68; trainees at CIMMYT from national programs: 10; invited experts from US and Australia: 9; representatives from other IARCs: 3; CIMMYT staff from outreach: 9; CIMMYT staff from headquarters: 22. Regional representation of national program participants was: Latin America and the Caribbean: 40; Africa 24; Asia 14, for a total of 41 countries. Most participants were from public sector institutions, but three were from the private sector, and several others had private sector experience. Absent was representation from NGOs.

The program included 36 oral presentations and 65 posters. About 80% of participants made presentations, either oral or as posters. The talks were generally of a high standard and simultaneous translation was provided throughout. The poster displays and the subsequent discussion of posters in the plenary sessions were exciting aspects of the meeting. The first two days of the symposium were devoted to scientific presentations and were followed by a field visit by about 90 participants to the Tlaltizapán Experiment Station, where participants observed harvests of demonstration materials, explanations of experimental procedures, and an overview of the CIMMYT Maize Program. The latter third of the meeting took a different tone: the papers were focused mainly on methodologies of direct use to national programs, and a whole day was devoted to consultation with national programs on the best way in which CIMMYT could help them meet their goals. Conference participants were divided into five large groups (Asia, lowland Africa, mid-elevation Africa, highland Latin America, lowland Latin America) and into small groups within each of these. Pre-selected issues were discussed for 2.5 hours, and reports presented to the plenary session next day. Topics addressed the extent and nature of stresses encountered by maize by region; types of products CIMMYT can best provide; global versus regional organization of maize improvement; germplasm exchange; key regional testing sites; organization and sharing of work ; and possible sources of donor support. The discussions confirmed the pre-eminence of drought and soil fertility (principally N) as the major abiotic constraints to maize production in the tropics and subtropics. The conference concluded with a panel discussion on issues affecting the transfer of technology related to stress-tolerance to the maize fields of small-scale farmers. A full report of these discussions has been presented elsewhere (Elings et al., 1996), and has already been used to mobilize funds from donor sources to support additional research on the conference theme.

The Extent of the Problem

While it was obvious that drought and low N are pervasive problems in tropical environments where maize is grown, it was clear that we lack quantitative estimates of the incidence and intensity of the stresses and of associated yield losses. Crop simulation models, in conjunction with global databases on climate and its variation over time, on soil properties and on the spatial distribution of the maize crop, all integrated through geographic information systems, have the capacity to answer these questions far more accurately now than a decade ago. Such answers can help researchers and their managers to establish breeding goals and to decide on the balance between crop improvement and crop management strategies. This is research that must be completed if we are to gain a sharper focus on the problem and its solution and make intelligent decisions relating to investments in breeding versus agronomy as a means of alleviating the effects of N and water shortages. The prospect of being able to predict the occurrence of region-wide drought, such as that resulting from *El Niño* events, is now a real one, though it will mainly affect crop management rather than crop improvement decisions. Increasingly crop simulation models, however, are providing guidance on the most promising crop management interventions to address water or N limitations.

Breeding vs. Crop Management

Breeding can only close perhaps 15-25% of the gap between realized yields and potential yield, as determined by the radiation and temperature regimes of a site. Improved crop management practices involving more effective uses of naturally-occurring supplies of N and water can probably close the gap a further 15-25%. The remainder of the gap, some 50-70% of potential yield, can only be met by exogenous additions of water and nitrogen. Breeding, then, cannot “green the desert”, but, since its benefits are embodied completely in a seed, it nonetheless remains the best alternative to many resource-poor farmers who cannot afford additional inputs or are simply unable to get access to them.

Earliness vs. Tolerance

Matching the phenology of the crop to the rainfall (and to some degree N) supply is the first important task for the breeder and agronomist, and early-maturing landraces are most commonly found in dry and infertile environments. An early-maturing cultivar will escape terminal drought stress in most dry years (and to some extent N stress as well), and gives stable though relatively low yields. However, earliness does not guarantee tolerance to stresses which occur at times other than the start and end of the season, and early cultivars generally lack yield potential for those good years when, contrary to expectations, rains are plentiful and fertility high. Multi-location trial data have reaffirmed the value of earliness *per se*, but more importantly, the value of tolerance in later-maturing cultivars that have the capacity to exploit good environments when they occur. Furthermore, our experience and that of others also show that N and water availabilities vary greatly from place to place in individual fields under tropical conditions (Bouma et al., 1997). Little research has been devoted to this phenomenon in tropical maize, but its documentation is an important future task. Even if we were able to predict the inter-annual variation in water and N supply, a single variety planted to a whole field in the tropics is commonly exposed to a wide range of water and N availability in any given crop cycle. High and spatially-stable production will then depend on that variety’s ability to perform well across the range of N and water availability encountered within a single field, as well as across fields and years.

