



CIMMYT

*Sustainable
Maize and Wheat
Systems for the Poor*

Book of Abstracts

The Genetics and Exploitation of Heterosis in Crops

An International Symposium



**Heterosis
in Crops**

**17-22 August 1997
Mexico City, Mexico**

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Foreword

Welcome to the “International Symposium on the Genetics and Exploitation of Heterosis in Crops.” Heterosis has significantly increased the productivity and quality of major crops in our century, contributing additional food, feed, fiber, and other important products. Several short symposia on specific aspects of heterosis have been organized in the past, but this is first time in nearly 50 years that some 450 scientists from more than 60 nations gather to discuss the subject in depth. Among other topics, this event will cover the genetic, physiological, biochemical, and molecular mechanisms underlying hybrid vigor; appropriate germplasm and breeding methodologies; and commercial strategies and methodologies for maximum and sustainable utilization of heterosis.

The *Book of Abstracts* provides descriptions of nearly 200 scientific presentations dealing with recent research on heterosis. The abstracts are extended; that is, they are intended to provide the reader with relevant details on materials and methods, results, and conclusions of the studies. Most are for posters presented at the symposium, in which case the title carries the corresponding code assigned to the poster. Abstracts of presentations by invited speakers are also included; full text versions will be published soon after the symposium in a proceedings by the American Society of Agronomy.

We are grateful to CIMMYT scientists M. Barandiaran, D. Beck, J. Betran, N. Bohorova, , S. Castellanos, H. Córdova, M. Kazi, S. Pandey, F. San Vicente, G. Srinivasan, W. Pfeiffer, and M. van Ginkel, who carefully reviewed the abstracts for scientific quality and value. We also thank CIMMYT science writer M. Listman for editing, formating, and overseeing production of this book. We have modified the abstracts for space, content, and clarity in many cases, but authors are still ultimately responsible for the quality of their submissions.

We welcome you once again, wish you a pleasant stay in Mexico, and hope your participation in the symposium will prove rewarding.

Timothy G. Reeves
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Organizing Committee

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Food Security; Poverty Alleviation; Natural Resource Protection -- Addressing Global Inequities through Agricultural Research Partnerships

T.G. Reeves

Director General, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico, D.F., Mexico

Introduction

"Every man, woman and child has the right to access to sufficient food to lead a healthy and productive life"; so said Pinstrup-Andersen and Pandya-Lorch (1997). The reality is however that we live in a world of stark contrasts; Serageldin (1997) sees the situation this way: "The top 20% of the world population consumes 83% of the world's income, while the remaining 80% live on 17%. A generation ago, that top 20% was 30 times as rich as the bottom 20%. Today they are 60 times as rich. And poverty is a global phenomenon. There are rich people in poor countries and poor people in rich countries. But poverty remains enormously more pervasive and acute in the south. In the 47 'least developed' countries of the world, 10 percent of the world's population subsists on less than 0.5 percent of the world's income. Some 40,000 people die from hunger related causes every day. Over a billion people are compelled to live on less than a dollar a day".

Similarly, in industrialized nations we have the luxury of deciding, at length, whether the risks of new technologies which could improve food productivity are worthwhile or not. Transgenic food crops are a classic example; currently in many developed countries there is public resistance to these products because people believe that the risks outweigh the benefits. This is not unnatural when one looks at the 'luxurious' benefits targeted by this technology in those countries: potatoes that don't turn brown when cut; more flavoursome foods; non-allergenic nuts; chocolate bars containing transgenic soybean... In stark contrast, biotechnology in developing countries is focused on traits such as insect-resistance and drought tolerance, which could help secure the next meal for the 1 billion needy; which could prevent the 40,000 dying each day of hunger and malnutrition related causes.

The Way Forward

It may be somewhat enigmatic, given the stark contrasts outlined above, to state that the solutions to these interrelated issues of poverty, food security, and natural resource management will only result from integrated global efforts that target each of the critical elements for success. Collectively we can prevail, individually we will only exacerbate the contrasts, a disaster for everyone north and south.

Swaminathan (1995) stated his belief that there can be enough food for feeding a global population of about 10 billion if certain strategies were widely adopted. He also pointed out, however, that even if food is available on the market, the poor will have no access to it unless they have opportunities for remunerative employment. He concludes "Hence, sustainable food production and consumption need integrated attention in national and international food policies."

The World Food Summit held in November, 1996, resulted in seven commitments to a Plan of Action and not surprisingly these covered political, social and economic issues in a framework of sustainable development. One of the actions proposed was:

- Increased food production, including staple food within the framework of sustainable management of natural resources (Shands 1997)

This paper mainly focuses on the technologies necessary for sustainable productivity increases in food production, particularly of the staple crops of maize and wheat, but also with reference to other crops.

Research challenges

The application of agricultural research outputs in both industrialized and developing countries has transformed food production: higher yields, reduced risks, lower unit costs, higher farm incomes and the resultant reduced food prices have benefited both rural and urban poor people (Pinstrup-Andersen

and Pandya-Lorch 1997) but the nature of the challenge we face to continue and increase these benefits is startlingly more difficult and complex in the coming decades.

Why? Because world population is growing at a rate of around 200 people/minute (mainly in the south) – an additional Mexico City three months. Agricultural land is being lost at a rate of millions of hectares/year; yield increases will therefore have to be the source of most of the production increases and the target is an average increase of somewhere between 1.5 to 3.0% p.a. every year for the foreseeable future. Unfortunately, there are no grounds to assume that yield increases obtained in the past decades can or will continue to grow at the same rates. How do we forecast the technologies required to achieve the required rates in a sustainable manner? Lastly, ironically, or indeed tragically, against this background, investment in public sector agricultural research is declining globally, but particularly in many countries of the south.

New paradigms

It is eminently clear therefore that our traditional agricultural research paradigm must change to meet these new challenges. We must find a way to focus the attention of the global agricultural research system on the problems, and opportunities of both south and north, with emphasis on the former. There is no single organization that has the resources, knowledge, and skills to overcome these complex global challenges. However, effective partnerships involving national agricultural research systems (NARS), CGIAR Centers; advanced research institutions; the private sector, NGOs and farmers can develop, and effectively utilize, the technologies necessary to help reduce the stark contrasts of today's world; through improved food security, reduced poverty and enhanced natural resources. Together we can prevail and prevail we must.

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Inbreeding and Outbreeding in the Development of a Modern Heterosis Concept

I.L. Goldman

Department of Horticulture, University of Wisconsin-Madison, 1575 Linden Drive, Madison, WI 53705
USA

Farming has always depended upon human-induced modifications of the natural world, and heterosis, meaning *ëto alteri* in Greek, is a prime example of technology in the service of agriculture. Unlike many key biotechnologies, however, its biological underpinnings remain poorly understood. Thus, the historical treatment here [also reviewed by East (1908), East and Jones (1919), Jones (1918), Zirkle (1952), Shull (1952), Hayes (1952), and Stuber (1996)] is concerned principally with those who recognized and exploited the phenomenon to the betterment of agriculture.

Heterosis, synonymous with hybrid vigor and a manifestation of the superiority of F_1 performance relative to parental performance, is fundamentally concerned with inbreeding and outbreeding; thus a consideration of its history must first treat the history of these two concepts. The significance of outbreeding in the development of superior animals such as the mule has been noted since Mosaic times. Careful outbreeding and likely unintentional inbreeding of domesticated plants was commonplace in early agricultural communities. Religious and moral teachings regarding human inbreeding likely preceded observations drawn from the experience of animal domestication by pastoral nations. Although relatively close inbreeding took place in early Egyptian and Greek cultures and among ruling classes in European societies, recognition of an incest taboo was commonplace in many of the world's cultures (Freud, 1912).

By the 18th century, hybridizers were careful to note the paradox between the dangers of close inbreeding and wide outbreeding. Koelreuter was the first hybridizer to comment upon heterosis and the first to suggest it resulted from outbreeding. Knight, Naudin, Mendel, and Darwin made significant contributions to the understanding of these phenomena during the 19th century, however they did not recognize the beneficial effects of outbreeding as opposite to the detrimental effects of inbreeding. Beal was influenced by Darwin and among the first to report increased yields with hybridization. Beal's work was repeated and confirmed by Morrow and Gardner at the University of Illinois in 1893 and 1894, who went as far as recommending alternate planting of varieties with detasseling to produce hybrid seed. Beal also trained Davenport and Holden who, along with East at the University of Illinois in 1900 pioneered inbreeding theory. Prior to this period, the primary aim of breeding programs was avoidance of inbreeding; thus hybrid vigor was said to work via the prevention of self-pollination. Breeders in this period focused on mass selection inspired by Darwin's *ëselection* principle.

Inspiration for the formal scientific study of inbreeding may have come indirectly from an association between East and the botanist Hottes, recently back from study in Europe with Correns. The rediscovery of Mendel's laws by Correns and others may have influenced East to think of line purification from inbreeding. It was not until a landmark paper by Shull in 1908 that the fundamental principle of inbreeding and its role in heterosis was clarified. In this work, Shull argued persuasively that selfing isolated homozygous lines; a fact which influenced East and helped to overturn the negative image of inbreeding to a positive benefit obtained by hybridizing inbreds. Shull coined the word heterosis in 1914. Commercially feasible F_1 maize hybrids were developed following Jones' 1918 proposition of the double cross.

Since the 1930s, exploitation of heterosis has spread to include many other crop plants. For many crops, the full benefit of heterosis has yet to be realized because inbreeding efforts are still in their infancy from a genetic point of view. Although some have criticized the move toward F_1 hybrids as driven more by profit rather than science, this argument does not address other benefits of F_1 hybrids such as

uniformity. Use of heterosis has fostered the development of a worldwide seed industry and dramatically altered the landscape of professional plant breeding, undoubtedly making a substantial contribution to research and development efforts in this discipline. The success of F1 hybrid technology has affected increases in food production in many regions of the world.

N.W. Simmonds remarked about certain aspects of plant improvement that "exact knowledge is inessential-otherwise plant breeding would be impossible...(and) there are situations in which it is perfectly reasonable to disregard formal genetics as such and talk in terms of a workable statistical abstraction." The development of inbreeding and outbreeding methods in exploiting the poorly-understood phenomenon of heterosis serves as an excellent historical example of a pragmatic merger between science and technology in the service of agriculture and humankind.

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Heterosis: Feeding People and Protecting Natural Resources

D.N. Duvick

Department of Agronomy, Iowa State University, Ames, IA 50011, U.S.A.

Introduction

Hybrid vigor, the increase in size or rate of growth of offspring over parents, has been carefully examined, given the name "heterosis", and utilized on a large scale for production of selected hybrids of plants and animals for the past 75 years. Field crops such as maize, sorghum and sunflower are now produced as hybrids in all of the industrialized world; they are also grown increasingly as hybrids in developing countries. Hybrid rice is grown extensively in China and is now introduced into India (Virmani 1994). Many commercial vegetable and flower crops are grown almost entirely as hybrids. Heterosis is credited for large increases in production per unit area and therefore for sparing large amounts of land for other uses such as environmentally benign nature preserves (Table 1). Examination of the historical record shows, however, that heterosis *per se* may have been only a catalyst rather than the primary cause of annually increasing yields for hybrid crops, worldwide.

Discussion

Hybrid maize was first bred and produced in the USA. The first hybrids yielded about 15% more than the better open pollinated varieties. Starting in the 1930s the area planted to hybrid maize started to increase rapidly and after 15 years 95% of the land in the US Corn Belt was planted to hybrid maize. Coincidentally, with the rise in plantings of hybrid maize, on-farm maize yields began to climb. They continued to climb after US maize plantings were essentially 100% hybrid (about 1965) and they are still rising (Fig. 1). Several studies have shown that about 50% of the yield gains since the 1930s is due to changes in management, such as increases in nitrogen fertilizer and higher plant densities, while the other 50% is due to changes in maize genotype (Duvick 1992). Inbred yields have increased over the years at nearly the same rate as the yields of their F₁ hybrids (Fig. 2), therefore heterosis has not increased, in fact it has decreased if calculated as percent advantage of hybrid over parents (Duvick 1984). Experiments demonstrate that yield gains in hybrid maize are due primarily to improvements in tolerance to abiotic and biotic stress, and that the improvements occurred in parental inbreds as well as in their hybrid progeny

Grain sorghum has been grown as hybrids for about 40 years (Doggett 1988) and sunflower for about 20 years (Miller 1987). Measurements of sequential changes in heterosis have not been made for either of these crops. Breeder observations indicate that for both crops modern inbreds are not uniformly higher yielding than inbred parents of the early years, therefore heterosis is somewhat greater since new hybrids outyield the older ones. However, in both crops some of the best new inbred parents are clearly more vigorous and higher yielding than their predecessors. As with maize, gains in hybrid performance of both crops are due primarily to improvements in traits that confer stability of performance; e.g., in disease and insect resistance, drought tolerance, staygreen (for sorghum), and standability. Parents as well as hybrids have acquired these improvements; they are not the unique product of heterosis. Thus, changes in traits that could just as well have been improved in the open pollinated varieties (but with more difficulty) are responsible for improved hybrid performance in sorghum and sunflower, as well as for maize.

Conclusions

Heterosis has been responsible for much of the annual yield gains in maize, sorghum, and sunflower, but its effect was indirect. Its indirect benefits include: 1) Precise genotype identification and multiplication. Instead of a random collection of hybrid/inbred plants in an open pollinated variety, the most superior hybrid combinations can be identified and reproduced at will in unlimited quantity. 2) Breeders of hybrid crops can react faster and with more options to meet changing times and changing

demands. New hybrids with needed new traits can be made and tested within one or two seasons, given a broad-based pool of inbred lines. 3) Farmers can easily identify hybrids as compared to their open pollinated varieties; they expect more from hybrids, they are more likely to provide extra inputs, and they keep constant pressure on breeders to make further improvements in hybrid performance. 4) The prospect of annual seed sales at profitable prices attracts private capital to hybrid breeding and sales. Therefore maize breeding and associated seed production and distribution technologies are doubly supported, by both public and private funds.

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Table 1. Estimates of the current annual global contributions of hybridization to production of maize, sorghum, sunflower. and rice.

Crop	% area planted to hybrids	% hybrid yield advantage*	% annual added yield	Annual added production (million t)	Annual land savings (million ha)
Maize	65	15	10	52	13
Sorghum	48	40	19	13	9
Sunflower	60	50	30	7	6
Rice	12	30	4	15	6

* Estimated gain in yield of hybrids over superior open pollinated varieties at time of hybrid introduction.

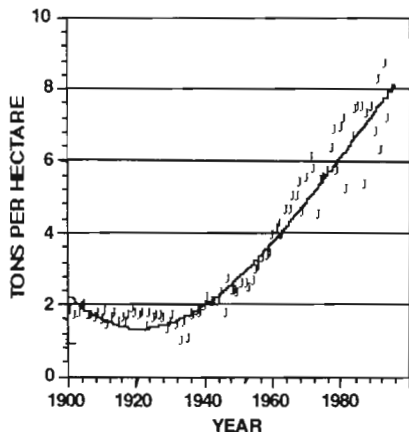


Figure 1. USA maize yields 1901 - 1996. Hybrid maize was introduced in about 1930 and was used on 100% of USA maize plantings by about 1965. (USDA NASS, "Agricultural Statistics").

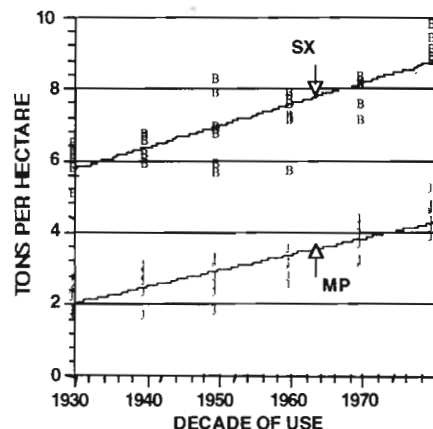


Figure 2. Yields of maize single crosses (SX) and the means of their parent inbreds (MP); widely used pedigrees in Iowa (USA) in each decade, 1930s through 1980s. (Duvick, unpublished data).

