

CENTRO INTERNACIONAL DE MEJORAMIENTO DE MAIZ Y TRIGO

INTERNATIONAL MAIZE AND WHEAT IMPROVEMENT CENTER

México

Lecture Notes

Breeding for Drought Tolerance in Tropical Maize

G.O. Edmeades

El Batan, Mexico

March 8 - April 2, 1993

LECTURE 1

Drought Course Outlines

A. Orientation:

1. Welcome to CIMMYT

1.1 CIMMYT: How is the center structured?

Director General: Dr. D. Winkelmann
Director of Research: Dr. R. Rowe
Director of Administration: Dr. C. Cafati

Programs

Maize (Dr. D. Hess and Dr. R. Wedderburn
Wheat (Dr. R.A. Fischer and Dr. G. Varughese
Economics (Dr. Derek Byerlee and Dr. R. Tripp)

Across-Program Activities

Training (for maize, Drs. W. Villena, F. Palmer, and R. Arias); Ing. Gilberto Hernandez; Liliانا Villasenor
Applied Molecular Biology (Dr. David Hoisington)
Biometrics (J. Crossa)
Information Services (T. Harris; library: E. Hesse)
Natural Resource Management (new section)

1.2 Headquarters and Outreach

About 65% senior staff are located in headquarters
35% senior staff located in Outreach

Outreach:

For Maize, these locations are:

Guatemala (1 agronomist for countries in Central America)
Cali, Colombia (2 breeders for Andean Region and Southern Cone)

Ghana - 1 agronomist, service to that single country
Kenya - 1 agronomist, and two conducting training courses, for eastern Africa

Harare - two breeders and 1 agronomist serving southern and parts of eastern Africa

Bangkok - 2 breeders assisting South Asia and sub-continent

Headquarters:

Programs:

Lowland tropical maize breeding: Head: Dr. S.K. Vasal

Mid-altitude and highland tropical maize:

Head: Dr. M. Bjarnason, assisted by Dr. Kevin Pixley

Stress Unit: Head: Dr. Jim Deutsch, assisted by Dr. David Jewell, Dr. John Mihm and Dr. Dan Jeffers

Physiology and Agronomy: Head: G.O. Edmeades, assisted by Dr. Renee Lafitte, Dr. Hector Barreto, Dr. Scott Chapman, Dr. Marianne Banziger, and Dr. Mohammed Ahmed, with help from Ing. Rafael Alvarado.

Germplasm Bank: Dr. S. Taba

International Testing: G. Srinivasan

1.3 The Maize Physiology Group

- Part of the Stress subprogram

- Principal activities are:

- development of methodologies that speed selection for tolerance to abiotic stresses
- development of source materials that will serve as reservoirs of drought tolerance for interested national programs
- understanding the effects of the environments on development and on yield
- development of calibration data sets so that we can detect useful crop models

- documentation of procedures and results from their use
- training

1.4 Areas of selection for tolerance to abiotic stress tolerance.

- Drought tolerance (40% of total activities)
- Tolerance to low nitrogen (15% total activities)
- Tolerance to general stresses such as plant density (15% total activity)
- Relationship among tolerances to all those stresses

1.5 How do products from this program affect other breeding programs?

- Exchange of information on techniques

- Exchange of elite germplasm as sources
- Intensive selection of elite germplasm from other units for specific lengths of time
- Evaluation of elite products (advanced inbred lines; preliminary evaluation trials)

1.6 How do germplasm products reach national programs?

- International testing system

Description

Types of materials tested

Progenies

Varieties

Preliminary materials (PETS; restricted)

Hybrids

- Special testing networks

1.7 The Drought Network (Introduction)

This is a group of national program collaborators who are committed to the identification and development of drought tolerant maize germplasm. The network provides a means of sharing new information on drought tolerance, and a means of sharing drought tolerant germplasm.

It consists of two types of cooperators:

1) Germplasm testing cooperators, who wish to participate in the testing of products which are thought to have enhanced drought tolerance.

2) Germplasm development cooperators, who have the facilities to handle progenies and lines under drought. Preferably, they have a means of managing drought intensity - such as through the use of irrigation at off-season nurseries, or in dry areas of the country, and have uniform and reasonably large test sites.

The Maize Drought Tolerance Network (MDTN) was established in 1989, and tested 2 variety trials and one progeny trial in 1989-90. The results from the majority of trials were published as a report in June, 1991.

1.8 Objectives of the drought course:

1. To familiarise maize drought tolerance network collaborators with breeding and selection methodologies, measurement and use of secondary traits, and plot management techniques which could be used to develop locally-adapted drought tolerant germplasm.
2. To promote the exchange of germplasm which could serve as a source of drought tolerance.
3. To build a sense of cooperation among national program colleagues.

4. To encourage participants to develop a strategy for improving drought tolerance in the germplasm currently being used within their own country programs.
4. To expose course participants to the wider range of products, techniques and germplasm that CIMMYT has to offer.
5. To collectively develop a strategy for managing the Maize Drought Tolerance Network that will benefit all participants.

1.9 Why should CIMMYT teach such a course?

Drought stress affects some 80 per cent of the maize production area in the tropics. In many of these environments, the effects of drought could be reduced by the selection and utilization of drought tolerant genotypes.

Over the past 15 years, CIMMYT has developed drought-tolerant varieties by performing selection for grain yield and correlated traits under carefully managed drought stress. During that time CIMMYT scientists have evaluated the specific value of a number of secondary traits. As well, methods for managing drought stress have been evolved, and methods of selection using primary and secondary traits have been developed. The analysis of progress made under selection has also given us a good understanding of the physiological basis of improved tolerance to drought stress.

Drought-tolerant varieties produced from CIMMYT's research are being used directly and indirectly by scientists from many national programs (over 120 seed lots have been shipped to 21 countries over the past 2 years). They are designed as source germplasm for use in breeding programs, rather than as varieties suitable for direct release. Because of this, further breeding for location-specific grain colour and type, and for disease resistances, may be needed before these can be released for direct use by farmers.

CIMMYT scientists will use this course to share their experiences in this type of research and their germplasm sources with course participants.

CIMMYT expects to learn from participants how it can better serve their needs in this important area.

1.10 Drought course outline (copies provided)

1.10.1 Drought and the maize plant

- 1) Definition and extent of drought, and its global importance to the maize crop (1 session)

- 2) Defining the target environment; risk
- 3) Soil factors in determining drought
- 4) The path of water through soil to plant and on to atmosphere; the concept of water potentials
- 5) Selection of germplasm, selection of progeny and evaluation of progress from the Tuxpeno Sequia study.
- 6) Stress-sensitive stages in the life of the maize plant
- 7) A drought tolerant ideotype for maize
- 8) Management options to manage water stress
- 9) Relationships between drought stress and other stresses

1.10.2 Breeding methodology

- 1) Basic genetics; sample size; genetics of drought tolerance
- 2) Theory of use of secondary traits
- 3) Choice of selection environment
- 4) Choice of breeding materials
- 5) Seed number, plot size and bordering
- 6) Experimental designs to control within-site variability; use of unreplicated nurseries
- 7) Choice of breeding methodology; incorporation of source germplasm into national breeding program activities.
- 8) Use of selection indices
- 9) Formation of source populations; example DTP1 and DTP2
- 10) Use of RFLPs and other molecular techniques to speed the breeding

1.10.3 Additional skills

- 1) Basic personal computer operations; use of programs ALPHAGEN; LATANOVA; the Selection Assistant
- 2) Measurement of soil and plant water potentials and stress levels

1.10.4 The Maize Drought Tolerance Network

- 1) What it is, its goals, and how we can organise it more effectively

1.10.5 Project work:

An assessment of the drought risk facing maize producers in home countries (need access to weather databases from trainees' countries); a proposed breeding strategy in which drought tolerance could be introduced into their on-going breeding programs. This will include considerations of the overall resources enjoyed by the specific national program; choice of germplasm; testing sites; utilization of drought tolerant cultivars when they have been identified or developed.

1.10.6 Field work:

- 1) Introduction to CIMMYT's drought tolerant germplasm
- 2) Ways of managing drought and their consequences
- 3) The assessment of secondary traits (ASI; leaf uprightnes; canopy temperature; senescence; tassel size;
- 4) Harvest procedures; shelled grain

Additional Reading placed on Reference:

1. CIMMYT, 1992. The CIMMYT Annual Report, 1991
2. Edmeades, G.O., D.L. Beck, and L. Martinez. 1991. The Drought Network Report, 1991

Drought Course Outlines

Lecture 2: Definition and extent of drought

(Prepare slides for this talk of symptoms as introduction)

1. Drought in various forms (slides)

Key periods (sensitivity of different periods will be discussed later). However:

- Establishment
- Flowering
- Grain filling

2. The target environment:

Show patterns of rainfall distribution, from the Cairo paper; point out the general types of distributions (slides)

Our target environment is usually one in which there is an uncertain start to the rains, followed by an increase in the probability of a certain amount of rain, followed by a relatively uncertain cessation date of the rains. Note that mean rainfall figures are only one guide to the adequacy of rain. If we have a dry spell around flowering, when maize is unusually susceptible to drought, it can greatly reduce yield without substantially reducing mean rainfall.

A common feature of drier tropical environments is high variability, both in seasonal totals and in rain fall distribution throughout the season. See the 75% probability figure for rainfall from the Ghana data, and the rainfall range bars. The intensity of drought also varies with soil depth and soil water holding capacity. Thus it seems that the *probability* of obtaining a given pattern of moisture stress is perhaps more useful than mean rainfall received in defining a target breeding environment. We need mean rainfall, variability of start and finish of rains (e.g. range of dates), and the probability of dry spells at various points throughout the rainy season.

Cumulative probabilities of yield in any one location (slide), predicted from crop models, highlight the potential of crop models in helping define the nature of the target environment. We will look more carefully at how appropriate our selection environment is when we come to consider genotype x environment effects.

3. The global importance of drought in tropical maize

Assembling the ME Database (1985-7)

1. Data are qualitative (guesstimates)

2. For drought there were four classes of response:

| | <u>Class</u> | <u>Est yld loss</u> |
|---------------------|--------------|---------------------|
| Rarely stressed | 1 | 5% |
| Sometimes stressed | 2 | 10% |
| Frequently stressed | 3 | 25% |
| Usually stressed | 4 | 40% |

Percentage Yield Losses due to Drought

- includes only southern China

- **By germplasm type**

| | ha ('000) | % loss | tons lost ('000) |
|-------------------------|------------------------------|---------------|-------------------------------------|
| Highland tropical | 3273 | 28 | 2199 |
| Transition zone | 2301 | 7 | 435 |
| Sub-tropical | 16632 | 15 | 7734 |
| Lowland tropical | 32720 | 15 | 8834 |
| Temperate | 5186 | 23 | 4890 |
| Developing world | 60561 | 17 | 24092 |

Percentage Yield Losses due to Drought

- includes only southern China

- **By Region**

| | ha ('000) | % loss |
|-----------------|------------------------------|---------------|
| South America | 17564 | 20 |
| Central America | 9089 | 15 |

| | | |
|-------------------------|--------------|-----------|
| West Asia/N. Africa | 2082 | 17 |
| West/C. Africa | 4366 | 12 |
| E & S Africa | 10953 | 13 |
| Asian subcont. | 7811 | 16 |
| E & SE Asia | 8786 | 14 |
| <hr/> | | |
| Developing world | 60561 | 17 |

Percentage Yield Losses due to Drought

- includes only southern China

- **By maturity class**

| | ha ('000) | % loss |
|-------------------------|------------------------------|---------------|
| Early | 15226 | 22 |
| Intermediate | 21421 | 13 |
| Late | 22437 | 15 |
| <hr/> | | |
| Developing world | 60561 | 17 |

Potential returns from drought related-research: E & S Africa

1. Assume that 20% of the yield loss due to drought is recoverable by selection within adapted germplasm
2. Regional production 13.6 m tons/year, av. yield 1.4 t/ha
3. About 13% of yield (or 1.78 m tons) lost annually to drought
4. Improved performance due to increased drought tolerance may equal 20% of 1.78m tons, or 356,000 tons/year,

worth about \$35 m annually

> > **CIMMYT's entire annual budget**

4. Escape, avoidance and tolerance - Levitt's definitions

Note that the full array of these types of responses are seen only when we survey a full array of species, from desert ephemerals and cacti to tropical rain forest species. We are going to define our discussion of mechanisms here to a much narrower range, those which are seen in the maize crop.

4.1 Escape:

Other species: only discuss it here; various mechanisms: - hard seed; delayed germination

- Earliness

Selecting for early maturing germplasm is an important means of increasing the reliability of production under drought caused by the shortness of the rainy season. (Note in particular the minor rainy season in Ghana)

It is important that the phenology of the crop matches the pattern of rainfall, but there are limits to how much this can be done in maize. As a rule of thumb, we consider that in the lowland tropics the limit of successful maize production is about 400-500mm of seasonal rainfall; in the midaltitude areas 350-450mm; and in the highlands 300-400mm; the decline in these numbers with increasing altitude reflects declining losses from evaporation because of lower mean temperatures at higher elevations. In sandy soils these figures are larger; in heavy clay soils figures are lower.

We should not confuse earliness with drought tolerance. Early germplasm, such as Katumani Composite, Makueni, Mata Hambre, Guajira 314, and others are relatively stable under drought, but principally because they miss the drought altogether

There is a price to be paid for early maturity, in loss of yield potential. Early flowering cultivars generally have fewer leaves, and a lower leaf area index. They often intercept a smaller proportion of radiation during the active growing season, and they intercept radiation for a shorter period.

We can define grain yield simply as: $\text{Grain yield} = [\text{radiation received} * \% \text{ incident radiation intercepted} * \text{number of days radiation is intercepted} * \text{radiation use efficiency} * \text{harvest index}]$.

Thus there is a general positive association between days to maturity and grain yield in maize and in many other species. Thus, in good seasons when the rains are longer than usual, a later maturing cultivar will normally outyield early maturing types. A better strategy therefore may be to use a later duration cultivar that was more stable under drought stress than the early maturing type. In dry conditions, this cultivar would yield as much as the early maturing "escaper", but in wet conditions, its greater yield potential would be

expressed. While this strategy actually increases the variability in grain production over time, it allows for a marketable grain surplus in good years.

When rains are highly variable at all points in the season, the later maturing type can also recover better, simply because physiologically "younger" plants retain this capacity to a greater degree.

Early maturing cultivars may also generally have a lower root length density and a shallower rooting depth. However, when the ratio of leaf area to root length was computed for sorghums of varying maturity, it was found that early types had a lower ratio than late types, suggesting that the ratio of water gathering capacity to water loss capacity (like a source:sink ratio) was higher in earlies, allowing them perhaps to maintain a higher leaf water potential at a given soil moisture potential (Blum, 1988).

We will be talking more about the need to fit cultivars better to the growing season as the course proceeds.

Where drought cannot be escaped:

A useful thought framework for thinking about drought in water-limited environments (Passioura, 1977; Ludlow and Muchow, 1990):

Consider that Grain yield = Amount of water transpired * Water use efficiency * Harvest index

or: $GY = W * WUE * HI$

- Amount of water transpired: affected by:

- Soil depth (shallow versus deep; shallow rooting versus deep rooting)
- Soil texture (amount of available water)
- Rainfall (net input; losses through runoff)
- Irrigation input
- Loss of water by weeds (losses in amount available fro the crop to transpire; can be dry season losses from weeds too)
- Loss of water by evaporation from soil surface (need for full ground cover as soon as posible). 20-25% total water lost by evaporation on a tropical alfisol in a typical maize-type rainy season, up to 30-60% on a Mediterranean type climate; mulches and management options
- Timing of water use to ensure that water is still available at drought-sensitive growth stages.

We would like the crop to exhaust all the water available by the end of the season, though this is a high risk procedure, simply because in a drier year when evaporative and transpirational demand by the crop is high, the crop may run out of water before we can get it to maturity (see our discussion on escape)

Research has generally shown (Tanner and Sinclair, 1983) that biomass production is linearly related to cumulative transpiration, that is biomass = water transpired x water use efficiency.

-Water Use Efficiency

Defined here as shoot biomass produced/amount of transpired water.

Water use efficiency is inversely proportional to vapor pressure deficit (VPD), that is the capacity of the atmosphere to absorb water. (Show the curve of absolute humidity versus temperature - do we have it?). The higher the temperature of the air, the more water vapor it can absorb, and the higher the VPD. Water use efficiencies are generally higher for C4 species than for C3 species. Note that apparent differences in WUE may reflect differences in chemical composition of the biomass, and also differences in soil evaporation. New data (from C12/C13 discrimination studies) have shown that small but significant differences in WUE exist within species.

At the whole crop level, WUE appears insensitive to drought, soil fertility and salinity. Some variation in WUE may be due to variation in respiration rate.

- Harvest Index

Ratio of economic yield to shoot biomass at maturity

Severe stress at flowering can drastically reduce harvest index in maize (See Robins and Domingo, 1953; find other refs). We will see much more of this in subsequent discussions.

-Survival versus production

In general we are interested in production rather than survival. Survival mechanisms are of interest only when they allow the plant to defer death, or loss of leaves, etc, so that it can survive through a difficult drought event, and to later resume production.

We defined grain yield as: $\{\text{Integral of } [\text{Radiation} * \% \text{ RI} * \text{RUE}] \text{ over time}\} * \text{HI}$. If survival mechanisms result in a reduction in % RI, or in RUE, or in HI, then production will be sacrificed.

The importance of survival versus production strategies depends very much on the timing of the stress. In general, the earlier the stress in the life of the plant, the more important are survival mechanisms. Where stress occurs late in the life of the crop (a terminal stress), there is little point in the plant having the capacity to survive, since its genetically programmed senescence pattern will automatically cause its demise.

If the crop is not going to escape drought it must either try to avoid experiencing tissue desiccation, or it must manage to tolerate it.

4.3 Drought avoidance:

These mechanisms basically allow the plant to maintain its turgor and tissue volume, and thus protect its tissues from stress.

- > Matching phenology with rainfall to ensure that sensitive periods do not coincide with times with a high probability of drought. Plants may use photoperiod responses to position the stress-sensitive reproductive period of the crop at the time when rainfall is the most reliable. (slide of photoperiod response in maize). The responsiveness of tropical germplasm to photoperiod can be an important consideration for those who work at latitudes greater than 25 degrees, where days may exceed 14 h during the photosensitive period of crop growth. Thus an early flowering type in a short day environment may well become a late flowering type in an environment with long days. A late flowering response (driven by photoperiod) could be useful where stress occurs early in the crop season. In general however, in today's agriculture, photoperiod responsiveness limits broad adaptation.

Developmental plasticity: found in some species especially indeterminate and tillering types, but very little in maize.

- > Remobilization of preanthesis biomass: relatively limited in maize, especially at flowering. Larger during grain filling.
- > Shortened anthesis-silking interval in maize as an indicator of more rapid ear growth. Another indicator of a successful change in partitioning resulting in an increase in harvest index, is an increase in ears per plant.
- > Loss of active leaf area and the regrowth of leaves when drought is lifted

-> **Maintenance of water uptake:**

- Osmotic adjustment; definition: the active accumulation of solutes within the cell. Through increased turgor, helps roots grow into dry soil, helps the tops "suck" more strongly, maintains active leaf area. Does not affect WUE. Increases or maintains harvest index. Risk that it may be associated with reduced yields because adjustment may reflect increase in concentration of solutes simply because growth is slowed. The underlying mechanism behind "hardening". Shown to occur especially in root tips. Maintenance of active leaf area may lead to increased water usage and sometimes more rapid tissue death. Important trait in intermittent stress conditions as it -> stable yields

- Depth of rooting, density of rooting. Are deep roots really needed to extract water? Root length density of 1 sufficient for water, but 5 needed for phosphorous (see Nottingham Easter School notes by Gregory).

- > Heat tolerance of seedlings

-> **Reduction of water loss:**

- Stomatal control; stomatal conductance. It is unlikely that stomatal conductance has a major role in regulating water usage from a crop which is planted at normal densities **unless** the stomates are almost closed. This is because the rate of water loss is determined by the crop boundary layer, rather than the leaf boundary layer. Where the planting density is low, or plants are erratically spaced, or the VPD is very high, then stomatal

conductance can conceivably play an important role. Stomatal control may play a more important role in maintaining internal [CO₂] than in regulating water loss in many canopies. Stomatal conductance, hence water use, may be a useful measure of the capacity of leaves to carboxylate. Triggered by root signals, and the vector is probably ABA. Production generally lowered.

- radiation shedding: rolling of leaves: function of the presence of bulliform cells on the leaf under surface, which permit the leaf to roll. Varies among maize genotypes. Little use if it occurs after the stomates are already closed. Production lowered. Where leaves senesce there is no regreening, so there is a severe loss of production. Other leaf movements: minimal in maize; become more erect when they roll; do not follow the sun.

- upright leaves reduce radiation load and increase radiation use efficiency. A form of radiation shedding with little productivity cost.

- waxy cuticle: waterproofs the leaf. Variation in leaf waxes in maize nowhere near as large as in wheat (bluish bloom) or sorghum and millets. Production maintained.

- low hydraulic conductance: tends to lower production if it leads to a reduction in stomatal aperture

- leaf reflectance: = radiation shedding; production cost

4.4 Desiccation tolerance:

- > Low lethal water status: the relative water content at which a leaf dies. Varies from -3Mpa in sorghum and millet to -13 Mpa in some forage grasses. It does not reflect the RWC or water potential at which stomates close, or that at which photosynthesis or respiration cease, therefore has little relationship with production.
- > Low water status at which essential metabolic processes, such as photosynthesis and respiration cease. Variation may be as much as 0.3 Mpa in maize.

Reading for Lecture 2

- *Bidinger, F.R., and J.R. Witcombe. 1989. Evaluation of specific drought avoidance traits and selection criteria for improvement of drought resistnace. p. 151-164. In: F.W. G. baker (ed.) Drought Resistance in Cereals. CABI, Wallingford.
 - *Blum, A. 1988. Plant Breeding for Stress Environments. CRC Press, Boca Raton, Florida
 - Grant, R.F., Jackson, B.S., Kiniry, J.R. and Arkin, G.F., 1989. Water deficit timing effects on yield components in maize. Agron J., 81:61-65.
 - *Ludlow, M.M. and Muchow, R.C., 1990. A critical evaluation of traits for improving crop yields in water-limited environments. Adv. Agron., 43:107-153.
 - Robins, J.S., and C.E. Domingo. 1953. Some effects of severe soil moisture deficits at specific growth stages in corn. Agron. J. 45:618-621.
 - *Tanner, C.B., and T.R. Sinclair. 1983. Efficient water use in crop production: Research or Re-search? p. 1-28. In: H.M. Taylor, W.R. Jordan, and T.R. Sinclair (eds). Limitations to Efficient Water Use in Crop Production. American Society of Agronomy, Madison, Wisconsin.
- * On reference in library

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Kenya - 1 agronomist, and two conducting training courses, for eastern Africa
Harare - two breeders and 1 agronomist serving southern and parts of eastern Africa

1. Choice of germplasm

- 1973 Data from rainfed sites of Experimental Variety Trials were used to identify a population with a high and stable yield. Only data from rainfed sites were used.
- Mean yield was significantly correlated (0.74*) with rainfall during the growing season
- Data were analysed using the Finlay-Wilkinson stability analysis (like the Eberhart-Russell analysis), and for similarity of response using a clustering technique.
- The race Tuxpeno had a slope of less than 1 and a higher than average mean yield across all sites.

Trial of 8 genotypes in Tlaltizapan

-> Normal irrigation

Irrigation withdrawn

-> At ear initiation (about 40 days after planting, and about 45 days before flowering)

-> At 10 days before flowering.

Tuxpeno was found to have a high drought tolerance index.

This index is:

Tuxpeno yield under drought
Tuxpeno yield under irrigation

Divided by:

Yield of all entries under drought
Yield of all entries under irrigation

(slide)

(slide)

Yield under non-stress:

- > Correlated with the drought susceptibility index ($r=0.76^*$), suggesting that selection simply for grain yield under non-stressed conditions might be sufficient for improving drought tolerance.
- > Two morphological traits were studied also:
 - ASI was correlated with the drought index (-.66*)
 - Stem elongation was correlated with the drought index (0.84*)

As a result, C₁₁ of Tuxpeno Crema I was selected for study under drought.

In the first cycle 85 full-sib families were grown under three water regimes:

- a) Well-irrigated control (WW, or RN))
- b) Mild flowering and severe grainfilling stress: or an intermediate stress, in which water was withdrawn about 14 d before flowering (IS)
- c) Severe flowering and grain filling stress, in which water was withdrawn about 40 days after planting (45 days before flowering) and not applied again. (SS)

Selection criteria:

- 1) Relative leaf and stem elongation rate (RLE)
- 2) ASI
- 3) Rate of leaf senescence
- 4) Shelled grain yield under WW, IS and SS conditions

- > Criteria were used as the basis for selecting groups of 10 best or 10 worst full-sib families from among the group of 85.
- > Where more than one characters was used during selection a selection index was used to decide which families were the desirable ones.
- > Data showed a significant water stress level * family interaction.
- > Experimental varieties were then retested under the same conditions:

Issues in the Tuxpeno Sequia study

1. What were the critical findings from this long-term selection experiment?
2. What were the useful secondary traits?
3. How successful was selection in a dry winter season in addressing main season problems?
4. Selecting at managed stress environments gave larger genetic gains at international sites than did selection based on international testing Why?

Reading for Lectures 3 & 4

- *Bolaños, J., and G.O. Edmeades. 1988. CIMMYT's strategies in breeding for drought tolerance in tropical maize. p752-54. In: P.W. Unger, W.R. Jordan, T.V. Sneed, and R.W. Jensen (eds). Challenges in dryland agriculture - a global perspective. Proceedings of the International Conference on Dryland Farming, Aug. 15-19, 1988, Amarillo/Bushland, Texas. Texas Agric. Expt. Stn., College Station, Texas.
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Lecture 5 Outline

In preparation for our visit to the field tomorrow I would like to introduce other aspects of our activities in drought in maize. I would like to consider two major areas this morning:

A: Introduction to remainder of CIMMYT's drought breeding program (will become clearer in field)

and

B: Ideotypes for drought tolerance: Choice of secondary traits and establishing the value of secondary traits

A: CIMMYT's approach to drought improvement

1. Short term approach versus long-term approach:

Short term approach:

Based on the principle of Blum (1983) which states:

"That in many elite populations and groups of varieties there exist drought-adaptive genes at low frequencies"

A careful selection procedure aimed at identifying those genes and increasing their frequency should result in reasonable levels of drought tolerance in elite germplasm. One example: Tuxpeno Sequia that we began describing yesterday afternoon.

This approach, in which selection pressure is deliberately high, should yield good results in short period of time, but genetic variability may also be quite quickly exhausted, and gains may not continue for long. The idea is to exploit the variability as quickly as possible, then move on to another population.

In this approach we have concentrated on the following elite populations:

1. La Posta Sequia, late white lowland tropical dent (matures in about 120 days), comes from a synthetic of 11 lines made up from the lowland tropical race, Tuxpeno. Carries reasonable levels of maize streak virus resistance, is about the number of days to flower as Tuxpeno Sequia, but is slightly later to harvest, and often yields 5-8% more grain. Suitable for West Africa, southern Africa, central America. Started with selection in 1986A in Tlaltizapan. Now in its 4th cycle of selection.

2. Pool 26 Sequia, late yellow lowland tropical dent, broad based in its composition, suitable for Brazil and for lower parts of the Andean region. Quite good levels of resistance to lowland diseases. May have some role in South Asia.

Somewhat limited in its applications. Started selection in 1986A in Tlaltizapan. Completed three cycles and discontinued.

3. Pool 18 Sequia: an early lowland tropical yellow dent/flint population, matures in about 90 days, suitable to parts of Asia. Reasonable resistance to lowland diseases. Dent or flint could be extracted from the population. Started selection in Obregon in 1986. Completed 3 cycles of selection, will probably be continued..

4. TS6: Tuxpeno Sequia C6: Late white lowland tropical dent. We have carried it forward as a separate population. It will be improved in the future in collaboration with Central American programs, in which CIMMYT tests it under two levels of drought in Tlaltizapan, and collaborators test it under two drought levels in Central America. It will be recombined on basis of across-site performance.

5. Zm601: This population is a cross of population 92 (from E & S Africa) and population 43, and carries some streak resistance. Late white sub-tropical dent. This is being improved jointly between CIMMYT Zimbabwe and CIMMYT Mexico. Now in its second cycle of testing.

Summarised characteristics of populations under improvement

Elite populations

| Ecology | Grain Type | Maturity (days,LT) | Breeding scheme | Cycles completed | Disease (R) or (S) |
|---------------------------------------|------------|--------------------|-------------------------------|------------------|---|
| <u>La Posta Sequia</u> | | | | | |
| LT | WD | 120 | Rec. S1 2 stage | 3.2 | Streak (R) H. maydis (R) Earots (PR) D. mildew (S) |
| <u>Pool 26 Sequia</u> | | | | | |
| LT | YD | 116 | Rec. S1 2 stage | 3 | H. maydis (R) Ear rots (R) Streak (S) D. mildew (S) |
| <u>Pool 18 Sequia</u> | | | | | |
| LT | YD/F | 90 | Rec. S1 2 stage | 3 | H. maydis (R) Earots (R) Streak (S) D. mildew (S) |
| <u>Pool 16 Sequia</u> | | | | | |
| LT | WD | 95 | FS/S1 2 stage 2 locs | 2 | Streak (R) Earots (R) D. mildew (S) |
| <u>Tuxpeno Sequia C6 (TS6)</u> | | | | | |
| LT | WD | 115 | Rec. S1 2 stage 2 locs? | 2.5 | H. maydis (R) Earots (PR) Streak (S) D. mildew (S) |
| <u>Zm601</u> | | | | | |
| MAT/ST | WD | 120 | Rec. S1 2 stage 2 locs | 1.5 | E. turcicum (R) P. sorghi (R) Streak (PR) Earots (PR) D. mildew (S) |

Breeding schemes: example: La Posta Sequia, Pool 26 Sequia;**(Also applies to Pool 18 Sequia, TS6 and Zm601)**

| Season | Station | Form S1s | Screen | Replicated Trial | Recombination |
|-----------------|----------------|-----------------|---------------|-------------------------|----------------------|
| Cycle 0: | | | | | |
| 85B | PR | 167 | | | |
| 86A | TL | - | - | 167-250 | |
| 86B | PR | - | - | - | 50 |
| Cycle 1: | | | | | |
| 87A | PR | 1000 | | | |
| 87B | OB | | 1000 | | |
| 88A | TL | - | - | 222 | |
| 88B | PR | - | - | - | 50 |
| Cycle 2: | | | | | |
| 89A | PR | 1000 | | | |
| 89B | OB | | 1000 | | |
| 90A | TL | - | - | 222 | |
| 90B | PR | - | - | - | 50 |
| Cycle 3: | | | | | |
| 91A | PR | 600 | | | |
| 91B | OB | | 600 | | |
| 92A | TL | - | - | 222 | |
| 92B | PR | - | - | - | 50 |
| Cycle 4: | | | | | |
| 93A | PR | 600 | | | |

Numbers vary especially in the initial screen, from 600-1500, but the replicated yield trial has almost always between 222-225 entries in 2 replications with 3 moisture stress levels, as described before.

A white dent early maturing population, Pool 16 Sequia, was improved also in conjunction with Dr. Diallo in West Africa, in Cycle 1 by full-sibs and in Cycle 2 by S1s. It was handed back to the Early Germplasm Development Unit after two cycles. This unit has also improved drought tolerance in many of their routine breeding programs, largely by testing these early and intermediate maturing materials under drought in Obregon and Tlaltizapan, often using plant density to amplify the effects of drought (look in Dave Back's terminal report)

Longer-term approaches to improved drought tolerance

Here we seek to develop populations which are composed of sources of tolerance to drought. This has entailed a screening of sources from:

- 1) Landrace collections in the Germplasm Bank
- 2) Elite selections from other programs with reputed drought tolerance
- 3) Elite selections from CIMMYT's own program with known drought tolerance

This will be a topic considered in considerably more detail in a later lecture and will not be considered in detail here. The first screen used about 15% germplasm directly traceable to a landrace collection; this led to the formation of DTP1; the second series of screens, far more thoroughly done, led to the formation of a new population, DTP2. DTP is in the process of its second cycle of improvement under drought via international testing. DTP2 has just entered the phase of S1 formation.

In summary: the long-term approach seeks to:

- 1) identify sources of variability for drought tolerance - a variety of traits if possible.
- 2) Recombine these to form a repository of genetic variability which national programs can use
- 3) Improve this population for agronomic traits
- 4) Test it internationally to improve its drought tolerance and to expose these materials to national programs.

Because of the increased level of genetic variability present in the population, we are assuming that greater gains can be made over time for a variety of traits.

Reminder about genetic variability: statistically it can be caused by a large proportion of low values of desirable traits, that is, rubbish, in the population.

This then is the summary of germplasm in process of improvement for drought tolerance at present. Evaluations of progress are underway, and we will review these in the field and in the class as time permits.

Long-term Source Populations

| Ecology | Grain Type | Maturity (days,LT) | Breeding scheme | Cycles completed | Disease (R) or (S) |
|--------------------|-------------------|---------------------------|---|-------------------------|--|
| <u>DTP1</u> | | | | | |
| LT/ST | Mixed | 110 | 4 HS/Rec.S1 2 stage Intern'l | 1.5 | D. mildew (PR) P. sorghi (PR) Streak (S) Earots (PR) |
| <u>DTP2</u> | | | | | |
| ST/LT | Mixed | 112 | 3HS/R 2 stage Intern'l | 0.5 | D. mildew (PR) P. sorghi (LPR) Streak (S) Earots (PR) |

Characteristics of drought tolerant ideotype of maize

1. Maturity (escape):

Objective: to fit available season length as well as possible; to provide stable yields in low rainfall periods because of drought tolerance, yet be of sufficient duration to exploit good rainfall conditions when they occur.

Direct measurement: flowering: simple; physiological maturity more difficult. Measurement of season length depends on historical data, not very precise. Could be grain moisture or black layer formation.

Indirect Measurement: brown husk stage; leaf senescence

Information available: considerable

Genetic variability: considerable

Heritability: High

Prospects for breeding: High, but should not be confused with drought tolerance.

2. Developmental plasticity (avoidance)

Objective: to allow the cultivar to suspend development under stress, and then resume with compensation when rain arrives. Maize carrying the *latente* characteristic is supposed to be able to do this, and sorghum shows some capacity to do this also.

Direct measurement: could be done through measurement of times to specific events, such as leaf appearance, flowering dates, etc. Not to be confused with silking delay, which shows no compensation when restarted. Difficult to identify.