Survival vs. Productivity

If grain yield is the goal of breeding for tolerance, then traits which promote *survival* are less likely to be useful than those which promote *productivity*. This is particularly true for stresses which occur at flowering. At this very susceptible stage in the development of the maize ear, grain sink capacity appears to depend on the flux of currently-formed photosynthate to the ear, a trait which is most easily measured as ear growth rate, a symptom of which is the rate at which emerged silks are growing. Traits which reduce the flux of assimilate to the ear in the two weeks either side of 50% anthesis, such as the closure of stomates, growth of competitive structures such as stems, roots and tassels, leaf rolling and early senescence may help the plant to survive and do not affect pollen shed, but they seem likely to decrease grain production. Traits which promote water capture, photosynthesis, increased ear growth, continued N uptake, remobilization of assimilates and delayed foliar senescence promote ear fertility and grain yield under stress at flowering, even though the survival of the plant may be jeopardized by what could be seen as a foolhardy usage of water.

Stress Tolerance at what growth stage?

While the incidence of drought is greatest at sowing and at the end of grain filling, the consequences of drought are greatest when it occurs at flowering. Drought at establishment, although severely affecting plant stand, can be compensated for by management options, such as replanting, reduced fertilizer application and intercropping. Repeatable terminal drought stress can be managed by using an earlier maturing variety. Around 80% of the variation in grain yield under severe drought stress, however, is accounted for by variation in numbers of grains per plant, itself largely affected by the degree of stress-induced barrenness, and few management options are available to farmers when drought occurs at this growth stage. Thus, a continued emphasis on tolerance to drought at flowering and during grain filling seems justified, and the breeder and physiologist must concentrate on exposing and utilizing genetic variation for mechanisms that affect barrenness and prolonged translocation of assimilates to the developing kernels.

Secondary Traits: Which Traits?

Grain yield under stress will remain the primary and most important trait during selection. The judicious use of secondary traits, however, has also been shown to improve overall selection efficiency, probably by more than 20% under severe stress caused by low N or drought. Useful secondary traits are: (i) genetically variable, with a genetic association with grain yield; (ii) moderate to high heritability; (iii) cheaper and / or faster to measure than grain yield; (iv) able to be observed at or before crossing time; (v) able to provide an estimate of yield potential before final harvest. Anthesis-silking interval is perhaps the best example of an effective secondary trait, provided environmental conditions are such that genetic variation for that trait is exposed. Most breeding programs use a combination of secondary traits with grain yield to develop a selection index for use in identifying superior genotypes. Although many secondary traits have been advocated over the years, few have been subjected to the test of these criteria, and even fewer have been evaluated in a planned set of experiments where selection for the trait alone, for grain yield alone, and for grain yield plus the trait have been compared. The advent of molecular markers in breeding programs opens new possibilities of being able to develop rapidly sets of near-isogenic lines with and without the trait of interest for comparison under field conditions, and of transferring the trait(s) efficiently to recipient stocks.

The present state of knowledge suggests that if improved and stable grain yield remain the prime objectives of maize breeding programs, then traits related to tolerance to stresses at flowering and during grain filling will be more important than tolerance during the vegetative growth stage, when farmers still retain some flexibility to replant in the event of a crop failure. Tolerance of factors leading to barrenness and an early cessation of grain filling is the route to follow, and traits which favor these, in order of importance, are ears per plant (or resistance to barrenness), anthesis-silking interval, delayed foliar senescence, leaf chlorophyll concentration, reduced tassel size, prolificacy, capacity to remobilize assimilates stored in the stem and husk, low canopy temperature, ability for the photosynthetic system to recover from stress, and unrolled upright leaves. Further analysis of the role of osmotic adjustment and of ABA in maize under drought seems warranted, and the search for additional secondary traits continues.