The Quantitative Genetics of Heterosis

K. R. Lamkey¹ and J. W. Edwards²

¹ USDA-ARS, Corn Insects and Crop Genetics Research Unit

² Department of Agronomy, Iowa State University, Ames, IA 50011

Quantitative genetics is the theory that links phenotype to genotype. Quantitative genetics, therefore, plays a central role in any plant improvement program, because the phenotype is what is visible to selection (Mayr 1997). Selection acts indirectly on the genotype, because the phenotype is caused by the interaction of the genotype with the environment (Mayr 1997). Quantitative genetics also plays a fundamental role in the manipulation and exploitation of heterosis, because heterosis is a phenotypic phenomenon.

For the purposes of this talk, heterosis is defined as the superiority of the hybrid over the midparent (the average performance of the two parents of the hybrid). Some would argue that this definition is not practically relevant and contend that superiority of the hybrid over the best parent is the best definition. This is true, particularly in those crops where there is little inbreeding depression. However, midparent heterosis has a clear quantitative genetic definition and is most easily manipulated in models.

Sprague (1983) identified two lines of investigation in the phenomenon of heterosis. The first is largely descriptive and is concerned with the frequency and magnitude of observed heterosis. There are many descriptive studies published in the literature. They usually take the form of a diallel and are concerned with the combining ability of the populations or lines included in the study. These studies rarely are concerned with the quantitative genetics of heterosis other than a description of the relative importance of general and specific combining ability. The second line of investigation has centered on causal factors at the biochemical-physiological level (see Rhodes et al. 1992 for a review). Although biochemical-physiological studies have shed much light on basic metabolic processes in the plant, it is debatable how much has been learned about the cause of heterosis.

The early descriptive studies, the rediscovery of Mendel's laws, and the development of quantitative genetics led to much speculation about the underlying quantitative genetic mechanisms of heterosis. The quantitative genetics of heterosis is important in manipulating heterosis in breeding programs. The efficiency and design of breeding programs is dependent on the relative importance of different types of gene action.

Gene action has been extensively studied in many species. The type of gene action controlling a trait is important in decisions regarding breeding methods, cultivar type (inbred, hybrid, synthetic), and the interpretation of results from quantitative genetic experiments. The study of gene action has been approached by studying the various types of genetic variance in populations and by generation means analysis (Sprague 1966). Both approaches have their pitfalls and we will discuss these studies and the general conclusions that can be drawn from them.

Gene action research, primarily in maize (*Zea mays* L.), led to the development of two prominent theories of heterosis: the dominance and overdominance hypotheses. We will generally discuss the relative importance of these two hypotheses as well as multigene theories (epistasis) of heterosis. Gene action is a fundamental property of quantitative genetic systems. Despite five decades of research in quantitative genetics, there is still debate over the types of gene action that predominate (Lamkey and Lee 1993). The reason for this is that estimates of gene action and gene effects have been averages over the whole genome. It is likely that there is a distribution of gene effects and the shape of the distribution is fundamental to designing breeding programs and quantitative genetics.

The role of inbreeding depression in heterosis and future research needs in the quantitative genetics of heterosis will also be considered.

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Dominance and Overdominance

J.F. Crow

Genetics Department, University of Wisconsin, Madison, WI 53706, USA

The prevailing opinion regarding the importance of overdominance in crop yields, especially in maize, and population variability, especially in *Drosophila*, has changed greatly during the past half-century. At the time of the Heterosis Conference at Iowa State College in 1950 (Gowen 1952), there was a large body of opinion that overdominance was of great importance.

The main arguments for overdominance were, first, the failure to achieve high-yielding inbred lines, emphasized by Hull and others. Second was the statistical estimate of dominance from the studies of Comstock and Robinson, which showed values in the overdominant range. My own argument, first presented in 1948, used Haldane's mutation load theory suggesting that elimination of deleterious recessives would increase performance (equated to fitness) by an amount equal to the haploid mutation rate. This was taken to be about 5%, not enough to account for hybrid yields. There was great emphasis on developing breeding schemes that could utilize overdominance along with additive variance (Gowen 1952).

Soon after, the evidence began to fall short. My own argument was weakened by the increasing realization that almost all "recessive" mutations are partially dominant. This automatically doubles the allowable increase in hybrids. Furthermore, estimates of the genomic mutation rate in *Drosophila* by Mukai and his associates gave values much higher than previously suspected. So my load argument completely lost its force. Also, selection for better inbred lines showed considerable success. These were better than hybrids of previous times, although not equal to the best contemporary hybrids. But they suggested that complete removal of deleterious recessives (and partial dominants) might bring yields up to the hybrid level. Finally, experiments by Gardner using Comstock and Robinson's "Experiment III" (Gowen 1952, p. 494) showed that the statistical overdominance declined in later generations after there had been a chance for linkage disequilibrium to dissipate. His results and similar ones by Moll et al. showed that statistical dominance declined steadily as linkage equilibrated so that after a few generations the value was in the partial dominance range (Crow 1993).

There was also a period in which ubiquitous overdominance in *Drosophila* was advocated by Dobzhansky and Wallace. The evidence for this has also gradually weakened. The most important evidence for partial dominance, rather than overdominance, comes from the mean persistence of mutations in *Drosophila* populations. The mutations studied were those which, when homozygous, cause minor decreases in viability. The mean persistence in populations from various experiments of different design suggest values in the range 50 to 150 generations. This is too small for complete recessiveness, and of course much too small for overdominants. Other evidence comes from direct measures of additive and dominance variance; the dominance component is too small to permit much overdominance. The *Drosophila* experiments have recently been summarized (Crow 1993).

Putting all the evidence together it seems unlikely that overdominance is making any large contribution to heterosis, at least in those species that have been extensively studied. Nevertheless, individual overdominant loci have been identified in many species. Molecular methods and QTL mapping may well reveal such loci. Even if these contribute only a small fraction of the variance, it may still be important to isolate and utilize them in breeding programs.

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Epistasis and Heterosis

C.J. Goodnight

Department of Biology, 115 Marsh Life Science Building, University of Vermont, Burlington VT 05405-0086, USA, <charles.goodnight@uvm.edu>

The standard additive dominance model of inbreeding depression and heterosis predicts that there should be a linear decline in fitness with increasing homozygosity. In contrast, experimental studies frequently find a non-linear change in fitness with inbreeding. This non-linear change in fitness is inconsistent with the additive dominance model, and suggests that interactions among loci are contributing to changes in fitness associated with changes in homozygosity.

In discussing the contribution of gene interaction, or epistasis, to heterosis and inbreeding, it is important to distinguish between the concepts of physiological epistasis and statistical epistasis. Physiological epistasis is the effect of interactions between loci on the phenotype of an individual. Physiological epistasis is a property of particular genotypes, and its values are independent of gene frequency. Statistical epistasis is the genetic variance within a population that can be attributed to interactions among loci. Statistical epistasis is a population level phenomenon, and unlike physiological epistasis, statistical epistasis changes as gene frequencies change. At some gene frequencies there may be physiological epistasis, but no statistical epistasis. On the other hand, if there is statistical epistasis there must also be physiological epistasis.

It is the concept of statistical epistasis that is important in understanding the effects of epistasis on inbreeding and hybridization. The most striking feature of populations with epistasis is that with inbreeding the additive genetic variance can increase. The additive genetic variance is the portion of the total genetic variance that can contribute to a response to selection. In contrast, traditional theory, which includes only additive effects, predicts that the additive genetic variance should decline with inbreeding. To find the source of this "new" additive genetic variance it is necessary to look between populations. Using a metapopulation extension of standard quantitative genetics it is possible to show that the increase in additive genetic variance associated with inbreeding occurs when the average effects of alleles shift relative to each other in the course of inbreeding. These results suggest that when there is epistasis the effects of alleles in hybrids may not be predictable from the performance in the inbred lines. The methods of metapopulation quantitative genetics can be used to measure the epistasis among lines and the predictability of the average effect of an allele when it is moved to a different genetic background. These models also suggest that forms of epistasis involving dominance are particularly important in inbreeding depression and heterosis. For example, dominance by dominance epistasis can potentially cause an increase in hybrid fitness (or yield) that is greater than would be predicted based on the inbred lines alone.

Inbreeding and Heterosis

J.B. Miranda Filho

Departamento de Genética, Caixa Postal 83, ESALQ- Universidade de São Paulo, 13400-970 Piracicaba, SP. Brasil.

The negative effects of inbreeding, known as inbreeding depression, are well known and due to the appearance of recessive, deleterious alleles in the homozygous state. In quantitative traits, inbreeding depression is quantified by the reduction in the mean that occurs only under dominant genetic effects; in other words, for traits with no dominance, no inbreeding depression is detected. The deleterious recessive major genes with qualitative inheritance may not only cause strong inbreeding depression but may also act as epistatic genes in that they can block important physiological pathways, precluding the expression of other quantitative genes of minor effects. An extreme example of such an epistatic effect is the recessive allele for albinism, which in homozygous condition leads to seedling death in a few days, precluding the expression of all other genes in the plant. The increase of homozygosity or the decrease in the frequency of heterozygous genotypes is a natural consequence of inbreeding and reaches its maximum rate through selfing, the most extreme form of inbreeding. Other less severe forms of inbreeding also lead to increases in homozygosity whose rate depends on the degree of parentage between the mating parents. The inbreeding coefficient (F) is the probability of randomly uniting gametes having alleles identical by descent. So F is the probability of homozygosity where the homozygotes carry alleles that are identical copies of the same allele in a common ancestor. The inbreeding due to small population size leads to an increase in the frequency of homozygotes at the rate of $1/2N_e$ (N_e is the effective population size) per generation. The reduction of the population size also causes genetic drift by which gene frequency (p) in a subpopulation departs from the original as a consequence of the dispersive process. After many generations of reduced size, the subpopulation tends to become homoallelic for all genes, meaning that some genes will be fixed ($p=1$) and others will be lost ($p=0$). However, some genes may be fixed or lost in just a few generations of inbreeding. The fixation of genes at frequencies $p=0$ or $p=1$ is the basis for the strong differentiation among old races with their own peculiar characteristics.

Heterosis depends on dominance and dominance types of epistatic genetic effects; in this sense no heterosis can be detected for a quantitative trait in a hybrid, in relation to the average of the parents, if genes controlling the trait act in a strictly additive way (no dominance). The phenomenon of heterosis is the opposite of the inbreeding depression in the sense that the vigor lost during inbreeding is recovered through crossing. However, although inbreeding depression and heterosis depend on dominance genetic effects, they are not merely the same phenomenon in opposite directions. In fact, when dealing with populations the inbreeding depression is an *intrapopulation* effect, while heterosis is expressed at the *interpopulation* level. Earlier studies on heterosis defined the phenomenon as merely the recovery of inbreeding depression caused by major genes visually detected. However, under a quantitative viewpoint, heterosis may occur whenever there is genetic divergence (differences in gene frequencies) between parents and some level of dominance controlling the trait. The recovery of vigor lost as a consequence of the effects of deleterious genes of large effects can be seen as a nullification of the epistatic effects (preventing full expression of other genes of minor effects) of the recessive major genes. If dominance controls a trait, heterosis will be a function of the distribution of allele frequencies. The maximum heterosis would be attained by crossing completely inbred lines fully contrasting in their allele frequencies; i.e., alleles with $p=0$ in one line and $p=1$ in the opposite line. The same principle is valid for crossing between populations, with the difference that there is a distribution of allele frequencies in the range $0 \leq p \leq 1$ for genes controlling a quantitative trait. Composite populations would have most of their genes with frequencies around 0.5 and a low frequency of genes with frequencies at the extremes of the distribution ($p=0$ and $p=1$). When crossing two populations of this kind heterosis will be expressed if their genes have some difference in allele frequencies; for example, genes with

frequencies at the left side of the distribution ($p < 0.5$) in one population and at the right side ($p > 0.5$) in the opposite population. Skewed distribution of allele frequencies would be expected in highly improved varieties (to the right) and in old local and unimproved varieties (to the left). Old races of maize possibly have many genes in an absorbing allelic state (fixed: $p=1$; or lost: $p=0$) and this should be the cause of relatively high heterosis when old, local races are crossed.

It is convenient to specify a reference population when dealing with heterosis. One should use h_o as the heterosis expressed in crosses between non-inbred populations. Any inbreeding effect (I) in the base populations will increase the heterosis in the same amount. Therefore, heterosis (h_i) in the cross between two inbred populations is actually an expression of $h_i = h_o + I$. Therefore, the effect I is part of the heterosis merely due to the recovery of the inbreeding depression of the parents; and h_o is the true heterosis expressed in the cross between the non-inbred populations. Crossing completely inbred lines ($F=1$) would express heterosis that is largely due to I , thus limiting the interpretation of heterosis as a measure of genetic divergence between contrasting parents.

Genotype-by-Environment Interactions and Selection Response

M. Cooper and D.W. Podlich

Department of Agriculture, The University of Queensland, Brisbane, Qld 4072, Australia

Introduction

Selection strategies are generally applied to improve the yield and quality performance of genotypes across environments (broad adaptation). Genotype-by-environment (GxE) interactions that result in a change in the rank of genotypes complicate selection for broad adaptation. Interactions can be distinguished on the basis of whether they are repeatable or non-repeatable within the target genotype-environment system. The presence of repeatable GxE interactions identifies cases of specific adaptations to types of environments encountered in the target population of environments (TPE). This component of genetic variation can be exploited by selection for positive interactions when these are adequately understood. Non-repeatable GxE interactions are a source of error that interfere with selection for both broad and specific interactions. Research on the genetic improvement of wheat in Australia has identified cases of repeatable GxE interactions. Our work on wheat improvement in the northern region of Australia is focused on population improvement by recurrent selection for grain yield and protein content in a highly heterogeneous TPE where the GxE interactions for grain yield are large (Cooper et al. 1996). Simulation methodology is being used to evaluate the influence of GxE interactions on short-, medium-, and long-term response to selection for different breeding and selection strategies (Fabrizius et al. 1996). The objective of this study was to use a computer simulation methodology to evaluate the influence of GxE interactions on the response to selection achieved by two alternative breeding strategies for the wheat recurrent selection program.

Methods

The QU-GENE simulation platform enables the design of E(NK) genotype-environment models for diploid or amphidiploid genomes; E is the number of different types of environments in the TPE, and for each type of environment N is the number of genes and K is the average number of genes involved in a set of genes that act epistatically upon each other. Using the E(NK) notation accounts for the different NK genetic models (Kaufmann 1993) that are nested within the different types of environments encountered in the TPE. Therefore, a type of environment is defined to correspond with a specific NK genetic model. The specification of different NK models for a TPE generates the GxE interaction within the genotype-environment system. The factors that can be manipulated in QU-GENE to define a genotype-environment system include 1) the number and frequency of types of environments; 2) heritability; 3) number of genes; 4) intra-locus gene action based on specification of midpoint (m), additive (a) and dominance (d) factors; 5) inter-locus gene action by specification of alternative epistatic models; 6) linkage groups based on specification of recombination frequencies; 7) the initial frequencies of the alleles at each locus; 8) the sets of genes that interact with the types of environments; and 9) the form of GxE interaction (e.g. heterogeneity of genetic variance and cross-over interactions). Simulation modules were designed to represent two recurrent selection strategies for the wheat germplasm enhancement program (GEP) (Fabrizius et al. 1996): 1) intermating facilitated by chemical sterilisation (C-GEP), and 2) intermating facilitated by a dominant male sterile gene (DMS-GEP). In both cases the selection units were S_1 families tested in ten environments sampled from the TPE. One cycle of both versions of the GEP corresponds to four years. A simulation experiment was conducted to investigate the influence of GxE interactions on short- (1 to 5 cycles), medium- (6 to 15 cycles), and long-term (16 to 25 cycles) response to selection for the two versions of the germplasm enhancement program. For a model based on 100 independent genes, three levels of GxE interaction were considered: 1) no GxE interaction (no GxE), 2) GxE interaction variation of about the same magnitude as genetic variation for average performance across environments ($GxE = G$), and 3) GxE variation greater than genetic variation for average performance across environments ($GxE > G$). In the study reported here, gene action was restricted to be additive within environment types, there was no epistasis and two levels of heritability were considered. The simulation modules for the C-GEP and DMS-GEP were run for 25

cycles (representing 100 years of breeding effort per run). A sample of 100 S_1 families was tested in each cycle and the best 20 were selected and these families were recombined as the base population for the next cycle. The simulation experiment was run 20 times for each combination of breeding program, genetic model and heritability and the mean results were investigated.