Indirect Measurement: ?

Information available: for maize, almost none.

Genetic variability: *Latente*? perhaps none at all

Heritability: ?

Prospects for breeding: Low

3. Root morphology (deep or intensive roots) (avoidance)

Objective: to extract a greater volume of water, either by exploring the soil more thoroughly, or by extracting water from a greater depth.

Direct measurement: observations of root distribution; harvesting of roots; very tedious; not possible on a scale required for breeding purposes

Indirect Measurement: biomass; water extraction patterns; predawn water potential; canopy temperature; timing of leaf rolling; rate of leaf death; rate of leaf and stem elongation; root vertical pulling resistance

Information available: little in a quantitative sense

Genetic variability: considerable

Heritability: moderate (O'Toole's review paper)

Prospects for breeding: Low/moderate

4. Root hydraulic conductivity (avoidance)

Objective: to slow the extraction of water from the soil so that more is conserved for later more critical times (e.g., slowing early water uptake to conserve water for flowering)

Direct measurement: observations of root xylem diameter; not possible on a scale required for breeding purposes

Indirect Measurement: water extraction patterns; slow rate of canopy expansion and early leaf rolling; predawn water potential; canopy temperature

Information available: little

Genetic variability: ? Some information for wheat

Heritability: moderate (Passioura and Richard's selection experiment with wheat)

Prospects for breeding: Low

5. Waxy leaf cuticle (avoidance)

Objective: to protect against loss of water by evaporation from leaf surfaces; to increase ratio of water loss through stomata (linked to CO₂ exchange) to water loss through cuticle.

Direct measurement: colorimetric measurement possible; score on waxy bloom

Indirect Measurement: biomass; water extraction patterns

Information available: ? some for wheat, sorghum and millets

Genetic variability: small in maize; large in sorghum and millets

Heritability: ?

Prospects for breeding: Low

6. Leaf angle (increases water use efficiency)

Objective: to reduce the intensity of radiation striking the leaf; to move down the light response curve for photosynthesis to where PHS is most efficient while keeping evaporation from leaf surfaces to a minimum. Detractions are that evaporation from soil surface is higher since more light strikes ground, and complete ground cover comes more slowly. Where a mulch covers the ground this may not be a problem.

Direct measurement: measurement (slow); simulation (slow); visual scoring (fast)

Indirect Measurement: not required

Information available: adequate, though not directly related to water use efficiency.

Genetic variability: large in maize

Heritability: high

Prospects for breeding: good

7. Leaf rolling (avoidance through radiation shedding)

Objective: to reduce radiation load on the leaf by avoiding the load, thereby reducing water usage and increases in canopy temperature. Such increases in temperature, decline in leaf water potential and high radiation load lead to photooxidation and loss of chlorophyll. Problem is if rolling merely identifies plants with a low water potential, or plants with a different capacity to respond to a given water potential. Cost of this trait: radiation not intercepted, biomass reduced. Good for intermittent early drought. Often not observed in post-flowering plants.

Direct measurement: visual score of rolling at the time of the day when symptoms are best observed.

Indirect Measurement: water extraction patterns

Information available: adequate

Genetic variability: large in maize

Heritability: relatively high

8. Photo-oxidation; chlorophyll destruction (desiccation tolerance)

Objective: under conditions of moisture stress and high radiation load, chlorophyll is destroyed essentially by damage to Photosystem II and the release of free radicals into the chloroplast.

Direct measurement: since maize does not recover by re-greening dead leaves, it is a very hard trait to measure except through detailed physiological measurements (photosynthesis, respiration; uncoupled respiration). Use of darkened leaf fluorescence output - the loss of light in a very short period following illuminance with a monotonic light source following darkening- indicates the degree of damage done by drought to the photosynthetic apparatus. The so called Fv/Fr ratio (variable fluorescence / fluorescence ratio) is used in this case. Relatively fast to measure in field. Some units no longer require that the leaf be predarkened. (See Selmani's thesis and Guei's recent paper). Other ways are to score directly for leaf bleaching.

Indirect Measurement: biomass production

Information available: reasonably adequate for greenhouse grown plants; less so for field conditions

Genetic variability: reasonable

Heritability: estimates are from.. to..

Prospects for breeding: reasonable

9. Rate of leaf senescence: (desiccation tolerance)

Objective: To delay the loss of active leaf area, since maize cannot restore leaf area once it is lost. This will depend upon the genetic program for senescence in the plant. Measurements should be adjusted for flowering dates by covariance adjustments. May be antagonistic to increased ear size under dry soils, since increased ear size increases demand for nitrogen, and in dry soils N will not easily move to the roots.

Direct measurement: visual score of proportion of total leaf area which is dead (fast); measurement of chlorophyll concentration using a photometer (quite fast); count of green leaves below the ear (slower);

Indirect Measurement: generally not needed; slight increases in biomass; maintenance of weight per kernel.

Information available: adequate

Genetic variability: quite large, but affected by ear size, flowering date and soil variation

Heritability: moderate-low

Prospects for breeding: reasonable; trait has inherent value, but negative correlation with sink size may be a problem.

10. Osmotic adjustment (avoidance)

Objective: increased turgor, helps roots grow into dry soil, helps the tops "suck" more strongly, helps maintain active leaf area. Increases or maintains harvest index. Risk that it may be associated with reduced yields because adjustment may reflect increase in concentration of solutes simply because growth is slowed. Maintenance of active leaf area and root growth may lead to increased water usage and sometimes more rapid tissue death when water runs out. Important trait in intermittent stress conditions. May carry a slight yield penalty.

Direct measurement: possible with bulk samples of leaf tissue, extraction of leaf sap and direct measurement, about 30 samples per hour/machine.

Indirect Measurement: high osmotic adjustment associated with increased water extraction; increased rates of leaf and stem growth under drought; delayed rate of leaf death (initially), cool leaf temperatures, continuing growth, reduced ASI, high weight per grain; slight increases in biomass.

Information available: adequate

Genetic variability: from 0-0.4Mpa in maize (up to 1.1 Mpa in sorghum)

Heritability: relatively high (realized about 0.46)

Prospects for breeding: reasonable; trait has less value in maize than in other spp.

11. Stomatal control (avoidance)

Objective: to prevent loss of moisture from stomates by selecting lines which have stomates partially closed; to select for stomatal sensitivity so plants could quickly sense when water is running out. A debatable trait. For terminal stress stomatal insensitivity is required, since this will use all available water and fix the maximum amount of carbon. For intermittent stress (more common in maize) sensitive stomates will conserve moisture, maintain turgor, but will reduce carbon fixation during closure and will allow the leaf temperature to rise. Does leaf stomatal conductance bear much relationship to resistance to water loss by the whole canopy which is determined by the canopy boundary layer?? Also involves heat tolerance, since leaves with closed stomates get very hot (up to 5°C hotter than the surrounding air).

Direct measurement: stomatal conductance: relatively slow to measure, varies greatly during the day and with the radiation load of individual leaves.

Indirect Measurement: canopy temperature; leaf rolling score;

Information available: good

Genetic variability: ?

Heritability: ? Probably relatively high, especially for conductance under well-watered conditions which may relate more to potential productivity than anything else.

Prospects for breeding: ? Poor

12. Germination at low soil water potential (desiccation tolerance/avoidance)

Objective: To obtain complete and uniform establishment even when rains fail. This will be done by rapid root development, high root/shoot ratio, osmotic adjustment, and high tolerance to desiccation in tissues. Also includes heat tolerance, since dry soil surface is often at about 50°C.

Direct measurement: grow seedlings in soil under a gradient of moisture and observe.

Indirect Measurement: laboratory measures of germinability against an osmotic gradient provided by salt or by large molecular weight mannitol. Often direct damage of the osmotica on the seedling is suspected. Relationship with field performance poor (Cuany thesis).

Information available: reasonable

Genetic variability: ?

Heritability: ?

Prospects for breeding: moderate?

13. Changes in hormone levels (avoidance)

Objective: The hormone abscisic acid has many and varied effects on the plant, but it is now considered to be one of the messengers which transmit root signals to the plant shoot which results in a closure to stomates (without the usual reduction in leaf water potential). *Latente* maize accumulates considerable ABA in its leaf tissues when droughted, and rolls in a marked fashion. Is high [ABA] good, or is it bad? In intermittent drought high ABA may be good - tides plant over till next rains. In terminal drought situations, high ABA may be bad since it inevitably reduces production. High ABA also appears to be linked to kernel abortion near flowering.

Direct measurement: can be quite quickly done with monoclonal antibodies specific to ABA, but the leaf extract requires cleaning up (removal of some pigments) first.

Indirect Measurement: Leaf rolling; biomass; kernel abortion; stomatal conductance

Information available: reasonable

Genetic variability: relatively high

Heritability: moderate (Quarrie's divergent selection)

Prospects for breeding: moderate?

14. Changes in metabolites (avoidance/desiccation tolerance):

Objective: it has been noted that proline and glycine betaine increase in plants exposed to drought stress. Do these metabolites protect the leaf (especially enzyme systems) from damage due to loss of turgor? Or are they merely symptoms of a damaged metabolism? Are high levels helpful or harmful? It is not known at this stage.

Another change that is sometimes seen is the presence of heat shock proteins. These are new genetic products associated with genes which are activated by high temperatures and in one report by moisture stress. They are thought to protect enzyme systems, but their precise function is not known. Seem more useful for intermittent stresses than for terminal stresses.

Direct measurement: tedious laboratory analyses

Indirect Measurement: osmotic concentration; osmotic adjustment

Information available: poor

Genetic variability: variation in proline and glycine betaine observed in tropical maize.

Heritability: ?

Prospects for breeding: ?

15. Partitioning of carbohydrates: (ASI, harvest index, ears per plant, tassel size, plant height, etc.) (avoidance).

Objective: Since severe stress in maize can reduce ear growth rates below a level critical for the successful survival of newly fertilized florets, the rapid growth of ears under stress is critical to their survival. The reduction in size of competing organs which are growing at the same time also helps increase this flux.

Direct measurement: the actual flux of assimilates to the ear is virtually impossible to measure, except perhaps through the use of radioactive labels (14 C labelled assimilate). Ear growth in the first 1-4 days after pollination is only about 20% that of the stem and less than that of the tassel (Edmeades, Daynard and Fairey, 1979). Possible through tedious repeated measurements of ear size.

Indirect Measurement: possible though the ASI; also related to reduced tassel size and shortened plant height. Another measure is ears per plant under stress, or a measure of barrenness. Harvest index under stress another indirect measure.

Information available: good

Genetic variability: considerable

Heritability: high

Prospects for breeding: good

16. Remobilization of preanthesis biomass: (avoidance)

Objective: to use carbohydrates stored in the stem as a buffer stock which can be remobilized when needed by the plant at critical times (e.g., at flowering or during grain filling). It appears that the maize plant ear at flowering has very limited capacity to remobilize carbohydrates stored in the stem prior to flowering, perhaps because the stem continues to increase in dry weight at this time and the ear is very small. During early ear growth (weeks 1-3) assimilates are stored in the stem which increases in biomass, and these can be remobilized by the filling grains if drought occurs at that stage. This will often result in severe lodging.

Direct measurement: the actual flux of assimilates to the ear is virtually impossible to measure, except perhaps through the use of radioactive labels (14 C labelled assimilate). Repeated harvests of ear and stem biomass may indicate degree of remobilization.

Indirect Measurement: Largely by defoliation (chemical (magnesium or potassium chlorate) or physical) during grain-filling. A measure is grain yield and weight per grain under stress. Harvest index under stress another indirect measure.

Information available: poor for maize; good for wheat

Genetic variability: ?

Heritability: ?

Prospects for breeding: probably good

17. Low lethal water status:

Objective: if we can select plants which are less damaged by low tissue water potentials (loss of turgor), this should be reflected in the rate of recovery when stress is lifted. Related to this is the water status at which essential metabolic processes, such as photosynthesis and respiration cease.

Direct measurement: detached leaf studies with measurement of relative leaf water content, rewatering and measurement of rate at which metabolic functions are restored. Since maize does not recover by re-greening dead leaves, it is a very hard trait to measure except through detailed physiological measurements (photosynthesis, respiration; uncoupled respiration)

Indirect Measurement: Rate of recovery when severely stressed plants are rewatered; relative rate of biomass addition when this happens.

Heritability: ?

Prospects for breeding: ?

18. Prolificacy (avoidance)

Objective: to avoid putting all the yield "eggs" in one basket, by selecting for more than one ear per plant. In good conditions we get prolifics; in bad conditions we reduce to at least one ear per plant. Key is whether the fate of the two upper ears is determined at the same time or not. In general, they are determined at the same time, so risk cannot actually be spread in time.

Direct measurement: simple; fast

Indirect Measurement: not needed

Information available: (on drought stress effects; poor)

Genetic variability: large

Heritability: high

Prospects for breeding: good

19. High grain yield under stress (all mechanisms)

Objective: This is the grand integrator of all the above traits when the plant is subjected to an array of moisture stress circumstances. It should be measured by shelling the grain, not estimating it from whole ears, since shelling percentage falls rapidly with stress at flowering. It should be expressed on the same area basis and moisture content for all cultivars. At issue is whether progress for increased grain yield can be accelerated by focusing on specific processes when yield is determined. Grain yield is highly correlated under stress ($r=0.90$) with kernel number per plant, so it makes sense to focus on process which determine this trait.

Direct measurement: not a problem; every breeding program is geared up to do it

Indirect Measurement: Ears per plant and ASI

Information available: good

Genetic variability: large

Heritability: moderate-low; subject to G*E

Information available: poor

Genetic variability: ?

Prospects for breeding: good

The maize drought-tolerant 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, has a waxy cuticle on upright dark green leaves which do not normally roll under stress. When drought-stressed 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 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. Its leaves will not accumulate proline under stress. It has a high grain yield under well-watered conditions, and 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..

Practical drought-adaptive traits

Time required to measure a trait: as a guide, a family needs to be characterised in about 2 minutes (or about a maximum of 20 seconds per plant, 5-6 plants per plots, 2 reps per family). Thus in one day (480 minutes), a researcher plus helper needs to be able to measure about 240 families or plots, for the trait to be a viable one.

Direct traits that fit the time requirements of a breeding program

- 1. Shelled grain yield :** indicates all drought adaptive processes, and related especially to all traits which imply greater volume of water available to the plant (osmoregulation; deep intensive rooting) and increased flux of carbohydrate to the developing ear at flowering (low damage to chlorophyll and chloroplasts under stress; changes in partitioning of carbohydrate). Fast to measure.
- 2. Delayed canopy senescence:** indicates osmoregulation, staygreen genes. (Fast to score, slower to measure)
- 3. Leaf rolling:** indicates radiation shedding, high ABA concentrations, low root water potentials, presence of bulliform cells (Fast to score)
- 4. Upright leaves:** indicates a canopy with high water use efficiency. (Fast to score).

5. Germination and establishment in dry soil: indicates capacity to maintain low shoot/root ratio; osmoregulation.

6. Osmotic adjustment: indicates directly the degree of active accumulation of solutes

Useful indirect traits that fit the time requirements of a breeding program:

1. ASI: indicates increased ear growth at flowering. (Fast to measure)

2. Reduced tassel size: also indicates increased ear growth at flowering (Fast to measure)

3. High ears per plant: prolificacy for increasing yield under good conditions; reduced barrenness for really tough conditions. (very fast to measure)

4. Maintained weight per kernel: indicative of delayed senescence and osmoregulation (slower to measure)

5. Relative leaf and stem elongation: indicative of deep and complete rooting; osmoregulation? (Slower to measure)

6. Canopy temperature: varies greatly with time of day, radiant load and wind. Indicates osmoregulation; stomatal control; root depth and intensity, etc. (Very fast to measure).

7. Root vertical pulling resistance: indicates extent and size of rooting system, though not the depth (slower to measure)

8. Score of leaf bleaching: indicates degree of photo-oxidation (Very fast to measure)

9. Leaf chlorophyll concentration: indicates degree of destruction of chlorophyll by photooxidation, and the degree of N deficiency associated with low soil moisture status. (Fast to measure)

10. Predawn leaf water potential: measures extent of rooting volume; osmoregulation (slow to measure).

Traits considered to be too slow for direct measurement during selection, but of value during evaluation of progress or in selection of parents for crosses:

- rooting depth and intensity
- root hydraulic conductivity
- wax level on leaves
- leaf fluorescence
- stomatal control
- abscisic acid concentrations
- metabolite concentrations
- harvest index

- remobilization of stored carbohydrates
- lethal water status
- recovery of metabolic functions when stress is lifted.

Which traits? There are many traits possible. Only by carefully examining the relationship between the trait and productivity, and the time taken to measure the characters, can a decision on the worth of secondary traits be taken. This will be considered in a subsequent discussion.

Lecture 5: Suggested reading

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Drought Lecture 6: Outline

Choice of Selection Environment

1. The target environment

This has already been introduced, and will be further discussed by Scott Chapman.

- Ideally we would like to test progenies, and at a later stage of selection, cultivars, under the environmental conditions under which they are expected to perform. The target environment comprises a population of environments representing the range of conditions the future genotype under selection is likely to meet. The problem comes when the factor that leads to great instability in performance occurs with low frequency, or is quite unpredictable in its timing.
- Unpredictability in time between seasons: The difficulty is that drought occurs perhaps in only 40% of years to a level of severity where yield is reduced by more than 50%. In a further 40% of years, drought occurs to a level which reduces yield by about 20%, and in the remaining 20% of years, yields are unaffected.
- Unpredictability in timing within a season: when in the season will the drought come? How intense will it be? Will it coincide with a sensitive stage in the life of the plant?
- Drought is normally unpredictable, and crops bred for rainfed summer season situations in the tropics must therefore be able to perform well in both dry and well-watered conditions.
- Given the uncertainties of the timing and intensity of drought stress, many researchers have concluded that the only sure way of breeding for drought tolerance is by extensive multi-location testing of progenies. We will look first at this aspect

2. Relevant breeding principles

Heritability: One of the most widely used parameters in comparing breeding strategies is heritability. Heritability (h^2) of a specific trait, such as grain yield, is defined as the heritable fraction of phenotypic variability. In terms of variance components derived from an analysis of variance of lines or plants grown in replicated trials at 2 or more locations, it is estimated by the ratio:

$$h^2 = \frac{\sigma^2_G}{\sigma^2_G + \sigma^2_{GE/l} + \sigma^2_{E/r}} \quad [1]$$

where σ^2_G is the genetic variance; σ^2_{GE} is the genotype by environment (G x E) variance, and σ^2_E is the error variance for r replications and l locations (Hallauer and Miranda, 1981).

Heritability (h^2) estimated by (1) is referred to as "broad sense heritability" because σ^2_G contains both a component due to additive gene effects (additive genetic variance = σ^2_A), and a component due to non-additive gene effects, mostly associated with dominance and epistasis. Since the latter cannot be fixed by selection (with the exception of hybrids and clones), it is the ratio of additive genetic variance over the phenotypic variance (defined as "narrow sense heritability") that is used to determine the response (R) per cycle of selection.

R is estimated by:

$$R = h^2 S \quad [2]$$

where h^2 is the heritability of a given trait and S the selection differential (the difference between the mean of the selected lines or plants and the mean of the population of lines or plants from which selections are made for the trait in question). The higher the estimate of heritability and the larger the selection differential, the more rapid the expected gain.

Thus gain (G) is estimated as:

$$G = (k) (\sigma_p) (h^2) \quad [3]$$

where k is a function of the proportion of individuals selected for crossing.

It is possible however, and often desirable, to estimate heritability from the results of selection experiments. From equation [2]:

$$h^2 = R/S \quad [4]$$

This estimate of heritability is called "realized heritability", and equals the response to selection/selection differential. It is an estimate of narrow sense heritability based on actual gains, and is perhaps the most valuable measure of heritability.

Estimates of heritability are not fixed attributes of a trait. The magnitude of the estimate is a function of how it is estimated. Thus the *relative* sizes of the estimates for several traits from a single experiment may be more useful than the absolute values in deciding which trait merits greater attention during selection.

From equation [1] it can be seen that, for a given trait, heritability varies according to the genetic material used and the environment(s) used for testing. In a highly variable environment (with a large plot-to-plot variation and a large σ^2_E , heritability will be reduced. However at any given value of σ^2_E for a specific trait, the estimate of heritability depends on the degree of genetic variability for that trait in the germplasm being tested.

It also depends on the degree to which this genetic variability can be expressed in the testing environment. If the stress is insufficient, or excessive, genetic variability can be masked and heritability will fall.

Management of stress levels is therefore a critical determinant of genetic gain.

Heritability is also reduced by the presence of a large σ^2_{GE} , as it often is the case in multilocation testing, a point which is taken up again when genotype by environment interactions and appropriate selection environments are considered.

3. Drought tolerance, yield potential and phenology:

If drought tolerance is defined simply by superior grain yield in dry environments, then yield potential in unstressed environments may be a useful selection criterion. In this case, higher yield in dry environments can be considered a "residual" effect of high yield potential (Blum 1988).

Fischer and Maurer (1978) proposed a susceptibility index, S , which was defined as

$$S = (1 - Y/Y_p)/D \quad [5]$$

where Y is grain yield under drought stress and Y_p is grain yield under unstressed conditions. D is the stress intensity. $D = 1 - X/X_p$, where X and X_p represent mean yield of all varieties under stressed and unstressed conditions, respectively.

From equation (1), $Y = Y_p(1 - SD)$, a mathematical construct which assumes that Y is made up of two components, Y_p and S . S was still positively correlated with yield potential in Fischer and Maurer's dataset, but has shown itself to be relatively independent of yield potential in other studies (see, for example, Ehdiae et al 1988)

Bidinger et al (1987a; 1987b) found that over 50% of the variation in grain yield of breeding lines of pearl millet when exposed to mid- and late-season stress could be explained by variation in yield potential and time to flower (escape). A multiple regression of stressed grain yield on unstressed grain yield and days to flower were fitted to mean data from the trial, and a drought response index (DRI) for each cultivar was computed as:

$$DRI = (Y_A - Y_{ES})/SE_S \quad [6]$$

where Y_{ES} and Y_A are the estimated and actual yields under stress for the cultivar and SE_S is the standard error of the multiple regression. This measure is related to equation [5]: where flowering dates do not vary, DRI is proportional to $1 - S$.

4. Genotype by Environment Interactions

Interactions between genotypes and environment occur when absolute differences among cultivars are not the same at all test locations within and across years, and have an important bearing on the breeding of better varieties (Allard and Bradshaw, 1964).

The resulting reduction in heritability (see Equation 1) impedes crop improvement for performance across environments (Baker, 1988).

Gains in plant breeding depend on the accurate identification of high yielding genotypes with temporal and spatial stability. Traditionally this has depended on multi-location testing of large numbers of cultivars, often over years. While this process is considered essential to the selection of stable adapted varieties, it is costly, and gains in its efficiency are always sought. For this reason considerable effort has been devoted to the analysis of $G \times E$ interactions.

Genotype x stress level interactions are of importance to us:

If they are not present to a significant degree, then we are just as well off selecting for drought tolerance in well-watered environments. Stressed environments are low yielding, and many consider them to have a low heritability for grain yield because genetic variance decreases and environmental variance rises (see Equation [1]).

Different patterns of G x E interactions are shown in Fig. 1. Case B is an example of G x E interaction of the crossover type, in which the ranking of the two cultivars reverses as stress levels increase. Experience with varietal tests suggests that cases A and D are the most common, followed by B and then C (Edmeades et al., 1989).

Since most breeders rank genotypes during selection even though the differences among them may not be statistically significant, the interactions of major significance are those involving crossovers and rank changes.

Analysis of G x E interactions of the crossover type are very important, since they may reveal cultivars with unique adaptive traits in either low or high yielding environments. This may signal the need to breed for specific adaptation to high and low yielding environments in separate programs.

It may also point to the need to combine superior performance in both environments in broadly adapted germplasm. The feasibility of the latter alternative also depends on whether adaptation to high and low stress environments are compatible. For example, does transgressive segregation arising from crossing lines 1 and 2 in Fig. 1B produce the situation shown in Fig. 1A?

Analyses of G x E interactions by statistical and physiological means and their interpretation in relation to the target environment are therefore critical determinants of important aspects of a breeding strategy, including the choice of the optimum environment for selection .

An understanding of the physiological basis of G x E interactions will also allow a more analytical approach to be taken to selection rather than one simply based on yield alone.

4.1 Statistical analyses of G*E interactions

This subject has recently been reviewed by Westcott (1986), Blum (1988), Baker (1988), Edmeades et al. (1989) and Crossa (1990). We include here a brief summary of the more useful numerical methods, but we must emphasize the value of simple graphical presentations of yield in different environments as the first step.

Ranking: When accompanied by plots of cultivar x environment means, this is one of the most simple, safe and neglected methods for preliminary examination of data from different environments. The number of times a genotype is ranked in the top, middle and bottom one third of entries at all sites (sometimes called stratified ranking) provides useful empirical information on genotype stability and performance.

Analysis of variance: The traditional approach has been to examine G x E through variance components derived from an across-location analysis of variance.

The breeder is frequently dealing with hundreds of genotypes in trials, and it is difficult to detect which of these give rise to a significant G x E term.

It does not detect stable genotypes, or interactions of the crossover type, nor does it help explain the causes of a significant genotype by environment interaction (Baker 1988a; Blum, 1988).

Joint linear regression: Here the performance of an individual cultivar at each location is regressed on an environmental index made up of the mean performance of all cultivars at each location (Fig. 2).

Although high mean yield has always been considered desirable, the definition of stability has remained hard to define. Finlay and Wilkinson (1963) considered a stable variety as one with a small slope, equating a slope of greater than one with an increasing sensitivity to environmental change. Eberhart and Russell (1966) partitioned the G x E interaction variance into that due to regression and deviations from regression, and considered a stable variety to have a slope of 1 with deviations from regression approaching zero. Blum (1988) noted that a high positive intercept is also an important indicator of a variety adapted to low yield environments, although slope and intercept are not independent.

If a cultivar suited to subsistence agriculture should have a slope of less than 1, a large positive intercept and small deviations from regression. But if farmers in the target area can market grain produced in excess of their needs, then a slope of greater than 1 is appropriate.

This method has some problems:

- there is a lack of independence between cultivar performance and the mean of the site (which increases as the number of cultivars decreases), and between the slope and the intercept. It should not be used with less than 6 genotypes.
- As well, estimates of slope and intercept are not fixed attributes of a genotype and depend on which set of genotypes is included in the analysis, so in a subsequent test with other cultivars a check entry may have a quite different slope and intercept.
- Outliers may have undue influence on estimates of slope, and should be noted and perhaps excluded.
- Deviations from regression can occur because of curvilinear responses of individual cultivars to the environment, or because of outstanding performance by that genotype at low yielding sites. Selecting genotypes on the basis of small deviations may lead to the rejection of the very genotype the breeder desires. If a single variety differs from all others in the trial in a specific drought tolerance mechanism, a breeder may reject that variety on the basis of large deviations from regression in low yielding sites.

- Slope and yield potential are often positively correlated (Fischer and Maurer 1978; Rosielle and Hamblin 1981), so slope may simply reflect the potential of the variety in good environments.
- Representation of a site only by the mean yield of all cultivars at that site may group sites with the same mean yield arrived at for very different reasons.

However, in spite of these limitations, the ease of this analysis and its simple graphical presentation make it a useful conceptual tool for many breeders working with limited computational resources and restricted capacity to further determine the underlying causes of G x E interactions

Analysis of patterns: If genotypes and locations can be grouped by similarity of response, then *patterns* of adaptation among cultivars and key testing locations can be identified, and a first step to understanding the underlying causes of G x E interactions will have been taken.

In general, methods of pattern analysis require considerable computational power, and care in interpretation is needed. Researchers at CIMMYT have had considerable success in analyzing data from wheat multilocation yield trials using an additive main effect and multiplicative interaction model (AMMI) (Gauch, 1988). The AMMI technique first applies the additive analysis of variance model to two-way data. Genotype yields are then adjusted at individual locations for principal component effects, which serves to reduce the influence of "noise" and the multiple changes in rank associated with noise that are commonly observed among sites.

Cluster analysis was applied separately to the location and adjusted cultivar within-location means from wheat trials at CIMMYT. Clusters of locations apparently bore no relationship to their mean yield level.

Numerical analysis methods that rely on grain yield of a annually changing group of genotypes under test as a sole measure of the environment suffer from non-repeatability over years. This is mainly because of year-to-year changes in weather, testing sites and in genotypes. More useful results perhaps could be obtained if cluster analyses were carried out on long-term means of environmental variables for the period of the growing season (e.g., Pollak and Pham, 1989), or the actual weather experienced during the trials.

Another useful approach, suggested by Fox and Rosielle (1982), would be to include a number of reference cultivars with known performance characteristics in each set of trials each year, and relate performance of each genotype to these.

Crop models: The development of sophisticated process orientated models that can predict mean genotypic response to several environmental factors (see, for example, Jones and O'Toole, 1987; Stapper and Harris, 1989) is providing new and exciting tools to breeders in their quest to understand and exploit G x E interactions, and may well point the way to future developments in this field.

4.2 Physiological Analysis of Genotype * Environment Interactions

It is essential that breeders conducting drought screening trials appreciate how the outcome of selection can be affected by the varying sensitivities to drought stress during the plant's life cycle and by variations in phenology among plants, families and lines.

Drought-sensitive stages in maize:

- Germination and seedling establishment are risky for crops which are sown at the onset of a rainy season. Uneven stand can be a major source of yield loss, and hence of G x E interactions.

- Important reductions in productivity can also occur because the expansion of leaf area is reduced by moisture stress (Boyer and McPherson, 1976).

- The most critical period for yield determination in cereals is at flowering. If drought at flowering is severe it can impair the development of reproductive tissues (e.g., Namuco and O'Toole, 1986). When less severe, drought reduces kernels per inflorescence (Boyer and McPherson, 1976), the effects of stress being largely mediated through assimilate supply on developing floret primordia. The reduction in kernel number is roughly proportional to the reduction in assimilate flux during that period (Edmeades and Daynard, 1979; Fischer, 1979). Maize is more sensitive than other cereals to water deficits at flowering because it is cross-pollinated and the flowers are separated physically on the plant (see Edmeades et al., 1992; Bolaños and Edmeades, 1993). Again, drought at flowering has much larger effects on grain yield than the same level of drought at other times in the life cycle of the crop.

- During grain filling, yield reductions occur largely because of reduced photosynthetic rates and by drought-induced foliar senescence (Fischer et al., 1983). Under these circumstances, genetic differences exist for the capacity to retranslocate stored, mobile preflowering assimilate to the grain (Blum et al., 1983).

- Much so-called "drought tolerance" is actually escape from drought by cultivars which mature before the season ends or which flower either earlier or later than the mean for the trial. The breeder must take considerable care in selecting for drought tolerance among cultivars which vary in flowering date and in maturity, and should try to maintain maturity constant. Where drought increases in intensity with time, and is managed to coincide with flowering, selection of superior S₁ maize families, based simply on grain yield, grain yield was negatively correlated with days to anthesis ($r = -0.40^{**}$, 233 df) for S₁ families of Pool 26 grown under moisture stress at flowering that increased in intensity with time (Bolaños and Edmeades 1988). When the 50 highest yielding lines were selected out of 235, the mean anthesis date of the selected fraction was 2 days earlier than the mean for the population.

Important note: In the presence of genotype x stress level interactions of the crossover type (e.g., Table 1), yield potential tends to become a poor selection criterion to improve yield in dry environments. Interactions of this type have been found in several crop species exposed to different types of stresses. There is evidence of similar types of interactions among progenies of maize when tested under a range of water stress environments (see Diallo and Rodriguez, 1987). Their consequences on breeding are of particular relevance in discussing one of

the more controversial issues in breeding for drought conditions, i.e. the choice of selection environment.

5. Choice of selection environment

- **Testing at a representative subset of environments:** The target environment comprises a population of environments representing the range of conditions the future genotype under selection is likely to meet. Because of limitations of resources, seed and time, selection has to be based on performance in only a subset of these environments. The optimum selection environment is that which maximizes the response to selection for performance of the genotype in the target environment.

- **The Coefficient of Variation "hangup":** There is an unfortunate tendency in some breeding programs which utilize multilocation testing to bias their selections by discarding data from droughted sites because the coefficients of variation (CV) from such sites are often high. Since CV is a ratio of the standard error to the mean, when mean yield falls the CV will automatically rise. Attention should rather be paid to the standard error of differences among means. When this begins to rise under stress, this may signal that the value of the selection site is being lost as spatial variation in available soil water (a function of spatial variation in soil texture and depth) is being exposed by increasing levels of moisture stress.

- **Decline in heritability under stress?** Selection for yield under moisture stress is generally considered less efficient than selection for yield under well-watered conditions because of observed declines in heritability for grain yield under drought (Rosielle and Hamblin, 1981). Heritabilities for yield often fall under stress because genetic variance falls more rapidly with increasing stress than environmental variance (Blum, 1988). However, the decline in heritability for grain yield is often not large until yield levels are reduced to less than 20% of yield potential (Fig. 3). Below this yield level genetic variability declines as yields of most genotypes approach zero.

- **Theoretical studies:** When the target environment is characterized by drought stress, the choice of selection environments is between those which are stressed and non-stressed. Theoretical aspects of this issue were discussed by Allen et al. (1978). They found that high yielding selection environments had an advantage over low yielding selection environments of 4% and 7% for wheat, and the best test site was one which adequately represented the environments under which the cultivar was expected to perform. From a theoretical study Rosielle and Hamblin (1981) concluded that selection for mean productivity across sites differing in stress level would increase yields in stress and non-stress environments. They suggested that if stressed sites occurred randomly in the target area, then 1 in 3 test sites should be a stressed site.

The choice of an optimum environment for selection can be treated as a case of correlated response to selection (Falconer, 1960). The correlated response in environment X when selection is done in environment Y is given by

$$CR_X = (r_A \cdot H_Y/H_X) R_Y \quad [6]$$

where CR_X is the correlated response in the target environment (X), R_Y is the direct response in environment Y, H_Y and H_X are the square roots of the

heritabilities of yield in environment X and Y, and r_A is the genetic correlation coefficient between grain yield in the two environments. If the genetic correlation is negative, (i.e., when a crossover G x E interaction occurs), it is obviously impossible to select in environment Y for improved performance in environment X.

Determination of whether a crossover interaction occurs among genotypes in the target environment, and the yield level at which it occurs is therefore important, and directly relevant to the choice of selection sites. This issue has recently been discussed recently by Lawn (1988) and by Ceccarelli (1989), whose arguments can be summarized as follows:

- The presence and type of G x E interaction depends on the range of test environments and on the definition of the target stress environment.
- Although a crossover type of genotype x environment interaction reduces heritability measured across the entire range of environments (see equation [1]), this does not necessarily imply a reduction in response to selection *within* a low yielding or *within* a high yielding macroenvironment.