Sources of Germplasm

There is no magic bullet: this conference has not identified one or two extreme sources of tolerance to drought and low N stress that all breeders can use, and there are very few such sources that have withstood the test of close examination. Resistance in the true sense (i.e., shows no symptoms of the stress) simply does not exist, and if it did it seems likely that yields would be very low. To quote Jorge Bolaños: "…..only rocks can *resist* drought and low N stresses….". Rather, consensus indicates that tolerance to these stresses can be developed through targeted breeding, and genetic variation for tolerance traits can be found by carefully searching for these traits in collections of germplasm at CIMMYT and elsewhere. Research reported here endorse the supposition of Abraham Blum (1983) that there is a relatively high frequency of drought-adaptive genes in our elite breeding populations, and that it is the art and responsibility of the breeder and physiologist to increase that frequency in the most efficient way possible.

CIMMYT's experience suggests that the most rapid short-term improvements in tolerance to drought and low N, while maintaining or increasing production under non-stressed conditions, can be made in elite maize germplasm through recurrent selection or by careful screening of inbred lines and topcross progenies from such germplasm. While landraces may possess tolerance characteristics, the characteristics are often linked with traits which result in low yields under well-watered and fertile conditions, and this handicap may take years to correct. Molecular markers, however, will greatly reduce the time taken to move specific traits from unimproved sources to an elite background, and for this reason it is too early for the long-term benefits of research on unimproved sources of tolerance to drought or low N to be properly assessed. In the meantime, however, it is prudent for national programs to focus on increasing stress tolerance and stability in their elite germplasm, rather than investing in research on landraces which often have mediocre yields when these stresses are not present.

Managed Stress Environments vs. Multilocation Testing

How do managed stress environments compare for selection efficiency with a random sample of environments encountered during multilocation testing in conventional selection programs? In general multilocation testing is a valuable means of improving broad adaptation of germplasm and for delivering improved germplasm to clients, and for a variety of reasons must be continued. Results presented at the symposium suggest that it will not result in significant improvements in tolerance to drought or to low N, though it may occasionally identify some outstanding stress-tolerant individuals which occur at a relatively low frequency within conventionally-improved populations. Evidence suggests that the use of managed stress environments is the most cost-effective means of improving tolerance to drought and low N, if these are the major objectives of a breeding program. Furthermore, for N stress at least, if the target environment has a loss of yield due to N stress of greater than 40%, it will be more efficient to select for that environment using a low N managed site than a high N site. For less intense stress levels, capitalizing on a "spillover" from constitutive traits such as high yield potential is likely to be the most effective way to select for improved performance. Where the target environments is characterized by losses of > 40-50% due to drought or low N, however, screening under severe stress is more likely to expose variation for facultative traits (such as osmotic adjustment) not expressed under less severe stress conditions. There are a number of ways in which artificial stress environments can be managed at little cost in a conventional program – staggered planting dates, high plant density, dry winter season nurseries, use of cereal intercrops to induce N deficiency, to name a few. The efficiency of multilocation testing for increasing stress tolerance can be also increased considerably by the use of efficient designs, by additional weighting of data obtained from stressed environments (rather than discarding them because the coefficient of variation was "unacceptably high"), by across-location analysis, by the deliberate siting of trials in low N fields or in areas known to have a high frequency of drought, and by the recording and use of relevant secondary traits.

Selection Methods that Work

In order to demonstrate the effectiveness of selection, it must take place under field conditions typical of the target environment, using realistic populations structured as full-sib or inbred families, and must show significant genetic gains over time in independent evaluation trials.