Results

There was a significant breeding-program \times genetic-model \times cycle interaction for population mean in the TPE (Fig. 1). With an increase in G \times E interaction there was a reduction in the rate of improvement of the population mean for both breeding programs. The C-GEP strategy consistently gave a higher rate of genetic improvement than the DMS-GEP but the advantage was reduced as G \times E interaction increased. In the first five cycles the advantage of the C-GEP was small but became more apparent from cycle six. When G \times E interaction was present the advantage of the C-GEP began to decrease from about cycle 20. This was in part due to the larger effective population size of the DMS-GEP relative to the C-GEP and a resultant reduction in the loss of favourable alleles due to drift by the DMS-GEP breeding strategy.

Conclusions

Simulation methodology can be used to investigate genetic models for genotype-environment systems and compare the effectiveness of breeding strategies. As our understanding of both the genetic architecture of the traits to be manipulated and the structure of the TPE improves, more realistic models can be examined. The simulation analysis approach can be used to complement theoretical and short term experimental investigations to quantify the impact of G \times E interactions on short, medium and long term responses to selection. For this analysis of the C-GEP and DMS-GEP versions of our recurrent selection program, G \times E interactions not only reduced response to selection but also influenced the relative merit of the two breeding strategies by decreasing the advantage of the C-GEP over the DMS-GEP relative to that observed when there was no G \times E interaction.

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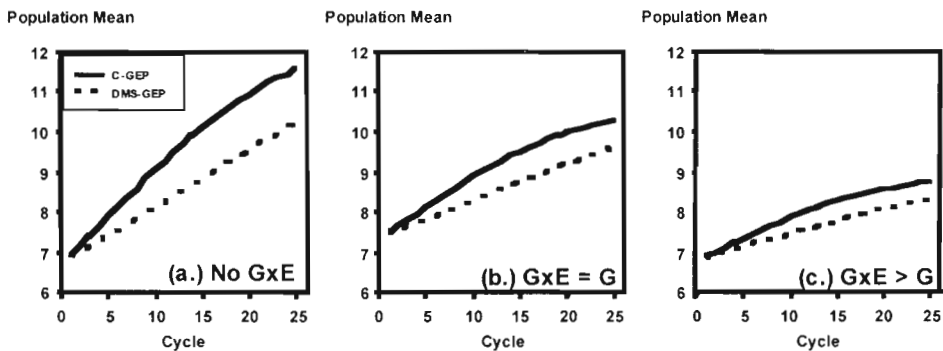


Figure 1. Simulated change of the population mean for two breeding strategies (C-GEP and DMS-GEP) for 25 cycles of recurrent selection for three G \times E interaction models based on a genotype influenced by 100 genes.

A1 - Genetic Effects of Heterosis in Maize Hybrid Yields

G. Todorovic¹, G. Surlan², I. Sataric¹, T. Zivanovic²

¹ Maize Research Institute, Zemun Polje, Belgrade-Zemun

² Faculty of Agriculture, Belgrade-Zemun

Introduction

Grain yield of maize is a quantitative trait determined by many genes whose effect is modified by environmental conditions. To apply the adequate breeding method, it is necessary to determine the genetic base and mode of inheritance of this trait.

Methods

Two single-cross maize hybrids (H_1 - ZPL735 × B432; H_2 - ZPL735 × ZPL439) with a common parent were selected for this study. Fourteen generations-families were analysed per each observed hybrid: P_1 , P_2 , F_1 , F_2 , BC_1 , BC_2 , $BC_1 \times F_1$, $BC_2 \times F_1$, $BC_1 \times P_1$, $BC_1 \times P_2$, $BC_2 \times P_1$ and $BC_2 \times P_2$. Generations, derived by self-pollination of back crosses (BC_{1s} and BC_{2s}), were also analysed. The 14 generations were evaluated in a randomised complete-block design with four replications at two locations in 1992 and 1993. The planting density was 71,400 plants ha⁻¹, standard agronomic practices for maize were applied. The estimation of gene effects for all studied traits was based on the analysis of generation means (Mather 1949, Hayman 1958, Jinks and Jones 1958, Mather and Jinks 1971 and 1982). High parent heterosis for yield was estimated. The interaction between additive, i.e. dominant gene effects and environmental factors for all studied traits were done after Mather and Jinks (1958), Bucio Alanis (1966) and Bucio Alanis and Hill (1966).

Results

The additive-dominant and interaction models revealed that dominant genes were of paramount significance in grain yield inheritance in both hybrids (Table 1 and 2). The differences in grain yield detected between studied hybrids are mainly caused by differences between dominant gene effects and their non-allelic interaction [l/dd]. Highly significant values of heterosis, evaluated in relation to the better parent, were obtained for grain yield in both hybrids. The dominant gene effects × environments interaction was more expressed in both hybrids than the additive gene effects × environments interaction (Table 3).

Conclusion

dominant and epistatic genes were of the primary importance for gain yield of the studied hybrids. The high positive values of heterosis point to the greatest significance in both, expression and inheritance, of this trait.

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Table 1. Additive-dominant model of the analysis of generation means for grain yield.

Year Location	1992				1993			
	Zemun Polje		Indjija		Zemun Polje		Indjija	
Hybrid	H ₁	H ₂	H ₁	H ₂	H ₁	H ₂	H ₁	H ₂
Gene effect								
[m]	63.15**	63.33**	62.84**	59.35**	58.63**	48.80**	59.21**	58.60**
[d]	0.52	1.37	2.58	1.49	3.13*	6.09**	0.06	5.12**
[h]	98.60**	71.80**	75.67**	53.75**	80.54**	73.62**	85.42**	62.17**
χ^2 test	13.120	36.204**	15.994	21.727*	83.672**	32.781**	8.687	22.492*
Scaling tests								
A	-11.320	21.910*	-8.990	20.230*	-44.800**	3.350	1.380	24.590**
B	3.380	22.420*	8.888	13.780	-22.900**	13.760*	8.530	-10.440
C	-13.320	36.830*	7.660	29.130*	-81.540**	-8.350	-0.530	6.870
X	16.860	-7.575	13.480	7.817	0.410	-5.195	9.045	-13.353
Y	1.780	2.535	10.630	13.003	-1.290	-6.145	7.385	8.233
Z	-0.710	-1.970	11.881	-0.420	-4.700	-16.410	6.000	8.540
Z'	-9.970	-7.010	2.485	-8.060	-8.060	-1.294	-5.140	7.560

Table 2. Interaction model of the analysis of generation means for grain yield.

Year Location	1992				1993			
	Zemun Polje		Indjija		Zemun Polje	Indjija		
Hybrid	H ₁	H ₂	H ₁	H ₂	H ₁	H ₂	H ₁	H ₂
Gene effect								
[m]	63.15**	58.39**	62.84**	52.12**	31.16**	18.77**	59.21**	46.68**
[d]	0.52	2.62	2.58	1.16	5.02**	8.17*	0.06	1.59
[h]	98.60**	114.50**	75.67**	97.00**	102.83**	148.25**	85.42**	101.08**
[i] aa		1.51		3.79	32.53**	31.38**		10.70
[j] ad		4.88		1.25	-11.39	-7.69		23.85**
[l] dd		-49.01**		-44.80	19.94	-45.17**		-29.74
χ^2 test	13.120	2.181	15.994	7.125	7.556	7.125	8.687	6.487

Table 3. Effects of basic gene effects x environments interaction on grain yield.

Environment	ZPLB 735 x B 432		ZPLB 735 x ZPLB 439	
	[d]x E	[h]x E	[d]x E	[h]x E
ZP 1992 : ZP 1993	-1.125	3.835	-2.665*	-3.235
IN 1992 : IN 1993	2.182	-3.982	-0.295	-5.635*
ZP 1992 : IN 1992	-1.190	10.085**	0.775	6.875**
ZP 1993 : IN 1993	2.117	2.267	3.145**	4.475*
ZP 1992 : IN 1993	0.993	6.102**	0.480	1.240
ZP 1993 : IN 1992	0.065	-6.250*	-3.440**	-10.110**

A2 - Selection of Parents and Prediction of Heterosis in Rice

C.H.M. Vijayakumar, M. Ilyas Ahmed, B.C. Viraktamath and M.S. Ramesha

Hybrid Rice Programme, Directorate of Rice Research, Hyderabad-500 030, India

Introduction

Magnitude of heterosis depends on the choice of appropriate parental lines. To increase the efficiency of heterosis breeding, there is a need for a simple and dependable criterion, to select the parental lines which would result in heterotic combinations without making all possible crosses among the potential parents and evaluating them. Several methods (per se performance, combining ability and genetic diversity, etc.) have been used to choose parents a priori with variable success (Virmani 1996). Studies on combining ability in relation to heterosis have been reviewed by Kim and Rutger (1988) and Virmani (1994). The results of such studies have not been much useful in choosing parents for yield heterosis, because yield is a complex trait which is determined by its components for which genes exist (Grafius 1959) and there are no studies to show that combining ability effects of certain traits are useful in predicting yield heterosis. Similarly, the genetic diversity studies using D2 statistic of Mahalanobis (1936) have been in use for selection of prospective parents of the hybrids. The results obtained from such studies have not been consistent in clearly demonstrating the relationships between divergence of the parental lines and the heterosis (Julfiquar et al. 1985; Li and Ang 1988; Peng et al. 1991; Virmani et al. 1991 and 1994), because they are influenced by type of material, selection of traits, etc. Often, the traits that contribute more to divergence have little to do with yield trait. Therefore, we tried to identify and establish a simple relationships between the traits of parental lines and the heterosis in their hybrids to facilitate choice of appropriate parental lines for obtaining heterotic combinations.

Methods

During wet season 1995 in International Hybrid Rice Observational Nursery (IRHON) consisting of 29 hybrids, 26 restorers and 3 maintainers, 3-5 plants were dissected in each of the hybrids and their respective restorers to identify the initiation of reproductive phase marked by the formation of a hairy like structure. At maturity, grain yield/m² and observations on several yield traits in five randomly selected plants were recorded. Besides, the number of days to 50% flowering (DFF) was also recorded. Seven traits viz., plant height (HT), number of panicles/plant (PN), panicle weight (PW), number of fertile spikelets (FS), spikelet fertility per cent (SFP), 100 grain weight (TW) and grain yield (GY) were used to classify the parents (restorers and maintainers). Initially, overlapping groups of parents were obtained for each trait based on DMRT. Then, a joint score over 7 traits was computed for each line following Arunachalam (1984). Using mean and standard deviation of joint scores, three groups: High, Medium and Low were made. The percentage of promising restorers (whose hybrid combinations showed better parent heterosis) was calculated for each group.

Results

The reproductive phase initiation (RI) was always early in hybrids. In hybrids with better parent heterosis ($H > R$), the reproductive phase duration i.e., from RI to DFF was more compared to the better; but with no change in growth duration. While, in hybrids whose grain yield was less than their restorers ($H < R$) there was no change in reproductive phase duration, but the growth duration was less compared to restorers. The distribution of parents based on DMRT followed by joint scoring revealed most parents (19/29) to be in Medium group. The two commonly used maintainers (CMS counterparts), IR 58025B and IR 62829 B were found in different groups i.e. Medium and Low respectively. Most (87%) of the promising restorers (whose hybrid combinations showed better parent heterosis) were from Medium group and only 13% of them belonged to High group. The per se performance of restorers belonging to High group was better. While, the Low group did not possess any promising restorer. A closer examination of relationship between parents revealed that heterosis resulted from the

complementation of traits between parents. The set of traits of restorers complementing with IR 58025A included SFP and TW, while those complementing with IR 62829A included PW, FS, SFP and TW.

Conclusions

The reproductive phase initiation was invariably early in hybrids and hybrids with better parent heterosis had similar growth duration as their restorer parent, but with extended reproductive phase duration indicated that a simple selection based on a comparison of growth duration between hybrids and restorers for heterotic hybrids is possible in the initial stages of hybrid development. Most of the restorers distributed in the High group were good for their per se performance, but the occurrence of a high frequency of promising restorers in the Medium group suggest that the selection of restorers for making hybrids should preferably be done from this group. Our preliminary analysis, of 1996 results have shown the similar trends. The analysis of yield heterosis of IR 58025A and IR 62829A hybrids showed that heterosis results from the complementation of traits between parents and they are different for different CMS lines. These results suggest that a preliminary evaluation of restorers and CMS lines is necessary to choose the appropriate parent combination of parents for obtaining the heterotic hybrids. As at a given time only 1-2 CMS lines are available for commercial use, then a thorough evaluation of restorers for various traits would help in choosing suitable ones for obtaining heterotic combinations.

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A3 - Genotype x Environment Interaction and Yield Heterosis in Rice

M. Ilyas Ahmed, C.H.M. Vijayakumar, B.C. Viraktamath, and M.S. Ramesha

Hybrid Rice Programme, Directorate of Rice Research, Rajendranagar, Hyderabad-500 030, India

Introduction

The potential of hybrid rice in increasing the productivity and production is well demonstrated in China and more recently in India. The large scale adoption of this technology in India in the coming years depends, among other factors, on identification of rice hybrids with stable performance in addition to high yield potential. Young and Virmani (1990) studied the stability of 140 rice hybrids and their parents using the Eberhart and Russell model and observed that hybrids were less stable than their inbred parents. Several authors (Hardwick and Wood 1972; Hill 1975 and Crossa 1990, etc.) have pointed out the statistical and biological limitations of regression analysis. The various methods of analysing trials data for stability or Genotype x Environment Interaction (GEI) have been reviewed in great detail by Lin et al. (1986) and Westcott (1986). Lin and Binns (1988) proposed a method based on a single parameter approach which uses the maximum response shown by a test entry including the check(s) at each location as a standard. The utility of this method to identify stable and widely adaptable hybrids in rice was examined by Ilyas Ahmed et al. (1996). They concluded that the method of superiority measure is simple and very useful. The top hybrids/entries identified by this method were stable and could be recommended for wider area. This paper further examines the response of stable hybrids in low and high yielding environments and stability of rice hybrid(s) against inbred varieties evaluated in a variety yield trial.

Methods

The data used in this study were taken from a National Hybrid Rice Trial (NHRT) conducted during wet season 1994 and from an Advanced Variety Trial (AVT) conducted during wet season 1996. The NHRT comprised 20 hybrids and 3 inbred check varieties, viz., 'Rasi', 'Jaya' and a local check. It was conducted over 12 locations in 10 states. The AVT consisting of 22 test inbreds, one hybrid (KMRH-2) and 3 inbred check varieties, viz., 'Ratna', 'Vikas' and a local check was conducted at 16 locations in 11 states of India. All the test entries were planted in RBD with 3 replications. The plot size was about 10 m² with a plant density of 44 hills/m². Detailed data on locations and cultural practices are available with the Directorate of Rice Research (DRR), Hyderabad, India. The statistical model used for analysing GEI/stability was superiority measure of Lin and Binns (1988). The top most stable hybrid, identified by this method was used for further study.

Results

The mean performance of the most stable hybrid as compared to mean maximum response (max. resp.) and mean of highest yielding check variety showed that the stable hybrid did not differ significantly from max. resp., while it was significantly superior to the mean of the check variety in both NHRT (667 kg/ha) and AVT (1061 kg/ha). The response of the stable hybrid was similar to the maximum response in NHRT. The difference between hybrid and check variety widened although not very clearly with the increase in location mean. There were doubts expressed in some quarters that the response may not be similar if hybrids are tested 1990 along with inbred. Therefore, one hybrid, KMRH-2 was evaluated along with 22 test inbreds in AVT. The response of the hybrid was close to the max. resp. and the gap between hybrid and check got widened very clearly as the location mean increased confirming that the yield advantage of hybrids is more pronounced in high yielding environments.

Conclusions

1. The method of superiority measure was useful in identifying high yielding stable hybrids that could be recommended for the whole of region of testing.
2. The stability of rice hybrids was comparable to inbreds as they are not significantly different from max. resp. at many locations, but superior to check variety.
3. The yield potential of hybrids was better expressed in high yielding environments than in low yielding environments.