Results reported for experimental varieties of maize reported by Fischer et al. (1983) showed this typical pattern of genotype x stress level interaction, but the cross-over point was near 2-3 t/ha for germplasm with a yield potential of 6 t/ha. CIMMYT's recent results (Fig. 4) based on the evaluation of progress in Tuxpeno Sequia suggest that selection for improved performance in low yielding environments have given added yield in both high and low yielding environments.

An important additional consideration:

When grain yield in both high and low yielding environments is limited by partitioning, and this is determined at a single stress-sensitive time in the life cycle of the crop, then gain in both environments will be maximized when a stress is applied that reveals the genetic variation that exists for that trait. The usefulness of this type of screening environment will depend very much on how much of the gains are transferred to the high yielding environment, and/or whether there exists a negative genetic correlation between the low yielding site and the high yielding site for this trait. There is no evidence that such a negative genetic correlation exists for ASI. As well, we see no evidence of a yield cost in good environments associated with yield gains in low yield environments.

(see slides)

For maize, when we test in a low-yielding stressed environment where the heritability of yield is falling, we see a rise in the genetic correlation between ASI and yield is high. In these circumstances ears per plant and ASI become accurately identified traits, and serve as surrogates for yield, so that continued gains in grain yield can be made.

Note that this does not rule out the possibility that under drought a variety selected for high yield potential in unstressed conditions could outyield selections made under stress simply by "spill-over" effects of high yield potential. However, for continued gains in performance under drought it will be essential to select for performance under carefully controlled conditions of drought (Blum, 1988). This seems particularly true for maize, and, remarkably, even suggests that gains in well-watered environments derived from selection made under drought may be

better than those gains made by selecting progenies at many environments under largely non-droughted conditions (Bolanos and Edmeades, 1993a).

In conclusion, the choice of the optimum environment for selection depends on the characteristics of the target environment, the breeding objectives, and the nature of the trait under selection:

- When the crop is grown in severe stress environments with a high probability of crop failures and very low probability of yields greater than 50% of unstressed yield potential, selection is most effective when conducted in stress environments which keep yields within the 20-50% unstressed yield potential range.
- When the crop is grown in a highly variable environment with similar probabilities of poor (<40% unstressed yield potential) and good yields (>80% unstressed yield potential), selection is most effective when conducted in both well-watered and moisture-stressed environments.
- When yields are restricted by a traits such as partitioning, the selection of the site will be the one which gives most precise expression of the trait.

Maximum efficiency in selection for drought tolerance demands that drought stress be managed in such a way that genetic variation for tolerance is fully and reliably expressed and easily identified. Richards (1982) suggested that environments where yield potential is reduced by 25-65% are suitable for selection for drought tolerance, but recommended that severely stressed environments (yield potential reduced >80%) should be avoided. However, statistical consideration aside, the choice of the appropriate test environment must be determined by the target environment. However, when stress becomes too severe, all cultivars yield similarly at yields approaching zero a fact illustrated by the decline in genetic variance under severe stress. Emphasis should be on selecting sites with the absolute minimum soil variability under moisture stress, and it is advisable to grow a test crop under drought on the plot area prior to beginning selection so that soil variation can be mapped and avoided. The problem of reduced heritabilities under drought can be partially overcome by increasing population sizes, by increasing the care with which parents of crosses are selected, or by special plot techniques (see below). These considerations are particularly important in the selection of parents for crosses and in selections made in early generations of segregating progeny when seed supply generally precludes multilocation yield testing. In later generations, or when seed supply permits, multilocation testing at representative sites within the target environment is considered essential, for it is only here that segregating lines can be exposed to the natural variation in plant water status encountered in the target environment.

6. Increasing the reliability and repeatability of moisture stress

The intensity of naturally occurring drought is normally difficult to predict, and where seed supply, land and capital are constraints most breeders have resorted to using irrigation or rainfall prevention techniques to impose a repeatable level of stress at an appropriate plant growth stage.

A: Dry season nurseries: stress level is controlled by withdrawal of sprinkler or furrow irrigation, have been used in several breeding programs. Here the soil

profile is usually fully charged at sowing and stress develops as water is used, encouraging deep rooting of genotypes. CIMMYT uses three managed moisture regimes to expose genetic variability for specific traits (Fig. 5):

- (i) Well-watered: target yield = 100%; exposes variability for grain yield; heritability for grain yield high, that for ASI and EPP lower
- (ii) Mild flowering and severe grain filling stress: target grain yield = 50%; exposes some variability for ASI and EPP, more for leaf senescence and less for grain yield. Heritability for grain yield still high, that for ASI and EPP rising.
- (iii) Severe flowering and grain filling stress: target grain yield = 10-20%; exposes maximum genetic variability for EPP, ASI, and least for grain yield, good variability for leaf rolling and leaf senescence. Heritability for ASI, EPP maximal, that for grain yield low, for leaf senescence moderate.

To these must be added the screening environment of Obregon, which exposes progenies to high temperatures, very high evaporative demand, long photoperiods as well as drought.

B: Early or Delayed planting dates: This is possible where irrigation facilities are available at the main station, and the length of the season is not controlled by frost. Delayed plantings are easier to manage, in that sowing and establishment can be at the height of the rains, and the crop should flower when the rains have ceased. It is probable that one additional irrigation application will be required 2-3 weeks after planting to ensure grain filling.

C: Line source sprinkler systems: imposes a gradient of stress down the progeny row (e.g. Wicks and Carson, 1987). This provides a response surface of yield to available water for each cultivar. Since small amounts of water are applied at regular intervals, the wetting front does not extend deep into the soil, thus encouraging intense but shallow rooting.

D: High plant densities: High plant densities are known to increase ASI. Density thus provides a means by which the variability for ASI can be exposed. When 80 S1 families of Pool 26 Sequia were grown under drought and under high density (106,000 plants/ha), the correlation between ASI observed under drought and density was only 0.29*. This disappointingly weak relationship suggests that drought and density effects on ASI may affect different genetic systems, and that density cannot fully replace drought in the pursuit of better floral synchrony. Studies on a group of about 20 early Corn Belt hybrids, however, showed a relatively strong relationship between ASI as a measure of drought tolerance and the optimum density at which grain was produced (Dow et al., 1984).

Variable plant density can also be used to provide variable levels of drought in the field (this has been used at CIMMYT by Dr. David Beck, who had two plant densities in each 5m row). Another method could be to have a range of plant densities down the row (each spacing between successive plants is reduced by 5-10%, for example). This technique would provide a variable level of drought and density to the progenies or varieties.

E: Tied versus untied ridges: This has been used by Diallo and Rodriguez (1987) as a means of imposing differential moisture stress in West Africa, where maize is grown on ridges under rain-fed conditions. They recorded mean yields of 3.3 and

4.7 t/ha under untied and tied ridges, respectively. In wet seasons, tied ridges may lead to local flooding and some yield reduction. Cannot control the timing of the stress except by breaking the ties part way through the season.

F: Rain-out shelters: provide a dry environment within the context of a normal growing season. These are expensive to install, fixed to one spot, and can only be used on a limited number of genotypes.

G: Field tests of seedling emergence: techniques have been developed at ICRISAT to test for the capacity of sorghum and millet seedlings to emerge from hot, crusted seedbeds that have been artificially created during the dry season (Soman et al., 1987).

Genotype x season and genotype x stress management method interactions when out-of-season nurseries are used for selection are of considerable concern for those who have used these methods (e.g., Bidinger et al., 1982; Seetherama et al., 1982). Will the selections made in dry season nurseries perform similarly in dry spells during the rainy season? Is the target environment rainfall pattern one of large infrequent falls or of many small falls? Evidence that selection for performance in out-of-season dry nurseries does not interact strongly with the type of growing season is provided by Bolanos and Edmeades (1993a), who showed that 79% of the gains reported in the dry winter season were also observed in rainfed seasons at other locations. For most other crops questions of season-specific adaptation remain unanswered, but dry season nurseries with supplementary irrigation continue to be widely used. Each of these special techniques, when carefully employed, can serve as a valuable adjunct to multilocation testing, but will not replace the need to test new genotypes in the environments and socioeconomic settings in which the new drought-tolerant cultivar is being expected to perform.

10. Conclusions

1. **Choice of selection environment:** if the breeding objective is to enhance stability and performance in an environment where low yields are the rule and high yields the exception, selection should be conducted in the presence of those stresses responsible for the low yields. Where probabilities of poor and good yields over time are roughly the same, selection can be better achieved by selecting both in the presence and in the absence of moisture stress.
2. **Special plot techniques:** these are designed to increase the reliability of drought while controlling the increase in the standard error of the difference among treatments under stress. Special attention must be paid to the possibility of genotype x selection season interactions when dry season/supplementary nurseries are used.

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* Recommended reading

Table 1: Yield performance of selected early tropical materials under drought stress and normal irrigation, Obregon 1991. Data show clear genotype x stress level interactions for grain yield between check entries and the early drought tolerant selections. (Source: D. Beck, pers. comm., 1991).

| Entry | Stressed | | Irrigated | |
|--------------------|-----------------|-----------------|-----------------|-----------------|
| | Yield (t/ha) | Best chk (%) | Yield (t/ha) | Best chk (%) |
| TEYF Drt.Tol.Syn.2 | 1.47 (4) | 156 | 4.28 (3) | 95 |
| Pool 18 Seq. BAS | 1.57 (1) | 167 | 4.18 (4) | 93 |
| Ext. Early Yel. C2 | 1.51 (2) | 161 | 3.60(16) | 80 |
| Checks | | | | |
| Muneng 8531 | 0.95(15) | | 4.52 (2) | |
| Poza Rica 8530 | 0.61(23) | | 3.57(17) | |
| LSD (0.05) | 0.39 | | 0.64 | |

Figures in brackets are yield ranks in trial

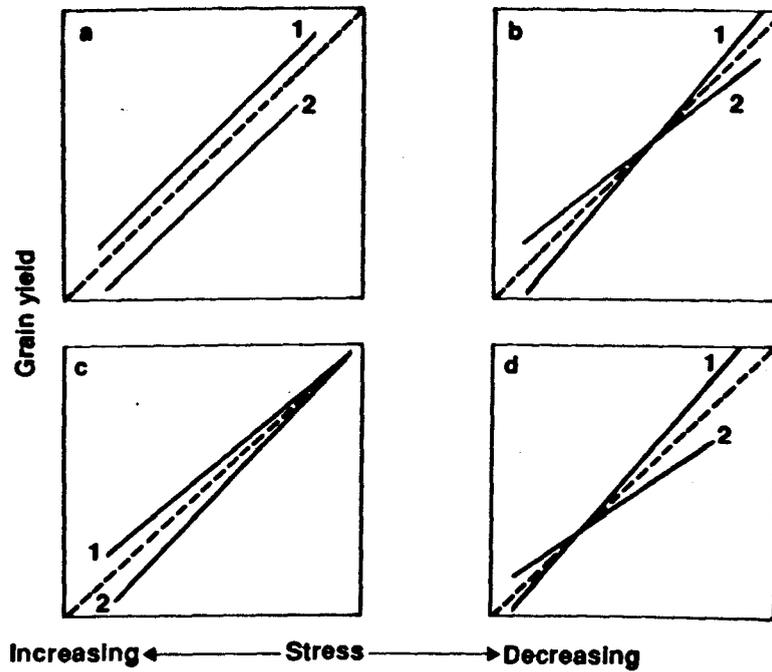


Fig. 1 Generalized yield responses of two cultivars, 1 and 2, to environments differing in stress level. The dotted line indicates the mean response of all cultivars (from Edmeades et al., 1989)

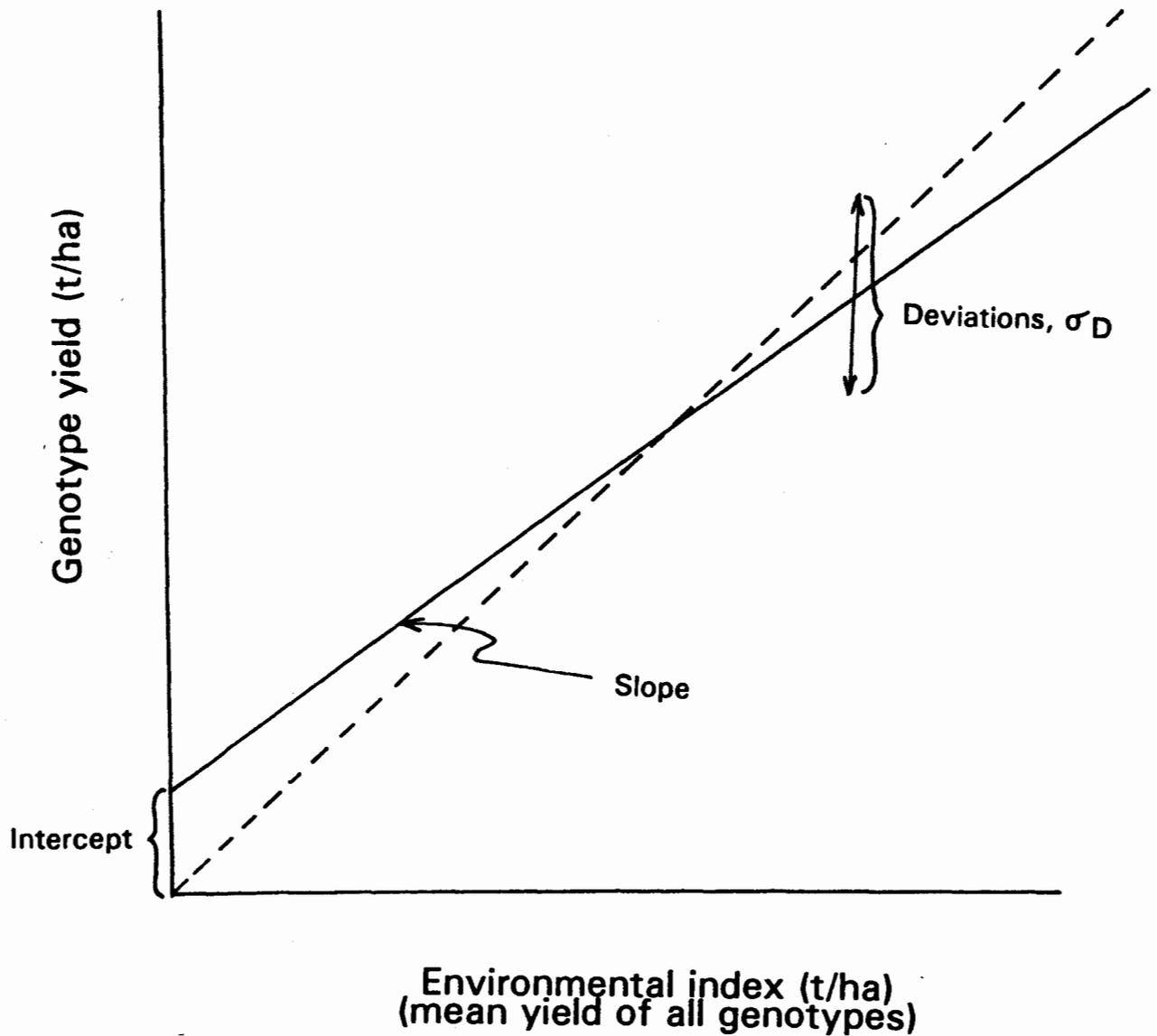


Fig. 2 Example of a joint linear regression of the performance of one genotype on the environmental index (the mean performance of all genotypes in that environment). Dotted line marks the 1:1 slope (After Eberhart and Russell, 1966)

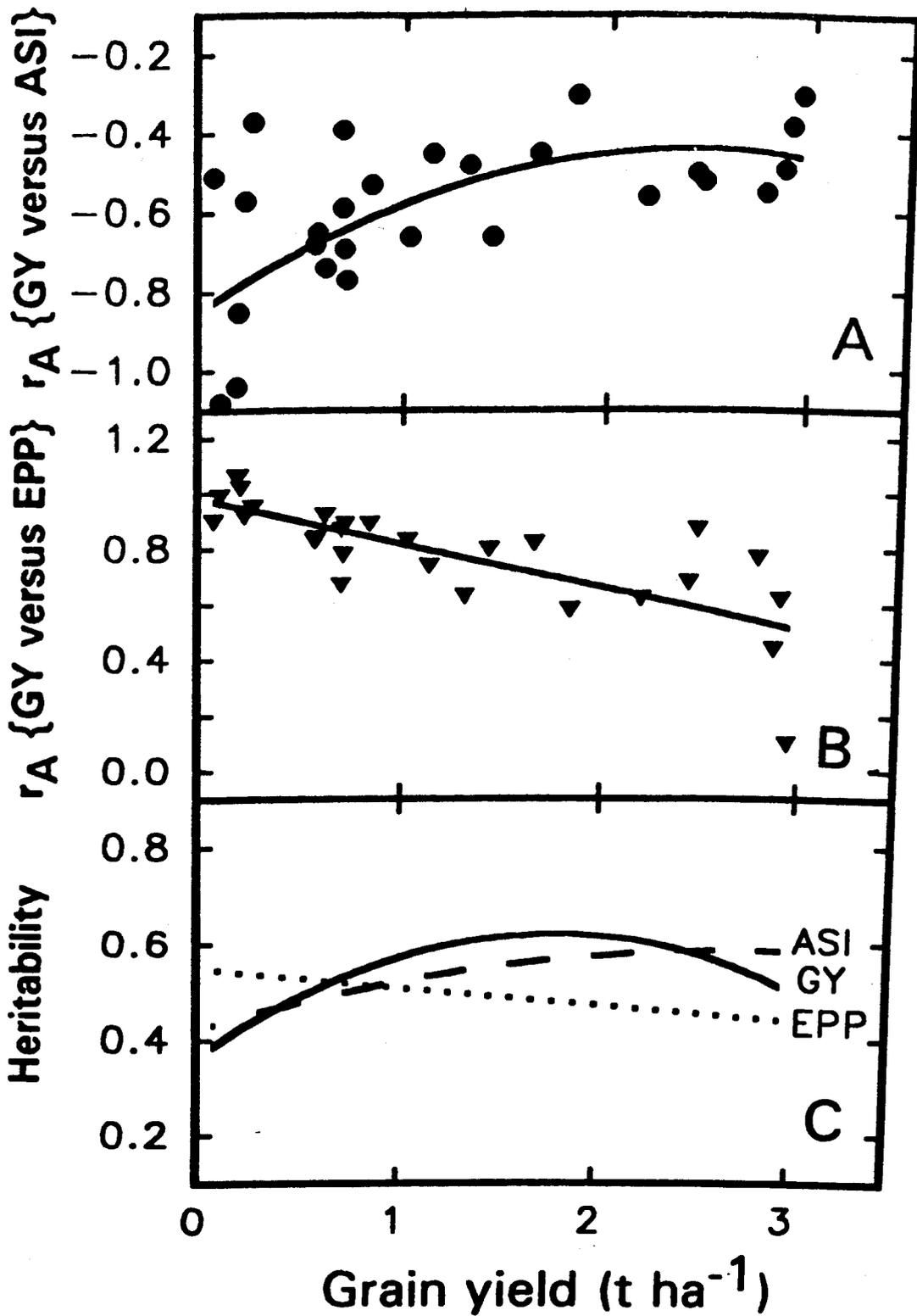


Fig. 3. The effect of yield level on genetic correlations (r_A) between grain yield (GY) and A) anthesis-silking interval (ASI), B) ears per plant (EPP), and C) the effect of grain yield level on broad-sense heritability of GY, ASI and EPP. Data are from 28 replicated S_1 progeny trials grown in México under several water regimes. Lines are fitted quadratic regressions.

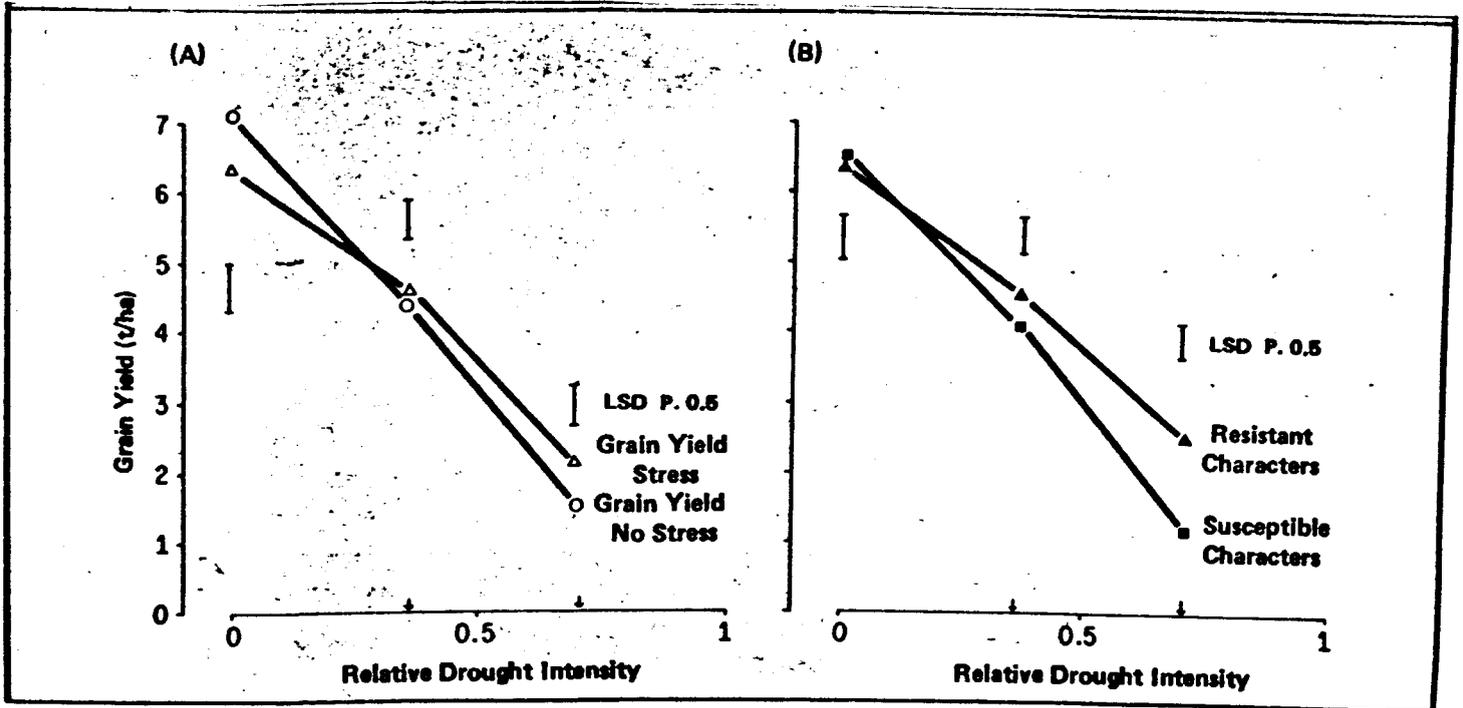


Fig. 4. Influence of moisture regime on performance of four experimental varieties of Tuxpeño Secuía when (A) selected for high grain yield under no stress and stress, and (B) for physiological characters related to resistance and susceptibility to drought, Tlaltizapan, 1976 (Fischer et al., 1983).

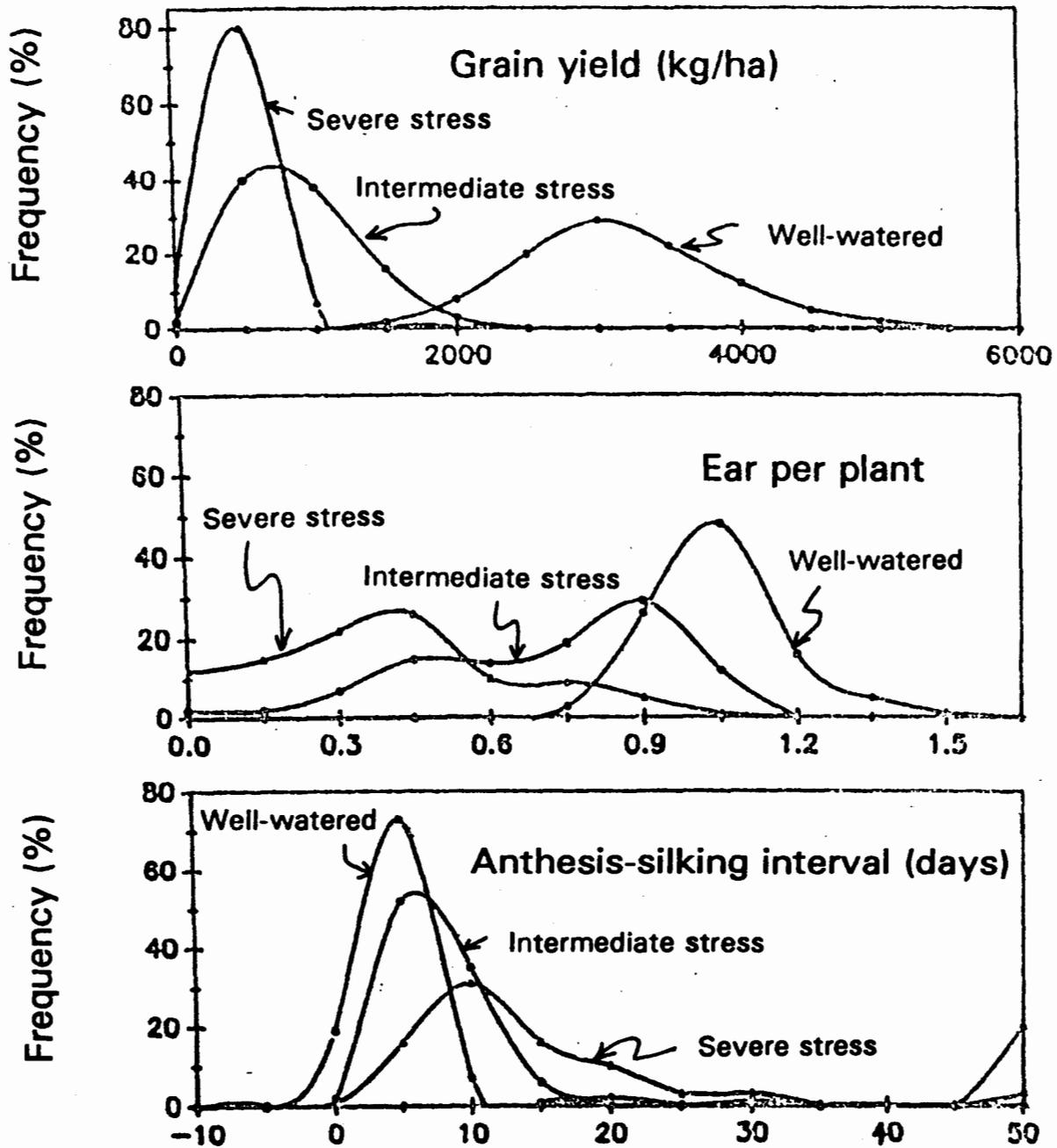


Fig. 5. Histograms of grain yield, number of ears per plant, and the anthesis-silking interval for 222 S1 lines of Pool 26 Sequia C₂ grown under three levels of water stress in Tlaltizapan, 1990

Drought Lecture Outlines - Lecture 7

Choice of Germplasm; Development of Source Populations

1. Background

CIMMYT's strategy in breeding for drought tolerance is twofold. The first focuses on the rapid improvement of drought tolerance in elite germplasm, and seeks to increase the low frequency of drought-adaptive alleles that normally exists within elite maize populations. This approach can result in a >30% increase in grain yield under conditions of drought at flowering and during grain filling that reduce potential yields from 6 t/ha to about 2 t/ha (Bolaños and Edmeades, 1993). Much of this gain has come about by changes in partitioning of biomass to the developing ear at flowering, resulting in an increase in grain numbers per ear and a decrease in barrenness. Very clearly, it is possible to make considerable progress for drought tolerance in elite material, yet much of this elite germplasm is close to a finished product, and the question remains as to how long gains in drought tolerance can continue to be made.

Characters seeming to lack variability in elite germplasm:

- 1) Establishment: No serious attention has yet been paid to problems encountered during establishment of elite germplasm (though we are now seeking to determine if there are heritable differences for this characteristic in the drought tolerant population (DTP1).
- 2) Selection in elite populations has not changed total biomass production, so has not changed water use efficiency (WUE). Although it seems unlikely that we will find much variability for WUE within the maize species, if such variability exists it is likely in unusual source materials.
- 3) There seems limited genetic variability in elite populations for delayed senescence under drought.
- 4) There is limited variability for osmotic adjustment.
- 5) There may exist greater unexploited "upside" variability for grain yield under stress, since this has been almost selected against in most multilocation testing schemes in the past.

Finally, there were indications that gains were declining in advanced selection cycles for improved drought tolerance in elite populations (Bolaños and Edmeades, 1993).

2. Objectives

These observations led to a second, longer term strategy in drought tolerance: the identification of donors of characteristics which would increase production under drought at no great cost to performance under well-watered conditions. It was considered necessary to combine these sources into a single population so that the unique genetic characteristics of each source material could be exchanged during the mixing phase in the formation of the population. This single population of populations could then be used as a vehicle for the transfer of this *reservoir* of variability to national programs.

The steps to be followed would be:

- 1) identify sources of variability for drought tolerance - a variety of traits if possible.
- 2) Recombine these to form a repository of genetic variability which national programs can use
- 3) Improve this population for agronomic traits
- 4) Test it internationally to improve its drought tolerance and to expose these materials to national programs.

Because of the increased level of genetic variability present in the population, we are assuming that greater gains can be made over time for a variety of traits.

At the outset it was considered unlikely that such a population would ever be used for direct release. Reasons for this relate to the almost impossible task of delivering in final product form an array of traits which a specific environment may require. This is particularly true for disease resistances needed at specific sites. Since rate of progress for a single trait is inversely related to the number of traits under simultaneous selection, if we were forced to select for disease reaction as well as drought, progress would be substantially slowed. As well, specific grain texture and colour requirements would require that we establish at least a white and yellow population, and perhaps a flint and dent version as well. This was beyond our current resources.

Given the above considerations, it was decided to establish initially a single population of mixed colour and texture and intermediate in maturity which could serve as a combined single source of drought tolerance in a tolerably acceptable agronomic background. Thus the Drought Tolerance Population-1 (DTP1) was established in 1986. Its agronomic performance was initially poor, so our first emphasis was to improve standability and disease resistance. In order to reduce bias from continuous selection at Tlaltizapan in the dry winter cycle, we have sent S1 progenies of DTP1 to interested collaborators in national programs for screening under the drought conditions they normally encounter (Edmeades et al., 1991).

3. Identification of source materials

This has entailed a screening of sources from:

- 1) Landrace collections in the Germplasm Bank
- 2) Elite selections from other programs with reputed drought tolerance
- 3) Elite selections from CIMMYT's own program with known drought tolerance

We have screened about 200 potential sources of drought tolerance (elite, landrace, hybrid and OPV) under drought and well-watered conditions at

Tlaltizapan. The elite sources were from countries other than Mexico (especially southern Africa, Thailand, USA, as well as CIMMYT's own program), and most were included on the basis of their reputed performance under drought elsewhere.

Each of these will be considered in turn:

3.1. Landrace accessions

We have relied almost exclusively on sources from the CIMMYT Maize Germplasm Bank for this phase of our work. General difficulties lie in the poor agronomic performance of this material (especially its height and lodging resistance), its narrow adaptation (especially its lack of disease resistance).

A total of 300 potential sources of drought tolerance were identified from CIMMYT's germplasm bank.

- These came either from sites described in the passport data as below 1000 m elevation and which had either an annual rainfall of less than 600 mm, or were from sites which were noted as dry.
- These were usually prescreened in the summer for agronomic performance (stalk strength, susceptibility to disease, low yield),
- A total of 160 were advanced for testing under drought in either late or early flowering trials.
- Criteria used in selection under drought were limited to what we could manage at Tlaltizapan. Each entry was grown in a replicated 3-row plot under two levels of drought stress during the winter. One stress level was normal irrigation, to observe yield potential.
- In the stressed water regime irrigation was withdrawn 3 weeks before anthesis, and the crop was severely stressed at flowering and during grain filling.
- A selection index was used to identify superior entries. This index placed weight on delayed foliar senescence, high osmotic potential (when measured), high grain yield and high ears per plant under stress, a short anthesis-silking interval, and lodging resistance under stress.
- The index maintained yield and flowering date under well-watered conditions.
- Compared with selection in elite germplasm, less emphasis was placed on performance under unstressed conditions, and more on delayed senescence and high osmotic activity.

A total of 6 trials involving germplasm bank materials were conducted between 1987 and 1993:

| Cycle | Trial number | # Germplasm Bank entries |
|--------------|---------------------|---------------------------------|
| 86A | 1283 | 1 |
| 87A | 1612 | 46 |

| | | |
|-------|--------------|-----|
| 88A | 1609 (late) | 35 |
| 89A | 1609 (early) | 32 |
| 90A | 1613 (late) | 34 |
| 91A | 1612 (late) | 12 |
| 93A | 1619 | - |
| Total | | 160 |

To this add 10 landrace collections from Hopi and Mojave Indian reservations, evaluated in 1988A.

There are problems encountered in such evaluation trials.

- The site used (winter, Tlaltizapan) limited the traits we could observe. We were unable, for example, to examine variability in ability to emerge from depth in a dry soil.

- In a number of trials the variability in flowering date among entries made it hard to distinguish escapes from those with genuine drought tolerance. We used the summer prescreening trials to stratify entries by flowering date, and then grew all early (or late) flowering entries in the same trials (see Table above). The passport data was not a precise guide to maturity, and many of the accessions are very photoperiod sensitive. Thus it was often difficult to get a fair comparison of ability to withstand stress at flowering, even with a prescreening trial the previous summer.