There have been relatively few of these studies reported here, largely because of their cost; this highlights an opportunity and a responsibility of international agricultural research centers (IARCs) that work in maize improvement. Nevertheless, research at CIMMYT has shown that selection under controlled stress conditions (managed low N fields; managed drought stress in a rain-free winter environment) has resulted in genetic gains in several elite maize populations of around 100 kg ha^{-1} yr^{-1}, or about 5% per year. There is emerging evidence that these methods are effective in germplasm varying in adaptation from the highland tropics to the temperate zone. These gains have been maintained over several cycles of selection without obvious diminution, and it is significant that they have also been accompanied by improvements in grain yield under unstressed conditions. The key elements of this selection process are:

- Use of managed stress environments to allow stress to be applied at critical points in the life cycle of the crop when genetic variation for stress tolerance is best displayed.
- Use of efficient experimental designs, specifically alpha (0,1) lattices.
- Monitoring performance in unstressed environments.
- Control of maturity from cycle to cycle so tolerance (not escape) is chosen.
- Use of elite germplasm, so improvement is from a high and stable base value.
- Consistent use of a carefully chosen group of secondary traits related to tolerance.
- Combination of all traits and environments into a selection index (or an ideotype) that permits weighting of each trait according to its perceived worth in that set of evaluations, and results in a single index value per genotype that can be used to identify superior genotypes for advance or recombination.

The fact that genetic improvements under drought are reported to result in similar rates of genetic gain under low N is of considerable significance. In other words, screening segregating progenies under managed drought stress that coincides with flowering is an efficient means of displaying genetic variation in partitioning of dry matter to the growing ear, and this also results in gains in grain yield under a stress induced by low N. Other evidence suggests that screening under drought also results in improved tolerance to stresses induced by high plant density and by shading. Thus managed drought stress imposed at flowering, provided early-flowering genotypes are recognized as escapes, is an effective means of increasing tolerance to a number of stresses occurring near flowering and which commonly result in barrenness.

The weak correlation observed between inbred line and hybrid performance challenges the strategy of evaluating inbred lines for *per se* production under drought and low N stress. This strongly suggests that the major emphasis in a pedigree breeding program should be on topcross or hybrid yield under stress rather than inbred line performance, especially at levels of inbreeding greater than S_3.

Uses of Source Germplasm

A number of papers reported the superior performance of specific populations or hybrids under stress conditions, even though these may not always be competitive with conventional populations or hybrids under unstressed conditions. How can this information be most effectively used? When inbred lines have been developed from populations improved for tolerance to drought or low N, they have resulted in a higher frequency of hybrids with tolerance to these stresses, when compared with the same population improved by conventional means. Thus, provided the performance of the source population is competitive under unstressed conditions, its use as a source of inbred lines will increase the chances of obtaining stress-tolerant hybrids. It is important to reinforce, however, the benefits of screening lines from conventionally-improved populations for tolerance to stresses. Although the frequency of occurrence of stress-tolerant hybrids will be lower when lines are extracted from such populations, it is likely that the performance of these hybrids will be superior under unstressed conditions and when challenged by pests and diseases.

While it may be unusual for source germplasm to be directly released to farmers, it may be effectively used on one side of an intervarietal cross or hybrid in combination with locally-adapted varieties or lines. This is proving to be the main means of utilizing sources possessing above average agronomic performance but lacking in local adaptation.

New developments in molecular techniques have greatly increased the value of sources that possess uniquely high levels of tolerance to stress but inferior agronomic characteristics. These serve as sources of lines for mapping the QTL associated with extreme degrees of tolerance, and using marker-assisted selection it is now possible to move alleles of interest to elite but susceptible lines and populations, with little linkage drag of inferior traits.

Roots

They are without doubt the great unexplored half of the plant, as Bob Loomis has so rightly said. Thus far, indirect measures of rooting capacity, such as electrical capacitance, ability to penetrate wax barriers, canopy temperature and pre-dawn leaf water potential have been used to assess rooting capacity, because of the difficulties of direct observation. Measurement methods, either as seedling measures, but more especially as direct indicators of size, intensity and efficiency of uptake, remain a major challenge and a bottleneck to a better assessment of whole-crop responses to stress. In the meantime, there are reports that suggest that a reduction in rooting intensity, especially near the soil surface, may be accompanied by an increase in ear growth, when water is withdrawn for several weeks around flowering. This suggests that optimal root growth and distribution will depend on the timing and nature of the stress, and that increased root growth in some circumstances may be accompanied by reductions in top growth and grain yield. Much remains to be done in this field, and it is a research area where molecular techniques may prove invaluable for transferring superior rooting traits to elite lines, once those traits are identified.