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A4 - Phylogenetic Relationship and Correlations Between Genetic Distances Using RAPD Markers and Specific Combining Ability in 28 Tropical Open Pollinated Maize Varieties

S.N. Parentoni, J.Magalhães, E.E.G. Gama, M.X. Santos, C.A.P. Pacheco, P.E.O. Guimarães, M.A. Lopes, M.J.V. Vasconcelos, E. Paiva.

Brazilian National Maize and Sorghum Research Center-CNPMS/EMBRAPA, C.P. 151-Sete Lagoas, MG. CEP 35701-970 - Brazil.

Introduction

The active maize breeding germplasm collection used at the Brazilian National Maize and Sorghum Research Center (CNPMS/EMBRAPA) comprises 28 open pollinated varieties. Based on the Brazilian experience the most useful heterotic patterns are Tuxpeño x Caribbean Flints and Swan. A more detailed identification of heterotic groups in these populations were conducted using diallel crosses (Santos et al. 1994). RAPDs have been used in many crops to assess phylogenetic relationships. They have also been used to study genetic variation among open pollinated varieties of red clover (Kongkiatngam et. al. 1996). Correlations between molecular marker estimated genetic distance and heterosis are generally low, when the whole dataset is used (Lee et al. 1989; Melchinger et. al. 1990). Recently, Lanza (1996) showed that the use of principal component analysis to assign parents to heterotic groups could increase these correlations. The objectives of this study were: a) to compare phylogenetic relationships among tropical open pollinated maize varieties using RAPDs and pedigree data; and b) to verify the relationship between genetic distance estimated with RAPDs and specific combining ability obtained from 5 and 10 environments.

Methods

Twenty-eight open pollinated varieties were used as parents of a diallel. The 28 parents and their 378 F₁ crosses were evaluated at five locations and two years in Brazil. Specific combining ability (SCA) was estimated for five locations in one year (Santos et al. 1994) and for 10 environments (Pacheco 1997). The SCAs from the 10 environments were used to obtain two heterotic groups: Group I (BR106, BAIII Tuson, Sint. Elite and CMS50) and Group II (BR105, CMS14C, BR111, CMS04N, ND and CMS04C).

The 28 open pollinated varieties were genotyped using RAPDs. A bulk of 100 seedlings was used to obtain the DNA from each variety. Up to now we have screened 30 primers which generated a total of 92 polymorphic bands. This RAPD data were used to obtain a distance matrix from which an UPGMA we generated a dendrogram for the 28 varieties. Genetic distances obtained with RAPDs markers for the whole dataset and for the two heterotic groups were correlated with: a) SCAs obtained from one year and five locations; and b) SCAs obtained from the 10 environments.

Results

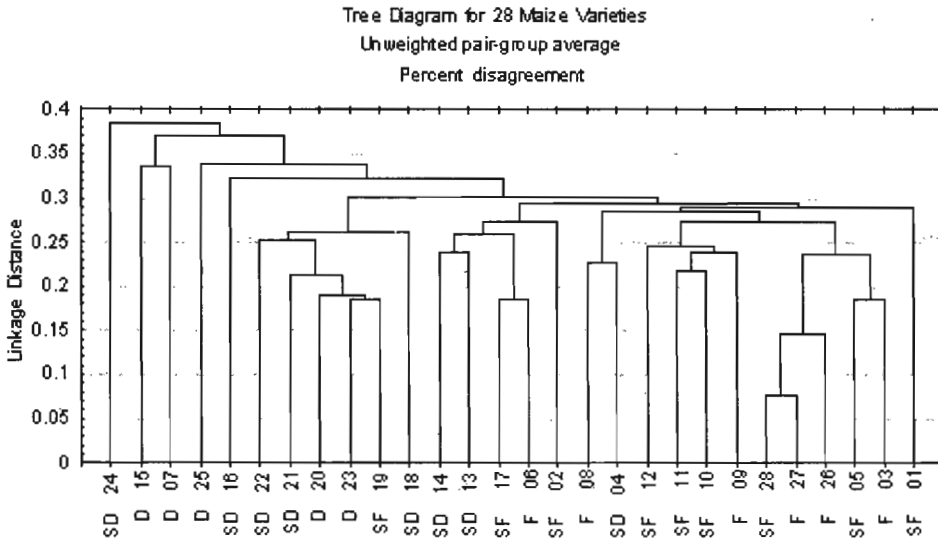
Phylogenetic data agreed with the known pedigree data. Flint and semi-flint genotypes tended to be grouped separately from the dent germplasm. However several clusters were observed in the dent germplasm (Figure 1). Correlations between genetic distances for each pair of parents and SCAs for the 378 F₁s in 10 environments was low and positive ($r=0.15^{**}$). Correlations between genetic distances and SCA were higher ($r=0.61^{**}$), when only the two heterotic groups were considered and the SCA data were obtained from 10 environments.

Conclusions

RAPD marker can be used to assess phylogenetic relationships among maize open pollinated varieties. The quality of SCA estimators can influence the relationship between SCA and genetic distances; the correlation increases as with the number of environments.

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Key to figure:

Genotype	Origin	Genotype	Origin
1 CMS-01	Mezcla Amarillo	15 BR-126	Dentado Composto
2 CMS-02	Antigua x Vera Cruz	16 CMS-28	Tuxpeño Amarelo
3 CMS-03	Amarillo Cristalino	17 CMS-29	Amar. del Bajío x Templados
4 CMS-4N	Amarillo Dentado Normal	18 CMS-30	Composto Amplo
5 CMS-4C	Amarillo Dentado Cerrado	19 BR-136	Sintético Cerrado
6 BR-105	Suwan DMR	20 CMS-39	Sintético Híbridos Brasileiros
7 BR-106	Composto Tuxpeño	21 CMS-50	Vega Precoce
8 BR-107	Composto Cateto	22 SINT. ELITE	Sint. / CNPMS Elite Inbreds
9 BR-111	Pool 21	23 CUNHA	Tuxpeño Brasileiro
10 BR-112	Pool 22	24 PH4	Varietade da Africa do Sul
11 CMS-14C	Pool 25	25 BAIH - Tusón	Tusón Brasileiro
12 CMS-15	Pool 26	26 SARACURA	Composto tolerante a encharcamento
13 CMS-22	Amarillo del Bajío	27 NITROFLINTE	Composto selecionado para eficiência a nitrogênio
14 CMS-23	Ant. x Rep.-Domin.	28 NITRODENTE	Composto selecionado para eficiência a nitrogênio

A5 - Genetic Analysis of Cytoplasmic Male Sterile Lines Available in P.R. China

Zhang T.Z., Guo W.Z., Liu K., Wang X.D., and Pan J.J.

Cotton Genetics and Breeding Research Lab, Nanjing Agric. University, Nanjing 210095, P.R.China

Introduction

The use of heterosis in upland cotton is very important for increasing cotton yield and improving fiber quality. An effective and economic way to produce the hybrid cotton seeds commercially is use of CMS lines. Since 1965, several kinds of CMS lines have been developed in the USA (Meyer 1975) and CMS line in *G. harknessii* cytoplasm has been used to develop hybrid cotton in India (Paroda and Basu 1993). There is much interest in the development of hybrid cotton in China.

Two kinds of hybrids produced via hand-emasculation and pollination and genetic male sterile lines are being grown in China, totalling around 200,000 hectares every year. Three types of CMS lines are presently available. One CMS line like DES-HAMS277 was introduced from the USA; Chinese scientists developed two other CMS lines, 104-7A (Jia 1990) and Xiangyuan-A (Zhou, Personal communication 1992). This study deals with the inheritance of restoration, RAPD analysis of chloroplast DNAs, and identification of RAPD markers linked with the fertility-restoring gene of three CMS lines available in China.

Methods

CMS lines were crossed with restorers to produce F_2 and BC populations to test the inheritance of restoration. A modified procedure of DNA extraction from plants with a high content of polyphenolics (Guo et al. 1996, Pich et al. 1993) was used. PCR reaction mixtures (25 μ l) contained 100 μ M each of dATP, dCTP, dGTP, and dTTP, 10 times reaction buffer (10mMTris-HCl, 50mMKCl, 2.0mMMgCl₂, and 0.001% Gelatin), 0.2 μ M arbitrary decamer primer, appropriate genome DNA, and 1 unit of TaqDNA polymerase.

The PCR reaction was as follows: a preliminary denaturation for 5 min at 95°C, 45 cycles of 1 min at 94°C for denaturation, 2 min at 36-37°C for annealing, and 2 min at 72°C for extension, and a final extension at 72°C for 7 min followed. A 15 μ l DNA sample was used for electrophoresis on 1.4% agarose gels. DNA was extracted and mixed to produce two mixed DNA pools from both ten fertile and sterile plants from a BC₃ segregating population of (0-613-2R x Simian3) Simian3 to develop new restorer by backcrossing in our lab. Bulked segregant analysis (Michelmore etc 1991) was employed to identify primer linked with fertility-restoring gene.

Results

Genetic analysis indicated that the fertility restoration to CMS lines was controlled by two pairs of independent dominant genes, R_{f1} , and R_{f2} , and R_{f1} is a completely dominant major gene and R_{f2} a partial one. Allelic tests suggested that a multiple allele rf_1^m at the rf_1 locus may exist in 104-7A CMS line and the male sterile gene of Xiangyuan-A is the same as that of DES-HAMS277. RAPD fingerprinting analysis of chloroplast DNA from these three kinds of CMS lines confirmed our genetic results. 104-A has the different amplified RAPD fragments in electrophoresis from the other two lines. It is supposed that 104-7A may be a new CMS type which is different from that in *G. harknessii* cytoplasm developed in USA. A total of 425 arbitrary 10-mer oligonucleotide primers were used to screen the two bulks of DNA pools. Three primers were identified to produce repeatable polymorphisms between paired bulks and their parents. Individual plant was tested of (104-7A x 0-613-2R) F_2 using these three primers. It is found that about one 300bp fragment amplified by OPV15 was linked with fertility-restoring gene R_{f1} , with a crossover value of 13.0+2.57%.

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A6 - The Use of Testers to Exploit Heterosis in Tropical Maize at CIMMYT

S.D. McLean*, S.K. Vasal, S. Pandey, and G. Srinivasan

International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico

Introduction

In the preliminary phases of hybrid maize development, inbred lines were tested for productivity and combining ability by crossing all inbreds in all possible combinations. It was soon realized that for a few hundred inbred lines, the single cross diallel was virtually impossible because of the large number of crosses required. A more efficient method, the inbred x variety or topcross, was suggested and utilized by Davis (1927). In the earlier years, the topcross consisted of crossing each inbred line with an open-pollinated variety (OPV) or tester, which gave a measure of general combining ability (GCA) and/or performance of the line in combination with the OPV.

Choosing a Tester

The best compromise for the topcross tester is to select a successful OPV from the area where the hybrid is to be grown. The best compromise for an inbred tester is to select a successful line unrelated to the inbreds being tested and from the target environment for the hybrid. However, at the onset of any hybrid evaluation, the breeder needs to determine the relative combining ability for the new inbred lines. Sprague and Tatum (1942) introduced the concepts of GCA and specific combining ability (SCA). Recurrent selection methods were introduced by several people (Jenkins, Hull, Comstock and Lonnquist) which expanded and broadened the use of the topcross or testcross. Hull (1945) concluded that the theoretically most efficient tester would be homozygous recessive at all loci and that homozygosity for dominance alleles at any locus should be avoided. If a tester contains only genotypes which are homozygous recessive then the tester was considered "weak". If on the other hand, the tester only contained genotypes which are homozygous dominant then the tester was considered "strong". All testers will give an equal measure of genetic variance if there is no dominance. As the level of dominance increases, a tester with a low frequency of favorable alleles shows a distinct advantage. Epistasis may be part of the reason why weak testers do not give the best differentiation of the genotypes. Other factors such as higher nongenetic and interaction variances after crossing with weak testers could also cause inconsistent results. In general, results indicate that poor performing testers (low GCA) are better than good performing testers (high GCA), and therefore low yielding testers are better than high yielding testers. In earlier years the philosophy for choice of tester when selecting for GCA was to utilize a broad base heterogeneous population as a tester. This tester would be the parental population or any unrelated broad based synthetic or unrelated OPV where maturity coincided with the genotypes being tested. When selecting for SCA, a narrow genetic base was utilized. This tester would be an unrelated narrow base synthetic or an unrelated inbred line or even an unrelated single cross which coincided with the maturity of the genotype being tested. However, studies by several people have shown that an inbred line tester gives relatively more information for GCA than SCA (Hallauer and Miranda 1988). Testers will change with the objectives of a program and the types of hybrids developed.

Defining a Tester

In 1953, Matzinger defined a "desirable" tester as one that combines the greatest simplicity in use with the maximum information on performance to be expected from tested lines when used in other combinations or grown in other environments. Rawling and Thompson (1962) stated that, for a "good" tester: 1) the genotypes under evaluation must be classified correctly, and 2) the tester must discriminate effectively among the genotypes being evaluated. Hallauer (1975) stated that a "suitable" tester should include simplicity in use, provide information that correctly classifies the merit of the genotypes, and the tester should provide the maximum genetic gain potential for the genotypes tested. Vasal (1995) defines a "practical" tester as a genotype which is unrelated and shows simplicity in functionality. It must provide information that correctly classifies the merit of the tested genotypes into heterotic groups,

and must differentiate effectively among the genotypes being evaluated. It must also increase the variance of testcross progenies and provide the maximum genetic gain for the tested genotypes.

Evolution of Testers in CIMMYT's Hybrid Maize Program

In the mid-1980s, in response to increasing demand for hybrids in developing countries, CIMMYT conducted eight combining ability studies on its populations and pools using diallels/ design II (CIMMYT 1987) and showing that the divergence in the germplasm used is crucial to developing hybrids. During 1985-1987, early generation lines (S_2 - S_3) were utilized as testers and several early generation hybrids identified (Han et al. 1991). During 1988-1990, 92 tropical and 88 subtropical lines were crossed with four inbred line testers and the resulting 720 single-cross hybrids evaluated in multi-location trials to class the lines into Groups A and B (Vasal et al. 1992a,b). CIMMYT also attempted using elite single crosses as testers and evaluating the resulting three-way hybrids in several multilocation trials. Based on these results, in 1993 CIMMYT began systematically categorizing its inbred lines into heterotic groups. This work established four heterotic groups for each grain color, reflecting specific grain types (i.e., dent and flint) preferred in tropical areas for human consumption. As of 1997, CIMMYT uses four elite testers within tropical white and yellow germplasm and has made them available to national programs. These tester lines will be crossed to national program lines and the combining ability patterns studied to classify national program germplasm into distinct heterotic groups. The lines are:

Early White	CLG1501: G15C22MH131#-1-3-4-1-1-BBB G16C19HC219-3-1-1-2-B-##	Early Yellow	G17TSRMH5-2-4-7-1-1-3-BB G18C19MH100-#-4-1-1-BBB
Late White	CML247: (P24F119*P24F54)-6-4-1-1-BB-f-# CML254: Tuxp. Seq. 149-2-BBB-##-1-BB-f-#	Late Yellow	CML287: (24F26*27F1)-4-1-B-1-1-BB-f-# CL00331: Sint. Am. TSR-23-3-2-3-2-BB-##

CIMMYT has used OPVs, narrow- and broad-based synthetics, single crosses, partial inbreds, and full inbred as testers. These have come from the parental population or from contrasting heterotic populations and mostly an unrelated, divergent inbred line from the lines to be tested. The change in testers over the last 10 years at CIMMYT has been "evolutionary" rather than "revolutionary"; the use of testers in most national research programs will likely follow a similar pattern.

Concerns for CIMMYT and National Programs

- Should standard testers be used by CIMMYT and national programs to standardize heterotic groups, such as in the USA between MO17 and B73?
- If standard testers are used, should this be by region, by mega-environment, or globally?
- Will use of standard testers narrow the global germplasm base?