3.2 Elite selections from other programs with reputed drought tolerance

These materials were either recommended from outreach staff or were already known to be drought tolerant. They included:

86A: Suwan 1; KSX 2301 (Thailand); Latente x Latente (via Burkina Faso) (USA); Ob. Sequia 8249; Ob. Sequia 8322; Ob. Sequia 8232 (CIANO); EV8443 SR BC4; EV8422 SR BC4; TZB Gusau SR BC2 (IITA); AN2 x AN1 (UAAAN); 3M075 (USA);

87A: Latente hybrid (DeKalb, USA); Suwan 2 (Thailand);

88A: Pioneer hybrids 3358, 3720, 3358, 3184, 3378, 3165, 3377 (USA); Pioneer Drought Resist. Synthetic (USA); Arizona 85721 (USA); two Nebraska selections (USA); R201 (Zimbabwe);

89A: CG4502; CG4526; CG4410; CG4512; CG4456; CG4352; CG4436; CG4403; CG4419 (all from South Africa); NS103; KK-DR(S) (Kansas); Drt Resist Synth. (IITA); Pioneer Drought Tol. Synth (Pioneer, USA); B73 x I137; E728 x I137; E728 x F2834; Oh43 x I137; I137 x M37 (South Africa); Pioneer 3165; B73 x Mo17 (USA); Latente hybrid (USA); Baja California synthetic

90A: (K303 x K301)S1; (Mo17W x K55)x(K301 x H28); (K55 x N28W)S2; (Zap. chico x K41) x K731; (Mo17 x K303)xK201G; K41; H28; (SD10 x H28) x K55)S2 (all from Kansas State, USA); 6 experimental hybrids from CIBA-Geigy;

G4385; G4393; G4666; G4734 (USA); KI14 (Thailand); CSM 8804; Ob. Seq. 8349 x 8332 (CIANO); Ghouta-1 (Syria)

91A: PNR 473; Kalahari Early Pearl; Katumani Composite B C12; Acr 88 TZUTSR-W; TZE Comp. 7; Gusau TZB SR BC5

93A: Suwan 3 C4; KS6 (S) C3; KSX 2301; KTX 2801; KTX 2802; KTX 3101 (Thailand); G5431; G5440 (Ciba Geigy, Thailand); USM Var. 2; USMARC 1188; USMARC 1887; USMARC 1888 (Philippines); Acr 88 TZUTSR; TZE Comp. 7; Gusau TZB SR BC5 (IITA); Pop. 49 SR; PR8326 SR; EV8725 SR; Pop. 22 DMR SR; PL150 PM SR (CIMMYT, Harare); Katumani BC3 SR (Kenya); Kito BC3 SR (Tanzania); Rampor 8075 (CIMMYT; Thailand); NS-1 (Thailand); Pool 16 Acr 88 (Cote d'Ivoire).

3.3 Elite selections from CIMMYT's own program with known drought tolerance or possible stress tolerance

We have relied here upon Blum's (1983) observation that in most elite germplasm there exist drought adaptive alleles at relatively low frequencies, and that these can be increased in frequency through judicious selection in carefully managed drought environments.

Materials examined include:

86A: Tuxpeno Reduced Tassel C8; ETO Blanco Red. Leaf y Tassel C3; Pool 23; Pool 25; Pool 26; Pop. 26; Pop 45; ARD Red. Tassel C6; Pop 62 (QPM); Pop. 64 (QPM); Pop. 66 (QPM)

87A:Pop. 30; Pop. 31; Seleccion Precoz; Pool 15; Pool 17; Pop. 49; H-28; Pop. 26; Pop. 34; Mata Hambre- Gujira 314;

88A: TL DR 8421; good and bad selections for predawn water potential; Puebla 209 x Pools 34 and 32; Planta pequena mazorca grande

89A: SPE C3; SPMAT CC3; Maize x Tripsacum C3; Tuxpeno Sequia C6 and C8;

90A: Pool 18 Sequia; Temperate Highland Swat '87; Batan 8786; Best selecions from La Posta Sequia, Pool 16 Sequia; Pool 26 Sequia; SPMAT; SPL;

91A: MBR 86 Across bugs; MBR 86 Chilo; LYF Sequia; LWF Sequia

93A: Latest selection of drought elite populations

4. Utilization:

Of the 13 components used to form DTP1, one was a direct bank accessions (Michoacan 21), and another (Latente x Latente) was directly traceable to a bank accession (also Michoacan 21).

4.1 History of DTP1

- 1986A Screen 22 varieties which were selected on the basis of high general stress tolerance (TL85B-1981-4) or known drought tolerance under three water regimes (normal irrigation; post-flowering stress; preflowering + post-flowering stress); identify best 13 based on yield and a wide array of drought adaptive traits.
- 1986B Cross 13 source materials in a diallel at TL; save 749 ears from 74 combinations.
- 1987A Grow 74 combinations from 86B in a 2 rep yield trial under two water regimes (normal irrigation; pre- and post-flowering stress in TL. At the same time, plant the 749 individual ears in 2.5 m rows in a half-sib block; save ears from this block according to the performance of specific crosses under drought; form C₀ from remnant seed of the 749 families.
- 1987B Plant 352 half-sib families at 66,000/ha in a half-sib block; select best ears from each family, rejecting less than 25% of each family; form C₁ from remnant seed of the 352 families. Cross 7 superior sources identified in 87A with the male bulk of Pool Sequia C₁.
- 1988A Plant 340 half-sib families at 66,000/ha in a half-sib block; apply light drought stress at flowering; select best ears from each family, rejecting less than 35% of each family; form C₂ from remnant seed of the 340 families.
- 1988B Plant 321 half-sib families at 66,000/ha in a half-sib block; plant at same density 39 families from superior crosses between sources with C₁ of Pool as females. Select best ears from each family, rejecting less than 25% of each family in area where pool is having new entries added; form C₃ from remnant seed of the 352 families. Cross 9 superior sources identified in 87A with the male bulk of Pool Sequia C₃.
- 1989A Make balanced bulk of 350 selected ears of previous cycle and sow as a bulk either side of a line source irrigation system. Apply irrigation weekly to provide a gradient of stress, and make selfs down that gradient. Select 350 ears which represent the same mean maturity as the bulk of the Pool and which have been formed in the driest area of the field. Observe 72 source materials under two water regimes in TL, and identify promising sources and promising crosses between good sources and the pool.
- 1989B Sow 350 S₁ families ear to row and sib-increase each family, while selecting the 222 most uniform. Cross superior source materials with the latest cycle bulk (C₄) of Pool Sequia before re-evaluation.
- 1990A Distribute 12 sets of the S₁ families in a replicated yield trial (alpha (0,1) lattice) to members of the drought network for testing. At the same time, test one set under normal irrigation, intermediate and severe stress at Tlaltizapan. Test sources and crosses of sources with the Pool, as well as S₃ synthetics under two water regimes in TL. Form C₅ from balanced bulk of the 250 selected S₁ families.
- 1990B Test 222 S₁ families under drought and irrigation in Obregon, and under rainfed conditions at PR.
- 1991B Recombine superior fraction of Pool;
- 1992A Form 500 new S1 families
- 1992B Observe 500 S1 families in Obregon (for drought); Pioza Rica and Batan (for disease); sib-increase selected S1 families
- 1993A Ship 13 sets of S1 progeny trial to network cooperators; grow three sets at Tlaltizapan.

4.2 Composition of DTP1

Sources of germplasm that have shown adaptation to drought in Tlaltizapan and good performance under drought at other locations have been recombined to form the drought tolerant population or DTP.

This population has sources from many areas included in it:

It included at formation:

| | |
|----------------------------|-------|
| Tuxpeno Sequia Cycle 8 EV | 14.4% |
| Latente x Cornbelt | 18.3% |
| Michoacan 21 | 14.2% |
| KSX 2301 | 7.3% |
| AN1 x AN2 | 7.4% |
| Obregon Sequia 8332 | 6.9% |
| Obregon Sequia 8322 | 7.0% |
| ARD Reduced Tassel C6 | 6.4% |
| Crosses of Pops 62, 64, 66 | 18.1% |

Later introductions were Pepitilla Brazil 2482; Sinaloa 31, and Nuevo Leon Gpo 2. (total introgression about 20%)

Final percentage by ecology is:

| | |
|------------------|-------|
| Lowland tropical | 60.1% |
| Subtropical | 21.6% |
| Temperate | 18.3% |

4.3 Breeding history of DTP2

After the major introgression of components, the new Pool (C₀ formed in 1991A cycle) entered a half-sib mixing period for 4 cycles, and in 1993A S1's were formed for the first time.

4.4 Composition of DTP2

The introgression of new material into DTP was made by crossing new and proven source materials (on basis of *per se* performance and on the basis of the performance of the cross between the source and DTP1, evaluated under drought) with the latest version of DTP1, and an elite set of S1 families identified from those under test internationally (but based on Tlaltizapan performance).

| Sources | Origin | % used |
|-------------------------------------|-------------|--------|
| 1. Pool 18 Sequia C1, best all, F2 | PR90A-651# | 4.0 |
| 2. Pool 16 Sequia C1, best all, F2 | PR90A-635# | 4.0 |
| 3. Pool 26 Sequia C1, best all, F2 | TL90A-1673# | 4.0 |
| 4. La Posta Sequia C1, best all, F2 | TL90A-1672# | 4.0 |

| | | |
|--------------------------------------|-----------------|-----|
| 5. Sint. de S3's, La Posta Seq., CO | TL89B-6651-1# | 4.0 |
| 6. Sint. de S3's, Pool 26 Sequia | TL89B-6652-1 | 4.0 |
| 7. Mezcla S3's de Pool 18, CO | TL89B-6648 | 3.2 |
| 8. Pioneer 3165, F2 | TL87B-6604-6# | 4.0 |
| 9. TS6 C1, mejor rend SS, F2 | PR90A-662# | 4.0 |
| 10. KSX 2301 | Thailand | 4.0 |
| 11. TL8421 x Latente. Burkina Faso | TL90A-16(69x68) | 4.0 |
| 12. DTP1 C2 x Tabloncillo Sinaloa 31 | TL87B-6644-2x8 | 4.0 |
| 13. CG 4419 white, F1 | CIBA-Gy Sth Afr | 4.0 |
| 14. R201, F1 | Harare, Zimb. | 4.0 |
| 15. Pool SPE C4, best all, F2 | PR89B-5623# | 4.0 |
| 16. Tamaulipas 25 x DTP1 C3 | TL88B-66(30X24) | 4.0 |
| 17. FRB73 x FRMo17 | Ill. Fd. Sds 86 | 4.0 |
| 18. KI14 x DTP1 C4 | TL89B-6641-22x1 | 4.0 |
| 19. [(SD10 x H28)x K55] x DTP1 C4 | TL89B-6641-23x1 | 4.0 |
| 20. Experimental hybrid #5 | CIBA-Geigy 89 | 5.3 |
| 21. Experimental hybrid #6 | CIBA-Geigy 89 | 2.7 |
| 22. G4734 | CIBA-Geigy 89 | 5.3 |
| 23. CSM 8804 (H-430) | Obregon '89 | 2.7 |
| 24. Ob. Seq. 8349 x Ob. Seq. 8332 | TL90A-16(66x67) | 5.3 |
| 25. SPMAT C4, best all, F2 | TL90A-1652# | 2.7 |

Each of these components was crossed to:

| | | |
|------------------------------|-------------|----|
| 1. Bulk of DTP C5 elite S1's | TL89B-6642# | 60 |
| 2. DTP C5 (240 fams), F1 | TL90A-1638# | 40 |

Crosses were made in the 1990B summer season. The number of crosses from each component, as a percentage of the total that formed this population, are listed alongside the origin in the list above.

The contribution of new germplasm to DTP2 by ecological class is as follows:

| | |
|--------------------------|-----|
| 1. DTP1 (various cycles) | 58% |
| 2. Lowland tropical | 27% |
| 3. Subtropical | 7% |
| 4. Temperate | 8% |

Combining the adaptation of DTP1, which contributed 58% of the germplasm to DTP2, gives the following adaptation breakdown for DTP2:

| | |
|------------------|-----|
| Lowland tropical | 65% |
| Subtropical | 15% |
| Temperate | 20% |

5. Total contribution of landrace materials to DTP1 and DTP2

When DPT2 was formed, two of the 25 components used in this introgression into DTP1 were drawn directly from the Germplasm Bank (Tabloncillo Sinaloa 31, and Tamaulipas 25). Thus 15% of the germplasm used in DTP1 and 11% used in DTP2 could be directly traced to Germplasm Bank accessions.

6. Adaptation

We anticipate that the adaptation of DTP1 will be oriented towards the lowland tropics, while that of DTP2 will be modified to suit the mid-elevation tropics. This is not the case at present.

7. Summary of Breeding Schemes used to date

| EcologyGrain | Maturity Type(days,LT) | Breeding scheme | Cycles completed | Disease (R) or (S) |
|--------------|------------------------|------------------------------------|------------------|---|
| DTP1 | | | | |
| LT/ST Mixed | 110 | 4 HS/Rec.S1 2 stage Intern'l | 1.5 | D. mildew (PR) <i>P. sorghi</i> (PR) Streak (S) Earots (PR) |
| DTP2 | | | | |
| ST/LT Mixed | 112 | 3 HS/R 2 stage Intern'l | 0.5 | D. mildew (PR) <i>P. sorghi</i> (LPR) Streak (S) Earots (PR) |

LT = Lowland tropical; ST = subtropical

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Drought Lecture Outlines

Lecture 8: Determining the Worth of Secondary Traits

Evaluation of the adaptive value of secondary traits begins with an assessment of its relationship to productivity in a field environment, an essential step because of the opportunity cost of a breeder's resources (Blum 1988).

Physiologists have been guilty in the past of recommending many traits which take far too long to measure and have little or no measurable effect on productivity.

In many cases physiologists have recommended selecting for specific traits on the basis of correlation analysis. Physiologists have used (and misused) correlation analyses to demonstrate associations between productivity and the expression of a trait. If the cultivars used in the study include poorly-adapted materials or unimproved germplasm from diverse genetic backgrounds, correlation analysis can often be misleading.

Some secondary traits, such as osmotic adjustment or leaf rolling may vary in their importance and expression with phenology, and it is important that they be observed at several times in the ontogeny of the crop so that the maximum degree of association with productivity can be observed.

Another problem with correlation analysis is that outlying values have a disproportionately large effect on the size of the correlation coefficient. This often suggests relationships where there are in fact, none.

Finally, in some cases, relationships between two variables are not linear. A good example is that between ASI and grain yield. When the scientist is dealing with large numbers of data points, he/she frequently omits to plot the data to see the underlying relationship. Linear correlations may well be increased in magnitude by appropriate transformations in this case. The linear correlation between ASI and grain yield has been observed to increase from -0.5 to -0.85 when ASI data have been log (square root) transformed (Bolanos and Edmeades, 1993).

Whenever phenotypic correlations are used to determine underlying associations between characters, care must be exercised to ensure that the associations are not simply a result of environmental differences, for example, in plant height or maturity. Ideally we would like to know the genetic correlation between the traits (see Falconer, 1960). This requires an estimate of environmental variance through replicated trials, and this is only sometimes available.

Phenotypic correlations are still one quite important means of estimating the adaptive worth of traits, and when used with care can help the breeder determine the association between productivity and a secondary character.

Data have been combined from many progeny trials in Table 1 to provide estimates of linear correlation coefficients between grain yield and a number of traits (see Table 1). The data for ASI are untransformed. An important question that should always be asked is: to what extent does selection in single row plots affect my results? Note that leaf erectness score in Table 1 is not associated with productivity. Is this because genotypes are being evaluated in single row plots, and if an erect leaved line is alongside and aggressive lax leaved type, it may be penalised in the subsequent competition for light? Slow root growth would similarly be penalised by aggressive rooting types. These differences due to the

outcome of competition among single row plots, would not hold up in large plots, and are therefore not useful.

Isogenic lines

A better but more costly way of determining the adaptive worth of a trait involves the development of isogenic lines. These are, however, never completely isogenic, and can continue to segregate for traits other than the one under study. Isogenic line comparisons work best for characters controlled by only a few genes, but the comparisons are only ever conducted in a few genetic backgrounds, and their general applicability is therefore questionable.

Divergently-selected sub-populations

Although these do not provide as precise a test of the adaptive worth of a specific trait as do truly isogenic lines, they can be produced quite rapidly, and represent a comparison of a trait present in a larger or smaller degree in two subpopulations differing principally in the degree of expression of the trait under question.

Population improvement methods allow the formation of sub-populations from the "best" and "worst" fraction of the population for the trait in question. For example, suppose the adaptive merit of large and small tassel size is to be examined in a maize population of 250 S₁ families grown out in a replicated yield trial as part of an on-going improvement program. Remnant seed of the 10 families with largest tassels are intercrossed and the resulting synthetic compared under drought stress with the bulk synthetic of all S₁ families and a similar synthetic made up of crosses among 10 families with the smallest tassels.

Considerable care must be exercised to ensure that the two fractions ("best" and "worst") are also compared with the cycle bulk, and that they do not differ by more than 1-2 days in mean male flowering date, or in any other trait which may affect their performance and which is not linked to the trait under study. Normally, the synthetics produced in this manner from divergent selection within a single cycle of recurrent S₁ selection, must be advanced to F₂ for a fair comparison with the cycle bulk or with other checks.

Within a recurrent selection scheme, such divergent synthetics for important secondary traits, or based on performance in specific selection environments (e.g., well-watered versus severe-stressed) can be produced each time the S₁ families are tested. Over the space of 3 cycles of recurrent selection it is therefore possible to obtain "replications" of the comparison between "best" and "worst", each replicate coming from a specific selection cycle. An example of this can be observed in the evaluation trials 1630, 1631 and 1632, currently in the field in Tlaltizapan. Here we will measure the original trait on which the synthetic was based (and thus get an idea of realized heritability, the ratio of actual difference/expected difference for the trait. Grain yield will provide a measure of the worth of the trait in terms of grain yield. Since it is easier to make progress selecting for low yield than for high yield, the divergent synthetics should always be compared to the cycle bulk.

Thus:

- the progeny trial provides information on genetic variability and heritability of tassel size, and the ease and speed of measurement of the trait in a breeding population:

- the trial of synthetics tests the adaptive value of tassel size and estimates realized heritability from a single cycle of selection.

Results from CIMMYT studies

As part of a study of selection methodology, we have formed divergently-selected synthetics for an array of traits in one or more of the selection cycles of each of the elite populations (La Posta Sequia; Pool 26 Sequia, Pool 18 Sequia, Pool 16 Sequia, and TS6). These traits are:

- Relative leaf and stem elongation
- Canopy-air temperature differentials
- Osmotic potential under drought
- Predawn leaf water potential
- Leaf death scores
- Leaf chlorophyll concentration
- Leaf erectness score
- Tassel branch number
- Anthesis-silking interval

We have also used the "ideotype" that we have defined in selecting superior families for recombination and developed divergently selected synthetics named "best all characters" or "worst all characters".

The first fully-replicated evaluation of these synthetics is currently underway in the field in Tlaltizapan at present.

Previous evaluations, usually conducted under two-three water regimes and in two replications, have been conducted on a limited range of synthetics, usually derived from a single set of S₁ families (that is, from within a single selection cycle). These trials have been:

88A: 1608 (evaluation of 14 synthetics from C0 of Pool 26 Sequia in 3 row plots, 3 replications, 3 water levels)

89A: 1608 (evaluation of 30 synthetics from C1 or C2 of Pool 18 Sequia and Pool 18 Sequia in 3 row plots, 2 replications, 3 water levels)

90A: 1610: Evaluation of divergent selection for predawn water potential and several other single-direction selections in La Posta Sequia and Pool 26 Sequia under line source.

1611: 14 synthetics from TS6 C0 under line source

1612: 6 divergent synthetics from Pools 16, 18, for osmotic concentration

Some of the results from these are presented below:

Tables 2 and 3: indicate the realised heritabilities for specific traits used in divergent selection. Show that the traits associated with partitioning and morphology are highly heritable, but that those associated with changed plant water status or N status are not.

From studies such as this, based on selection made in small single row plots, we can say that the following about the realized heritability of traits:

High

- ASI
- Tassel size
- Leaf erectness

Moderate

- Osmotic concentration
- Leaf death score

Low

- canopy temperature differential
- relative leaf and stem elongation rate
- predawn leaf water potential
- leaf chlorophyll concentration

Tables 4 and 5 illustrate the *adaptive value* of the trait in question, under two levels of drought. Much of the benefit of "best all" over "worst all" seems to come from changes in ASI. Cool canopy selections appear to perform quite well, as do erect leaved types, high chlorophyll concentration selections, and especially small tasseled types. Strangely, the selection for delayed foliar senescence is among the poorer, and the best elongation rates were associated with lower grain yields.

Data from "best all" and "worst all" have been graphed as a stability diagram, (Fig. 1) and shows consistent performance of the best selection over the worst at all yield levels. Note that all of these selections are made *within* selection cycles.

The "best all" and "worst all" selections of La Posta Sequia and Pool 26 Sequia were tested at 17 locations in the first set of Drought Network Trials (Table 6), and showed consistent performance of the best over the worst selections in cycle 1. (see analysis of variance, Table 7). When graphed as stability graphs against the mean yields of each site, their response was quite consistent (Fig. 2 and 3, attached).

Conclusions

The preferred method of selection involves a combination of direct and indirect selection using traits whose associations with productivity have been established to augment selection for yield. A simple selection index made up of standardized values of desirable secondary traits and grain yield under stressed and unstressed conditions with appropriate weights provides one relatively easy way to incorporate data from secondary traits into the selection process. This seems appropriate, since other researchers have concluded that there seems to be no single plant trait conferring drought resistance, but that superior performance is associated with a combination of traits (Blum, 1988; Bolaños and Edmeades, 1993a).

The procedure outlined resembles ideotype breeding, where breeding efforts are directed towards selecting a plant type consistent with best available knowledge of crop physiology (Rasmusson, 1987). It differs from it in a minor way in that the breeder rarely has a "model" plant in mind, but rather seeks to augment traditional selection for yield by using traits which show direct associations to productivity, or which are less influenced by inter-cultivar competitive effects in small plots than is grain yield.

It is noteworthy, however that Rasmusson (1987), in a recent review of ideotype breeding, suggested that where enhanced yield potential is a major breeding goal the breeder might consider making 75% of the breeding effort yield-based and 25% trait oriented. This advice may well apply to those who seek to select for increased grain yield under moisture stress, since the farmer will be far less impressed by how his crop obtained its yield than by the yield itself.

Thus, within CIMMYT's maize program, selection is now for:

High intensity

- High shelled grain weight over all moisture regimes
- short ASI
- reduced barrenness under stress
- constant days to flower

Moderate intensity

- delayed canopy senescence
- small tassel size
- maintained kernel size during grain filling under stress
- unrolled, dark green leaves

Mild intensity

- upright leaves
- reduced lodging under stress
- good husk cover
- reduced canopy temperature (when measured)

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*** Recommended reading**

**** Placed on reference in the library**

Table 1. Linear correlation coefficients ($P < 0.01$) between grain yield under severe drought stress and various traits, determined from 905-2449 S₁ progenies from five lowland tropical maize populations.

| | n | r |
|-----------------------------------|------|-------|
| Ears per plant | 2449 | 0.77 |
| Kernels per ear | 2227 | 0.50 |
| Kernels per plant | 2227 | 0.90 |
| Kernel weight | 2227 | 0.46 |
| Days to 50% anthesis | 2449 | -0.40 |
| ASI | 2449 | -0.53 |
| Leaf and stem extension rate | 1321 | 0.10 |
| Canopy-air temperature difference | 1089 | -0.27 |
| Leaf rolling score | 2033 | -0.18 |
| Leaf erectness score | 2033 | NS |
| Leaf death score | 2449 | -0.11 |
| Chlorophyll concentration | 905 | 0.17 |
| Tassel branch number | 1793 | -0.16 |
| Plant height | 2449 | NS |

Scores: 1 = unrolled, upright or green
5 = rolled, lax or dead

Table 2. Realised gains for traits in divergently selected experimental synthetics of Pool 26 Sequia C₀ formed from the best and worst 10 out of 222 S₁ families for various morphological and physiological traits, when evaluated under well-watered and droughted conditions in Tlaltizapan, Mexico, 1988.

| Characteristic | Cycle | Best | Worst | F(tmt) | LSD |
|--|-------|-------|-------|--------|------|
| Leaf death score | 4.67 | 4.04 | 5.54 | *** | 0.59 |
| Photo-oxidation score | 3.83 | 3.33 | 4.41 | *** | 0.63 |
| Ear leaf chlorophyll (ug/cm ²) | 56.96 | 59.96 | 54.36 | *** | 4.13 |
| Leaf erectness score | 3.00 | 2.56 | 3.33 | NS | 0.59 |
| Canopy temperature (°C) | 0.86 | 0.52 | 0.22 | NS | 1.78 |
| Leaf & stem expansion (%) | 57.90 | 53.89 | 60.91 | NS | 5.82 |

*** Difference between best and worst synthetics for trait significant at P < 0.001

NS Not significant at P < 0.001

LSD is at P = 0.05

Score of leaf death scale 1-9, 1 being most green

Score of photo-oxidation scale 1-9, 1 being least affected

Score of leaf erectness scale 1-5, 1 being most erect

Canopy temperature is $T_{leaf} - T_{air}$

Canopy and leaf expansion is a percentage of well-watered control

Table 3. Realised gains for traits in divergently selected experimental synthetics of Pool 18 Sequia C₀ and TS6 C₀, formed from the best and worst 10 out of 222 S₁ families for various morphological and physiological traits, when evaluated under well-watered and droughted conditions in Tlaltizapan, Mexico, 1988.

| Trait | Cycle | Best | Worst | Heritability |
|--|-------|-------|-------|---------------|
| <u>Pool 18 Sequia</u> | | | | |
| Leaf & stem ext. (%) | 62.1 | 65.3 | 75.4 | non-heritable |
| Canopy temp. diff (°C) | -0.98 | -1.78 | -1.78 | non-heritable |
| Leaf death score | 3.84 | 3.70 | 4.03 | heritable |
| Ear leaf chlorophyll (ug/cm ²) | 52.6 | 49.3 | 47.8 | non-heritable |
| ASI | 5.5 | 3.0 | 11.5 | heritable |
| TBN | 18.8 | 12.9 | 22.9 | heritable |
| <u>TS6 C₀</u> | | | | |
| Leaf & stem ext. (cm) | 32.3 | 33.4 | 36.9 | non-heritable |
| Leaf erectness score | 3.63 | 2.75 | 3.88 | heritable |
| Leaf death score | 3.29 | 2.61 | 3.81 | heritable |
| Ear leaf chlorophyll (ug/cm ²) | 63.0 | 60.7 | 64.4 | non-heritable |
| ASI | 7.9 | 0.4 | 15.9 | heritable |

Score of leaf death scale 1-5, 1 being most green
 Score of leaf erectness scale 1-5, 1 being most erect

Canopy temperature is $T_{leaf} - T_{air}$
 Canopy and leaf expansion is a percentage of well-watered control

Table 4. Grain yield (t/ha) of maize synthetics selected bidirectionally for individual traits and groups of traits from a late (Pool 26) and and early maturing (Pool 18) lowland tropical population, when evaluated under irrigation and drought stress in Tlaltizapan, Mexico, 1988-89

| | Pool 26 | | Pool 18 | |
|------------------------------------|-------------|-------------|-------------|-------------|
| | Irrigated | Stress | Irrigated | Stress |
| Cycle 0 | 4.93 | 1.58 | 2.85 | 0.90 |
| Best for "all" | 5.19 | 2.37 | 3.02 | 1.44 |
| Worst for "all" | 3.72 | 0.60 | 2.30 | 0.96 |
| Shortest ASI ^a | 4.67 | 1.59 | 3.08 | 1.74 |
| Longest ASI ^a | 3.50 | 0.86 | 1.79 | 1.10 |
| Cooler T _c ^b | 4.20 | 1.46 | - | - |
| Warmer T _c ^b | 3.95 | 1.09 | - | - |
| Erect leaves | 4.42 | 1.58 | 3.23 | 1.63 |
| Lax leaves | 3.70 | 1.13 | 2.68 | 1.42 |
| High leaf chlorophyll ^c | - | - | 2.93 | 1.58 |
| Low leaf chlorophyll ^c | - | - | 2.51 | 1.18 |
| Low TBN ^d | - | - | 3.00 | 1.90 |
| High TBN ^d | - | - | 2.43 | 1.41 |
| LSD (P=0.05) | 1.07 | 1.12 | 0.75 | 0.82 |

^a Anthesis-silking interval observed under moisture stress.

^b Canopy temperature measured under moisture stress.

^c Chlorophyll content (mg/cm²) of ear leaf under moisture stress.

^d Primary tassel branch number under irrigation.

Table 5. Grain yield (kg/ha) of experimental synthetics (ES) formed from Pool 26 Sequía C₀ and evaluated under well watered and droughted conditions in Tlaltizapan, Mexico, 1988.

| Experimental synthetic | Moisture stress regime | | |
|--------------------------------------|------------------------|---------|------|
| | Well-watered | Drought | |
| Pool 26 Sequía C ₀ | | 4934 | 1582 |
| Best for all characters | | 5188 | 2370 |
| Worst for all characters | | 3722 | 598 |
| Best yield under drought | | 4589 | 1997 |
| Best yield under well-watered | | 5137 | 1073 |
| Best ASI | | 4670 | 1588 |
| Worst ASI | | 3503 | 862 |
| Best leaf & stem expansion, drought | | 4225 | 1477 |
| Worst leaf & stem expansion, drought | | 4891 | 1737 |
| Best "stay green", drought | | 4148 | 762 |
| Worst "stay green", drought | | 3844 | 1045 |
| Lowest canopy temperature | | 4202 | 1461 |
| Highest canopy temperature | | 3946 | 1092 |
| Erect leaves | | 4420 | 1577 |
| Lax leaves | | 3696 | 1127 |
| F treatment (19, 38 df.) | | ** | NS |
| LSD (P=0.05) | | 1067 | 1122 |
| C.V. (%) | | 14.9 | 50.1 |

** Significant at P=0.05; NS = not significant

TABLE 6

DEVT LATE Set: Means and across location regressions of grain yield of each entry on mean grain yield of each site.

| Ent. No/Pedigree | Mean yield | Inter-cept | Slope | R2 | Freg | Anth. date | ASI (days) | Ears/plant |
|---------------------|------------|------------|-------|------|--------|------------|------------|------------|
| La Posta Seq. C1F2 | 3.25 | -0.37 | 1.17 | 0.92 | 161.96 | 69.55 | 3.14 | 0.87 |
| La Posta Seq. BA | 3.15 | -0.10 | 1.05 | 0.95 | 316.48 | 68.87 | 1.78 | 0.90 |
| La Posta Seq. WA | 2.89 | -0.29 | 1.03 | 0.86 | 94.09 | 70.83 | 3.22 | 0.80 |
| La Posta Seq. Bsync | 3.20 | 0.08 | 1.01 | 0.94 | 256.90 | 69.29 | 1.65 | 0.89 |
| La Posta Seq. BY,SS | 2.97 | -0.44 | 1.10 | 0.89 | 126.09 | 69.45 | 1.94 | 0.88 |
| Pool 26 Seq. C1F2 | 2.97 | 0.19 | 0.90 | 0.97 | 465.34 | 66.64 | 2.62 | 0.85 |
| Pool 26 Seq. BA | 3.13 | -0.02 | 1.02 | 0.96 | 386.01 | 66.07 | 2.90 | 0.90 |
| Pool 26 Seq. WA | 2.60 | -0.27 | 0.93 | 0.89 | 117.35 | 66.52 | 3.66 | 0.78 |
| Pool 26 Seq. Bsync | 2.92 | 0.06 | 0.92 | 0.92 | 162.26 | 66.36 | 2.05 | 0.89 |
| Pool 26 Seq BY, SS | 3.13 | 0.03 | 1.00 | 0.91 | 149.40 | 65.82 | 1.72 | 0.90 |
| DTP1, C4 | 3.13 | 0.00 | 1.01 | 0.87 | 102.50 | 63.88 | 2.42 | 0.90 |
| Tuxpeno Seq. C6 | 3.21 | 0.51 | 0.87 | 0.85 | 85.20 | 67.97 | 1.32 | 0.91 |
| Tak Fa 8536 | 3.33 | 0.39 | 0.95 | 0.94 | 215.87 | 67.45 | 2.83 | 0.92 |
| Palmira 8425 | 2.82 | -0.07 | 0.93 | 0.92 | 168.36 | 66.95 | 2.59 | 0.89 |
| Check 1 | 3.56 | 0.50 | 0.99 | 0.68 | 31.84 | 68.47 | 2.42 | 0.91 |
| Check 2 | 3.33 | -0.20 | 1.14 | 0.91 | 148.38 | 65.99 | 2.58 | 0.90 |
| Number of sites: | 17 | 17 | 17 | 17 | 17 | 14 | 13 | 16 |

Notes: All check entries from individual sites are combined in this analysis

Table 7. Combined analysis of variance of grain yield for late varieties in Drought Experimental Variety Trial, with preplanned comparisons between cycle bulks and best and worst selections. Data from check entries have been deleted from the data set.

| Source | Df | Sums of Squares | Mean Squares | F | Prob>F |
|-----------------------|-----|-----------------|--------------|----------|--------|
| Location | 16 | 572.4688 | 35.7793 | 130.96** | 0.0001 |
| Variety | 13 | 8.4972 | 0.6536 | 2.39** | 0.0051 |
| La Posta Seq C1 vs BA | 1 | 0.0901 | 0.0901 | 0.33 | 0.5665 |
| La Posta Seq BA vs WA | 1 | 0.5363 | 0.5363 | 1.96 | 0.1627 |
| Pool 26 Seq C1 vs BA | 1 | 0.2322 | 0.2322 | 0.85 | 0.3576 |
| Pool 26 Seq BA vs WA | 1 | 2.3718 | 2.3718 | 8.68** | 0.0036 |
| Others | 9 | 5.2669 | 0.5852 | 2.14** | |
| Location x Variety | 208 | 56.8271 | 0.2732 | 2.66** | |
| Pooled Error | 561 | 230.1747 | 0.1023 | | |

** Denotes significant at P=0.01

Fig. 1.