Statistical Considerations

Stresses reduce mean performance and genetic variance, and although error variance also falls, it does not do so as rapidly, and coefficients of variation and heritabilities tend to fall as stress levels intensify. In general, heritability does not decline disastrously until stress has reduced yields by around 75 to 80%. The use of the coefficient of variation to assess the worth of trials grown under stress conditions is a practice that should be discontinued; rather, researchers should focus be on ways in which error variance can be reduced. Efficient experimental designs are critically important in increasing the efficiency of selection under stress; in fact, the increased selection efficiency resulting from the use of an efficient incomplete block design can be as great as that obtained from the use of secondary traits during selection, and a lot cheaper to implement! Where lines and cultivars are evaluated across environments, the use of analyses such as AMMI and SHMM can further increase our capacity to identify stable high yielding varieties.

Reality Test: Field Performance and Farmer Acceptance

Don Duvick has emphasized the need to ensure that stress tolerant selections are adequately tested in farmers' fields, under typical production conditions. None of the findings reported at this symposium has value if it does not result in improved field performance, and we assert that much of the technology discussed in this volume is now ready for that test. Recently two externally-funded projects with NARS, CIMMYT and IITA in sub-Saharan Africa have commenced operations. These projects, aimed at improving tolerance of locally-adapted germplasm to these stresses, are evidence of our readiness to move from a methods development phase to deployment in order to obtain impact in the fields of resource-poor farmers, particularly in regions characterized by variable rainfall and declining soil fertility levels. Participatory breeding approaches must find a greater use in these research activities. Through these we expect to identify new ways of managing stress that are suited directly to farmers' circumstances. The resulting varieties will (and must) meet the needs of farm families in terms of texture, taste, color, husk cover, resistance to storage insects and diseases, and in the production of non-grain biomass.

Networking

Genotype x environment interactions virtually preclude global networks directed specifically towards improving drought and low N tolerance, even though two of these networks remain in existence. Regional networks addressing tolerance to these stresses were, however, endorsed by participants (Elings et al., 1996), and are being established in sub-Saharan Africa. In other areas (Latin America; Asia) networks that focus on these and other regionally-specific stresses, such as tolerance to acid soil and waterlogging, will be established as funds from donors become available and as regional scientists express their specific need for such networks and volunteer their screening facilities. In the meantime, there is no reason why broadly adapted sources (inbred lines; synthetics; populations; prebreeding populations) cannot be made available on a limited basis to scientists worldwide, nor why global networks cannot continue to serve as a vehicle for distribution of information specific to these stresses.

CIMMYT's Role in Networking and Research

CIMMYT can help facilitate and execute regional testing networks focusing on selection for stress tolerance by coordinating network activities such as trial design, dispatch and reporting; maintenance of genetic diversity for stress tolerance in a regionally-adapted form; mobilizing and managing regionally-focused donor funds for national program support; exchanging information through conferences and visits; and facilitating the exchange of seed among national programs and between private seed companies and national programs. CIMMYT also continues to have an important role in strategic research – in establishing efficient protocols for marker-assisted selection and line conversion, determining the worth of secondary traits, identifying new sources of genetic variation for stress-adaptive traits, developing new source germplasm, and testing new statistical approaches to error control in the field, etc.

The Role of the National Programs

We are in an era of intellectual property rights, reduced government funding to national programs, and the privatization of research, factors which are each restricting the free exchange of valuable germplasm. Networking is greatly enriched by a willingness of national programs to share germplasm and information. Imaginative ways to share information and germplasm are required, without loss of control over critical intellectual property. The crossing of elite germplasm into heterotic germplasm pools that represent the major heterotic responses in the region, for example, can be carried out without releasing inbred lines to a second party, yet the process will expand the range of germplasm available for inbred line development to all participating national programs. Similarly, there is no *a priori* reason why early generation lines cannot be freely shared in a regional testing network. CIMMYT and IITA, as "honest brokers", can do (and are doing) much to facilitate this process and protect the rights of individual national programs, provided IARCs and national programs recognize that they are equal partners in this process.

We can each accomplish a great deal more if we work together than if we work alone. Resource-poor maize farmers of the tropics and subtropics should expect no less.

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