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A7 - Genetic Analysis of Abiotic Stress Tolerance in Tropical Maize Hybrids

F.J. Betrán, D. Beck, G.O. Edmeades, J.M. Ribaut, M. Bänziger and C. Sanchez

International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 México D.F., México

Introduction

Improvement for drought tolerance (DT) at flowering and for improved performance under low nitrogen (N) has been accomplished in open-pollinated varieties by recurrent selection using managed stress environments (Bolaños and Edmeades 1993, Byrne et al. 1995, Lafitte and Edmeades 1994). Edmeades et al. (1996) showed that population improvement for stress tolerance in open-pollinated varieties increases the probability of obtaining stress-tolerant hybrids. CIMMYT is using these populations as source germplasm to develop abiotic stress tolerant lines and hybrids. The objectives of this study were to: 1) study the genetic control and modes of gene action for ST; 2) examine dosage rate for ST in hybrids as well as the role of hybrid vigor in tolerance; 3) estimate the relationship between line per se and hybrid performance under stress and normal conditions; 4) estimate combining ability for a group of promising lines under stressed and unstressed environments.

Materials and Methods

A five-line diallel was developed from La Posta Sequía C₃, four from Tuxpeño Sequía 6 C₁, seven CIMMYT maize lines (CMLs) and P1, and experimental line used to map the anthesis silking interval (ASI). Lines per se and their hybrids were evaluated separately in trials planted side-by-side using alpha (0,1) lattice designs under drought stress, low N and optimal conditions. Traits measured include grain yield, ears per plant, days to 50% anthesis and silking, ASI, plant and ear height, root and stalk lodging, root capacitance, erect leaves, tassel size, and disease scores. Under drought stress, scores were taken for leaf rolling, leaf senescence, and tassel blasting. Individual analyses of variance were conducted with the SAS MIXED procedure, and a Griffing Method IV Diallel analysis was used to estimate GCA for the lines in all environments. GCA and SCA equivalent variance components (VC) of mean squares were calculated using a fixed model for the diallel design. Lines were fingerprinted using 60 probes distributed across the genome. Allelic composition was used to calculate Nei's genetic distances.

Results

Grain yields for hybrids under severe drought stress (SS) and intermediate stress (IS) were 13% and 50% of grain yield (GY) under well watered conditions (WW). For lines, GY under SS and IS were 5% and 48% of GY under WW. ASI environment means ranged from essentially zero in WW conditions to 8.2 days for hybrids under SS. Lines showed smaller ASI under drought stress than hybrids. With increasing drought stress, phenotypic variation decreased for GY but increased for ASI. The GCA and SCA genetic variance components for GY were smaller for stressed environments than for well-watered environments. The relative importance of GCA vs SCA, expressed as the ratio between additive vs. total genetic variance components, increased with stress level (Fig. 1), suggesting the presence of dosage effects and the need for drought tolerance in both parental lines to obtain acceptable hybrid performance under drought. CML339 had the highest GCA under drought conditions and across environments (Table 1). CML 258 had the second highest GCA across environments and under intermediate drought stress. Under low N, non-additive effects were more important than additive effects and a significant number of cross-over's were observed between the GCA of lines under low N and high N. Hybrids including the lines CML341, CML344 and CML254 had good performance under low N conditions (Table 1). The DNA-marker classification of lines agreed with pedigree and source germplasm information.

Conclusions

GCA effects became more important under drought. This suggests the need for DT in both parental lines to obtain acceptable hybrid performance under drought. Non-additive effects were more important than additive effects in determining hybrid yields under low N. Significant interactions were observed between combining abilities under low and high N. CML 339 had the highest GCA under drought stressed, non-stressed, and across all environments. CML 344 had superior GCA under low N. Our preliminary data show the potential use of molecular markers to estimate relationship among tropical maize inbred lines.

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Table 1. Grain yield GCA effects for the best lines under severe drought stress (TLSS), intermediate drought stress (TLIS), well-watered conditions (TLWW, PRWW), low N stress (LOWN) and across environments (ACROSS).

LINES	PEDIGREE	TLSS	TLIS	TLWW	PRWW	PR LOWN	ACROSS
CML 339	LA POSTA SEQC3-H297-2-1-1-1-3-#	0.590	1.508	2.406	1.226	-0.302	0.990
CML 340	LA POSTA SEQC3-H20-4-1-1-2-3-#	0.397	0.436	0.471	0.107	-0.160	0.198
CML 341	LA POSTA SEQC3-H1-2-2-2-1-1-#	-0.078	-0.110	-0.120	-0.428	0.329	0.101
CML 344	TS6c1-F118-1-2-3-1-2-#	-0.159	0.688	0.352	-0.887	0.588	0.102
CML 254	TS-149-2-BBB-##-1-BB-f	0.274	0.248	0.126	0.824	0.414	0.487
CML 258	21C5HC218-2-3-B-###-B-1-BBB-f	0.157	1.246	1.831	1.320	-0.451	0.685
S.E. Diff. between two effects		0.086	0.217	0.266	0.227	0.158	0.215

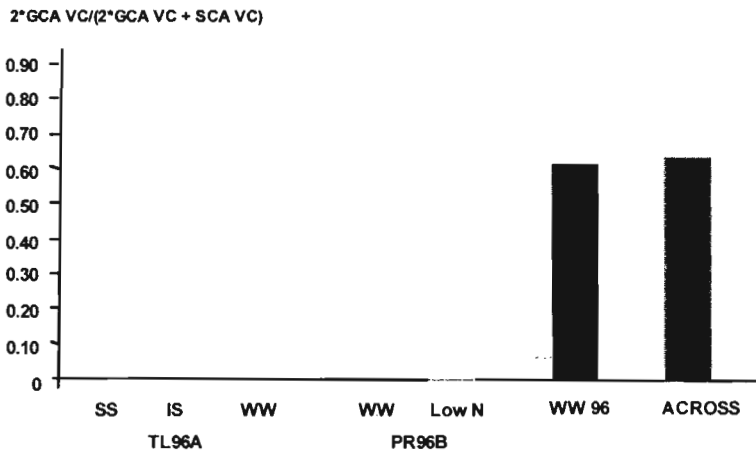


Figure 1. Relative importance of general and specific combining ability for GY expressed as the ratio: $2*GCA VC / (2*GCA VC + SCA VC)$, where GCA VC and SCA VC are equivalent variance components considering a fixed model.

A8 - Genetic Analysis of Adaptation Differences Between Highland and Lowland Tropical Maize

I. Armstead,¹ C. Jiang,² M. Hayward,¹ H.R. Lafitte,³ G.O. Edmeades,² D. Hoisington,² and J.A. Deutsch⁴

¹ Crop Genetics Division, IGER, Plas Goggerdan, Aberystwyth SY23 3EB, UK

² CIMMYT, Apdo Postal 6-641, 06600 Mexico D.F., Mexico

³ IRRI, P.O.Box 933, Manila, Philippines

⁴ Zeneca Seeds, RR#2 Marshall, Missouri, USA

Introduction

Although maize as a species has an extremely broad range of adaptation (Fischer and Palmer 1983) there are distinct germplasm groupings which show specific adaptation to the lowland tropics, the mid-elevation tropics and subtropics, the highlands, and temperate environments. Some of this adaptation is due to varying disease resistance and photoperiod sensitivities (Edmeades et al. 1994), but there are also fundamental differences in their response to temperature (Lafitte and Edmeades 1997). Understanding the genetic basis of this thermal adaptation would enhance our ability to improve yield under cool or warm environments or for stable yield in both.

Materials and methods

Two inbred lines were extracted by continuous selfing, one from a lowland population (S_8 , from CIMMYT Pop. 21) and one from a highland population (S_5 , from CIMMYT Pool 1). An F_2 population was developed from the cross between the two inbreds and DNA extracts from leaf samples from individual F_2 plants shortly before flowering were used to derive a linkage map based on genotypic information on 86 markers and 307 individuals. At the same time $F_{3,4}$ families were produced by selfing F_2 individuals followed by plant-to-plant crosses within each F_3 family. A total 161 of these $F_{3,4}$ families were evaluated in 1993 at four CIMMYT experimental stations, each representing a different thermal regime (Poza Rica winter, $T_{mean} = 22.6^\circ\text{C}$; Tlaltizapán summer, $T_{mean} = 24.4^\circ\text{C}$; El Batán summer, $T_{mean} = 16.7^\circ\text{C}$; Toluca summer, $T_{mean} = 12.7^\circ\text{C}$). Plot size was a single row 2.5 m long, and within- and between-row plant spacings were 0.20 m and 0.75 m. The design used at each site was an alpha (0,1) lattice in two replications. Joint analyses of composite interval mapping (Jiang and Zeng, 1996) over sites were performed for mapping quantitative trait locus (QTL) and for testing QTL by site interaction when a QTL was detected.

Results

Variation among families and family \times site interactions were highly significant (Table 1). Allelic effects characteristic of their origin were indicated at each site by significant correlation between biomass production and the proportion of alleles from highland (or lowland) parental lines in each family (Fig. 1). Significant and positive correlation with heterozygosity was also observed in all four sites, indicating that heterosis itself increases biomass production (Fig. 1). Seven QTL were detected for biomass production, four of which showed significant QTL \times E interaction and a clear pattern in the direction and magnitude of the estimated allelic effects from lowland to highland (Fig. 2). These QTL in combination contributed on average 0.34 of the phenotypic or about 0.60 of the genetic variation in each of the 4 sites. Similar results were observed for traits such as grain yield and flowering date.

Conclusion

Adaptation of a genotype to a specific thermal regime may be the consequence of long-term natural selection with allelic substitution at many loci. However, using molecular markers a few QTL have been identified which are responsible for most of the difference in biomass production among sites (about 0.70 of the interaction). Although most alleles expressed in favor of their origin, alleles with positive effects on all testing sites were observed. These may come from both populations, especially the lowland

population, which suggests that the biomass production of highland germplasm could be enhanced by the judicious introgression of specific lowland alleles.

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Table 1. F_{3,4} family means and variances for biomass (g/m²) at each thermally-diverse site (lowland, PR; mid-altitude, TL; highland, BA; extreme highland, TO), and across sites.

Parameter	Estimates in each site				Joint estimates
	PR	TL	BA	TO	
Mean	408	865	1011	544	707
Variance	7090	33191	21444	20757	V _g =5597, V _{gxe} =4757

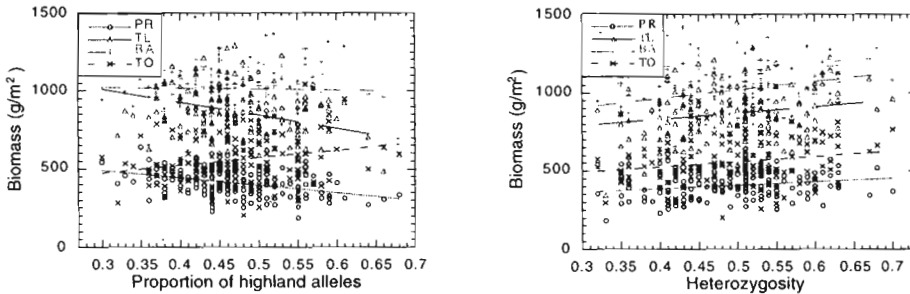


Fig. 1. Relationship of biomass to the proportion of alleles originating from the highland parent, and to the degree of heterozygosity in each family, when evaluated over four thermally-diverse sites in Mexico.

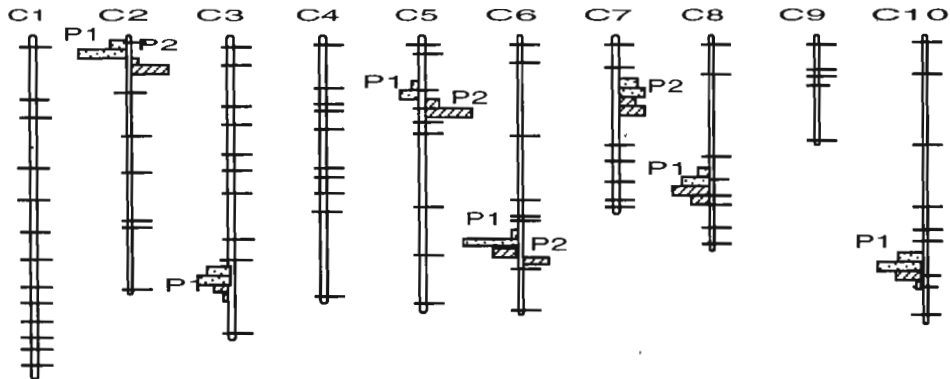


Fig. 2. RFLP linkage map of tropical maize, based on the segregation of 86 loci in 307 F₂ individuals. P1 and P2 indicate the direction and magnitude of the lowland or highland allelic effect, whichever is bigger, at four thermally-diverse testing sites (PR [top], TL, BA and TO [bottom]).

A9 - Plant Improvement Through Molecular Markers: A New Approach

J.M. Ribaut and F.J. Betrán

Applied Biotechnology Center and Maize Program, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico DF

Introduction

Two phases of selection common in plant breeding programs are the creation of variability by crossing appropriate materials and the selection of suitable individuals among the recombining progeny. The use of molecular markers at early stages of recombination can increase selection efficiency, but also reduce possibly useful genetic variation. Our new strategy describes the use of molecular markers in large F_2 segregating populations derived from crosses between elite lines. The novelty of our approach is double: 1) it allows to fix efficiently specific genomic segments, while maintaining allelic variability in the rest of the genome for future selection, and 2) it benefits from the contribution of two or more elite parental lines, to generate new source germplasm. The large plant screening requires in this new marker-assisted selection (MAS) scheme is now possible through reliable, PCR-based molecular markers (Ribaut et al. 1997). This strategy works for both cross- and self-pollinated plants and quantitative and qualitative traits.

The strategy

Potential parental lines are chosen from elite material that is outstanding for a trait(s) of interest. To be selected as parental lines, elite lines should have a high potential allelic complementarity at loci controlling the target trait(s) and good combining ability for later recovery of hybrid vigor (phase I, Fig. 1).

To identify genomic regions of interest, each selected parental line is crossed with a tester line to develop a segregating F_2 population (Phase II A, Fig. 1). Testers can be common for all parental lines, and should show a poor expression of the target trait(s) and/or be elite line belonging to heterotic pool other than the tested parental line. After genome mapping (parental line x tester line; Lander et al. 1987), loci involved in the expression of target traits can be identified by comparing field performance (F_3 families) with allelic distribution of segregating genotypes (F_2 plants) along the genome (Lander and Botstein 1989). Only genomic regions that show good stability across environments and large effects are considered in the next step.

Concurrently with the above, large F_2 populations can be developed by intercrossing the selected elite parental lines (Phase II B, Fig. 1). Selection within large F_2 populations is conducted using PCR-based markers that identify polymorphisms for the target genomic regions previously identified for each parental line. A combination of different loci with favorable alleles contributed by one or the other parental line is considered. Only F_2 plants whose genomes are fixed for those alleles are selected. No additional selection pressure is applied on the rest of the genome. The F_2 population size before selection, and the number of desirable fixed loci involved in the design will determine the number of F_2 plants selected. By selecting only those individuals homozygous for the allele of interest, the F_2 population will be reduced by a factor of four for each genomic region considered. By recombining plants across families, the allelic segregation at non-selected regions is recovered, and a synthetic population can be created.

Breeders can use the resulting materials to develop new genotypes that meet farmers' needs in specific environments.

Comments and conclusion

For lines representing distinct genetic pools, the development of more than one F_2 population is important. Thus, line recycling takes place within a single heterotic group, and later on the crossing of lines developed from different F_2 populations will ensure the recovery of heterosis and good hybrid vigor. The selection scheme described may constitute the first step of a more complex selection process. Selected material fixed at specific loci can be improved by crossing it with elite lines favorable for other traits in a pyramidal genetic improvement strategy.

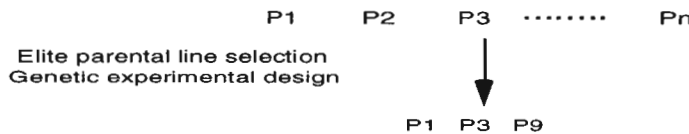
After MAS, the resulting plants should possess 1) quality, conferred by the fixed alleles at specific genomic position, and 2) diversity, due to allelic segregation in the rest of the genome, providing wide adaptability for future selection.