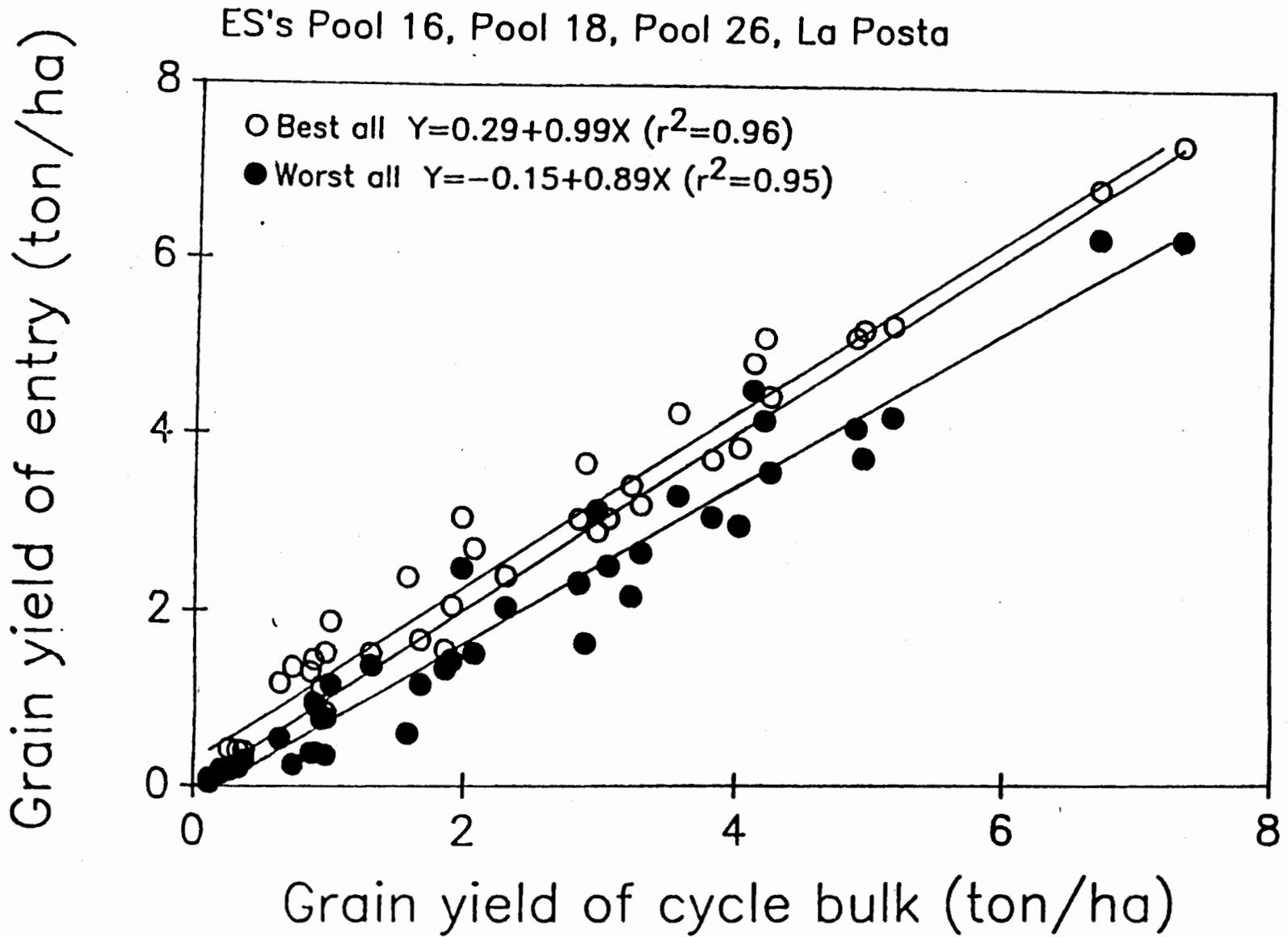


Fig. 2 Joint linear regressions of individual site yields on mean site yields for best and worst selections based on all traits related to drought tolerance for the population La Posta Sequia C1

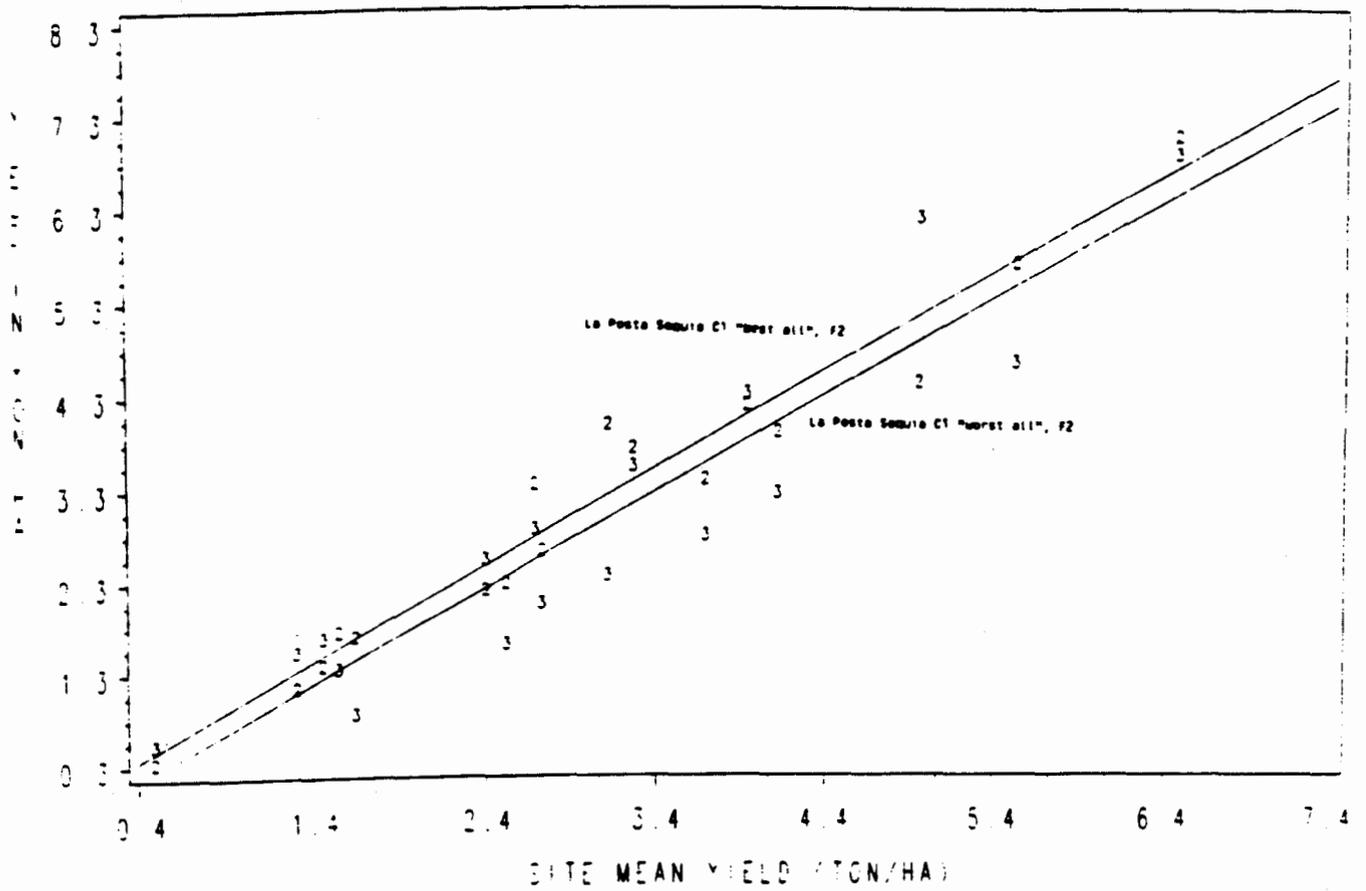
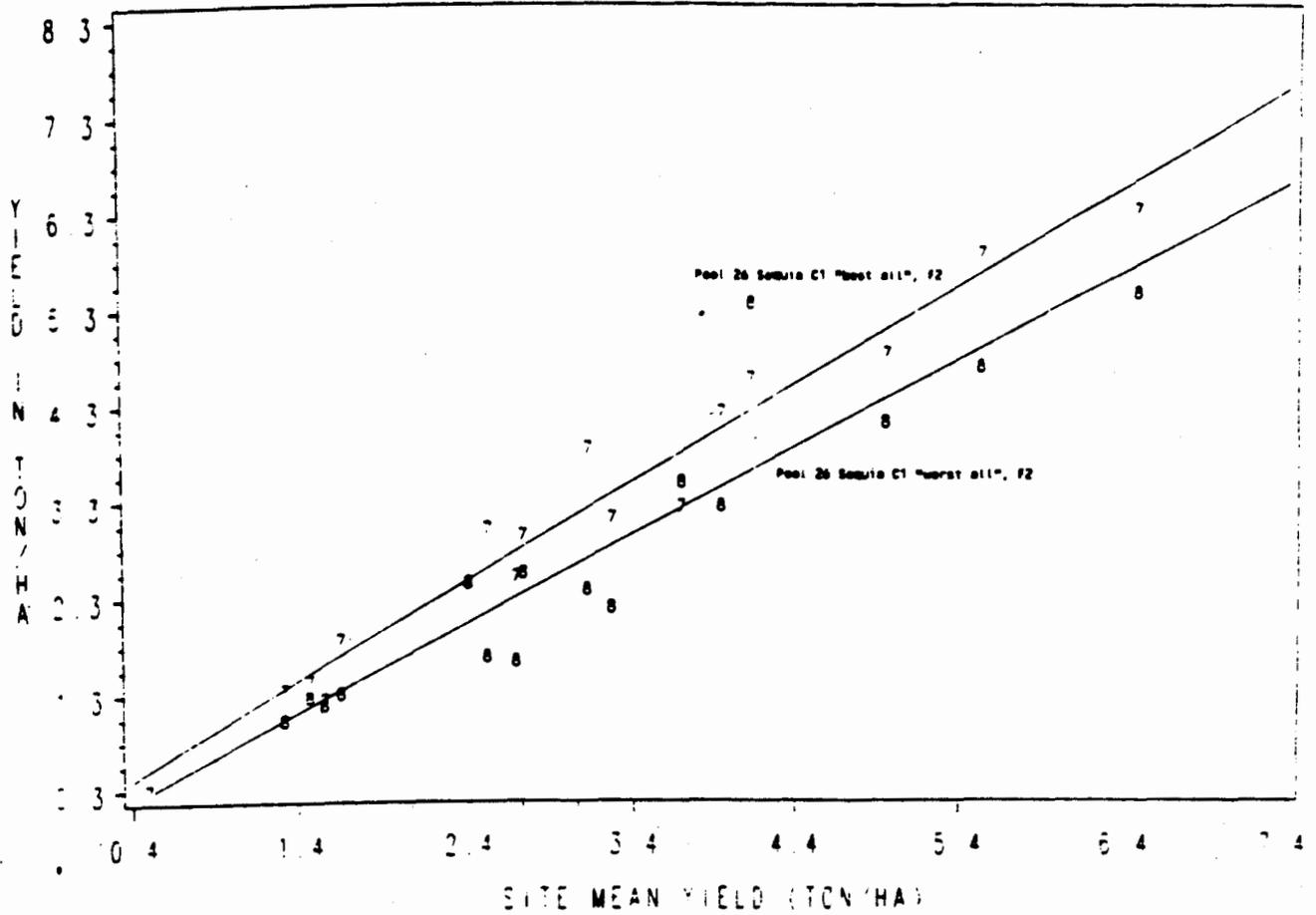


Fig. 3. Joint linear regressions of individual site yields on mean site yields for best and worst selections based on all traits related to drought tolerance for the population Pool 26 Sequia C1



Value of Selection for Osmotic Potential in Tropical Maize

J. Bolaños and G. O. Edmeades

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ABSTRACT

Osmotic adjustment, the lowering of osmotic potential (ψ_s) under drought, is considered a desirable component of drought tolerance since it has been shown to maintain turgor, growth, and photosynthesis at lower water potentials. This study attempted to determine the relative merits of selecting for osmotic adjustment and low ψ_s under drought in lowland tropical maize (*Zea mays* L.). During 3 yr of trials in Mexico that examined 204 maize landraces, elite open pollinated populations (OPPs), experimental synthetics (ESs), and hybrids, osmotic adjustment averaged 0.10 MPa and ranged from 0.54 to -0.23 MPa. Only 7% of genotypes showed a capacity to adjust by more than 0.40 MPa, a level considered minimum for them to serve as sources for the trait. Variation for ψ_s under drought for 222 to 225 S₁ progeny of three maize populations ranged from -1.04 to -1.79 MPa. Divergent selection within each population for high and low ψ_s under drought resulted in the formation of ESs which differed in ψ_s by an average of 0.17 MPa when grown under a line source moisture gradient. Realized heritability for ψ_s averaged 0.46. The ESs selected for high and low ψ_s did not yield differently from the cycle bulk, suggesting little adaptive value for ψ_s . Correlations between several traits indicative of performance under drought and osmotic adjustment or ψ_s under drought generally were weak, inconsistent, and non-significant. These studies suggest that selecting for increased capacity to adjust osmotically or low ψ_s under drought does not appear advantageous in lowland tropical maize.

DURING WATER STRESS some plant species can increase the concentration of their cell sap solutes over those of well watered controls. Such osmotic ad-

Maize Physiologists, Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT), J. Bolaños, 12 Calle 1-25, Zona 10, Edificio Geminis, Torre Norte, Oficina 1606, Guatemala, Guatemala; and G.O. Edmeades, Apdo. Postal 6641, México D.F., 06600, México. Received 6 Sept. 1990. *Corresponding author.

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justment has been considered a desirable component of drought tolerance since it has been shown to maintain or increase turgor, stomatal conductance, photosynthesis, expansive growth, and soil-water extraction, and to decrease rates of leaf senescence in the face of increasing moisture stress (13). High capacity for adjustment has been used as a direct selection criterion in several crops under improvement for drought tolerance (3,9,14). However, in assessing the value of osmotic adjustment, results are often confounded by genetic differences among genotypes for other traits. An effective test of the adaptive value of osmotic adjustment can be found by comparing genotypes differing in ψ_s in an otherwise nearly isogenic background (3,5). In one of the few studies of this kind, Grumet et al. (9), working with barley (*Hordeum vulgare* L.) isopopulations that differed in ψ_s by only 0.10 MPa, reported a significant reduction in productivity associated with low ψ_s .

In maize (*Zea mays* L.), genotypic variation for osmotic adjustment has been reported (17,18), with adjustment of up to 0.4 MPa under slowly developing water deficits in field studies (1,6), and up to 0.5 MPa under controlled conditions in pots (2,21). The study reported here was performed within the framework of CIMMYT's (International Maize and Wheat Improvement Center) on-going breeding program designed to improve drought tolerance in maize adapted to the lowland tropics (4). The objectives were to as-

Abbreviations: ASI, anthesis-silking interval; DAP, days after planting; ESs, experimental synthetics; EPP, ears per plant; LDS, leaf death score; LRS, leaf rolling score; masl, meters above sea level; OPPs, open pollinated populations; PV, pressure-volume; RWC, relative water content; h^2 , realized heritability; S, selection differential; R, response to selection; Ψ , total leaf water potential; and ψ_s , osmotic potential.

certain the relative merits of selecting for osmotic adjustment and low ψ_s under drought as part of a conceptualized drought tolerant maize ideotype. Specific objectives were:

1. To develop a simple, rapid, and effective method for measuring ψ_s in maize selection programs.
2. To determine the extent of genetic variability for ψ_s , its adjustment in response to drought, and its adaptive value under stress in a wide array of temperate and tropical maize germplasm, including landraces from semi-arid environments, open pollinated populations (OPPs), experimental synthetics (ESs), and hybrids.
3. To determine the adaptive value and realized heritability of ψ_s , by developing ESs differing only in ψ_s by divergent selection within three lowland tropical maize populations under improvement for drought tolerance.

MATERIALS AND METHODS

Field Site and Crop Husbandry.

Maize under selection for adaptation to drought was planted in November during the dry winter seasons of 1987–1988, 1988–1989 and 1989–1990 at the CIMMYT Experimental Station in Tlaltizapan, Mexico [18°N, 940 m above sea level (masl)]. During this season (November – April) there was no appreciable rainfall so the crop depended almost completely on stored and applied water. Short-wave radiation increased seasonally from 18.0 to 24.0 MJ m⁻² d⁻¹, air vapor pressure varied from 1.0 to 1.2 kPa, daily temperature maxima and minima averaged 32 and 12°C, and Penman ET₀ increased seasonally from 4 to 9 mm d⁻¹. Vegetative growth was initially slow due to cool temperatures, but grainfilling was hastened as temperatures rose later in the season, so that grainfilling accounted for only 40% of the total crop duration. The soil is a calcareous vertisol 1.3 to 1.8 m in depth (isothermic Udic Pellustert) with a pH of 7.6, and unadapted germplasm received one to two foliar applications of a 1% FeSO₄ aqueous solution to alleviate symptoms of lime-induced chlorosis. Fertilizer was applied as 150:21.8 kg N:P ha⁻¹, with half the N and all the P being applied at planting and the remaining N sidedressed 40 d later. The crop was kept free from weeds, insects, and diseases.

Germplasm Examined for Osmotic Potential.

This comprised (Table 1):

1. Sources: A range of genotypes were screened as potential sources for osmotic adjustment and other drought adaptive traits. During the 3 yr of trials we examined 204 genotypes. 39% of these were unimproved cultivars and landraces from CIMMYT's germplasm bank collected from semi-arid sites in Mexico and Central America, which were under 1200 masl and received less than 400 mm annual rainfall: 19% were elite lowland tropical CIMMYT OPPs as cycle bulks or ESs, 12% were temperate F₁ hybrids, 10% were the F₂s of the F₁s, and 20% were crosses between the foregoing classes and a population formed from recognized genotypes with good performance under drought. These genotypes were sampled for ψ_s under drought and well watered conditions near anthesis after the crop had shown signs of moisture stress.
2. The S₁ progeny (first generation inbred): These were formed from three elite CIMMYT lowland tropical maize populations under recurrent selection for improved drought tolerance in S₁ selection schemes. These were: 222 S₁s from Pool 16 Sequia C₁ (P16S C₁), a tropical early white dent; 222 S₁s from Pool 18 Sequia C₁ (P18S C₁), a tropical early yellow flint/dent; and 225 S₁s from Tuxpeño Sequia C₆ (TS6 C₆), a tropical late white dent whose development has been described elsewhere (7). These were sampled for ψ_s under drought near anthesis.
3. The S₃ progeny (third generation inbred): These were formed from two elite CIMMYT lowland tropical maize populations under recurrent selection for improved drought tolerance. These were: 49 S₃s from Pool 26 Sequia C₀ (P26S C₀), a tropical late yellow dent population; and 41 S₃s from La Posta Sequia C₀ (LPS C₀), a tropical late white dent population. These were sampled for ψ_s under drought near anthesis.
4. The ESs at the F₁ stage: These were formed by recombining 10 S₁ progeny of the above populations selected divergently for high and low ψ_s under drought and their respective population bulks, also at the F₁ stage. These were sampled for ψ_s along a line source moisture gradient at regular intervals throughout the season.

Low ψ_s under drought, as well as capacity for high osmotic adjustment, were considered desirable traits as part of a conceptualized drought tolerant ideotype of maize which in-

Table 1. Description of trials in which ψ_s was determined for maize under selection for drought tolerance at Tlaltizapan, Mexico, during the winter seasons of 1987–1988, 1988–1989, and 1989–1990. WW refers to well watered conditions, and SS to severe stress; DAP is days after planting.

| Trial | Entries | Reps | Plot size | Moisture levels sampled | Dates sampled | Anthesis date | Plants sampled |
|--|---------|------|-----------|-------------------------|-----------------------|---------------|----------------|
| | | | | | | | |
| Sources for osmotic adjustment | | | | | | | |
| 1 | 60 | 2 | 3R†2.5m | WW-SS | 68,87 | 81 | 10 |
| 2 | 72 | 2 | 3R 2.5m | WW-SS | 86,96 | 80 | 10 |
| 3 | 72 | 2 | 3R 2.5m | WW-SS | 89 | 81 | 10 |
| S ₁ Progeny (1988–1989) | | | | | | | |
| 4 | 222 | 2 | 1R 2.5m | SS | 84 | 76 | 6–8 |
| 5 | 222 | 2 | 1R 2.5m | SS | 78 | 73 | 6–8 |
| 6 | 225 | 2 | 1R 2.5m | SS | 96 | 92 | 6–8 |
| S ₃ Progeny (1988–1989) | | | | | | | |
| 7 | 49 | 2 | 1R 2.5m | SS | 82 | 87 | 6–8 |
| 8 | 41 | 2 | 1R 2.5m | SS | 82 | 91 | 6–8 |
| S ₁ 's during recombination (1989 summer) | | | | | | | |
| 9 | 60 | 1 | 1R 5.0m | WW | 38,52,66 80,94,101 | 68 | 10 |
| ES's during evaluation (1989–1990) | | | | | | | |
| 10 | 9 | 2 | 3R 3.0m | 4 Hydric regions | 57,71 87,98 | 81 | 10 |

† Number of rows.

cluded other adaptive physiological and morphological traits measured simultaneously in the same nurseries (4).

Source and Progeny Evaluation Trials.

Water was applied by sprinkler for germination, and thereafter by furrow irrigation. Two moisture regimes were used for measuring ψ_s in trials evaluating sources (Trials 1, 2, and 3; Table 1): (i) well watered, with irrigation of approximately 60 mm of water every 10 d, and (ii) stressed, by withholding irrigation about 3 to 4 wk before anthesis and allowing the crop to complete its life cycle with stored soil moisture only. In trials of S_1 and S_3 progenies (Trials 4, 5, 6, 7, and 8; Table 1) ψ_s was only measured under the stressed water regime above. Stress development was relatively slow because of large soil water-holding capacity (>200 mm) and deep rooting, but it intensified with time. Compared to irrigated controls, stressed genotypes had slower canopy expansion, leaf rolling before tassel emergence, delays of silk emergence in excess of 10 d, and yield reductions of up to 75%.

Experimental design for each trial and each moisture regime was an alpha (0.1) lattice design in two replications (16). Planting density was 5.3 plants m^{-2} , obtained by overplanting and thinning. Plot size varied with the trial (Table 1), and measurements were taken on well bordered plants in the central row. Adjacent families acted as borders on single-row plots, and adequate borders were planted around the sides of the entire trial. Anthesis-silking interval (ASI) was determined as the difference between days to 50% silking minus days to 50% anthesis per plot. Visual scores of leaf rolling (LRS) were recorded under drought before tassel emergence, and of leaf death (LDS) on both treatments on three occasions during grain filling when phenotypic differences became obvious. The scale used was 1 (turgid, green) to 5 (rolled, dead). Scores of each trait were averaged before analysis. Ears were hand-harvested from the bordered section of the central one to two rows of each plot and shelled. Grain was dried to constant weight at 80 °C in a forced air oven.

Determination of Osmotic Potential.

Plots were sampled for ψ_s at predawn (0500–0700 h) within the 2 wk bracketing anthesis after the crop had shown signs of reduced canopy expansion and midday leaf rolling (Table 1). At predawn the tissue experiences the maximum rehydration during the diurnal cycle and has reached hydric equilibrium with soil water potential. One or two disks 5 cm in diameter were punched from the uppermost fully expanded leaves on each of six to 10 plants for a total of 10 to 12 disks per plot. Samples from a plot were bulked and immediately wrapped in a plastic bag and frozen. Tests showed that similar values were obtained whether the tissue was frozen using dry ice (–80 °C) or a deepfreeze (–18 °C). Samples were thawed 24 to 48 h later, and their sap was mechanically expressed. The osmolality of this sap was immediately measured with a Wescor Vapor Pressure Osmometer Model 5100B (Wescor, Logan, UT). No attempt was made to correct for apoplastic dilution, and leaf samples were not artificially rehydrated to 100% relative water content (RWC) prior to freezing. Osmolality was converted to ψ_s by assuming 1.0 mol kg^{-1} to be equal to –2.48 MPa. Osmotic adjustment was considered as the difference in ψ_s between droughted and well watered treatments, and as positive if the tissue accumulated solutes under drought, i.e., had a more negative ψ_s under drought than under well watered conditions.

Values of ψ_s in the range of –0.70 to –3.00 MPa were determined from expressed sap by the vapor pressure osmometer and were compared with those obtained from intact leaf disks cut from the same samples using a Wescor

HR-33T dew point thermocouple psychrometer equipped with C-52 sample chambers. Measurements by vapor pressure osmometry agreed well with measurements by thermocouple psychrometry. Experimental error in determining ψ_s was examined by taking six repeated samples of 10 disks each from the same plot of six single-cross hybrids (all plants of a given hybrid assumed to be genetically identical) under well-watered conditions (uniform soil water content).

Predawn (0500–0700 h) leaf water potentials (Ψ) were determined per plot within 1 to 3 d of the sampling date for osmotic adjustment in trials involving sources under droughted treatments (Trials 1 and 2; Table 1), but not on progeny (Trials 4, 5, 6, 7, and 8; Table 1) to ascertain that there were no important differences among genotypes in hydration at the time of sampling. Four uppermost fully expanded and fully exposed leaves per plot were cut and wrapped in moist cheesecloth. Within 2 min of excision their balancing pressure, measured on the central mid-rib, was determined with a pressure chamber (Soil Moisture Corporation, Santa Barbara, CA) to the nearest 0.05 MPa. In Trials 9 and 10 (Table 1), and in the well irrigated plots of Trials 1, 2, and 3, predawn leaf Ψ was not measured since samples were always collected the predawn immediately after irrigation and were assumed to be fully hydrated (leaf Ψ near zero).

Divergent Selection and Realized Heritability for Osmotic Potential.

Based on measurements of ψ_s made under drought at about the time of anthesis on the S_1 progeny of P16S C_1 , P18S C_1 and TS6 C_0 (Table 1), S_1 families in each population, 10 with the highest ψ_s and 10 with the lowest ψ_s , were selected to form ESs for high and low ψ_s (selection intensity of 4.5%). The 20 S_1 families selected were similar to the population bulk for all other traits and differed only in ψ_s . The mean of the 20 families was less than 0.5 standard deviation units from the population mean for yield, yield components, anthesis date, ASI, LRS, and LDS, but about 2.5 to 3.0 standard deviation units from the population mean for ψ_s .

For recombination, the 10 S_1 families per ES were each planted from remnant seed in 16-plant 5-m long rows in the summer season of 1989. Plant-to-plant crosses were made along families in the maximum number of combinations possible. Individual crosses were shelled and a balanced bulk of 200 kernels from each ear was made for each ES. The bulk of each population was formed in a similar manner by planting a mixture formed from four remnant seed from each S_1 family and making crosses among 300 randomly selected plants.

The ψ_s was determined at regular intervals [38, 52, 66, 80, 94, and 101 d after planting (DAP); Trial 8, Table 1] on each individual S_1 family, and the 10 families per ES averaged. Samples were routinely collected during predawn (0500–0700 h) after a rainfall or irrigation, so samples were assumed to be fully hydrated. During this season Penman ET_0 averages 5 to 6 mm d^{-1} and air vapor pressure increases to 2.2 to 2.5 kPa. Diurnal water deficits therefore were much less pronounced than in the winter season, and this provided an opportunity to determine whether the S_1 families responded differently for ψ_s in these two quite distinct environments.

The ESs formed for high and low ψ_s , and the population bulk, were all planted at the F_1 stage in the winter season of 1989–1990. Cultural practices were similar to those described above except that stress was imposed using a line source sprinkler irrigation gradient (22). The gradient was started at 43 DAP and irrigations were applied weekly at 0600 h to replenish crop ET at the wet end of the line source. Crop rows were planted perpendicularly to the irrigation line and were divided into four hydric regions each 3 m in length. Tests with catch cans showed that the three drier hydric regions, H1 (driest hydric region), H2 and H3, received, re-

spectively, 46, 77 and 89% of the water received by the wettest hydric (H4) region. The coefficient of variation (CV) of the water applied to different plots within a hydric region was less than 8%. Plot size was three rows 0.75 m apart, and each plot ran the full length of a hydric region. No alleys were left between hydric regions, and no borders were removed during harvest, though adequate borders were planted around the sides of the entire trial.

The nine genotypes in each hydric region were independently randomized in a randomized complete block design with genotypes considered as fixed effects and hydric regions as random effects. Genotypes were further subdivided into a factorial arrangement of three populations and three ESs. The design was replicated twice, once on each side of the irrigation line. Values of ψ_s were determined at regular intervals (57, 71, 87, and 98 DAP) (Trial 10, Table 1) in all hydric regions the day after irrigation was applied. Time of sampling was treated as a sub-plot within hydric regions as main plots in a split-plot design. Ears were hand-harvested from all rows of each plot, and grain was dried to constant weight at 80 °C in a forced air oven. Yields were expressed on an oven-dry weight basis.

Realized heritability (h^2) for ψ_s was calculated as $h^2 = R/S$ (10), where R is response to selection and S the selection differential. Selection differential was the difference in ψ_s between the mean of the selected 10 S_1 progeny for each ES and the population mean during selection in the dry season of 1988–1989 when S_1 progeny was evaluated. Response to selection was the difference in ψ_s between the ESs and the cycle bulk when evaluated under the line source in the dry season of 1989–1990, and measured at the same ontogenetic stage as that used during selection. This procedure was followed for both high and low ψ_s selections in each population. In order to standardize the units for different years, seasons (rainy summer vs. dry winter), and vigor levels (S_1 vs. F_1 of crosses among S_1 s), S and R were each expressed as a percentage of the mean for each trial. This was preferred over the normal method of standardizing differentials in standard deviation units (8) since only three ESs from each population were evaluated compared to 222 to 225 S_1 progeny during selection.

RESULTS

Osmotic Adjustment in Source Germplasm.

Values reported are the means of two sampling dates in 1987–1988 and 1988–1989, but represent only one sampling date in 1989–1990 (Table 1). Mean osmotic adjustment in response to drought was relatively small in the range of source germplasm tested (Table 2). In 1987–1988 ψ_s in irrigated controls differed from that in droughted plots by -0.04 MPa, indicating negative adjustment. In 1988–1989 mean adjustment was 0.06 MPa, and in 1989–1990 a more significant adjustment of 0.26 MPa was detected. All groups of maize germplasm tested, whether unimproved landraces from semi-arid regions, elite CIMMYT improved OPPs and ESs, temperate F_1 hybrids and their F_2 s, or crosses of superior sources, gave generally similar mean values for ψ_s under both treatments (Table 2). The standard error of differences (S_d) among means for a given germplasm class was similar across classes and years and averaged 0.10 MPa. Maximum osmotic adjustment observed was 0.32 in 1987–1988, 0.22 in 1988–1989, and 0.54 MPa in 1989–1990, indicating that some genotypes possessed significant ability to adjust and could serve as sources for the trait in a breeding program. Only 7% of tested genotypes adjusted in excess of 0.40 MPa and 36% of the genotypes showed minor negative osmotic adjustment, i.e., loss of solutes under stress as compared to values under well irrigated conditions. Mean predawn leaf Ψ under drought at the time of sampling was -0.32 MPa (range from -0.10 to -0.67 MPa, $S_d = 0.08$ MPa) in 1987–1988 and -0.41 MPa (range from -0.14 to -0.69 MPa, $S_d = 0.14$ MPa) in 1988–1989. Predawn leaf Ψ under drought was not measured in 1989–1990. Samples collected from well irrigated plots were assumed to be fully hydrated since they

Table 2. Osmotic potential (ψ_s) under droughted and irrigated conditions and osmotic adjustment for source germplasm tested at CIMMYT's breeding nurseries at Tlaltizapan, Mexico, during the winter seasons of 1987–1988, 1988–1989 and 1989–1990. Osmotic adjustment was considered positive if ψ_s was more negative under drought than under well watered conditions. Measurements were collected within 10 d of anthesis for all germplasm reported. S_d refers to standard error of differences among genotypic means.

| Number | Drought | | Irrigated | | Osmotic adjustment | | | |
|-------------------------------|----------|-------|-----------|-------|--------------------|-------|-------|-------|
| | ψ_s | S_d | ψ_s | S_d | Mean | Max | Min | |
| MPa | | | | | | | | |
| 1987–1988 - 60 Sources | | | | | | | | |
| Landraces | 29 | -1.27 | 0.11 | -1.29 | 0.09 | -0.02 | 0.32 | -0.22 |
| Trop. Improved | 8 | -1.24 | 0.05 | -1.28 | 0.08 | -0.04 | 0.09 | -0.17 |
| Temperate F_1 | 2 | -1.36 | 0.09 | -1.37 | 0.11 | -0.01 | 0.12 | -0.15 |
| Temperate F_2 | 13 | -1.26 | 0.10 | -1.26 | 0.09 | 0.00 | 0.20 | -0.23 |
| Crosses | 8 | -1.18 | 0.06 | -1.33 | 0.06 | -0.15 | -0.01 | -0.21 |
| Mean | 60 | -1.25 | 0.10 | -1.29 | 0.09 | -0.04 | 0.32 | -0.23 |
| 1988–1989 - 72 Sources | | | | | | | | |
| Landraces | 25 | -1.30 | 0.08 | -1.25 | 0.06 | 0.06 | 0.16 | -0.04 |
| Trop. Improved | 17 | -1.40 | 0.06 | -1.33 | 0.05 | 0.07 | 0.21 | -0.05 |
| Temperate F_1 | 12 | -1.27 | 0.05 | -1.21 | 0.08 | 0.07 | 0.21 | 0.00 |
| Temperate F_2 | 8 | -1.27 | 0.08 | -1.19 | 0.06 | 0.08 | 0.17 | -0.02 |
| Crosses | 10 | -1.31 | 0.07 | -1.27 | 0.05 | 0.04 | 0.22 | -0.06 |
| Mean | 72 | -1.32 | 0.08 | -1.26 | 0.08 | 0.06 | 0.22 | -0.06 |
| 1989–1990 - 72 Sources | | | | | | | | |
| Landraces | 26 | -1.72 | 0.12 | -1.40 | 0.06 | 0.31 | 0.54 | 0.02 |
| Trop. Improved | 14 | -1.81 | 0.12 | -1.48 | 0.11 | 0.33 | 0.51 | 0.19 |
| Temperate F_1 | 10 | -1.58 | 0.14 | -1.44 | 0.12 | 0.14 | 0.33 | -0.21 |
| Crosses | 22 | -1.74 | 0.09 | -1.52 | 0.08 | 0.23 | 0.44 | 0.04 |
| Mean | 72 | -1.72 | 0.13 | -1.46 | 0.10 | 0.27 | 0.54 | -0.21 |

Table 3. Linear correlation coefficients (*r*) between several traits indicative of performance under drought and (†) osmotic adjustment, and (‡) ψ_s under drought, in source germplasm grown at Tlaltizapan, Mexico, in 1987-1988, 1988-1989, and 1989-1990. Osmotic adjustment was considered positive if ψ_s was more negative under drought than under well watered conditions. In 1988-1989, leaf rolling scores were not determined.

| | df | Grain yield | Anthesis silking interval† | Ears per plant | Leaf rolling score‡ | Leaf death score‡ | Days to anthesis |
|--|----|-------------|----------------------------|----------------|---------------------|-------------------|------------------|
| Osmotic adjustment (MPa) | | | | | | | |
| 1987-1988 | 58 | -0.18 | 0.01 | -0.10 | 0.23 | 0.16 | -0.08 |
| 1988-1989 | 70 | 0.20 | -0.23 | 0.26* | - | 0.01 | -0.25* |
| 1989-1990 | 70 | -0.24* | 0.16 | -0.21 | -0.08 | -0.26* | 0.29* |
| Osmotic potential (ψ_s) under drought (MPa) | | | | | | | |
| 1987-1988 | 58 | 0.02 | -0.08 | 0.04 | 0.17 | 0.17 | -0.19 |
| 1988-1989 | 70 | -0.48** | 0.44** | -0.55** | - | -0.24 | 0.64** |
| 1989-1990 | 70 | 0.10 | 0.02 | 0.05 | 0.18 | 0.13 | -0.01 |

*,** Significant at *P* < 0.05, 0.01, respectively.
 † Days to 50% silking minus days to 50% anthesis per plot.
 ‡ Leaf rolling and death scores on scale from 1 (unrolled, green) to 5 (rolled, dead).

were always collected the predawn immediately after an irrigation.

Non-significant correlations were observed between osmotic adjustment and traits indicative of crop water relations and performance under drought (Table 3). For ψ_s under drought, correlations were also non-significant and inconsistent, except for 1988-1989 when low ψ_s under drought was significantly associated with high yield, high ears per plant (EPP), short ASI, and earlier maturity (Table 3).

Variation for Osmotic Potential within Elite Populations.

These plants were sampled for ψ_s under drought after reduced canopy expansion and midday leaf rolling became visible. The S_1 (P16S C₁, P18S C₁, and TS6 C₀) and S_3 progeny (LPS C₀ and P26S C₀) within each population showed considerable variation for ψ_s under drought, ranging from -1.04 to -1.79 MPa (Fig. 1). Inbreeding appeared to increase mean ψ_s , but not the range. The maximum range for ψ_s under drought within a population was 0.53 MPa and the mean S_d for family differences was 0.08 MPa. The 10 S_1 families chosen for recombination into ESs for high and low ψ_s were selected out of these 222 to 225 S_1 s from each population (indicated by arrows in Fig. 1).

Weak and inconsistent correlations were observed between ψ_s and traits indicative of performance under drought across populations (Table 4). Correlations be-

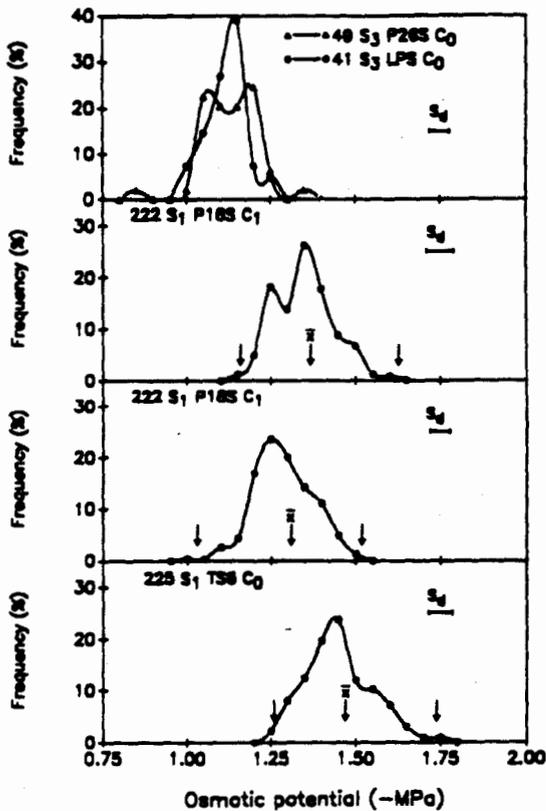


Fig. 1. Frequency distributions for ψ_s under drought for S_1 and S_3 progeny from several elite CIMMYT lowland maize populations in Tlaltizapan, Mexico, during the dry season of 1988-1989. Arrows indicate mean ψ_s , and mean for 10 selected families with highest and lowest ψ_s . S_d refers to standard error of differences among families.

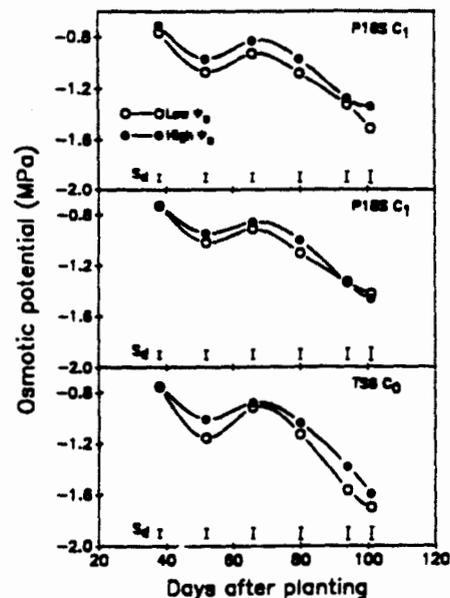


Fig. 2. Seasonal course of ψ_s for S_1 families selected for high and low ψ_s from three maize populations (a) P16S C₁, (b) P18S C₁, and (c) TS6 C₀, during the well watered summer rainy season of 1989 at Tlaltizapan, Mexico. Each data point is the mean of 10 S_1 families. S_d refers to the standard error of differences between groups.

Table 4. Linear correlation coefficients (*r*) between several traits indicative of performance under drought and osmotic potential (ψ_s) under drought for S₁ and S₂ progeny from several tropical maize populations, Tlaltizapan, winter 1988–1989.

| | df | Grain yield | Anthesis silking interval† | Ears per plant | Leaf rolling score‡ | Leaf death score‡ | Days to anthesis |
|------------------------|-----|-------------|----------------------------|----------------|---------------------|-------------------|------------------|
| S ₁ progeny | | | | | | | |
| P16S C ₁ | 220 | -0.23** | 0.30** | -0.33** | -0.30** | -0.18* | 0.34** |
| P18S C ₁ | 220 | 0.01 | -0.03 | 0.06 | 0.02 | -0.34** | 0.20** |
| TS6 C ₀ | 223 | -0.01 | 0.08 | 0.02 | 0.08 | -0.17* | 0.15* |
| S ₂ progeny | | | | | | | |
| P26S C ₀ | 47 | -0.17 | 0.08 | -0.16 | 0.41** | 0.08 | 0.21 |
| LPS C ₀ | 39 | 0.18 | -0.09 | 0.19 | -0.03 | -0.19 | 0.02 |

*,** Significant at *P* < 0.05 and 0.01, respectively.

† Days to 50% silking minus days to 50% anthesis per plot.

‡ Leaf rolling and death scores on scale from 1 (unrolled, green) to 5 (rolled, dead).

tween ψ_s and LDS, however, were consistently negative, while between ψ_s and days to anthesis they were consistently positive. This meant that progeny with lower ψ_s under drought (higher solute concentration) had higher rates of leaf senescence and earlier maturity, suggesting that ψ_s may be more a function of ontogenetic stage rather than tissue age.

Divergent Selection for Osmotic Potential.

The S₁ lines selected for low ψ_s under drought in the dry season of 1988–1989 also showed lower ψ_s in the wet summer season of 1989 during recombination than the lines selected for high ψ_s (Fig. 2). A similar trend was observed in each population examined, the differences in S₁ progeny remaining consistent over the two seasons. Values of ψ_s declined steadily with ontogeny from -1.0 MPa at 40 DAP to -1.5 MPa during mid-grainfill in all S₁s. Differences between S₁ families selected for high and low ψ_s were small early in the season, but increased to around 0.09 MPa (7.8% of a mean of -1.08 MPa) when averaged across all populations near anthesis (Fig. 2). The difference in

ψ_s for the same lines during selection in the previous winter season ranged from 0.33 to 0.39 MPa (25% of a mean of -1.40 MPa) at a similar ontogenetic stage (Fig. 1).

After recombination, ESs formed for high and low ψ_s , as well as the cycle bulk for the three populations sampled, ranked as predicted for ψ_s when measured at several ontogenetic stages while being evaluated under the sprinkler irrigation gradient during the dry season of 1989–1990 (Fig. 3, Table 5). Differences in ψ_s between ESs selected for high and low ψ_s were small early in the season, but increased to 0.17 MPa near anthesis across all three populations (Fig. 3). A similar trend of increasing osmotic concentration with ontogeny was observed, ψ_s decreasing from -1.05 to -1.60 MPa from 57 to 98 DAP across the three populations evaluated (Fig. 3). Again, limited osmotic adjustment across the irrigation moisture gradient was detected. Mean ψ_s across the three populations decreased non-significantly from -1.30 MPa in the wettest hydric region to -1.36 MPa in the driest region.

Grain yield decreased from 4.2 to 1.6 Mg ha⁻¹ along the line source irrigation gradient, but no significant

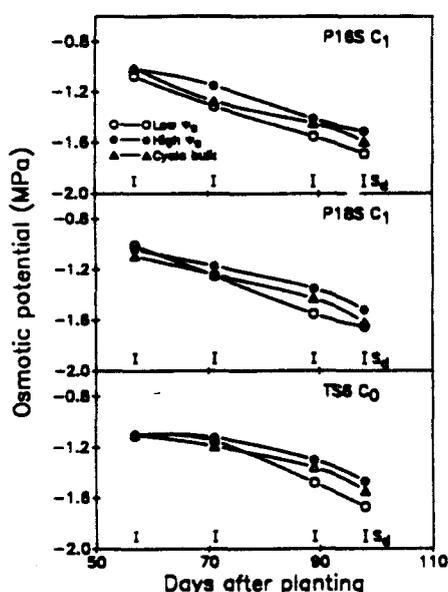


Fig. 3. Seasonal course of ψ_s for ESs selected for high and low ψ_s , and the cycle bulk of three maize populations (a) P16S C₁, (b) P18S C₁, and (c) TS6 C₀, averaged over a line source irrigation gradient during the winter season of 1989–1990 at Tlaltizapan, Mexico. S_d refers to the standard error of differences among ESs.

Table 5. Analysis of variance for ψ_s (MPa) and grain yield (Mg ha⁻¹) for data from Trial 10, where three ESs (high ψ_s , low ψ_s , and cycle bulk) from three populations (P16S C₁, P18S C₁, TS6 C₀) randomized within four hydric regions under a line source irrigation gradient in two reps.

| | ψ_s | | Grain yield | |
|-----------------------|----------|-------------|-------------|-------------|
| | df | Mean Square | df | Mean Square |
| Reps | 1 | 0.012 | 1 | 1.416 |
| Hydric Regions | 3 | 0.049*** | 3 | 23.169** |
| Error (a) | 3 | 0.002 | 3 | 0.415 |
| Populations | 2 | 0.035 | 2 | 2.385 |
| ES's | 2 | 0.292*** | 2 | 0.498 |
| Pop × ES | 4 | 0.008 | 4 | 0.596 |
| Hyd × Pop | 6 | 0.007 | 6 | 1.656*** |
| Hyd × ES | 6 | 0.002 | 6 | 0.163 |
| Hyd × Pop × ES | 12 | 0.005 | 12 | 0.190 |
| Error (b) | 32 | 0.009 | 32 | 0.240 |
| Time of Sampling | 3 | 3.802** | | |
| Error (c) | 3 | 0.038 | | |
| Time × Hyd | 9 | 0.011 | | |
| Error (d) | 9 | 0.005 | | |
| Time × Pop | 6 | 0.038*** | | |
| Time × ES | 6 | 0.038*** | | |
| Time × Pop × ES | 12 | 0.007 | | |
| Time Hyd × Pop | 18 | 0.005 | | |
| Time × Hyd × ES | 18 | 0.003 | | |
| Time × Hyd × Pop × ES | 36 | 0.004 | | |
| Error (e) | 96 | 0.005 | | |

*, **, *** Significant at *P* < 0.05, 0.01, and 0.001, respectively.

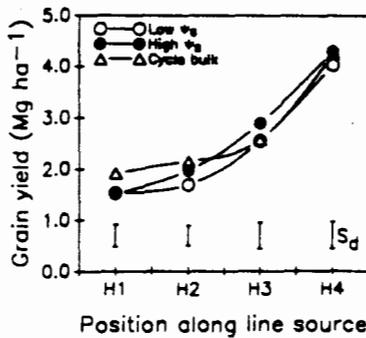


Fig. 4. Grain yield of ESs selected for high and low ψ_s , and the cycle bulk averaged for three maize populations as affected by hydric region (H1 = wettest, H4 = driest) when grown under a line source irrigation gradient during the winter season of 1989-1990 at Tlaltizapan, Mexico. S_d refers to the standard error of differences among ESs.

differences were detected among the ESs selected for high and low ψ_s , and the cycle bulk (Fig. 4, Table 5). A small non-significant reduction in yield was detected in both the ESs selected for high and low ψ_s , compared to the cycle bulk as stress intensified (Fig. 4).

Differences in ψ_s , detected at about the time of anthesis were used as the observed response (R) to calculate realized heritability, since selections were based on data also collected near anthesis. Selection differentials (S) in the dry season of 1988-1989 ranged from 0.16 to 0.22 MPa (11.3 to 15.2% of the mean ψ_s) and the observed response when evaluating the ESs during the dry season of 1989-1990 ranged from 0.04 to 0.13 MPa (2.5 to 8.9% of the mean ψ_s) (Table 6). Realized heritability (h^2) for ψ_s , ranged from 0.22 to 0.70 and averaged 0.46 across all populations examined and for both directions of the divergent selection (Table 6).

DISCUSSION

Evaluation of the Method.

Since ψ_s varies with RWC, it is normal practice to rehydrate excised leaves to full turgor prior to determining ψ_s . This procedure adds considerably to the time required to complete each measurement, and may result in unknown changes in metabolism and solute concentration during rehydration. We collected samples at predawn when leaves experience their greatest rehydration in their diurnal water balance, and were not artificially rehydrated to full turgor before measurement. Samples for irrigated plots were assumed to be fully hydrated (predawn leaf Ψ near zero) since they were always collected the predawn immediately after irrigation. For droughted plots, predawn leaf Ψ during sampling for ψ_s , averaged -0.32 and -0.41 MPa in 1987-1988 and 1988-1989 (it was not measured in 1989-1990). This predawn Ψ is equivalent to around 96% RWC from previously observed pressure-volume (PV) curves (unpublished data, CIMMYT). A ψ_s of -1.25 MPa at 96% RWC would be increased only to -1.20 MPa if RWC was raised to 100% by rehydration, according to the Vant-Hoff relationship. Differences in hydration level between irrigated and droughted treatments could then be expected to account for at most a lowering of ψ_s by 0.05 MPa from its fully rehydrated value.

In developing an appropriate screening technique

Table 6. Selection differentials, observed response, and realized heritabilities of ESs selected for high and low ψ_s , under drought in three elite tropical maize populations (P16S C₁, P18S C₁, and TS6 C₀). Selections were made in the winter season of 1988-1989, and evaluations in the winter season of 1989-1990 at Tlaltizapan, Mexico.

| Population | Selection differential | | Response differential | | Realized heritability |
|-----------------------------------|------------------------|-----------------|-----------------------|-----------------|-----------------------|
| | MPa | Percent of mean | MPa | Percent of mean | |
| For low osmotic potential | | | | | |
| P16S C ₁ | 0.18 | 13.1 | 0.10 | 7.1 | 0.54 |
| P18S 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 ψ_s | | | | | 0.58 |
| For high osmotic potential | | | | | |
| P16S C ₁ | 0.16 | 11.3 | 0.04 | 2.5 | 0.22 |
| P18S 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 |

for use in breeding programs, relative differences among genotypes are often more important than absolute accuracy. Predawn leaf Ψ among genotypes varied from -0.10 to -0.67 in 1987-1988 and from -0.14 to -0.69 in 1988-1989, with a maximum difference of 0.57 MPa. From observed PV curves such differences in leaf Ψ are roughly equivalent to a 6 to 7% difference in RWC among the same genotypes. Using the Vant-Hoff relationship, this means that 0.08 MPa of a mean leaf ψ_s of -1.25 MPa could be due to genotypic differences in rehydration at the time of sampling. This error was smaller than the S_d among genotypic means derived from analyses of variance of ψ_s (See Table 2 and Fig. 1).

The mean experimental error of determining ψ_s by repeated measurements of the same plots of hybrids sampled after full rehydration was 0.11 MPa. Thus errors associated with ψ_s , determined on samples from the same plot were greater than those associated with lack of hydration at the moment of sampling. We arbitrarily considered a capacity for an osmotic adjustment of 0.40 MPa as a minimum to justify inclusion of a cultivar in a crossing program, based on considerations of additional soil water extraction, stomatal aperture and expansive growth. The accuracy of the method described allowed us to distinguish genotypes which met this criterion. Added precision obtained from rehydration did not, in our view, compensate for the disadvantages of this procedure. By eliminating the step of rehydrating, but including time taken for predawn sampling, 20 plots per hour could be processed with one osmometer and two staff, a rate well suited to screening large numbers of genotypes in breeding programs.

Genetic Variation for Osmotic Adjustment and Osmotic Potential under Drought.

In general little capacity for osmotic adjustment was detected in the wide range of tropical and temperate maize germplasm examined (Table 2). Mean osmotic adjustment for 204 sources over 3 yr of sampling was a mere 0.10 MPa in environments where drought reduced yield by more than 75%. Only 7% of all geno-

types showed a capacity to adjust by more than 0.40 MPa, and 36% of all genotypes showed minor negative osmotic adjustment, that is, a higher solute concentration under well watered conditions than under droughted conditions. Osmotic adjustment of ESs between hydric regions differing markedly in stress level was a non-significant 0.06 MPa, also confirming that little solute accumulation occurred in response to moisture stress.

The modest adjustment observed in this study contrasts with published reports up to 0.40 MPa difference in ψ_s between droughted and irrigated treatments for maize under apparently similar field conditions and on similar tissue (1,6,17,23). For maize cultivars grown under controlled environments in pots stressed by withholding water, osmotic adjustment in excess of 0.50 MPa has been reported (2,18,21). In other crops, such as wheat (*Triticum aestivum* L.) and sorghum (*Sorghum bicolor* Moench), adjustment under drought in excess of 1.0 MPa has been observed (3,12,14).

One possible reason for our inability to detect significant differences between irrigated and droughted treatments in osmotic adjustment could be the atmospheric aridity of the Tlaltizapan winter environment. Even well irrigated plants faced severe diurnal water deficits as midday leaf Ψ declined to values approaching -2.0 MPa during the season (unpublished data, CIMMYT). Since predawn Ψ was normally around -0.2 to -0.3 MPa, this meant that leaves operated at low turgor and low water content throughout most of the day. Therefore, even well-irrigated plots may have been operating at their limit for active solute accumulation.

Despite the inability to detect differences in ψ_s between irrigated and droughted treatments, solute concentration increased steadily with ontogeny in both treatments. In droughted treatments, ψ_s decreased seasonally from -1.00 to -1.60 MPa, demonstrating that a mechanism for accumulating solutes was still functional. The rate and size of the increase with crop development was consistent with other field reports, (6,11,20,23). Since water content as a percentage of total biomass usually declines as the crop matures, perhaps the seasonal lowering in ψ_s observed across both irrigation regimes is more a function of decreasing absolute tissue water content than active accumulation of solutes.

Significant genetic variation in ψ_s under drought among source genotypes and among S_1 families of elite lowland maize populations was detected (Table 2, Fig. 1). This variation was several times larger than that observed for osmotic adjustment per se, and it was for this reason that the heritability of this trait, rather than adjustment, was studied. Two of the elite parent populations, TS6 C_0 and LPS C_0 , are derived from similar germplasm, and should be expected to produce lines with similar ψ_s as comparable stages of ontogeny if inbreeding had no effect. However, S_3 lines from LPS C_0 had higher mean ψ_s than the S_1 lines from TS6 C_0 (Fig. 1), suggesting that the capacity to accumulate solutes may decrease with increasing levels of inbreeding. Hybrid vigor apparently had little effect, since no consistent differences were detected between F_1 temperate hybrids and their F_2 s, or between hybrids and OPPs (Table 2).

Low ψ_s can arise from an increased capacity to accumulate additional solutes as an active adaptation to drought stress, or it may arise from a constitutive capacity for high solute concentration in the cell. Both mechanisms should be effective in maintaining turgor. Evidence for the constitutive nature of the trait is provided by the consistent ranking between arid and wet seasons of S_1 families selected for high and low ψ_s (compare Fig. 1 and 2), and the reasonably high heritability detected for ψ_s . However, the fact that even in well-irrigated plots the same lines had ψ_s values higher by about 0.3 MPa (0.12 mol kg^{-1} less solute concentration) under the rainy summer environment than under the dry winter conditions, argues that the constitutive level of solute concentration is influenced by the atmospheric aridity of the environment.

Differences between families having high and low ψ_s were still obvious after the two divergent fractions were separately recombined and bulked as F_1 s (Table 5). Realized heritability for ψ_s averaged 0.46 (Table 6) and was considerably higher than that commonly observed for grain yield in maize (10). This means that the method of determining ψ_s was effective in identifying true genetic differences during selection. Had the families and synthetics been evaluated in the same season under identical conditions this estimate would probably have been even higher. An estimate of 34% for the broad-sense heritability of ψ_s was obtained by Thomas (19) in *Lolium perenne* L.

Association between Osmotic Adjustment, Osmotic Potential, and Productivity.

The generally weak and inconsistent associations between osmotic adjustment or ψ_s under drought per se and other measures of performance under drought in a wide array of germplasm may have been partly due to accumulated errors in the measurement of adjustment, which is the difference of two measurements each with an associated error. It is unlikely that such errors were completely responsible for non-significant associations between yield and this trait. There is apparently little association between the variation in ψ_s per se and performance under drought in lowland tropical maize germplasm.

This conclusion was also supported by yield data from the ESs. Although the ψ_s of the high and low selections was significantly different throughout much of the season (as much as 0.17 MPa), yields were not significantly different from each other or from the cycle bulk even under quite severe stress (Fig. 4). The non-significant trend towards a higher yield by the cycle bulk in the two driest hydric regions may even imply a cost associated with both high and low ψ_s . These data agree somewhat with those of Grumet et al. (9) who found negative costs associated with high constitutive solute concentration in barley isopopulations developed for differing ψ_s . However, they disagree with the findings of Morgan et al. (14) who observed that wheat lines with lower ψ_s under drought also extracted more soil water, produced more biomass and grain, and had a better overall water use efficiency. The fact that significantly lower ψ_s did not result in higher yield under stress may be because an increase of osmotic concentration of 0.17 MPa had little or no effect on the capacity of the plant to take

up water or to maintain turgor. Alternatively, lower ψ_s may come about passively because of reduced growth rather than because of active accumulation of solutes, and this may offset the benefits of high solute concentration under stress. In the latter case, selection of lines with low ψ_s , or a capacity to adjust under stress, may merely be selecting lines which have enhanced survival under drought, but which have limited capacity for growth. Munns (15) estimated that a 30% reduction in expansive growth without reduction in photosynthetic rate due to stress would account for a passive increase of solute concentration of about 0.10 to 0.20 MPa.

In conclusion, limited osmotic adjustment was detected in a wide range of lowland tropical maize germplasm, even in landraces collected from semi-arid environments. In contrast, useful genetic variation for constitutive levels of ψ_s under drought was detected within elite CIMMYT maize populations and its heritability seemed relatively high. However, the trait was only weakly associated with performance under drought in the wide array of germplasm examined and did not result in yield gains under stress in ESs that differed in ψ_s by 0.17 MPa. Selection for increased capacity to adjust osmotically or for low ψ_s as desirable drought adaptive traits in lowland tropical maize cannot be endorsed at this time.

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Selection Indices

The central problem is:

- How to improve a crop for more than one trait at a time?
- How to use data from secondary traits to improve the primary trait?

Most Selection Indices consist of:

1) a linear function of phenotypic values (P), in which the observed value for each trait is given some weighting (b), and **each is summed to make an index, I:**

$$I = b_1P_1 + b_2P_2 \dots b_nP_n$$

2) The more sophisticated take into account the phenotypic (or better still, the **genotypic**) **correlations** between traits to avoid the problem of "double weighting"

3) The weights used in many selection indices relate to **economic value** of each trait. e.g.,

"How much is X units of lodging worth in terms of kg of grain yield?"

4) **Problems of scaling:** how can we put each variable on the same scale? How can you compare leaf scores (1-5) with yield (in kg/ha)?

HISTORY OF SELECTION INDEX METHODOLOGY

I. INTRODUCTION

In most crop improvement programs, there is a need to improve more than one trait at a time. Recognition that improvement of one trait may cause improvement or deterioration in associated traits serves to emphasize the need for simultaneous consideration of all traits which are important in a crop species. Selection indices provide one method for improving two or more traits in a breeding program.

This chapter reviews the basic strategy behind the original development of selection indices and some of the modifications that have been developed subsequently. The concepts of optimum selection indices, restricted selection indices, and of other modifications, are introduced. Some of the problems associated with applying these methods to crop improvement are presented.

II. THE BASIC STRATEGY OF OPTIMUM SELECTION INDICES

The use of a selection index in plant breeding was originally proposed by Smith,¹ who acknowledged critical input from Fisher.² Subsequently, methods of developing selection indices were modified, subjected to critical evaluation, and compared to other methods of multiple-trait selection.

Today, it is generally recognized that a selection index is a linear function of observable phenotypic values of different traits. The observed value for each trait is weighted by an index coefficient. Symbolically,

$$I = b_1P_1 + \dots + b_iP_i + \dots + b_nP_n$$

where P_i represents the observed phenotypic value of the i^{th} trait, and b_i is the weight assigned to that trait in the selection index. With three traits, say, yield, days to maturity, and protein concentration, an index (I) for a particular genotype might be

$$I = 0.3 \times \text{yield} - 1.4 \times \text{days to maturity} + 4.7 \times \text{protein concentration}$$

Then, if the observed yield on a particular genotype was 1800 kg/ha, maturity was 94 days, and protein concentration was 12.4%, the index value for that genotype would be

$$I = 0.3 \times 1800 - 1.4 \times 94 + 4.7 \times 12.4 = 466.68$$

The purpose of using a selection index in plant selection is usually stated as an attempt to select for improved "genotypic worth" of the population. In order to understand what is meant by the term "genotypic worth", one must first have an understanding of what is meant by "genotypic value". If a particular genotype is tested in a large number of environments, its average phenotypic value would be considered to be its genotypic value. Thus, genotypic value is a true value in the sense that it is a measure of the average performance of the genotype within some reference population of environments. As such, genotypic value can rarely be measured, and any estimates of the genotypic value must be by indirect methods (see Chapter 3).

FROM:

R.J. Baker (1986). Selection Indices in Plant Breeding. CRC Press, Boca Raton, Florida. p. 1-12.

Genotypic worth (W) is defined as a linear function of unobservable genotypic values in which the genotypic value of each trait is weighted by a known relative economic value. In symbols,

$$W = a_1G_1 + \dots + a_iG_i + \dots + a_nG_n$$

where G_i is the unobservable genotypic value of the i^{th} trait and a_i is the relative economic value of that trait. In terms of the example mentioned above, one might consider that an increase of 100 kg/ha in yield has the same economic value as a decrease of 1 day in maturity or an increase of 0.25% in protein concentration. If so, the relative economic values would be 0.01 for an increase of 1 kg/ha in yield, -1.0 for an increase of one day in maturity, and 4.0 for an increase of 1% in protein concentration. Thus, if a particular genotype were known to have genotypic values of 2000 kg/ha for grain yield, 100 days for maturity, and 15% for protein concentration, its genotypic worth would be

$$W = 0.01 \times 2000 - 1.0 \times 100 + 4.0 \times 15 = -20.0$$

If genotypic and phenotypic values have a multivariate normal distribution, there will be a linear regression of genotypic worth on any linear function of phenotypic values. In fact, such a regression may exist with distributions which are not normal. If a linear regression of genotypic worth on phenotypic values does exist, the expected change in genotypic worth due to use of a linear selection index (I) will be

$$\Delta W = (W_s - W_u) = b_{w_i}(I_s - I_u) = \frac{\sigma_{wI}}{\sigma_I^2}(I_s - I_u)$$

where ΔW is the response to selection, W_s is the average genotypic worth of the selected sample, W_u is the average genotypic worth of the unselected population, I_s is the average index value of the selected sample, I_u is the average index value for the unselected population, and b_{w_i} is the linear regression of genotypic worth on the selection index. If changes in genotypic worth and the selection index are expressed in terms of their respective standard deviations, then

$$\Delta W = (W_s - W_u) \frac{\sigma_w}{\sigma_w} = \frac{\sigma_{wI}}{\sigma_I^2} (I_s - I_u) \text{ and}$$

$$\frac{\Delta W}{\sigma_w} = \frac{(W_s - W_u)}{\sigma_w} = \frac{(I_s - I_u)}{\sigma_I} \frac{\sigma_{wI}}{\sigma_I \sigma_w} = \frac{(I_s - I_u)}{\sigma_I} r_{wI}$$

Rearrangement of the regression equation in this way shows that expected response to index selection, when expressed as a fraction of the standard deviation of genotypic worth, is equal to the product of the standardized selection differential and the coefficient of linear correlation between genotypic worth and the selection index. Since the standardized selection differential will depend only upon the intensity of selection, development of a selection index requires the use of index coefficients that maximize the correlation between genotypic worth and the resulting selection index.

III. OPTIMUM SELECTION INDICES

Smith¹ is usually credited with the initial proposal to use selection indices for the simultaneous improvement of several traits in a breeding program. Smith introduced the concept

that the genotypic worth of a plant could be expressed as a linear function of the genotypic values of several traits. In an example, it was considered that an increase of 10 in baking score, or a decrease of 20% in infection by flag smut, was as valuable as an increase of 1 bushel/acre in the yield of wheat, *Triticum aestivum* L. Relative values for increases of one unit in each of the three traits were $1/1 = 1.0$, $1/10 = 0.1$, and $1/20 = 0.05$. The genotypic worth (W) of a plant or line could therefore be expressed as

$$W = 1.0 \times \text{genotypic value for grain yield} \\ + 0.1 \times \text{genotypic value for baking score} \\ - 0.05 \times \text{genotypic value for flag smut infection}$$

Smith,¹ following a suggestion by R. A. Fisher,² argued that since it could not be directly evaluated, genotypic worth might best be estimated by a linear function of observable phenotypic values. As indicated previously, the expected change in genotypic worth is

$$\Delta W = (W_s - W_u) = b_{w_i}(I_s - I_u)$$

If phenotypic values of all traits in the index are normally distributed, the index itself will be normally distributed. With truncation selection for genotypes with high index scores, the selection differential ($I_s - I_u$) can be written as $k\sigma_I$, where k is the standardized selection differential and depends only upon the proportion of the population that is selected. In this case, expected response to selection is

$$\Delta W = (W_s - W_u) = k\sigma_I b_{w_i}$$

For this reason, Smith¹ argued that index coefficients should be chosen to maximize the product of the standard deviation of the index and the regression of genotypic worth on the index. Since

$$r_{w_i} = \frac{\sigma_{wI}}{\sigma_I \sigma_w} = b_{w_i} \frac{\sigma_I}{\sigma_w}$$

and since σ_w is constant for any population, maximizing the product of the standard deviation of the selection index and the regression of genotypic worth on the selection index is identical to maximizing the correlation between genotypic worth and the selection index.

Smith¹ showed that the index coefficients which maximized this expression for response to selection were those obtained by solving the set of simultaneous equations which can be expressed in matrix form as $\mathbf{Pb} = \mathbf{Ga}$. For three traits, this set of equations would be written in algebraic form as follows.

$$b_1\sigma_{p(1)}^2 + b_2\sigma_{p(1)2} + b_3\sigma_{p(1)3} = a_1\sigma_{G(1)}^2 + a_2\sigma_{G(1)2} + a_3\sigma_{G(1)3} \\ b_1\sigma_{p(1)2} + b_2\sigma_{p(2)}^2 + b_3\sigma_{p(2)3} = a_1\sigma_{G(1)2} + a_2\sigma_{G(2)}^2 + a_3\sigma_{G(2)3} \\ b_1\sigma_{p(1)3} + b_2\sigma_{p(2)3} + b_3\sigma_{p(3)}^2 = a_1\sigma_{G(1)3} + a_2\sigma_{G(2)3} + a_3\sigma_{G(3)}^2$$

In these equations, a_i is the relative economic value of the i^{th} trait, $\sigma_{G(i)}^2$ and $\sigma_{p(i)}^2$ are the genotypic and phenotypic variances of the i^{th} trait, and $\sigma_{G(ij)}$ and $\sigma_{p(ij)}$ are the genotypic and phenotypic covariances between the i^{th} and j^{th} traits. Methods for solving such a set of equations will be discussed and illustrated in Chapter 8.

Table 1
GENOTYPIC AND PHENOTYPIC PARAMETERS FOR
THREE TRAITS IN A HYPOTHETICAL POPULATION

| Parameter | Trait | | |
|-------------------------|------------------|--------------------|----------------|
| | Yield (kg/ha) | Maturity (days) | Protein (%) |
| Mean value | 3000 | 100 | 10 |
| Genotypic variance | 100,000 | 8.0 | 0.60 |
| Phenotypic variance | 250,000 | 10.0 | 1.00 |
| Heritability | 0.40 | 0.80 | 0.60 |
| Relative economic value | 0.01 | -1.0 | 4.0 |

| | Pairs of traits | | |
|------------------------|-----------------|---------------|------------------|
| | Yield-maturity | Yield-protein | Maturity-protein |
| Genotypic correlation | 0.3 | -0.5 | 0.0 |
| Genotypic covariance | 268.3 | -122.7 | 0.0 |
| Phenotypic correlation | 0.4 | -0.6 | -0.2 |
| Phenotypic covariance | 632.4 | -300.0 | -0.63 |

The nature of these equations might be better understood by reference to a set of hypothetical data for three traits (Table 1). Based on the parameters given in Table 1, the following three equations could be solved to give the index coefficients required for simultaneous improvement of grain yield, maturity, and protein concentration.

$$\begin{aligned}
 250,000 b_1 + 632.4 b_2 - 300.0 b_3 &= 0.01(100,000) - 1.0(268.3) + 4.0(-122.47) = 241.820 \\
 632.4 b_1 + 10.0 b_2 - 0.63 b_3 &= 0.01(268.3) - 1.0(8.0) + 4.0(0.0) = -5.317 \\
 -300.0 b_1 - 0.63 b_2 + 1.00 b_3 &= 0.01(-122.47) - 1.0(0.0) + 4.0(0.60) = 1.175
 \end{aligned} \tag{1}$$

The estimation of index coefficients for an optimum selection index will require knowledge of the relative economic values of traits as well as the genotypic and phenotypic variances and covariance among these traits. It will be seen that a major obstacle to the use of selection indices is the effort required to obtain suitably precise estimates of the required variances and covariances.