References

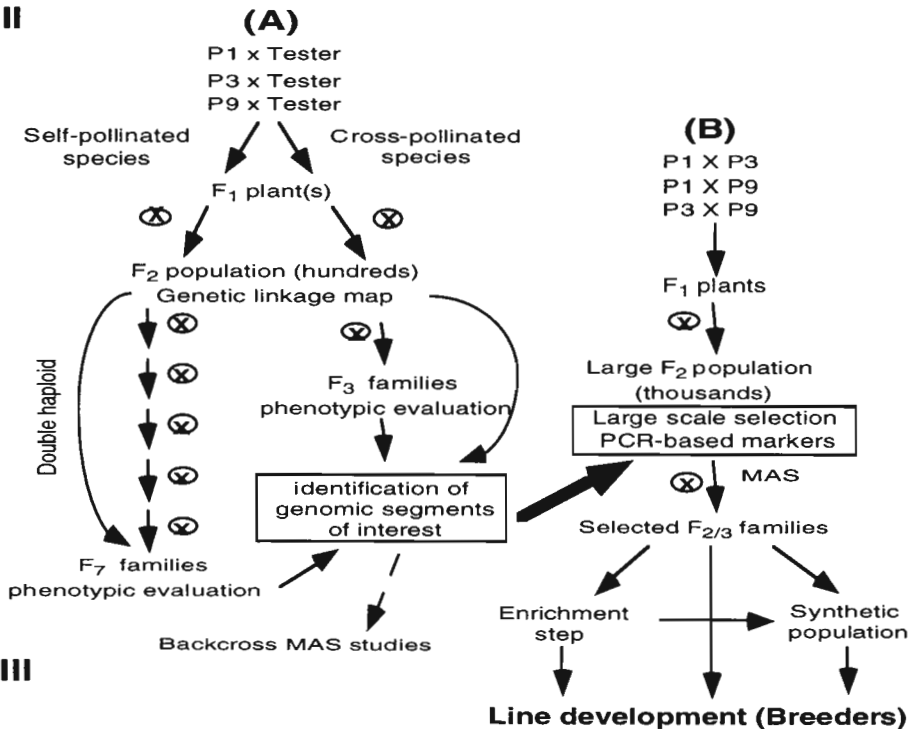
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Figure 1. Large scale F_2 population MAS.

Phase I



Phase II



Phase III

A10 - Gene Dosage and Heterosis

A. Dogra,^{1,2} J.A. Birchler,³ E.H. Coe²

¹Genetics Area Program, ²Department of Agronomy, ³Division of Biological Sciences, University of Missouri - Columbia, MO 65211, USA

Heterosis is the phenomenon by which the performance of an F_1 , generated by crossing of two genetically different individuals, is superior to that of the better parent. In maize, heterosis can be observed even at the very early developmental stages, e.g., seedling emergence, leaf appearance rate and elongation. Also, heterosis is observed in height, size of leaves, number of nodes per plant, length and angle of branches, tassel morphology, length of ear, number of grains per row, root length, diameter and penetration. These factors together result in a greater yield producing larger kernels on larger ears. Though heterosis has been studied for over eighty years, the causal factors at the biochemical level remain virtually as obscure as they were years ago.

One approach to understanding heterosis would be through the study of mechanisms of reactions responsible for growth and development in general, since heterosis for the most part is a manifestation of a superior growth rate of a hybrid over its parents. We plan to characterize heterosis at the molecular level using the enzyme sucrose phosphate synthase (SPS), as one of the criteria for measuring heterosis. SPS, which is involved in sugar metabolism, has been recognized as playing a role in heterosis. The level of SPS is thought to be rate limiting for growth, as it controls sugar transport in the plant. Activity of SPS in leaf extracts correlates positively with the leaf sucrose content; this supports the proposal that sucrose synthesized by SPS reflects the sucrose pool available for transport.

SPS has been mapped to chromosome arms 3L and 8L. Using the B-A translocation system in maize, we have created the dosage series of these chromosome arms in two inbred lines, B73 and Mo17, and their hybrids. Using a dosage-indicative RFLP marker for each of these arms, we will determine if the expression of SPS increases with the increasing dosage or if its expression is dosage compensated. If there is a dosage effect, we can determine whether reduced levels of SPS become rate limiting on growth and restrict the manifestation of heterosis phenotypically by correlating with the level and activity of SPS with various morphological characteristics of heterosis in maize.

A11 - Heterosis Estimation for Different Quantitative Maize Characteristics Using Highland and Subtropical Progenitors

R. Gaytan-Bautista and J.S. Padilla-Ramirez

INIFAP-Campo Experimental Pabellon, Apdo. Postal 20, 20660 Pabellon de Arteaga, Ags.

Introduction

Heterosis is defined as the result of the interaction of several independent factors coming from the progenitors and expressed in the hybrid, which normally has greater yield potential than its progenitors (De la Loma 1963). Thus, heterosis estimation is very important in maize to identify the best combinations of progenitors to form potential hybrids and to study gene action (Paccapelo 1993). Maize hybrids involving germplasm from different origin or with broad genetic diversity typically have higher heterosis (Moll et al. 1965; Castro et al. 1968). However, there is little information about heterosis estimation in progenitors developed from highland x subtropical germplasm. The purpose of this research was to study the genetic variability using different methods of heterosis.

Methods

The study was conducted during the summer of 1992 at the Buenavista experiment station, Saltillo, Coahuila, Mexico (25° N; 1,743 masl), which belongs to the Universidad Agraria Antonio Narro. The maize genotypes evaluated were seven progenitors from the highlands (females), 12 subtropical progenitors (males), 40 crosses coming from the highland x subtropical progenitors, and two commercial hybrids (AN-44 and AN-447); all materials were provided by CIMMYT. The experimental design was a randomized complete block with three replicates and the experimental unit consisted of one row of 5 m. Heterosis estimation was determined in only 15 hybrids, due to emergence problems in some subtropical progenitors. We estimated mid-parent heterosis, high-parent heterosis (heterobeltiosis), and % over the best commercial hybrid check (useful heterosis); in this case AN-447. The variables included were grain yield, weight of 100 seeds, dry matter, and days to male flowering.

Results

The range of grain yield for the highland progenitors varied from 662 to 3,769 Mg ha⁻¹, with a mean of 2,048 Mg ha⁻¹. The grain yield of the subtropical progenitors ranged from 1,093 to 4,927 Mg ha⁻¹, with a mean of 2,932 Mg ha⁻¹. Yield of the hybrids ranged from 4,193 to 8,876 Mg ha⁻¹, with a mean of 6,741 Mg ha⁻¹. Heterosis for grain yield ranged from 50.7 to 618.7%, while heterobeltiosis varied from -14.9 to 80.2% and useful heterosis ranged from -36.0 to 35.3% (Table 1).

Conclusions

All estimated heterosis for grain yield was positive, heterobeltiosis was positive in 13 out of 15 cases, and useful heterosis was positive in only 5 out of 15.

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Table 1. Estimated heterosis (%) for different agronomic characteristics in maize.

Hybrid	Grain yield			Wt. of 100 seeds			Dry matter			Days to anthesis		
	H	HB	HU	H	HB	HU	H	HB	HU	H	HB	HU
P2 x P49	190.2	31.9	-0.9	42.0	1.2	-14.2	452.9	119.1	-42.5	2.3	-10.9	-11.9
P4 x P34	237.8	60.9	20.8	26.0	7.4	-8.9	131.7	58.5	-58.4	-10.2	-13.2	-14.0
x P53	618.6	28.0	-3.8	26.8	-4.1	-18.7	537.1	52.5	-50.0	-2.6	-11.3	-12.3
x P60	50.7	33.0	-0.1	-11.3	-10.2	-23.9	183.9	106.2	-45.9	-7.7	-12.4	-13.3
x P34	137.0	43.2	7.6	1.9	-4.1	-18.7	89.1	87.2	-50.9	-6.5	-13.5	-14.4
P15 x P35	303.5	80.1	35.3	38.5	12.7	-4.5	34.8	20.5	68.4	-6.3	-13.9	-14.8
x P40	98.5	8.9	-18.2	28.7	10.5	-6.3	53.9	17.9	-69.1	-4.4	-13.5	-14.4
x P44	145.1	16.6	-12.4	14.8	-1.8	-16.8	85.4	42.2	-62.7	-2.9	-13.5	-14.4
x P45	215.7	-12.2	-34.1	20.3	-7.6	-21.7	90.4	10.7	-70.9	-7.6	-15.3	-16.2
P18 x P35	217.2	59.5	19.8	28.9	18.8	0.7	63.4	11.0	-70.9	-7.3	-14.6	-15.5
x P42	246.2	22.8	-7.8	50.1	24.5	5.6	221.9	3.8	-72.8	-6.4	-14.6	-15.5
x P45	266.9	22.7	-7.8	49.2	30.7	10.8	202.8	11.1	-70.9	-8.9	-16.4	-17.3
x P46	136.5	-14.9	-36.0	24.1	14.9	-2.5	253.5	19.6	-68.6	-5.2	-16.4	-17.3
x P47	259.0	52.1	-14.2	33.1	34.2	13.8	282.8	65.9	-56.5	-9.6	-15.7	-16.6
x P48	120.3	50.1	12.8	28.5	23.9	5.0	185.6	33.8	-64.9	-8.7	-15.3	-16.2

H = heterosis; HB = heterobeltiosis; HU = useful heterosis.

A12 - Heterosis for Root Potential in Maize

S. Kuruvadi, H.A. Paccapelo, and B.A. López

Universidad Autónoma Agraria Antonio Narro, Saltillo, Coahuila, México, CP 25315

Introduction

Several researchers have suggested that breeding for improved root systems in annual crops such as cereals and grain legumes could significantly improve their yield under drought (Hurd 1974; Blum 1982; Kuruvadi and Smith 1986 and Kuruvadi and Aguilera 1990). Turner (1979) stated that the variation of root growth between species determines differences in drought resistance. Utilization of genetic variation in improving crop varieties requires knowledge of the heritability, heterosis, and genetic control of root system traits. This study estimates heterosis for root potential in 15 crosses of maize.

Methods

Ninety S₁ lines derived from a broadly-based population were evaluated at two locations. Six outstanding lines were chosen as parents, based on grain yield, good agronomic characteristics, and differing genetic background. Selected lines were crossed on station in all possible combinations, excluding reciprocals, to obtain seed of 15 hybrids. The root potential of the 6 parents and 15 F₁ progenies were evaluated in the greenhouse using black colored polyethylene bags 110 cm long and 23 cm diameter. These bags were filled with well-sieved, fumigated soil. The experimental unit comprised two seedlings of each genotype per bag. Plants were watered as needed. A randomized block design with two replications was used. After flowering in all entries, soils was washed from the roots with a gentle spray of water. The roots recovered were oven dried and the dry weights determined. The heterosis percentage was calculated over mid- and high parent for root dry weights.

Results

Mean root dry weight varied from 7.16 to 11.59 g in parents and 7.91 to 16.24 g in hybrids (Table 1, Fig. 1). Three lines (8, 9 and 5) and four hybrids (7x8, 3x8, 5x8 and 5x9) produced the greatest root mass. Heterosis over mid-parent value for root dry weight ranged from -25.3 to 93.6% and 10 out of 15 hybrids manifested positive mid-parent heterosis. Heterosis over the better parent for this trait varied from -31.6 to 71.8% and 8 out of 15 F₁ progenies surpassed their better parent. Crosses 3x8, 7x8, 5x8 and 5x9 showed a high-parent heterosis of 71.8, 68.8, 27.8, and 12.6% respectively, for root dry matter.

Conclusions

Increased root mass may result from greater density or depth of root growth; both can provide increased extraction of soil water and maintenance of high water potentials to avoid the effects of drought.

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Table 1. Mean and heterosis for root dry weights in six parents and 15 hybrids in maize.

Parents	Root dry weight (g)	Crosses	Root dry weight (g)	Heterosis (%) for root dry weights	
				Over mid parent	Over better parent
Line 3	8.95	3x5	10.53	2.7	- 8.9
Line 5	11.56	3x6	8.40	- 18.2	- 27.5
Line 6	7.16	3x7	9.74	4.9	1.2
Line 7	9.62	3x8	15.38	91.1	71.8
Line 8	11.59	3x9	11.81	15.9	3.2
Line 9	11.44	5x6	8.91	- 22.9	- 23.1
Mean	10.05	5x7	7.91	- 25.3	- 31.6
LSD (5%)	4.08	5x8	14.77	57.8	27.8
		5x9	13.02	13.2	12.6
		6x7	12.39	16.9	6.9
		6x8	9.24	- 1.4	- 20.3
		6x9	8.74	- 24.1	- 24.6
		7x8	16.24	93.6	68.8
		7x9	11.75	11.6	2.71
		8x9	10.30	10.8	- 9.7
Mean	-	11.27	-	-	
LSD (5%)	-	4.08	-	-	

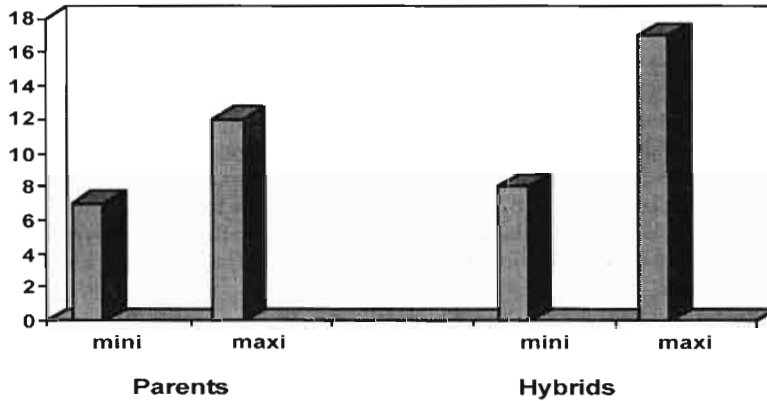


Figure 1. Minimum and maximum quantity of root mass recovered in parents and hybrids in maize.

A13 - Mapping Heterosis QTLs in Maize Grown Under Various Stress Conditions

J.R. LeDeaux, C.W. Stuber

U.S. Department of Agriculture, Agricultural Research Service, and
Department of Genetics, North Carolina State University, Raleigh, NC

Introduction

Genotype x environment interactions are generally recognized as being important to plant breeding (Kang and Gauch, 1996; Moll et al., 1978). Increasing productivity while growing crops in increasingly stressful environments is a challenging endeavor. To address this issue and other issues related to mapping quantitative trait loci (QTLs) and their environmental interactions, we applied different types of stress to maize populations of lines derived from a hybrid that was at one time the most widely grown hybrid in the USA. We have mapped the positions of QTLs involved with yield and ear height.

Methods

A recombinant inbred (RI) population was constructed by selfing 206 F₂ offspring of a Mo17 x B73 F₁ for several generations. The F_{2:6} generation was crossed to B73 and the F_{2:7} generation was crossed to Mo17. Each backcross population was grown at two locations in North Carolina over two years. For each year-location and each population, eight replications were planted. Half the replications were subjected to severe drought stress, the other half were provided adequate moisture; one half had nitrogen applied at 56 kg/ha, the other half at 224 kg/ha; one half were planted at high density (71,600 plants/ha), and the other half at low density (35,800 plants/ha), such that each of the eight possible combinations of treatments was present in one of the replications. Plots were planted in two rows, 3.6 m long, with 0.9 m spacing between rows. Several traits were measured for each plot. The RI lines in this population have been extensively characterized genotypically using several SSR, RFLP, and isozyme markers (Senior et al., 1996). Each line has been scored for 208 different polymorphic markers that map to 199 distinct loci.

The data comprise a 2 x 2 x 2 x 2 x 4 factorial design at each locus: two different alleles per marker locus, two levels of moisture, two levels of nitrogen, two different planting densities, and four different year-locations. The data for yield and ear height were analyzed for each marker locus using SAS proc GLM (SAS, 1990). The number of degrees of freedom (DF) for the error term depended on how many lines were successfully scored for the particular marker in question, but the average DF for the backcross to Mo17 was 5384, and for the backcross to B73, 5801. The relatively few markers that were scored as heterozygotes were treated as missing values. An effect associated with a marker was deemed significant when the P-value of the F-test for that effect was <0.001. This relatively low value was chosen because of multiple tests.