In some cases, relative economic values of some traits included in the index may be set to zero. These secondary traits are not of any direct economic importance, but may serve to enhance overall response in genotypic worth. In these cases, the right hand sides of the index equations need to be modified by dropping any terms for which the corresponding economic value has been set to zero. Furthermore, estimates of genotypic variances or covariances of these particular traits will no longer be required to develop optimum index coefficients. In fact, Smith¹ considered an example where genotypic worth was equal to the genotypic value of grain yield alone, but where the selection index was to include information about ear number per plant, average number of grains per ear, average weight per grain, and weight of straw, all expressed on logarithmic scales.

The Smith¹ method of developing selection indices will be referred to as an "optimum" index in the sense used by Williams.⁴ This is to differentiate this method from more recent modifications to the original proposal. If genotypic and phenotypic values are distributed with a multivariate normal distribution, the index coefficients calculated from population parameters in the way proposed by Smith¹ will give maximum response in genotypic worth.

In practice, however, one will use estimates of the corresponding population parameters and the resulting index coefficients will be estimates of the optimal index coefficients. Williams⁴ referred to these indices as "estimated" indices.

Hazel² took a slightly different, but equivalent, approach to the development of selection indices. The equation for expected change in genotypic worth can be modified in the following way.

$$\Delta W = (W_s - W_u) = b_{w1}(I_s - I_u) = b_{w1}k\sigma_{I1} = k \frac{\sigma_{w1}}{\sigma_{I1}} = k r_{w1} \sigma_w$$

Since σ_w will be constant for a given population and a given set of relative economic weights, the maximum response to index selection will be achieved if the correlation between genotypic worth and the selection index is maximized. Hazel² used this relationship as the basis for choosing index coefficients.

The equations given by Hazel² are equivalent to those given by Smith.¹ Dividing both sides of the i^{th} equation by $\sigma_w \sigma_{P_{i1}}$, the equations of Smith can, for three traits, be written as follows.

$$b_1 \frac{\sigma_{P_{11}}}{\sigma_w} + b_2 r_{P_{12}} \frac{\sigma_{P_{12}}}{\sigma_w} + b_3 r_{P_{13}} \frac{\sigma_{P_{13}}}{\sigma_w} = r_{P_{1W}}$$

$$b_1 r_{P_{21}} \frac{\sigma_{P_{11}}}{\sigma_w} + b_2 \frac{\sigma_{P_{22}}}{\sigma_w} + b_3 r_{P_{23}} \frac{\sigma_{P_{13}}}{\sigma_w} = r_{P_{2W}}$$

$$b_1 r_{P_{31}} \frac{\sigma_{P_{11}}}{\sigma_w} + b_2 r_{P_{32}} \frac{\sigma_{P_{12}}}{\sigma_w} + b_3 \frac{\sigma_{P_{33}}}{\sigma_w} = r_{P_{3W}}$$

Hazel² used the method of path coefficients to show that the right hand side of the i^{th} equation can be expressed as

$$r_{P_{iW}} = h_i \sum_j a_j r_{G_{ij}} \frac{\sigma_{G_{ij}}}{\sigma_w}$$

where summation is over the subscript j of the economically important traits, and h_i is the square root of the heritability of the i^{th} trait.

Using the parameters from Table 1, the variance of genotypic worth is given by

$$\begin{aligned}
 \sigma_w^2 &= (0.01)^2 (100,000) + (-1.0)^2 (8.0) + (4.0)^2 (0.60) \\
 &+ (2)(0.01)(-1.0)(268.3) + (2)(0.01)(4.0)(-122.47) \\
 &+ (2)(-1.0)(4.0)(0.0) = 12.4364
 \end{aligned}$$

Thus, $\sigma_w = (12.4364)^{1/2} = 3.5265$. If Equations 1 are each divided by the corresponding phenotypic standard deviation and by σ_w , they take the following form.

$$141.7825 b_1 + 0.3586 b_2 - 0.1701 b_3 = 0.1371$$

$$57.7080 b_1 + 0.8967 b_2 - 0.0565 b_3 = -0.4768$$

$$-85.0695 b_1 - 0.1786 b_2 + 0.2836 b_3 = 0.3332$$

Since the Hazel's equations can be derived directly from those of Smith's by dividing each side of each equation by the same constant, both sets of equations will give the same estimates for the index coefficients.

From Hazel's terminology, one can see that, in calculating optimum index coefficients, one must have knowledge of (1) the genotypic variance of each trait, (2) the genotypic correlations between each pair of traits, (3) the heritability of each trait, (4) the phenotypic variances of each trait, and (5) the phenotypic correlations between each pair of traits. Hazel's equations emphasize the point that the development of optimum selection indices requires estimation of numerous population parameters.

Hazel's developed selection indices for the simultaneous improvement of three traits in swine, *Sus domesticus*, based on (1) two of the three traits measured on juvenile animals, (2) those same two traits plus a third trait measured on the animal's mother, and (3) those same three traits plus the average of the first two for the litter in which the animal was born. These examples serve to show that the traits considered important in determining genotypic worth need not all be included in the index. Furthermore, the index may include traits other than those specified in the definition of genotypic worth, as well as traits measured on relatives of those undergoing selection.

In developing selection indices, Hazel's cautioned that the indices developed for one herd may not be widely applicable. Relative economic values may differ from locality to locality or with the nature of the operation. Genotypic variances and covariances may differ from herd to herd and phenotypic variances and covariances may differ because of different management practices. Moreover, initial estimates of population parameters may be subject to large estimation errors.

For genotypic worth defined as the genotypic value of a single trait, say trait 1, the Smith's equations, for a three trait index, are as follows.

$$b_1\sigma_{P(1)}^2 + b_2\sigma_{P(1)2} + b_3\sigma_{P(1)3} = \sigma_{G(1)}^2$$

$$b_1\sigma_{P(1)2} + b_2\sigma_{P(2)}^2 + b_3\sigma_{P(2)3} = \sigma_{G(2)}^2$$

$$b_1\sigma_{P(1)3} + b_2\sigma_{P(2)3} + b_3\sigma_{P(3)}^2 = \sigma_{G(3)}^2$$

In a similar way, the equations of Hazel's simplify to

$$b_1 \frac{\sigma_{P(1)}}{\sigma_{G(1)}} + b_2 r_{P(1)2} \frac{\sigma_{P(2)}}{\sigma_{G(2)}} + b_3 r_{P(1)3} \frac{\sigma_{P(3)}}{\sigma_{G(3)}} = h_1$$

$$b_1 r_{P(1)2} \frac{\sigma_{P(1)}}{\sigma_{G(1)}} + b_2 \frac{\sigma_{P(2)}}{\sigma_{G(2)}} + b_3 r_{P(2)3} \frac{\sigma_{P(3)}}{\sigma_{G(3)}} = h_2$$

$$b_1 r_{P(1)3} \frac{\sigma_{P(1)}}{\sigma_{G(1)}} + b_2 r_{P(2)3} \frac{\sigma_{P(2)}}{\sigma_{G(2)}} + b_3 \frac{\sigma_{P(3)}}{\sigma_{G(3)}} = h_3$$

If, for the population characteristics given in Table 1, the relative economic values of days to maturity and protein concentration were set to zero, the equations for developing a selection index to improve yield alone would be as follows.

$$250,000 b_1 + 632.4 b_2 - 300.0 b_3 = 100,000$$

$$632.4 b_1 + 10.0 b_2 - 0.63 b_3 = 268.3$$

$$-300.0 b_1 - 0.63 b_2 + 1.00 b_3 = -122.47$$

If several traits have economic importance, Henderson's has shown that the optimum selection index for total genotypic worth can be obtained by first developing indices, I_i , for each trait and then weighting each index by the economic value of the corresponding trait. Thus, if I_i is the selection index for the i^{th} trait, then

$$I = a_1 I_1 + \dots + a_i I_i + \dots + a_n I_n$$

is the optimum index for improving overall genotypic worth. The advantage of this approach is that changes in relative economic values will not require calculation of new selection indices for each trait. All that will be required is a reweighting of the original indices.

For the example considered above, one would estimate index coefficients for an index, I_y , for increasing yield, for an index, I_M , for increasing days to maturity, and for an index, I_p , for increasing protein concentration. All three indices would be linear functions of yield, days to maturity, and protein concentration. Then, an index for the simultaneous improvement of all three traits would be

$$I = 0.01 I_y - 1.0 I_M + 4.0 I_p$$

IV. RELATIVE EFFICIENCY OF INDEX SELECTION, INDEPENDENT CULLING, AND TANDEM SELECTION

Three methods of selection, which are recognized as appropriate for simultaneous improvement of two or more traits in a breeding program, are index selection, independent culling, and tandem selection. A selection index is a single score which reflects the merits and demerits of various traits. Selection among genotypes is based on the relative values of the index scores. If selection is conducted for several generations, one might consider using the same index in each generation.

Independent culling requires the establishment of minimum levels of merit for each trait. An individual with a phenotypic value below the critical culling level for any trait is removed from the population. With tandem selection, one trait is selected until it is improved to a satisfactory level. Then, in the next generation, selection for a second trait is practiced within the selected population, and so on for the third and subsequent traits. Differences among the three basic approaches are demonstrated diagrammatically in Figure 1.

Hazel and Lush⁶ investigated the relative efficiencies of these three selection methods. They considered expected response to truncation selection when phenotypic values are normally distributed, and when both genotypic and environmental correlations between traits are zero. For index selection, expected response in overall genotypic worth is

$$R_i = k \{a_i^2 h_i^2 \sigma_{P(i)}^2 + \dots + a_n^2 h_n^2 \sigma_{P(n)}^2\}^{1/2}$$

where k is the standardized selection differential, σ_p is the phenotypic standard deviation, h^2 is the heritability, and the subscripts refer to the traits included in the index.

For independent culling of uncorrelated traits, response in overall genotypic worth is expected to be

$$R_i = a_i h_i^2 k_i \sigma_{P(i)} + \dots + a_n h_n^2 k_n \sigma_{P(n)}$$

where k_i is the standardized selection differential corresponding to the fraction saved when culling for the i^{th} trait. For single trait (tandem) selection, expected response is

$$R_i = k \sigma_p h^2$$

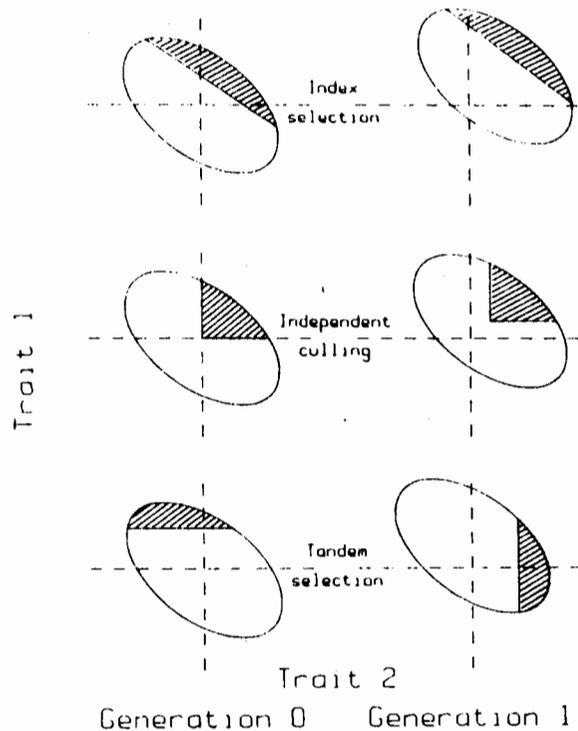


FIGURE 1. A diagrammatic comparison of index selection, independent culling, and tandem selection for two negatively correlated traits.

To further facilitate comparison of the three selection methods, Hazel and Lush⁶ considered only those cases for which the product of relative economic value, heritability, and phenotypic standard deviation, was the same for all traits. Under these more restrictive conditions, expected responses to one cycle of selection for each method can be expressed as follows.

$$\text{Index:} \quad R_1 = n^{0.5} k a h^2 \sigma_p$$

$$\text{Independent culling:} \quad R_2 = n k_i a h^2 \sigma_p$$

$$\text{Tandem:} \quad R_3 = k a h^2 \sigma_p$$

In these equations, k depends upon the fraction p of the population selected by tandem or index selection while k_i depends upon culling of a fraction p_i^n for each of the n traits. Under these very specific conditions, index selection will be $n^{0.5}$ times as efficient as tandem selection, regardless of selection intensity. Hazel and Lush presented a geometric argument as to why this should be so.

These equations also show that independent culling for uncorrelated traits is always intermediate in efficiency to index and tandem selection. Independent culling is expected to approach the efficiency of index selection as the number of traits decreases, and as the selected portion of the population becomes smaller (more intense selection). The advantage

of independent culling over tandem selection will decrease as the number of traits increases and when selection becomes less intense. Although Hazel and Lush⁶ found it necessary to use several restrictive assumptions to compare efficiencies of the three methods of multitrait selection, their results provided a strong argument for the use of selection indices in breeding programs.

The simplified equations of Hazel and Lush⁶ cannot be applied to the hypothetical population described in Table 1. First, the genotypic and phenotypic correlations between each pair of the three traits would have to be zero. Then, it would be necessary for the relative economic weights to be changed to -0.79 and 3.33 for days to mature and protein concentration, respectively, if the traits were to be considered equally important in the sense specified by Hazel and Lush.

Young⁷ also evaluated these selection methods, but with fewer restrictive assumptions, and came to similar conclusions. Young first considered relative responses to the three selection methods when traits were independent, but not of equal importance. Under these conditions, index selection is more efficient than tandem selection, with the advantage becoming greater as the number of traits increases and as the relative importances of the traits approach a common value.

In comparing index selection with independent culling, Young⁷ first estimated the optimum culling levels for each of the uncorrelated traits. The superiority of index selection over independent culling was greatest when the traits were of equal importance and when selection intensity was low to intermediate.

In considering relative efficiencies of selection for correlated traits, Young⁷ limited discussion to two traits. Both genotypic and phenotypic correlations have important effects on the relative efficiencies of the three selection methods. Generalization of the results is difficult. However, it does seem that selection using an optimum index will always be at least as efficient as selection based on optimum culling levels. Similarly, selection using optimum culling levels should always be at least as efficient as using tandem selection.

Finney⁸ suggested more generalized formulas for studying the relative efficiencies of these three selection methods. Central to Finney's proposal was the concept that covariances between genotypic values of individual traits and overall genotypic worth play a key role in determining the relative effectiveness of the three methods. Expected change in genotypic worth in response to selection for a single trait is proportional to the ratio of the covariance (between genotypic value for that trait and the total genotypic worth) to the phenotypic standard deviation for that trait. If one of these ratios is far larger than any other, tandem selection for that trait, or independent culling with high selection intensity for that trait, should give responses in overall genotypic worth which are close to that expected from index selection. Finney suggested that such an approach would have allowed Young⁷ to develop results with wider applicability. For the traits listed in Table 1, the ratio of the covariance between genotypic value and genotypic worth to the phenotypic standard deviation is 0.48 for yield, -1.68 for days to maturity, and 1.17 for protein concentration. Since these three values are similar, it is likely that index selection would be considerably more effective than independent culling or tandem selection for improving genotypic worth.

Pesek and Baker⁹ used computer simulation to compare tandem and index selection in advanced generations of inbred species. They considered selection among random F_6 plants from a cross between two homozygous parents, and then among F_7 progeny of the selected plants. For tandem selection, equal proportions were selected for one trait in the F_6 and for the other in the F_7 . A selection index was calculated from the F_6 data and used to select in both generations. Their simulations were based on a 10 locus genetic model and included only negative genotypic correlations varying from -0.95 to 0.0 , heritabilities from 0.3 to 0.8 , and ratios of relative economic importance of 0.5 to 1.5 . Their results indicated that index selection should be considerably more efficient than tandem selection for improving genotypic worth for two negatively correlated traits.

In some applications, a selection index based on several traits is used to improve a single trait. It is not difficult to show that, if the index coefficients are reliable estimates of the optimum coefficients, and if the trait included in the definition of genotypic worth is included in the index, selection based on the index will always give greater response than direct selection for that trait by itself. When index coefficients are chosen to maximize the correlation between an index and the genotypic value of one trait, the correlation will always be greater than the correlation with the phenotypic value of that trait, provided that trait is included in the index.

V. RESTRICTED SELECTION INDICES

Kempthorne and Nordskog¹⁰ considered that breeders may sometimes wish to maximize genotypic worth while restricting change in some traits. As an example, they described a case where a poultry breeder wished to maximize economic value based on egg weight, body weight, egg production, and fraction of blood spots, while maintaining body weight at an intermediate level. They calculated such an index. The index was equal to the unrestricted index multiplied by a modifying matrix. In general, imposing a restriction on changes in any trait will reduce the correlation between genotypic worth and the resulting index, and will therefore reduce expected response to selection. The extent of the reduction will depend on the particular correlational structure of the population.

Tallis¹¹ provided a further extension of the restricted selection index. Rather than restricting response to a fixed value, Tallis developed a method for restricting response to a proportion of a fixed value. If the value is specified as zero, the Tallis index is the same as that of Kempthorne and Nordskog.¹⁰ Harville¹² described such indices as having proportionality constraints. This terminology is more suitable than the "optimum genotype" terminology used by Tallis.¹¹ Harville¹² considered the case where selection is meant to improve genotypic values of different traits by specified amounts.

Pesek and Baker,¹³ in considering the problem of assigning relative economic weights, proposed that selection indices be developed by specifying "desired genetic gains" for each trait. They developed a method for calculating a selection index that would move the genotypic means in the desired direction. Their method appears to be a specific case of the proportional constraint method developed by Tallis.¹¹ While Pesek and Baker¹⁴ did refer to Tallis¹¹ paper, they apparently did not realize that their method of "desired gains" was identical to that of Tallis when proportionality constraints are attached to all traits in the index. Similarly, a more recent paper by Yamada et al.¹⁵ also appears to be identical to that of Tallis.¹¹

Tai¹⁶ developed a generalization of the Pesek and Baker index that could be applied when some of the traits in the index are not constrained. It appears that the modification proposed by Tai was covered in an earlier paper by Harville.¹⁷ The indices of Harville,¹⁷ Tai,¹⁶ and Pesek and Baker¹⁴ are all equivalent to that of Tallis¹¹ if constraints are specified for all the traits in the index. If constraints are not applied to all traits, then it appears that the Tallis¹¹ index is not as efficient as that developed independently by Harville¹⁷ and by Tai.¹⁶

VI. GENERAL SELECTION INDICES

Hanson and Johnson¹⁸ noted that any selection index is calculated from a specific population of genotypes tested in specific environments and questioned whether or not such an index could be used as a general index in a breeding program. They suggested it would be more efficient to combine information from a series of experiments to obtain an average or general index. In averaging data from several experiments, the purpose would be to develop an index which would maximize response in reference to all possible genotypes evaluated

over all possible environments. They argued that an adequate criterion would be to choose index coefficients so that average genotypic worth would be maximized. Since an exact solution is impractical, they recommended that index coefficients be estimated from pooled genotypic and phenotypic variance-covariance matrices, and that the average undergo a correction to give final estimates. Hanson and Johnson provide a worked example for two populations of soybean, *Glycine max.* Caldwell and Weber¹⁹ also discussed the possibility of developing general selection indices for use in crop breeding.

VII. OTHER MODIFIED SELECTION INDICES

Elston²⁰ considered the problem of ranking individuals based on their phenotypic values, and proposed a multiplicative index for this purpose. In the Elston index, data for each trait are transformed so that high values are desirable and distributions are similar, at least in number of modes. The index is then constructed by subtracting the minimum sample value for each trait and forming the product of the adjusted values. This procedure is based strictly on phenotypic values and does not require estimation of genotypic and phenotypic parameters. In a sense, the index assumes that each trait receives equal emphasis in the selection or ranking process.

In assessing the use of selection indices, Williams¹ evaluated the use of a base index. A base index was defined as one in which the relative economic values are used as the index coefficients. The index is similar to that of Elston²⁰ in that it does not require estimates of genotypic and phenotypic parameters. Williams¹ noted that the optimum index of Smith² adjusts the weighting coefficients in an attempt to correct for differences in genotypic variability, as well as for correlations between traits. The base index should approach the optimum index in efficiency if correlations between traits are small, and if the variability for each trait reflects its relative importance.

VIII. SUMMARY

The optimum selection index for improving a specified linear function of genotypic values is a linear function of phenotypic values in which the weights attached to each phenotypic value are chosen to maximize the correlation between genotypic worth and the selection index. Estimation of optimum index coefficients requires knowledge of genotypic and phenotypic variances and covariances among traits, or, equivalently, of heritabilities and of genotypic and phenotypic correlations among traits. An index for a case where relative economic values are nonzero for more than one trait can be calculated by first calculating an index for each trait and then weighting the individual indices by the relative economic values of the corresponding traits.

For simultaneous improvement of genotypic worth of several traits, index selection should always be at least as effective as independent culling which, in turn, should always be at least as effective as tandem selection. The advantage of using an optimum index will be greater if the relative economic values are equal, and if genotypic correlations between traits are low or negative.

There are instances where a plant breeder may wish to improve genotypic worth while restricting change in one or more traits to some particular value, or at least to some proportion of a specified value. Theory has been developed for estimating indices which meet the requirements of fixed or proportional constraints. It is apparent that people working in plant breeding have not been fully aware of these theoretical developments. More recent papers on restricted selection indices suggest that earlier proposals might not result in optimum response.

Indices based on average estimates of genotypic and phenotypic parameters, while never

having as great a predicted response as specific selection indices, often show realized responses that are in close proximity to those obtained by using specific indices. Such generalized indices may give the best average response.

Other modifications to the selection index methodology include the use of a base index, where relative economic values are used for index coefficients, and a weight-free index based solely on observed phenotypic values.

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THE APPLICATION OF SELECTION INDICES IN CROP IMPROVEMENT

I. INTRODUCTION

Much of the recent literature on the use of selection indices for crop improvement concerns self-pollinated crops or maize, *Zea mays*. This reflects the amount of research being conducted with these species rather than the effectiveness of selection indices in their improvement.

The various applications of selection indices can be divided into two major groups. The first group includes those instances where the objective is to improve a single quantitative trait. In this group, selection indices may incorporate data from related traits, or from the same trait in related plants, to increase the effectiveness of selection.

The second group of applications includes those instances where the objective is to improve two or more traits simultaneously. In this group, significant problems arise in assigning relative economic weights to the various traits. Because of this problem, researchers have developed modified methods, such as base indices, restricted indices, and multiplicative weight-free indices.

The purpose of this chapter is to review recent literature on selection indices, and, by so doing, to provide a background on the types of selection problems for which selection indices have been considered. This review also serves to illustrate some of the methods used for estimating genotypic and phenotypic variances and covariances.

II. APPLICATIONS INVOLVING IMPROVEMENT OF A SINGLE QUANTITATIVE TRAIT

Smith¹ introduced the concept of a linear selection index by developing an index for improved grain yield of wheat, *Triticum aestivum*. He concluded that using an index based on yield, yield components, and straw weight would result in greater response in yield than would selection for yield itself. Similar conclusions have been reached by Murthy and Rao² in a study of lodging resistance in barley, *Hordeum vulgare*. They concluded that an index based on plant height and weight of the main shoot would give only 75% as much improvement in lodging angle as would selection for lodging angle itself. However, they considered that it is easier to measure plant height and main stem weight than lodging angle, and that the index would therefore provide a useful basis for improving lodging resistance.

Rosielle and Brown³ assessed the use of selection indices for improving traits related to *Septoria nodorum* resistance in wheat. They evaluated yield, yield components, and disease symptoms on infected and disease-free (fungicide control) plots of F_2 -derived F_3 lines from six wheat crosses. They found that using severity of disease on the flag leaf and on the head as secondary traits failed to provide much advantage in selecting for improved yield or increased seed weight under diseased conditions.

Thurling⁴ evaluated several selection indices for improving yield of rapeseed, *Brassica campestris*, in western Australia. Two full-sib families within each of 32 half-sib families were evaluated in two blocks at a single location. Smith's¹ method was used to calculate several selection indices for improving yield and expected responses were compared. Indices based on yield components alone would not result in as much response as selection for yield *per se*. However, indices based on yield components and certain vegetative characteristics resulted in a higher expected response than selection for yield alone. The difficulty of conducting an extensive evaluation of a selection index over several environments led the author to question the practical value of selection indices.

Drought Course Lecture Outlines - Lecture 10

1. The Maize Drought Tolerance Network

1.1 Why have a Maize Drought Tolerance Network?

National program awareness: the basis for the Drought Network is the sharing of germplasm and methodology among concerned national programs, and with CIMMYT. This will ensure that national programs are fully aware of stress tolerant germplasm being developed, and they will be in a position to utilise it immediately, if they so desire.

The network provides a vehicle by which information and methodology can also be shared. This will be through exchange of technical reports, through the distribution of the Drought Network Report after each round of testing, and through training courses such as the present one.

National program involvement: By using the network as a means for testing and developing drought tolerant germplasm, national program scientists will have an important stake in the development process. The germplasm so developed will be theirs to use as they think fit. As well, cooperators could contribute germplasm, selection information and general guidance to the network.

Broad adaptation of germplasm under development: During the development of the population Tuxpeño Sequía it was apparent that some of the gains in "drought tolerance" (perhaps 21% of the total gains) were due to improved adaptation of this germplasm to the Tlaltizapan site (Bolaños and Edmeades, 1993). This highlighted the need to develop and test drought tolerant germplasm at a number of sites in our cooperating countries.

2. Mechanisms of germplasm sharing and improvement

2.1 Drought Tolerant Populations: The idea that one or two populations should serve as a reservoir of genetic variability for drought tolerance was put into practice by CIMMYT's Maize Physiology Program, and the Drought Tolerant Population-1 (DTP1) was formed in 1986. In 1989 this population was considerably upgraded by a major introgression of drought tolerant germplasm, to form DTP2. These populations are composed of about 60-65% lowland tropical germplasm, about 15-20% subtropical germplasm and about 20% temperate germplasm. Both are mixed grain colour and texture, and are intermediate in maturity. Yields of 10-11 tons/ha have been reported from them under unstressed conditions in Tlaltizapan, a mid-altitude disease-free test environment. Under stress, their performance has been among the best of the elite drought tolerant populations, but at this stage of their development, it has been no better.

2.2 Means of improving these populations: the present selection scheme is a recurrent S1 selection scheme in two stages. In the first stage about 600 S1 families are formed at Poza Rica under disease pressure in the A (winter) cycle. These are then subjected to testing in Obregon (heat and drought), Poza Rica (lowland tropical diseases), Batan (mid-altitude diseases), and at Tlaltizapan (agronomic performance). At the same time, each S1 family is sib-increased at Tlaltizapan, families being eliminated on the basis of their general performance at other sites as the season progresses. Finally, based on across-location observations, a core group of 222 families is selected for international testing. The recombination of the superior fraction is based on across-location performance. Lattice-adjusted yields from each site are passed to the

Selection Assistant program, where weights are placed on yields from each site according to yield level, incidence of drought, etc, and a superior fraction of 40 families is identified and recombined.

The testing phases requires almost 2 years. During this time there are opportunities for improving each S1 family by advancing to S2 and selecting one superior S2 to represent that family in recombination, etc. Thus far this has not been done.

2.3 Strengths of this approach: It brings together germplasm of widely different adaptations, mixes it and allows a series of recombinations which will permit genes for drought tolerance mechanisms to be recombined with genes good agronomic performance. Thus germplasm from widely different backgrounds can be combined into a single entity. If this is then shipped to cooperators in a form which they can use to extract inbred lines, synthetics, etc. The population is open-ended, in that a major introgression is planned each 4-5 years as new source materials are identified and proven to have superior performance.

A second major advantage is that it gets around a number of problems of seed quarantine and proprietary rights. The population becomes a Mexican entity, produced here in Mexico. If we attempted to ship the individual components, especially hybrids, we would quickly run into problems of quarantine (e.g., seed produced in southern Africa, but shipped from Mexico - we cannot state anything about the seed production conditions), and proprietary rights (this is my F1 hybrid!). When components are merged into a single population, many of these objections are eliminated.

2.4 Weaknesses of this approach:

It is probably impossible to have a single population that meets the needs of specific countries and sites. This confines the role of these materials to source germplasm, that will be used in a back-crossing program within national programs.

A central problem with both populations is disease resistance. In the process of pursuing drought tolerance among sources, little or no attention has been paid to the associated disease resistances that the sources carry. In doing so CIMMYT has argued that specific disease resistances are best added to the germplasm in the regions and zone of adaptation that the germplasm is designed to serve. Genes for downy mildew resistance exist in low frequency in both populations. DTP1 carries no streak resistance and there is a low frequency of streak resistance in DTP2. Neither is strongly resistant to *H. maydis*, *E. turcicum*, *P. polysora* or *P. sorghi*. Ear rots will be a problem where disease pressure is high. Fortunately, in most drought-prone areas, the air is generally dry, and conditions for severe fungal disease epidemics are less favourable than in standard lowland tropical environments.

Insect resistance: There is a low frequency of genes for insect resistance in DTP2.

The adaptation of these populations to specific sites and specific requirements for grain color and texture is a central issue in their further development.

Extraction of lines with clean true colour may well be a problem. Early experience with these materials suggests that it will be comparatively simple to extract clean white lines from these populations, but that yellow lines from either will be a weak in colour.

2.5. Identification and verification of drought tolerant sources in national programs: CIMMYT feels certain that there are excellent sources of drought tolerance already in existence in national programs. It is to be hoped that these will be entered in trials of drought tolerant

germplasm that are grown as part of the Network activities. These would then be identified as drought tolerant materials at the site where that trial was grown, and in the next round of testing these entries could be more widely tested.

The problem we encounter with this approach is one of seed supply and quarantine. Take for example the case of single cross hybrids. If 7kg of seed of a desirable is supplied by a national program cooperator, present quarantine arrangements here in Mexico require that all of this seed be grown first under isolation in Mexico. CIMMYT can obviously not increase seed of a SX hybrid, nor would it be reasonable to expect national programs to supply us with lines to make the hybrid here.

To avoid this difficulty we may have to ship seed from specific locations to other cooperators in the region, that is, form small networks within regions that exchange superior entries for further testing under drought.

Another approach is to receive superior source materials from national programs at CIMMYT, along with data on their regional performance, retest them here in Tlaltizapan under relatively neutral conditions, and to form a new Drought Tolerant Population, or to introgress these new sources into the existing populations (DTP3? DTP4?). Such introgressions will probably have to be organized along lines of specific adaptation: for example, lowland tropical; mid-altitude tropical; yellow grain; white grain.

3. Who constitutes the Maize Drought Tolerance Network?

The Network is made up of individuals in national programs (public and private) who share an interest in developing drought tolerant maize germplasm. The Network will be coordinated by CIMMYT, under the auspices of the UNDP Maize Stress Project.

We recognise that there will be two groups of network cooperators: a larger group which will be primarily interested in testing synthetics and varieties being developed within the network. Generally they will conduct such tests in the normal rainy season, and will contribute locally adapted drought tolerant varieties for testing across a wider range of sites by other collaborators. We refer to these as **testing cooperators**.

A second smaller group of cooperators will concentrate on the development of drought tolerant germplasm through a recurrent testing scheme of S1 (or full-sib) families under conditions of carefully controlled drought. The development of population(s) will be coordinated from CIMMYT with national program help, and they will serve as the repository for genes associated with drought tolerance. Populations would therefore be open-ended, and introgressions of superior germplasm will take place from time to time as appropriate. We refer to this group as **development cooperators**.

How would this network differ from the normal group of CIMMYT's international germplasm testing cooperators?

We believe that over time cooperators in the drought network will be distinguished by:

- 1) Interest in the problem of drought tolerance in maize, and a national responsibility to breed for areas affected by drought.
- 2) Access to good testing sites. Such sites should have deep uniform soils typical of the region in which drought occurs, and should have a high probability of a reliable dry period

occurring in a growing season which is either the normal maize season or a dry season not very different in temperature regime to the normal growing season.

- 3) For **development cooperators** the capacity to supply supplemental irrigation at the site is important. The source of water should be reliable all year around, good quality sprinkler/gravity irrigation systems should be available, and drainage of excess water should be uniform and rapid. Sites relying on furrow irrigation should be well-levelled. If possible the site should be close to a meteorological station so that daily rainfall, windrun, temperatures and pan evaporation data can be reported.
- 4) For **all cooperators** the capacity to observe anthesis-silking interval on a family basis, to score leaf loss from below-ear senescence and above-ear firing, and the capacity to recognize tassel blasting when it occurs is important.
- 5) Some familiarity with instruments which measure plant water potential (pressure chamber, infrared thermometer, porometers) is an asset, but is by no means essential.
- 6) We prefer to measure shelled grain yields since shelling percentage is often affected by flowering stress. Access to a sheller would therefore be essential. For certain trials, especially those conducted by development cooperators, we will also need weights of 100 kernel samples at oven-dry moisture percentage (or at a moisture content defined by a good electronic moisture tester). Access to moisture testers, and perhaps balances and ovens will be needed in those cases.

These requirements represent a desirable end point in cooperation, one which we can work towards together. We emphasize that the current absence of some of these facilities should not prevent an interested cooperator from becoming part of the Drought Network.

4. Network Activities to Date

4.1 First round of testing:

Please refer to Edmeades et al. (1991), the report of the first round of testing, a document held on reference in the Library.

The trials reported here were announced in mid-1989, and seed of three trials (the DEVT Early Trial, DEVT Late trial, and the S1 progeny trial of the population DTP1) were sent out for testing by interested cooperators in 1990. Results were returned in late 1990 and early 1991. All trial data reaching CIMMYT by May 31, 1991 were included in this analysis.

Methods and Materials

A: Materials under test:

All populations under test in the DEVT trials were derived from CIMMYT populations, with appropriate places in each trial for local check entries.

Pool 16 Sequía: Pool 16 is an early white dent population. This population is based mainly on crosses among a large number of early and late white dent materials from México, the Caribbean, Central and South America and Asia. Prior to selection for drought tolerance, approximately 12 cycles of recurrent half-sib family selection had been conducted in CIMMYT's back-up unit primarily for early maturity, but also for better plant type, improved yield, tolerance

to high plant density, and to stalk rot. Pool 16 is well adapted to short season dry environments in sub-Saharan Africa. In the early 80s a version of it was partially converted to streak resistance by IITA and SAFGRAD Programs, and underwent recurrent selection for improved performance in Ivory Coast, using tied and untied ridges to impose differential water stress. Selection at CIMMYT was initially within this version of the population, but in Cycle 1 the CIMMYT and SAFGRAD versions were combined. Synthetics under test in the present trials were derived from C0, which was tested as 196 full-sib families in a replicated trial under three water regimes in Tlaltizapan in 1987A. Synthetics based on the 10 best and worst families for an index of traits used during selection (see Bolaños et al, 1990; Edmeades et al., 1990) were created and advanced to F2, and entered in the DEVT Early Trial.

Pool 18 Sequía: Pool 18 is an early yellow dent population. The origins of Pool 18 Sequía are generally similar to those of Pool 16, except that selection for drought tolerance was based solely on the CIMMYT version of the population. Recently selection in this population has been for a more a flinty grain type. Synthetics under test in the present trial were derived from C0, which was tested in two stages: 1500 S1 families were created and tested in an observation nursery in Obregon under heat and drought stress in 1986. Remnant seed of the best 250 of these was planted in a replicated trial under three water regimes in Tlaltizapan in 1987A. Synthetics based on the 10 best and worst families for traits used as part of a selection index were created and advanced to F2, and entered in DEVT Early Trial.

La Posta Sequía: La Posta is tropical late maturing white dent population of Tuxpeño germplasm, relatively tall and vigorous, with a considerable level of resistance to streak virus. This population had undergone recurrent full-sib family improvement in CIMMYT's International Progeny Testing Trials (IPTTs) for 6 cycles prior to its conversion by CIMMYT to streak resistance at IITA. Synthetics under test in the present trials were derived from C1 of La Posta Sequía. Cycle 0 was tested as 167 S1 families in a replicated trial under three water regimes in Tlaltizapan in 1987A, and the best 40 families were recombined to form C1. One thousand S1 families were created and tested in an observation nursery in Obregon under heat and drought stress in 1987. Remnant seed of the best 225 of these was planted in a replicated trial under three water regimes in Tlaltizapan in 1988A. Synthetics based on the 10 best and worst families for traits used as part of a selection index were created and advanced to F2 in 1988A, and entered in DEVT Late Trial.

Pool 26 Sequía: Pool 26 is a tropical late yellow dent population, made up mainly of materials from Central America, México, Colombia, the Caribbean and Asia. It contains a small amount of US Cornbelt germplasm. It is relatively tolerant to stunt and has good yield potential. When families from this population were being assembled to form Pool 26 Sequía, 38% of the families of C0 were derived from a fraction of Pool 26 which had been improved specifically for resistance to Fall Armyworm. Cycle 0 was tested as 250 S1 families in a replicated trial under three water regimes in Tlaltizapan in 1987A, and the best 50 families were recombined to form C1. One thousand S1 families were created and tested in an observation nursery in Obregon under heat and drought stress in 1987. Remnant seed of the best 232 of these was planted in a replicated trial under three water regimes in Tlaltizapan in 1988A. Synthetics based on the 10 best and worst families for traits used as part of a selection index were created and advanced to F2 in 1988A, and entered in the DEVT Late Trial.

Drought Tolerant Population-1 (DTP1): Intermediate maturity mixed grain color and type, tropical and subtropical adaptation. This formation of this population has been described in previous lectures.

In 1989A a bulk of C4 was planted under a linesource irrigation system and selfs were made at varying distances from the irrigation line. At harvest 600 ears were selected from the driest area of the linesource. In 1989 these were screened in Obregon under drought and heat, for

disease in Poza Rica, and for general performance in Tlaltizapan in 1989A. On the basis of performance at these three sites, the best 350 were sib-increased under well-watered conditions to provide additional seed, and the best 222 were finally selected for international testing.

National Program Check entries: Cooperators were requested to select check entries that matched the general entries for the trials in maturity.

B: Trials

Early Drought Experimental Variety Trial (DEVT-E):

Germplasm under test: For the most part entries in this trial were either experimental varieties (made up from the best fraction of full-sib families) in the case of Pool 16, or were synthetics formed by crossing superior S₁ families selected on the basis of all traits observed (e.g., "best all characters", or "small tassel size", or "best for all traits" and "worst for all traits"). Note that the entry list was not constant during this trial series because of seed supply constraints. Thus two versions of entries 2, 7, 8 and 11 were under test.

Entries were as follows:

| | |
|--|---------------|
| 1.Pool 16 Sequía, C ₀ F ₂ | PR89A-696# |
| 2(1).Pool 16 Sequía, "best all", C ₀ F ₂ (sites 1-17) | PR88B-5641# |
| 2(2).Pool 16 Sequía, best yield RN, C ₀ F ₂ (sites 18-21) | PR88B-5629# |
| 3.Pool 16 Sequía, "worst all, C ₀ F ₂ | PR88B-5642# |
| 4.Pool 16 drought synthetic, high yld, F ₂ | PR88A-210# |
| 5.Pool 16 drought synthetic, good ASI, F ₂ | PR88A-213# |
| 6.Pool 16 Across 86, F ₃ | TL89B-6696# |
| 7(1).TEW Synth. resistant to <i>Phyllacora</i> , F ₂ (sites 1-17) | PR89A-224 |
| 7(2).Tropical Early White Drought Synthetic (sites 18-21) | PR89B-5216-B |
| 8(1).Pool 15 Synthetic, F ₂ (sites 1-17) | PR86B-5233# |
| 8(2).Tropical Early Yellow Drought Synthetic (sites 18-21) | PR89B-5216-D |
| 9.Pool 18 Sequía, C ₀ F ₂ | TL87B-6655# |
| 10.Pool 18 Sequía, small tassel size, C ₀ F ₂ | PR88B-5623# |
| 11(1).Pool 18 Sequía, "best all", C ₀ F ₂ (sites 6-21) | TL89B-6699-5# |
| 11(2).Pool 18 Sequía, "worst all", C ₀ F ₂ (sites 1-5) | TL89B-5626# |
| 12.Pool 18 Sequía, best ASI, C ₀ F ₂ | PR88B-5616# |
| 13.Rattray Arnold (1) 8149 | PR88B-5085# |
| 14.Across 8530 | TL87A-1049# |
| 15.Local check 1 | |
| 16.Local check 2 | |

Notes:

- 1) Entries 4 and 5 were developed from CIMMYT's version of Pool 16, based on Back-Up Unit selections of 500 S₁ families at Tlaltizapan. They do not carry streak resistance.
- 2) Entry 6 is an across-location selection of 12 FS families found to be superior under drought at Tlaltizapan and in Burkina Faso.
- 3) Entry 7(1) showed good general vigor and is a synthetic of S₁ families showing resistance to *Phyllachora maydis*.
- 4) Entry 8(1) was developed from CIMMYT Pool 15 in a similar manner to Entries 4 and 5
- 5) Entry 10 has shown promise in tests in México, and resembled a "best all" selection.
- 6) Entries 13 and 14 are stable high yielding experimental varieties from CIMMYT's International Testing Program. Entry 13 is later maturing than most other entries.
- 7) Entries 15 and 16 were supplied by the cooperator.

Test locations:

1. Tucuman, Argentina, 27 S 65 W, 481 masl. Mean yield = 5.3 tons/ha, Dr. N Baracco
2. Lodana, Ecuador, Mean yield = 2.1 tons/ha, Ings. Segundo Reyes and Daniel Alarcon
3. Hualtaco Piura, Peru. 5 S, 81 W, 29 masl, Mean yield = 4.3 tons/ha, Ing. Jose Moran
4. Harare, Zimbabwe, 18 S, 31 E, 1506 masl, Mean yield = 2.2 tons/ha, Dr. K. Short
5. Golden Valley, Zambia, 14 S 28E, 1200 masl, Mean yield not recorded (lodged by termites); Dr. C. Mungoma
6. IARI, New Delhi, India, 28 N, 77 E, 228 masl, Mean yield = 4.7 tons/ha, Dr. N.N. Singh
7. Godhra, India, 23 N, 74 E, 119 masl, Mean yield = 1.4 tons/ha, Dr. M.D. Arja
8. Tak-Fa, Thailand, 16 N, 100 E, 86 masl, Mean yield = 2.3 tons/ha, Dr. C. Kitbamroong
- 9 & 10. Obregon, Mexico, 27 N, 100 W, 20 masl, Mean yield = 2.8 tons/ha and 2.8 tons/ha (rain interfered), G. Edmeades
11. Sinematiali, Cote d'Ivoire, 9 N, 3 W, 305 masl, Mean yield = 2.7 tons/ha, Dr. A. Diallo
12. Poza Rica, Mexico, 21 N, 97 W, 60 masl, Mean yield = 3.4 tons/ha, G. Edmeades

Data lost in transit: Ngabu, Malawi

Data arrived late: Ilonga, Tanzania; Awasa, Ethiopia; Siete Lagoas, Brazil.

Trial methodology

A rainfall gauge was supplied with each trial set and monthly rainfall totals for each site were reported along with the trial results.

DEVT-E and DEVT-L: Each trial consisted of a 4 x 4 alpha (0,1) lattice (Patterson and Williams, 1976) in 4 replicates. Plot size was normally 4 rows 5m long, 0.75-0.80m apart, and the plants were usually 20cm apart in the row in DEVT-E (66,000 plants/ha) or 25 cm apart in DEVT-L (53,000 plants/ha). Actual densities ranged from 40,000 plants/ha to 66,000 plants/ha. Cooperators were asked to record days to 50% anthesis, 50% silking, scores of foliar senescence, stand counts at harvest, lodging, ear number, grain moisture at harvest, shelled grain yield from a bordered plot area (6.38-6.60 m²), and if possible weight of 100 representative grains from each plot.

Anthesis-silking interval and yield components were calculated where possible, and yields adjusted to 15% grain moisture. Data were subject to analysis of variance. The relative efficiency of the lattice design compared with a randomized complete block design ranged from 0% to 52% (average 15%) for the early maturing trial, and ranged from 0 - 177% (average 35%) for the late maturing trial. In the tables which follow, all data are given as lattice-adjusted means. An across-site analysis of variance based on lattice adjusted means for grain yield at each site was carried out, using the pooled error from the individual site analyses as a measure of average error. Sites were considered random effects. Pre-planned single degree of freedom

comparisons were carried out in the late maturing dataset where the entries remained the same at all 17 locations.

In addition, joint linear regressions (Blum, 1988; Eberhart and Russell, 1966) were carried out in which yield of an individual genotype was regressed on mean yield at each site.

Across location yields:

| Entry | Yield t/ha | Anthesis d | ASI d |
|---|---------------|---------------|----------|
| 1. Pool 16 Sequía, C ₀ F ₂ | 3.11 | 53.7 | 1.99 |
| 2. Entry 2 | 3.30 | 53.8 | 1.51 |
| 3. Pool 16 Seq., "worst all", C ₀ F ₂ | 3.15 | 53.9 | 1.83 |
| 4. Pool 16 Drt Syn, high yld, F ₂ | 2.74 | 51.9 | 2.04 |
| 5. Pool 16 Drt Syn, good ASI, F ₂ | 2.72 | 52.4 | 1.93 |
| 6. Pool 16 Across 86, F ₃ | 3.27 | 53.2 | 1.98 |
| 7. Entry 7 | 2.51 | 53.3 | 2.68 |
| 8. Entry 8 | 3.28 | 53.3 | 1.71 |
| 9. Pool 18 Sequía, C ₀ F ₂ | 2.66 | 50.5 | 2.61 |
| 10. Pool 18 Sequía, small tass. C ₀ F ₂ | 2.81 | 50.3 | 2.30 |
| 11. Entry 11 | 2.73 | 50.3 | 2.59 |
| 12. Pool 18 Sequía, best ASI, C ₀ F ₂ | 2.46 | 51.1 | 2.47 |
| 13. Rattray Arnold (1) 8149 | 3.69 | 57.8 | 1.63 |
| 14. Across 8530 | 3.54 | 54.2 | 2.15 |
| 15. Local check 1 | 3.64 | 56.9 | 1.61 |
| 16. Local check 2 | 3.72 | 57.8 | 2.36 |

Discussion

A total of 21 sets of the early maturing trial were distributed for testing, and 12 returned useful results, a return rate of 57%.

High yielding sites (5): Data from Tucuman represented a test of yield potential rather than drought tolerance. Despite the high yields, the coefficient of variation for yield in this trial was very high (42%). The two check entries outyielded the best CIMMYT entry (Rattray Arnold (1) 8149) by a significant 26%. Pool 16 Sequía entries generally outyielded those from Pool 18. Plants at this site were tall, presumably because of photoperiod effects.

A similar pattern of yields was seen at Piura, Peru, where the check, Costeño-36, outyielded the best CIMMYT entry (Pool 16 Across 86) by a significant 34%. At Delhi, India (Table 1-6), also a high yielding location, Pool 16 Sequía "best all" (5.44 t/ha) was only 0.74 t/ha less than the highest yielding check, Harsha. Yields were also relatively high at Sinematiali, Ivory Coast (Table 1-11), where little stress was encountered at flowering. Here the check entry, TZEComp 3 x 4, outyielded Pool 16 Sequía "worst all" and Across 8530 by a non-significant margin. Poza Rica, México, was a relatively unstressed site, though heavily lodged at flowering. The most lodging resistant entry, Rattray Arnold 8149, also the latest to flower, gave the highest yield.

Low yielding sites (6): Yields were considerably reduced by drought at Lodana, Ecuador. The highest yielding entry was Rattray Arnold 8149, but several entries from Pool 16 Sequía and the check entry, INIAP-526, performed creditably. Low yields were recorded from Harare, Zimbabwe, caused by a combination of drought and *Puccinia sorghi* infection. Here the best check outyielded the best CIMMYT entry (Rattray Arnold 8149) by a non-significant 8%. Among the early maturing entries (flowering in less than 66 days), the check hybrid R201 and Across 8530 proved the best. Godhra, India, was also a low yielding site, but largely because of waterlogged conditions caused by 1302 mm of rainfall during the growing season. Several CIMMYT entries outyielded the best check, Arun, but not by a significant margin.

Drought reduced yield significantly in the trial at Tak-Fa, Thailand. At this site several varieties (Pool 16 Across 86; Pool 16 Sequía "best all"; Rattray Arnold 8149; Across 8530) non-significantly outyielded the best local check, NS 1. Yields at two trials planted in Obregon were remarkably similar, largely because unexpected rain eliminated planned differences in water stress between the two trials. The highest yielders were again Rattray Arnold 8149, Across 8530, Pool 18 Sequía "low tassel branch number" and Pool 16 Sequía C0.

Across sites: There were significant variety and variety x location effects in the analysis. It is important to note that mean yields were 3.08 t/ha, and this is relatively high for droughted trials. We must conclude therefore that relatively few sites were severely affected by drought, and that yields therefore were largely a reflection of unstressed yield potential.

The highest yielding entries were the checks which were not significantly different from Rattray Arnold (1) 8149 or Across 8530, the two CIMMYT reference entries. The superiority of the checks is not unexpected, especially in a trial series which was not severely drought stressed, since the checks would have possessed disease resistance required for site-specific adaptation. Rattray Arnold 8149 was 4-7 days later to flower than entries from the CIMMYT drought program, and since many sites were relatively unstressed, this variety demonstrated its high yield potential. It is also clear however that this variety possesses considerable capacity to yield well in low yielding environments, since the intercept obtained by joint linear regression was 0.85 t/ha. Across 8530 however, is relatively early (54.2 days to flower, versus 50.5 d for Pool 18 Sequía and 53 d for Pool 16 Sequía), and performed very creditably.

Grain yield was significantly and negatively correlated with ASI ($r = -0.63^{**}$, 14 df), highlighting the continuing importance of this trait in selecting drought tolerant early maturing germplasm.

Individual trait selections showed inconclusive results. In general, selections based on ASI (entries 5 and 12) showed slightly smaller ASI's than the trial mean. The best yielding entries in Pool 16 Sequía and Pool 18 Sequía were, respectively, Entry 2 (mainly the selection "best all") and Entry 10, "low tassel branch number".

Late Drought Experimental Variety Trial (DEVT-L):

Germplasm under test: For the most part entries in this trial are synthetics formed by crossing superior S_1 families selected on the basis of traits observed.

Entries were as follows:

- | | |
|--|------------|
| 1. La Posta Sequía, $C_1 F_2$ | PR89A-676# |
| 2. La Posta Sequía, "best all", $C_1 F_2$ | PR89A-682# |
| 3. La Posta Sequía, "worst all", $C_1 F_2$ | PR89A-683# |
| 4. La Posta Sequía, "best sync", $C_1 F_2$ | PR89A-679# |

| | |
|---|-------------|
| 5. La Posta Sequía, "best GY, IS, SS" C ₁ F ₂ | PR89A-677# |
| 6. Pool 26 Sequía, C ₁ F ₂ | PR89A-662# |
| 7. Pool 26 Sequía, "best all", C ₁ F ₂ | PR89A-668# |
| 8. Pool 26 Sequía, "worst all", C ₁ F ₂ | PR89A-669# |
| 9. Pool 26 Sequía, "best sync", C ₁ F ₂ | PR89A-665# |
| 10. Pool 26 Sequía, "best GY, IS, SS" C ₁ F ₂ | PR89A-663# |
| 11. Drought Tolerant Population 1, C ₄ | TL89A-1627# |
| 12. Tuxpeño Sequía C ₆ | TL89A-1642# |
| 13. Tak Fa 8536 | TL87A-1038# |
| 14. Palmira 8425 | TL88A-1099# |
| 15. Local check 1 | |
| 16. Local check 2 | |

Notes

- 1) Entry 12 is a bulk of Cycle 6 of Tuxpeño Sequía
- 2) Entries 13 and 14 are stable high yielding experimental varieties from CIMMYT's International Testing Program.
- 3) Entries 15 and 16 were supplied by the cooperator.

Test locations:

1. Tucuman, Argentina, 27 S 65 W, 481 masl. Mean yield = 6.6 tons/ha, Dr. N Baracco
2. Lodana, Ecuador, Mean yield = 2.7 tons/ha, Ings. Segundo Reyes and Daniel Alarcon
3. Hualtaco Piura, Peru. 5 S, 81 W, 29 masl, Mean yield = 4.3 tons/ha, Ing. Jose Moran
4. Harare, Zimbabwe, 18 S, 31 E, 1506 masl, Mean yield = 3.3 tons/ha, Dr. K. Short
5. Golden Valley, Zambia, 14 S 28E, 1200 masl, Mean yield 1.9 tons/ha; Dr. C. Mungoma
6. Choluteca, Honduras, 13 N, 87 W, 48 masl, mean yield = 0.5 tons/ha, Ing. N. Moradlaya.
7. IARI, New Delhi, India, 28 N, 77 E, 228 masl, Mean yield = 4.9 tons/ha, Dr. N.N. Singh
8. Godhra, India, 23 N, 74 E, 119 masl, Mean yield = 1.3 tons/ha, Dr. M.D. Arha
9. Tak-Fa, Thailand, 16 N, 100 E, 86 masl, Mean yield = 3.2 tons/ha, Dr. C. Kitbamroong
- 10 & 11. Obregon, Mexico, 27 N, 100 W, 20 masl, Mean yield = 1.5 tons/ha and 2.4 tons/ha, G. Edmeades
12. Sinematiali, Cote d'Ivoire, 9 N, 3 W, 305 masl, Mean yield = 2.7 tons/ha, Dr. A. Diallo
13. Poza Rica, Mexico, 21 N, 97 W, 60 masl, Mean yield = 3.9 tons/ha, G. Edmeades
- 14, 15, 16 and 17: Tlaltizapan, Mexico, 19 N, 99 W, Four regions from a line source irrigation scheme. Mean yields were: 1.7, 2.6, 2.9 and 5.5 tons/ha; J. Bolanos

Data lost in transit: Ngabu, Malawi

Data arrived late: Ilonga, Tanzania; Awasa, Ethiopia; Siete Lagoas, Brazil.

Trial methodology: see early maturing trial.

Results:

| Entry | Yield t/ha | Anthesis d | ASId |
|---|------------|------------|------|
| 1. La Pos Seq, C ₁ F ₂ | 3.25 | 69.6 | 3.14 |
| 2. La Pos Seq, "best all", C ₁ F ₂ | 3.15 | 68.9 | 1.78 |
| 3. La Pos Seq, "worst all", C ₁ F ₂ | 2.89 | 70.8 | 3.22 |

| | | | |
|--|------|------|------|
| 4. La Pos Seq, "best sync", C ₁ F ₂ | 3.20 | 69.3 | 1.65 |
| 5. La Pos Seq, "B GY, IS,SS" C ₁ F ₂ | 2.97 | 69.5 | 1.94 |
| 6. Pool 26 Seq, C ₁ F ₂ | 2.97 | 66.6 | 2.62 |
| 7. Pool 26 Seq, "best all", C ₁ F ₂ | 3.13 | 66.1 | 2.90 |
| 8. Pool 26 Seq, "worst all", C ₁ F ₂ | 2.60 | 66.5 | 3.66 |
| 9. Pool 26 Seq, "best sync", C ₁ F ₂ | 2.92 | 66.4 | 2.05 |
| 10. Pool 26 Seq, "B GY, IS,SS" C ₁ F ₂ | 3.13 | 65.8 | 1.72 |
| 11. DTP1, C ₄ | 3.13 | 63.9 | 2.42 |
| 12. Tuxpeño Sequía C ₆ | 3.21 | 68.0 | 1.32 |
| 13. Tak Fa 8536 | 3.33 | 67.5 | 2.83 |
| 14. Palmira 8425 | 2.82 | 67.0 | 2.59 |
| 15. Local check 1 | 3.56 | 68.5 | 2.42 |
| 16. Local check 2 | 3.33 | 66.0 | 2.58 |

Discussion

A total of 27 sets of the late maturing DEVT trial were distributed, of which 17 (52%) provided usable results.

High yielding sites (6): Yields at Tucuman, Argentina, and Hualtaco Piura, Peru, were largely unstressed by drought, and generally showed superior performance by La Posta Sequía C₁ and the local checks. The site at Delhi, India, had a mean yield of 4.93 t/ha, and several entries, notably La Posta Sequía "worst all", La Posta Sequía C₁, La Posta Sequía "best yield, severe stress", Pool 26 "best yield, severe stress", Tak-Fa 8536 and Palmira 8425, outyielded the best check, Harsha. Poza Rica, México was little affected by drought stress but was severely lodged prior to flowering. Here Tuxpeño Sequía C₆ recombination was the highest yielder, closely followed by La Posta Sequía "best ASI". The two wettest zones of the linesource trial at Tlaltizapan were also classed as high yielding sites. At the drier of these two sites Tuxpeño Sequía C₆ produced the highest yield, while at the wetter site higher yield potential genotypes (such as La Posta "best yield, severe stress" and Pool 26 Sequía "best yield severe stress", DTP1 C₄, and the two checks) improved their overall performance.

Low yielding sites (11): We assume that low yields at these sites was caused by drought stress, though disease, such as *Puccinia sorghi*, was undoubtedly another cause of yield loss at some sites (e.g., Harare, Zimbabwe).

At Lodana, Ecuador, several entries, notably Tak-Fa 8536, La Posta Sequía "best all", La Posta Sequía "best ASI", and Palmira 8425 outyielded the best local check, INIAP-526, though not by a significant margin. At Harare, Zimbabwe, Tuxpeño Sequía C₆, selected in Harare for rust resistance, significantly outyielded all other entries. The superiority of the check entry, MM502, was especially marked at Golden Valley, Zambia, where it outyielded all other entries by a large margin. Yields were severely reduced in Choloteca, Honduras, and the CV for yield exceeded 80%. We decided to retain this site in the across-site analysis because the standard error for difference was similar to that of other higher yielding sites. In general Tuxpeño-based varieties showed superiority here, especially Tuxpeño Sequía C₆. At Godhra, India, yields were low, but largely because of flooding. A number of entries outyielded the local checks under these circumstances, the best yielders being La Posta "best ASI" and Tak-Fa 8536.

The entries La Posta Sequía C₁, La Posta Sequía "best yield, severe stress" and Tak-Fa 8536 gave yields which were 10% better than the best local check, NS 1 when grown at Tak-Fa, Thailand. Tuxpeño Sequía C₆ yielded poorly, a result which is typical of its performance throughout much of South Asia. Both trials grown in Obregon, despite being irrigated to

produce separate levels of stress, fell in the low yield group. In the severely stressed trial, the highest yielders were an F1 synthetic of S4 lines developed at Obregon, and Tak-Fa 8536. In the higher yielding trial this result was repeated, though Tuxpeño Sequía C6 and La Posta "best ASI" also performed well. Several entries outyielded local checks at Sinematiali, Ivory Coast, the best of these being Pool 26 Sequía "best yield, severe stress" and Pool 26 Sequía "best all".

The two drier areas of the linesource were classed as low yielding sites. Here, the station where most CIMMYT drought selections had been made, the individual trait selections performed more or less as predicted, and grain yield showed a strong dependence on ASI ($r = -0.65^{**}$, -0.68^{**} for very dry and dry zones respectively, 14 d.f). The earliest entries from Pool 26 showed some advantage over later flowering varieties. DTP1 proved to be the highest yielder across both of these dry sites, but it was also the earliest to flower and therefore escaped some of the intense moisture stress that developed over time.

Across sites (17): Highest across-sites yields were reserved for the check entries, followed by Tak-Fa 8536, La Posta Sequía C1 and Tuxpeño Sequía C6. Analysis of variance showed that the "best all" selection for La Posta Sequía and Pool 26 Sequía were, respectively, non-significantly and significantly superior to their "worst all" counterparts. When expressed graphically, it was clear that the superiority of the "best all" selections is maintained across all yield levels without crossover, and that the margin of superiority of the best selection is relatively constant, i.e., they had roughly similar joint regression slopes, but joint regression intercepts are the source of their differences. Grain yield was weakly and non-significantly correlated with ASI in this data set ($r = -0.33NS$, 14 df).

Progeny Trial S1 families of Drought Tolerant Population 1

Germplasm under test: 222 S1 families of DTP1 and three check entries supplied by the cooperator.

Test sites:

1. Harare, Zimbabwe, 18 S, 31 E, 1506 masl, Mean yield = 1.7 tons/ha, Dr. K. Short
2. Golden Valley, Zambia, 14 S 28E, 1200 masl, Mean yield 1.3 tons/ha; Dr. M. Vidakovic
3. IARI, New Delhi, India, 28 N, 77 E, 228 masl, Mean yield = 3.5 tons/ha, Dr. N.N. Singh
- 4 & 5. Tak-Fa, Thailand, 16 N, 100 E, 86 masl, Mean yield = 3.8, 3.7 tons/ha, Dr. C. Kitbamroong
6. La Lujosa, Honduras, Mean yield = 1.2 tons/ha; Dr. L. Brizuela
- 7 and 8. Obregon, Mexico, 27 N, 100 W, 20 masl, Mean yields = 0.8, 1.3 tons/ha; G. Edmeades
9. Sinematiali, Cote d'Ivoire, 9 N, 3 W, 305 masl, Mean yield = 2.6 tons/ha, Dr. A. Diallo
- 10, 11 and 12. Tlaltizapan, Mexico, 19 N, 99 W, 3 water regimes; Mean yields were: 0.2, 1.0, and 2.4 tons/ha; J. Bolanos

Data were lost from Ngabu, Malawi. Data arrived late from Siete Lagoas, Brazil; Awasa, Ethiopia; Ilonga, Tanzania, and were not used in the across-location data analysis, nor in the selection of families for recombination.

Trial methodology: Each trial consisted of a 15 x 15 alpha (0,1) lattice in 2 replicates. Plot size was normally 1 row 5m long, rows 0.75-0.80m apart, and the 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 were asked to record 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 m²). Anthesis-silking interval was calculated and yields adjusted to 15% grain moisture. Where unshelled ears were weighed, a shelling

percentage of 0.70 was assumed. Data were subject to analysis of variance. The relative efficiency of the lattice design compared with a randomized complete block design ranged from 0% to 82% (average 15%). All data are given as lattice-adjusted means.

Selection of the best 10 families at each site was based on a selection index in which ASI, grain yield and ears per plant were the major selection criteria. An across-site selection of the 10 best families (to create Across 89DTP1) and the 35 best families (for recombination of the population) was done using a selection index comprising yields at each site, weighted according to the level of drought we believed existed at each site, as well as ASI where it had been carefully observed. Linear correlations were conducted between yields at each site to identify sites which selected similar progeny. An across-site analysis of variance was not carried out.

Discussion

A total of 18 sets of the DTP1 S1 Evaluation trial were prepared and distributed, and usable results were returned from 11 locations (61% return rate).

At each site the best 10 families were selected based on data supplied from each site. In general several of these families outyielded the check entries, the major exceptions being Golden Valley, Zambia where the hybrid MM-501 was outstanding, and Tak-Fa, Thailand, where NS 1 yielded very well. Check entries Chorotega B-105 and Lujosa B-106 were also high yielding at La Lujosa, Honduras, and Ac 87TZUTSR-W was the top yielder at Sinematiali, Ivory Coast. At Tlaltizapan, México, the S1 progeny were grown under three carefully managed stress levels as part of a larger progeny trial.

The 10 best families identified at each site have been recombined to form a synthetic. Within each family we attempted to select grain colors appropriate to each of the sites where selection took place. As well, an across-sites selection for recombination was formed based on data from all sites. Synthetics under formation at Tlaltizapan, México in 1991B are:

| Name | Families | Grain color [*] |
|------------------------------|----------|--------------------------|
| Harare 89DTP1 | 10 | White |
| Golden Valley 89DTP1 | 10 | White |
| Delhi 89DTP1 | 10 | Yellow |
| Tak-Fa (1) 89DTP1 | 7 | Yellow |
| Tak-Fa 89DTP1 | 10 | Yellow |
| La Lujosa 89DTP1 | 10 | White |
| Obregon 89DTP1 | 10 | Mixed |
| Sinematiali 89DTP1 | 10 | White |
| Tlaltizapan 89DTP1 | 10 | Mixed |
| Ngabu(1) 89DTP1 ^a | 10 | White |
| Across 89DTP1 | 10 | Mixed |
| Siete Lagoas 89DTP1 | 10 | Yellow |
| Ilonga 89DTP1 | 10 | White |
| Awassa 89DTP1 | 10 | White |
| Recombination DTP1 | 35 | Mixed |

* Some canary yellows are expected in the white selections

^a Based on observations supplied by cooperator, Dr. E. Sibale

Most of these were made up of 10 best S1's at each location, which were intercrossed, advanced to F2 and then retested in the 1993 series of trials. Limited amounts of seed from each of these is available on request.

Linear correlations between yields at different sites were calculated. In general the degree of association among sites in México, Central America and Thailand was weakly positive, but often statistically significant. The sites in India, Zambia and Zimbabwe showed little association with yields elsewhere or with each other. Possible reasons for this may be severe infestation by *Puccinia sorghi* in Harare, severe drought and very low yields at Golden Valley, Zambia, and flooding of the site at Delhi, India.

Grain yields were significantly negatively correlated with ASI at Taltizapan ($r = -0.62^{**}$, -0.46^{**} , -0.47^{**} for severe stress, intermediate stress and well-watered environments, respectively), a result which is consistent with that observed in other populations (Bolaños and Edmeades et al., 1993b).

Summary Discussion

The first set of trials conducted by the Drought Network has resulted in several requests from cooperators for germplasm observed under test in their environments. Distribution and exchange of germplasm is therefore already taking place, and will accelerate with the next round of testing. Our ability to identify drought tolerant genotypes was somewhat disappointing, especially among early maturing germplasm, largely because many testing sites lacked the capacity to control the intensity and timing of drought. Some cooperators were, however, able to do a good job of controlling moisture stress, and returned excellent data. Others were unable to observe the anthesis-silking interval, and we feel that this, along with grain yield, are key traits in selecting for drought tolerance.

These shortcomings in our first set of collaborative trials highlight the need to develop better screening facilities at key sites, and to increase input from the CIMMYT sites in México where the desired level of control over moisture stress exists. They also indicate the need to increase the level of awareness of moisture stress management and of the value of key traits such as ASI.

The relatively new and raw population, DTP1, showed a surprisingly large range of genetic variability for traits that relate to performance under drought, and rapid progress towards drought tolerance should be possible. The trials have been a successful means of identifying new sources of drought tolerance in national programs. We look forward to observing some of the outstanding check entries in other environments, and view these as potential sources of drought tolerance for inclusion in DTP1 and DTP2

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- * Recommended reading.
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Issues for Discussion

A: Population Improvement:

Concept: Is the concept of a single population which serves as a reservoir of genetic variability for drought tolerance a valid one? What are its limitations?

Composition: how should a population be put together? Should it be on the basis of the per se performance of the components under drought? Should it be on the basis of heterotic groups? On the basis of adaptation? On the basis of grain colour? Maturity?

Breeding methodology: How should such a population be improved? How can we deal with genotype x environment interaction?

- Should CIMMYT concentrate on working this population for ASI (using full sibs, for example) at HQ, and form S1's for testing every third cycle?
- Should we consider using reciprocal recurrent selection with a heterotic population chosen because of its widespread use in the target area?
- Should within family improvement be carried out during the period while the S1 families are under test?
- Should S1 families be tested, or should topcrosses onto S2 families? Full-sibs?

Adaptation: If we have to split this population should the first split be by colour? The second by adaptation (disease reaction)? The third by maturity? To what extent do you think national programs can handle these modifications?

Use: How do you envisage using this population? What form can CIMMYT deliver it in to be the most effective? Would you prefer to identify an elite fraction in your own country, and then retire it from the population and tune it to your own needs?

Addition of source germplasm: How should source germplasm be most efficiently identified? How should it be added to the population?

Frequency of testing: How often should we test this population? How important is international testing relative to detailed improvement in Mexico?

DTP2: What should be done with DTP2? Should we merge the best fraction of DTP2 with DTP1 and then split the result for colour? Should we change the adaptation of one to LT and the other to ST, or are they too similar in background?

B: Network Activities:

Germplasm testing: How do you envisage the development of trials under test? With an increasing number of local entries versus CIMMYT entries? with hybrids and OPVs in the same trial? With how many entries in total? How often should such trials be run? Would you be prepared to help CIMMYT evaluate the effectiveness of selection in a cycles of selection trial?

National program entries: How do we incorporate national program entries? Should they be confined to their particular region of adaptation (e.g., Asian entries tested only in Asia, African entries tested only in Africa?)

- If we run an international drought trial how do we get around quarantine problems for seed imports and redistribution of hybrids?

Help with site development: Assuming the network can get access additional funds (not very likely) what additional assistance might network cooperators require?

Exchange of information: What information should be exchanged through the drought network? Local trials of drought-tolerant germplasm? Trials of sources at CIMMYT? Evaluations of progress at CIMMYT and other locations? Published papers? Network reports? Is there a need for a newsletter, say twice a year, with all people contributing a paragraph?

Conference(s): Should we aim to have a three day conference in which each of us reports on current progress for drought tolerance, funded under the UNDP Stress Project?

Other: Are there other functions of the Network which we have overlooked?