Results

In the backcross to Mo17, 146 of 199 markers were significantly associated with differences in yield between the two alleles. Of these markers, three linked markers from chromosome 1 had significant interaction effects with drought stress (Table 1). Two markers from chromosome 5 (Table 1) and one from chromosome 7 (Table 1) had significant interaction effects with nitrogen stress. No markers had significant interaction effects with density or higher order interactions. Similarly, in the backcross to B73, 154 markers were associated with differences in yield. Of these, four from chromosome 8 had a significant interaction effect with density (data not shown). There were no other significant marker x stress interaction effects in the backcross to B73.

Similar results were found for ear height. In the backcrosses to Mo17 and B73, 128 and 131 of 199 markers, respectively, were significantly associated with differences in ear height. Of these, only four linked markers from chromosome 8 in the backcross to Mo17 had significant interaction effects with drought stress. No other marker x stress interaction effects were significant for ear height. In every case

where there was a marker x stress interaction, the stress reduced the effect of the QTL in question; i.e. there was never a situation where one allele was better than the other in the absence of stress and was worse in the presence of the stress (e.g., see Table 1).

Conclusions

Relatively few loci showed interaction effects with the stresses in this study, and the sum of these effects is only a small percentage (<5%) of the sum of the locus effects themselves. This is consistent with results observed in other studies in maize where few QTLs were identified that were affected by the environment in which the plants were grown (Beavis and Keim, 1996; Veldbloom and Lee, 1996; Stuber et al., 1992). Given these results, one may expect that the lines bred for superior performance in non-stress environments would also perform well in stress environments, at least for the stresses used in this study. However, this may not be the case for wider crosses involving lines that were not specifically bred for temperate regions.

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Table 1. Yield averages and negative \log_{10} (P-value) associated with the F-test for those markers that showed significant interaction effects with a particular stress and their immediate neighboring markers in the backcross to Mo17. Marker position is the chromosome followed by the position in Haldane cM based on the map of Senior et al. (1996).

Stress factor	Marker position	B73	Mo17	B73	Mo17	Marker x stress F test -log(P)	B73	Mo17	Marker F test -log(P)
		allele without stress kg/ha	allele without stress kg/ha	allele with stress kg/ha	allele with stress kg/ha		allele comb. avg. kg/ha	allele comb. avg. kg/ha	
Moisture	1_77	6016	5824	4078	4046	1.93	5048	4935	4.80 *
	1_80	6058	5796	4100	4037	3.07 *	5079	4917	7.85 *
	1_102	6036	5794	4097	4046	3.00 *	5067	4921	6.73 *
	1_115	6089	5755	4128	4008	3.41 *	5110	4881	16.06 *
	1_116	6079	5765	4137	4015	2.90	5108	4891	14.38 *
Nitrogen	5_99	5405	4975	4964	4709	2.54	5185	4842	30.78 *
	5_104	5444	4924	4976	4673	3.90 *	5210	4799	45.50 *
	5_108	5429	4949	4973	4677	3.07 *	5201	4813	42.92 *
	5_110	5338	5025	4910	4737	1.85	5124	4881	16.71 *
Nitrogen	7_39	5284	5047	4830	4784	2.59	5057	4915	4.89 *
	7_47	5323	4995	4870	4747	3.06 *	5096	4871	11.01 *
	7_58	5326	5071	4883	4821	2.87	5104	4946	6.83 *

* Significant at 0.001 level.

A14 - Relative Importance of Additive, Dominance, and Epistatic Effects for Maize Yields in Acidic- and Nonacidic Soils

H. Ceballos¹, S. Pandey² and L. Narro²

¹Universidad Nacional de Colombia, Sede Palmira; ²International Maize and Wheat Improvement Center (CIMMYT). Apdo Aereo 6713, Cali, Colombia

Introduction

Maize yields are low on acid soils (pH < 5.6) mainly because of Al and Mn toxicities and Ca, Mg, and P deficiencies. Although maize is not tolerant to acid soils, it is grown on more than 8 million ha of acid soils in the tropics. Tolerance to acid soils in maize is quantitatively inherited. Additive, dominance, and additive x environment variances play an important role in the expression of tolerance (Borrero et al., 1996; Pandey et al. 1994). Little is known about the importance of epistatic effects in the expression of maize traits under acid soil conditions.

Methods

Through divergent selection in three acid-soil tolerant populations (SA4, SA5, and SA7), tolerant (PT) and susceptible (PS) S₅ lines were selected and crossed to obtain the three respective F₁ hybrids. The tolerant lines from populations SA4 and SA5 were also crossed with a susceptible S6 line from Tuxpeño-Sequía (TXP). Five F₁ hybrids were produced: SA4-T x TXP (Set 1); SA4-T x SA4-S (Set 2); SA5-T x TXP (Set 3); SA5-T x SA5-S (Set 4); and SA7-T x SA7-S (Set 5). The following generations were obtained for each set: backcross to the tolerant (BT) or susceptible parent (BS); F₂; F₃; second backcross to the tolerant (BTT) or susceptible parent (BSS); and selfing of the backcross to the tolerant (BT) or susceptible parent (BS). Segregating families were represented by an average of 44 ears (across sets and families), ranging from an average (across sets) of 39 ears for BTT, to 51 ears for F₃. The second backcross generations from Sets 3 and 4 were not included. The five sets were evaluated in three acidic environments (Quilichao, Villavicencio, and Villavicencio) and one non-acid environment (Palmira). A randomized complete block design with three replications was used (except at Quilichao were two replications were used). Experimental units had a varying number of 5m rows (from one to four) depending on the genetic uniformity of the family and were planted to provide about 53,000 plants ha⁻¹. Plots were hand-harvested and grain yield, adjusted to 155 g kg⁻¹ moisture, was calculated. A grain:ear ratio of 80% was assumed. A quantitative generation mean analysis (Mather and Jinks 1977) was performed for each set using the model:

$$Y = M + A ca + D cd + AA caa + AD cad + DD cdd$$

where M is the intercept, A is the pooled additive effect, D is the pooled dominance effect, and AA, AD, and DD are the pooled digenic additive by additive, additive by dominance, and dominance by dominance epistatic effects, respectively. ca, cd, caa, cad, and cdd are the corresponding coefficients of these effects in the equations of expectation of generation means. The weight used in the regression analysis was the inverse of the variance of the generation mean. The sequential sums of squares derived from the addition of each genetic effect in the model, including digenic epistatic effects, were used to determine the relative importance of each effect (Allen and Cady 1982).

Results and Conclusions

Mean yield at Palmira was 3.59 t ha⁻¹; 0.51 t ha⁻¹ in acid soils (Table 1). The phenotypic correlation coefficient between yield in acid soils and non acid soils was 0.81**. Much of the sum of squares for yield was accounted for by the additive and dominance effects, the latter being the most important (Table 2). The means of R² values for a model that excluded epistatic effects were 0.83, 0.57, and 0.91 for Villavicencio, Quilichao and Palmira, respectively. In general, the higher the coefficient of variation of the trials, the higher the proportion of the total sum of squares accounted for by epistatic effects. The correlation between these two parameters was 0.74**. Generally, epistatic effects reached statistical significance only for Sets 2 and 3 at Villavicencio. Epistasis tended to be more relevant in acid soils for Sets 3 and 4. The high proportion of the total sum of squares explained by epistatic effects for Set 1 at Quilichao is probably due to the variable soil conditions there (CV = 119%). Epistasis does not seem

important in the expression of yield under acid soils, but was more important than in non-acid soils. This could be due to the higher experimental errors typically resulting at acidic locations.

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Table 1. Mean yield (t ha⁻¹) of different generations derived from five sets of crosses evaluated at three acid soil locations and in one non-acid soil location (Palmira) in Colombia.

	Across acid soil locations					Palmira				
	Set 1	Set 2	Set 3	Set 4	Set 5	Set 1	Set 2	Set 3	Set 4	Set 5
PT	0.41	0.59	0.39	0.22	0.05	2.98	3.41	2.23	1.74	1.90
PS	0.14	0.10	0.21	0.15	0.02	2.21	0.65	2.01	0.91	1.62
F1	1.16	1.87	1.37	0.91	1.53	8.68	7.73	7.27	4.24	9.35
F2	0.86	0.61	0.44	0.36	0.72	4.66	3.88	3.54	2.29	4.62
F3	0.36	0.38	0.27	0.28	0.41	3.79	2.64	2.61	1.98	3.21
BT	0.90	0.85	0.69	0.31	0.98	5.32	5.51	4.30	3.41	4.71
BTT	0.58	0.82	--	--	0.34	5.01	4.90	--	--	3.59
BT	0.59	0.46	0.28	0.40	0.48	3.78	3.50	3.02	1.59	2.98
BS	0.67	0.45	0.38	0.17	0.60	4.84	3.31	4.59	2.38	5.16
BSS	0.46	0.24	--	--	0.24	3.52	1.69	--	--	3.37
BS	0.34	0.27	0.27	0.15	0.35	3.49	2.06	2.59	1.49	2.88
Mean	0.63	0.60	0.48	0.31	0.49	4.39	3.57	3.57	2.23	3.94
LSD0.05	0.20	0.35	0.22	0.21	0.22	0.78	0.68	0.82	0.66	1.14

Table 2. Relative importance of additive, dominance, and digenic epistatic effects, measured as % of total sum of squares accounted for the respective genetic coefficients. The coefficient of determination (R²) corresponds to the model that excludes epistasis.

df	Set 1	Set 2	Set 3	Set 4	Set 5	Mean
<i>Villavicencio-1 + Villavicencio-2</i>						
Additive 1	15.23*	40.67*	2.99	26.39*	15.23	20.10
Dominance 1	78.97**	39.84**	80.15**	33.94*	81.49**	62.88
Epistasis 3	5.02	16.70*	16.21*	32.82	1.87	14.52
R ²	0.94	0.81	0.83	0.60	0.97	
<i>S. de Quilichao</i>						
Additive 1	13.52	78.73**	1.24	12.28	3.30*	21.81
Dominance 1	3.05	7.70	38.36	36.89	89.43**	35.09
Epistasis 3	50.56	3.34	39.74	39.39	4.17	27.44
R ²	0.16	0.86	0.40	0.49	0.93	
<i>Palmira</i>						
Additive 1	1.96*	43.85**	0.60	4.09	1.38	10.38
Dominance 1	95.26**	46.12**	94.16**	74.39**	93.85**	80.76
Epistasis 3	2.11	4.26	4.08	3.42	2.06	3.19
R ²	0.97	0.90	0.95	0.78	0.95	

*, ** Significant at the P ≤ 0.05 or P ≤ 0.01 probability level, respectively.

A15 - Prediction of Heterosis in Wheat Using Coefficient of Parentage and RFLP - Based Estimates of Genetic Relationship

J.F. Barbosa-Neto,¹ M.E. Sorrells,² and G. Cisar³

¹ Department of Crops, Universidade Federal do Rio Grande do Sul, Faculdade de Agronomia, Av. Bento Gonçalves 7712, CEP: 91501-970, Porto Alegre, RS, Brazil. E-mail: jfbn@pro.via-rs.com.br

² Hybritech Seed International, Inc., 6025 West 300 South, Lafayette, IN, USA, 47905-9278.

³ Department of Plant Breeding and Biometry, Cornell University, Ithaca, NY, USA, 14853.

Introduction

Maximizing genetic diversity between inbreds is a major goal in hybrid breeding programs to maximize heterozygosity in the progeny. Evaluation of hybrids for heterosis or combining ability in the field is expensive and time consuming. As a result, pedigree information (Smith et al. 1990), morphological traits (Souza and Sorrells 1991a; Souza and Sorrells 1991b), biochemical data (Smith and Smith 1988), and DNA based markers (Melchinger et al. 1990; Martin et al. 1995) have been used extensively to study genetic diversity and heterosis. Results have been inconsistent for predicting heterosis. Smith et al. (1990) reported that measures of similarity based on restriction fragment length polymorphisms (RFLPs) and pedigree knowledge could be used to predict superior hybrid combinations in maize. On the other hand, Melchinger et al. (1990) and Dudley et al. (1991), working with different sets of maize cultivars, detected a low correlation between combining ability and RFLP based genetic distance. The purpose of this study was to characterize genetic diversity in a set of winter wheat lines using pedigree information and RFLP markers and to correlate these relationship estimates with heterosis for grain yield, test weight, days to heading, and plant height.

Material and Methods

Genetic relationships of 112 wheat (*Triticum aestivum* L.em Thell.) lines were estimated using 41 DNA clones hybridizing to 273 DNA fragments and by calculating coefficient of parentage (COP). Genetic relationship was estimated using the distance index proposed by Barbosa-Neto (1995); its value ranges from zero (total similarity) to one (complete dissimilarity). Heterosis was estimated for 722 hybrids grown in multiple locations with 189 being tested in more than one year.

Results

The average RFLP-based genetic distance index (DI) was 0.35. Mid-parent heterosis for grain yield ranged from -20% to 57% and high-parent heterosis from -22% to 47%. The correlation between RFLP - based estimates of genetic distance and COP was non-significant (-0.33). Coefficient of parentage was significantly correlated with heterosis for all traits in 1991 but not in other years (Table 1). Genetic distance based on RFLPs scored in this study was not correlated with heterosis in any of the years tested (Table 2).

Conclusions

Neither RFLP-based genetic distance nor coefficient of parentage were promising predictors for heterosis in wheat. The presence of heterosis for grain yield in wheat was demonstrated; however, the genetic diversity in this large group of soft red winter wheat was limited, with an average of 88% similar RFLP fragments. This narrow germplasm base may explain, in part, the absence of correlation between heterosis and RFLP genetic distance. On the other hand, the analysis of the genetic diversity in a breeding population can contribute to the incorporation of new source genotypes to increase variability. In addition, with this information, genetic pools can be accurately assembled in order to explore more efficiently the variability present.

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Table 1. Correlation between coefficient of parentage and grain yield, test weight, days to heading, plant height, mid-parent heterosis (MP), and high-parent heterosis (HP) in 1991, 1992, 1993, and 1994. *, ** a = 0.05 and a = 0.01. † Sample size in parenthesis.

Trait	1991	1992	1993	1994
Grain Yield	0.00(160)†	-0.11(61)	0.10(164)	-0.13(191)
MP heterosis	-0.41(160)**	-0.18(53)	-0.12(162)	-0.15(179)*
HP heterosis	-0.30(160)**	-0.04(61)	-0.13(164)	-0.09(191)
Test weight	-0.06(88)	0.00(60)	-	-0.02(47)
MP heterosis	-0.43(86)**	-0.28(52)*	-	-0.36(27)
HP heterosis	-0.25(86)*	-0.12(60)	-	-0.10(45)
Days to heading	-0.18(159)	-0.28(61)	-	0.08(190)
MP heterosis	0.24(159)**	0.18(53)	-	0.15(179)*
HP heterosis	0.25(159)**	0.19(61)	-	0.10(190)
Plant height	-0.20(60)*	-0.26(61)	-	-0.30(47)**
MP heterosis	-0.43(57)*	-0.21(53)	-	-0.19(27)
HP heterosis	-0.18(60)	-0.09(61)	-	-0.11(45)

Table 2. Correlation between RFLP distance index and grain yield, test weight, days to heading, plant height, mid-parent heterosis (MP), and high-parent heterosis (HP) in 1991, 1992, 1993, and 1994. *, ** a = 0.05 and a = 0.01. † Sample size in parenthesis.

Trait	1991	1992	1993	1994
Grain Yield	0.15(293)†**	0.15(98)	0.09(272)	0.05(308)
MP heterosis	0.09(293)	0.18(88)	0.09(267)	0.02(284)
HP heterosis	0.05(293)	0.11(98)	0.05(272)	0.05(308)
Test weight	0.23(139)**	0.43(97)**	-	0.42(86)**
MP heterosis	0.04(137)	0.18(87)	-	0.19(49)
HP heterosis	-0.02(137)	-0.09(87)	-	0.06(81)
Days to heading	0.05(292)	-0.18(93)	-	-0.05(308)
MP heterosis	0.03(292)	-0.08(84)	-	-0.03(284)
HP heterosis	-0.06(292)	-0.15(93)	-	-0.11(309)
Plant height	0.04(96)	0.03(98)	-	0.05(85)
MP heterosis	0.28(89)**	0.13(85)	-	0.18(49)
HP heterosis	0.15(96)	0.06(98)	-	0.06(80)

A16 - Line X Tester Analysis for Drought Tolerance in Tropical Maize

G. Castañón¹, D. Jeffers², H. Hidalgo³, O.H. Tosquy⁴, R. Arano⁵, and B. Raygoza⁶

^{1,3,4} Researchers, Maize, Plant Pathology, and Rice Program, Campo Experimental Cotaxtla (CECOT)-INIFAP, A. Postal 429 Col. Centro. Veracruz, Ver. México CP 91700. Tel 98-29-34-83-54.

² Maize pathologist, CIMMYT, Apdo. Postal 6-641 06600 México, D. F. México

^{5,6} Professors, Centro de Bachillerato Tecnológico Agropecuario 36 (CBTA 36), Ignacio de la Llave, Ver. México

Introduction

Although total precipitation in the humid tropics often exceeds 900 mm per year, it is common that the yield of maize decreases considerably in this area due to drought spells during the growing season. Edmeades *et al.* (1994) indicated that maize yield losses due to drought in the lowland tropics typically approach 9.0 millions. Drought can affect maize in the tropics at any growth period, though grain yield reductions are often most severe when drought occurs at flowering. Shaw (1977) indicated that maize is very sensitive to drought during tasselling and pollination. Different breeding methods have been used to study drought tolerance in maize (Edmeades *et al.*, 1994; Peña and Martín del Campo, 1993). Combining ability studies on drought tolerant maize lines were reported by Cantú and Gómez (1992). We present results on the general and specific combining ability of selected, drought tolerant lines.

Materials and Methods

Recurrent selection was performed using S₁ lines of Tuxpeño Sequía Cycle 1 during 1994B. The lines of families were evaluated under an irrigation-drought system during 1995A at Cotaxtla Experiment Station (CECOT). For the irrigated trial, water was supplied throughout the growing season, whereas the drought trial was left without water for 45 days during the final crop growth stages up to grain filling. Field data taken included grain yield and plant and ear height. Other variables observed were foliage color, senescence rate, leaf wilting, and tassel size, all on 1-5 scales. Selection was based on the differential averages of all traits under both moisture regimes. Ten percent of the selected S₁ families were crossed by hand with CML 254 and CML 273 of the CIMMYT Maize Program during 1996A. Fifty-two such testcrosses and the two testers were evaluated during 1996B at San Andrés Tuxtla and Ignacio de la Llave, environments which differ in precipitation, temperature, relative humidity and soil type. The trials used an incomplete block design and were analyzed as per the methods of Arunachalam (1974), Rojas and Sprague (1952), Vyas and Pokhriyal (1985). Traits measured were bad ear covering (BEC), rotten ears (ER), grain yield (GY), and dry matter (DM) as a measure of maturity.

Results

The analysis of variance shows significant differences for environments for ER, DM, and GY (Table 1). Similarly, tester differences were significant for ER, GY and DM. For the lines, significant differences were observed only for BEC and DM. Tester x line interactions were significant only for DM. For the remaining variables the testcrosses were similar and there was no effect of the tester on the lines. Generally the variance of the testers was higher than the variance of the lines and testers x lines, which indicates that the characters studied showed additivity.

Conclusions

The results establish the effectiveness of evaluating lines under simultaneous irrigation and drought. Given that the testers did not influence the lines, the general and specific combining ability are due solely to the lines.

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Table 1. Analysis of variance for testcrosses of drought tolerant lines. 1996B.

SV	df	BEC	ER	DM	GY
E	1	13.5 NS	59.8 *	0.28 **	84751277 **
R(E)	2				
T	1	6.3 NS	25.6 **	0.12 **	24419697 **
E X T	1	11.6 NS	25.4 **	0.01 NS	16769975 **
L	25	11.8 **	2.9 NS	0.04 **	2426084 NS
E X L	25	5.1 *	3.6 NS	0.02 **	3624505 NS
T X L	25	4.2 NS	1.9 NS	0.02 **	2654037 NS
E X T L	25	2.9 NS	4.0 NS	0.01 NS	2353057 NS
Error	102	3.3	3.1	0.01	2752423

A17 - Genetic Analysis of Maize Generative Organs

M. Stojakovic, J. Bocanski, G. Bekavac, Jockovic, B. Purar

Institute of Field and Vegetable Crops, 21000 Novi Sad, Yugoslavia

Introduction

Half-sib recurrent selection (HS-RS) is frequently used for population improvement. The HS-RS procedure was efficient in the selection for grain yield (Russell et al. 1973; Lamkey 1992). After five cycles of HS-RS in the populations Kolkmeier and Lancaster, their combining abilities were improved, while the grain yield was at the level of the initial population (Kolkmeier) or decreased (Lancaster) (Walejko and Russell 1977). Because pollination is critical in maize development, more attention has been paid recently to the study of pollination mechanisms (pollination and silking) under stress conditions (Herrero and Johnson 1981; Guei and Wasson 1992; Bolanos and Edmeades 1993). The objective of our study was to test the variability of the characters of generative organs of two synthetic maize populations under drought conditions. Another objective was to select the best S₁ progenies and recombine them for the next cycle of HS-RS.

Materials and Methods

The population NS 796 A/92 was formed by crossing the domestic inbred line NS 796/II (from the local population Vukovarski zuti zuban) and the inbred lines from BSSS synthetic: B73, A632, CM105, H100 and B68. Out of 218 S₂ or S₃ lines, 13 were selected after testing at three locations (Srbobran, Bajmok, Uljma) in 1991. The population NS 2040 B/92 was formed by crossing the inbred lines originating from BSSS synthetic from different periods of selection: NS1141, NS119, NS568, CM105 and NS298 (local germplasm). Fifteen of 220 S₂ or S₃ lines were selected and crossed after evaluation at three locations (Srbobran, Bajmok, Uljma) in 1991. In 1992, 300 plants per population were grown, and approximately 200 plants were selfed. The S₁ families obtained were crossed with the inbred tester Mo17-46 in 1993. In 1994 and 1995 field trials were established (with the selected HS families) according to the method of the nested design - random model (Cochran and Cox 1957) at two locations (Novi Sad and Srbobran).

Results and Discussion

The populations had similar average grain yield (7.20 t/ha and 7.31 t/ha), but NS 2040 B/92 had more barren plants than NS 796 A/92 (Table 1). Silking occurred three days after male flowering in both populations. The population NS 796 A/92 had 2% lower grain moisture than the population NS 2040 B/92, while both populations had similar number of ears per plant (0.99, i.e., 0.96).

Although the genetically divergent populations of different origin (local germplasm is dominant in the population NS 796 A/92 and American germplasm is dominant in NS 2040 B/92) were studied, there were no clear differences between them. The masking effect of dominant alleles of elite inbred tester and the interaction of dominant alleles of the population and tester may be the cause for no clear differences between examined traits. Fewer barren plants and more ears per plant in the population NS 796 A/92 than in NS 2040 B/92 indicate its better adaptability to local conditions. Additionally, NS 796 A/92 has a shorter vegetative growth period, so the critical phase of the development (pollination) is finished before the period of severe drought (July and August). To increase the frequency of favourable alleles for the traits that affect the grain yield under drought conditions (percent of barren plants, number of ears per plant, delayed silking), several cycles of HS recurrent selection should be performed in combination with the inbred progeny selection in the population NS 796 A/92. On the other hand, direct selection for grain yield would be more efficient in the population NS 2040 B/92, as it has a higher average yield and higher genetic variance for yield than NS 796 A/92.

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Table 1. Means of selected traits for two synthetic maize populations.

Population	Grain yield (t ha ⁻¹)	Barreen plants (%)	Delayed silking	Grain moisture (%)	No. of ears per plant
NS 796 A/92	7.20	5.96	3.10	25.32	0.99
NS 2040 B/92	7.31	8.83	3.02	27.53	0.96

Table 2. Variance components, heritability and coefficients of variation of HS families in the population NS 796 A/92.

Trait	V _g	SEV _g	V _p	h ² (%)	SE _{h²}	CV _g (%)	CV _p (%)
Grain yield	0.19	0.08	0.37	52.00	0.22	6.06	8.41
Barren plants	15.45	6.53	29.49	52.38	0.22	56.48	78.04
Delayed silking	0.24	0.12	0.51	46.18	0.23	15.69	23.08
Grain moisture	0.32	0.11	0.53	59.99	0.21	2.24	2.89
No. of ears per plant	0.001	0.00	0.00	58.88	0.22	1.83	2.39

Table 3. Variance components, heritability and coefficients of variation of HS families in the population NS 2040 B/92.

Trait	V _g	SEV _g	V _p	h ² (%)	SE _{h²}	CV _g (%)	CV _p (%)
Grain yield	0.63	0.19	0.92	68.68	0.21	10.90	13.15
Barren plants	19.62	7.98	36.26	54.10	0.22	50.18	68.22
Delayed silking	0.22	0.14	0.59	38.28	0.23	15.68	25.34
Grain moisture	0.96	0.34	1.58	60.52	0.21	3.55	4.57
No. of ears per plant	0.001	0.00	0.00	66.71	0.21	5.35	6.55

A18 - Changes in Quantitative Traits in Synthetic Maize Populations

J. Bocanski, D.J. Jockovic, M. Stojakovic, and G. Bekavac

Faculty of Agriculture, Trg. D. Obradovica 8, 21000 Novi Sad, Yugoslavia,
Institute of Field and Vegetable Crops, M. Gorkog 30, 21000 Novi Sad, Yugoslavia

Introduction

The main target of all plant breeding programs is the broadening of genetic variability within the source population in order to develop new superior lines which are subsequently used for the development of new varieties or hybrids. This aim is reached by using either double-cross hybrids, populations with broad or narrow genetic base, backcrosses or top-cross populations. Long-term maize breeding programs use recurrent selection to develop and exploit new genetic variability. The first synthetic maize population, Iowa Stiff Stalk Synthetic (BSSS), was developed in 1933. Synthetics were formed as raw materials that resisted lodging and had good yield potential (Sprague 1946). Sixteen lines, selected for a reduced tendency to lodge, were recombined in 1933 and 1934. Recurrent selection of half-sibs (HS-RS) was started with BSSS in 1939, using the double-cross hybrid Iowa 13 as a tester. In 1949, reciprocal recurrent selection of half-sibs (HS-RRS), an efficient method for the improvement of general and specific combining ability, was started between BSSS and Iowa Corn Borer Synthetic No. 1 (BSCB1(R) (Comstock et al. 1949). Summarizing the fifty years of recurrent selection of BSSS, Lamkey (1992) found that the synthetic's yield per se was increased by 164 kg/ha (3.9%) per cycle, i.e., by 59 kg/ha (CO-C4) and 317 kg/ha (C4-C7) per cycle. The combining ability of BSSS with the inbred Mo17 increased by 135 kg/ha (1.99%) per cycle (Helms et al. 1989). Walters et al. (1991) found that the yield of HS (Mo17) progenies increased from 6.18 t/ha to 6.92 t/ha, i.e., by 1.2%, per cycle. The objective of this investigation was to study FS and HS (Mo17) for changes in quantitative traits under selection.

Methods

Three maize synthetics were selected for study: BSSSC0, BSSSC7 and ZPSIN2C2. The latter was obtained by recombining six lines plus a balanced pollen mixture of 12 varieties from Dalmatia which resisted lodging. Reselected BSSS lines were used to develop that synthetic, four of them of the B73 type, two of the B14-B37 type. Changes in plant height, ear height, harvest index, and grain yield were measured in 100 full-sib and half-sib (Mo17) progenies. The experiment was conducted over two years at two locations and with two replicates per location. Mean values among the experiments were compared by *t* and *t'* tests, depending on whether the variances were homogeneous or not.

Results

Seven cycles of recurrent selection of half-sibs (HS-RS), for yield, with BSSS (BSSSC0), using the double cross hybrid Ia13 as a tester, brought significant reductions in plant height in the FS progenies (Table 1). Plant height was significantly increased in the HS progenies of BSSSC7, compared with BSSSC0 (Table 2). The FS and HS progenies of ZPSIN2C2 were significantly taller than the corresponding BSSSC7 progenies. Ear height was significantly reduced in the FS progenies over the seven cycles of HS-RS for grain yield. In the HS progenies, ear height was significantly increased. The FS and HS progenies of ZPSIN2C2 had a significantly greater ear height than BSSSC0. Selection increased the harvest index per se in FS progenies and in the six test crosses (HS progenies × Mo17). Harvest index of the FS and HS progenies significantly increased. The FS progenies of ZPSIN2C2 were significantly different from the corresponding progenies of BSSSC7 in harvest index, whereas HS progenies of the two populations did not differ for the trait. Grain yield significantly increased in the FS progenies and in the HS progenies with Mo17. Both FS and HS progenies of ZPSIN2C2 were significantly higher yielding than the corresponding progenies of BSSSC7.

Conclusions

BSSS populations underwent certain changes in quantitative traits during recurrent selection for grain yield. The seven cycles of HS-RS for grain yield of BSSS using IaDC13 as a tester resulted in highly significant increases in plant height and highly significant reductions in ear height. Harvest index was increased in the FS and HS (Mo17) progenies by 0.71% and 1.00% per cycle, respectively. Grain yield was increased by 0.72% and 2.40% per cycle, respectively.

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Table 1. Mean values and significance of differences in quantitative traits of the FS progenies of BSI populations.

	Plant height (cm)	Ear height (cm)	Harvest index (HI)	Grain yield (g/ per plant)
(1) BSSSC0	208.24 B10.62 [#]	93.70 B10.44	0.41 B10.003	89.03 B12.46
(2) BSSSC7	196.56 B10.57	82.98 B10.34	0.43 B10.003	93.52 B12.14
(3) ZPSIN2C2	223.99 B10.62	92.49 B10.37	0.45 B10.003	127.91 B12.84
Significance				
(1-2)	**	**	**	*
(1-3)	**	ns	**	**
(2-3)	**	**	**	**
#	Mean values of the progenies			
**	P < 0.01			
*	P < 0.05			
ns	P > 0.05			

Table 2. Mean values and significance of differences in quantitative traits of the HS progenies of BSSS populations.

	Plant height (cm)	Ear height (cm)	Harvest index (HI)	Grain yield (g/ per plant)
HS (Mo17) [#]				
(1) BSSSC0	217.21 B10.41	90.13 B10.28	0.45 B10.002	120.02 B11.20
(2) BSSSC7	231.63 B10.45	101.57 B10.26	0.48 B10.002	140.18 B11.13
(3) ZPSIN2C2	239.93 B10.49	104.45 B10.30	0.48 B10.002	156.00 B11.25
Significance				
(1-2)	**	**	**	**
(1-3)	**	**	**	**
(2-3)	**	**	ns	**
#	Mean values of the progenies, HS (Mo17).			
**	P < 0.01			
*	P < 0.05			
ns	P > 0.05			

A19 - RFLP Heterozygosity and Hybrid Performance in Australian Sorghum

D.R. Jordan^{1,2}, Y.Z. Tao², I.D. Godwin¹, R.G. Henzell³, M. Cooper¹, and C.L. McIntyre²

1 Department of Agriculture, The University of Queensland, Brisbane, Qld. 4072.

2 CSIRO Tropical Agriculture, St Lucia Qld 4067.

3 Department of Primary Industries, Hermitage Research Station, Warwick Qld 4370.

Introduction

Numerous studies have been carried out to assess the potential of using RFLP markers to predict heterosis in hybrid maize (Bernardo 1992, Bernardo 1994, Goldshalk et al. 1990, Lee et al. 1989, Melchinger et al. 1990 and Smith et al. 1990). The results of the maize studies have been variable, with correlations between marker diversity and performance varying considerably, depending on the type of material used in the experiment. In general, parental diversity as measured by molecular markers showed higher correlations with performance when the parents were related, as opposed to crosses between unrelated parents (e.g., crosses within heterotic groups of maize as opposed to crosses between lines from different heterotic groups). Sorghum is closely related to maize, however there is little published work on the use of molecular markers to predict performance of hybrid sorghum. Heterotic groups in sorghum are not as formal as those of maize. In addition, genetic diversity in Australian sorghum lines appears to be relatively narrow (Jordan et al 1996), suggesting that RFLP markers may be of value in predicting performance. This abstract reports on work in progress to determine the feasibility of using molecular markers to predict hybrid performance in sorghum. In addition the use of heterozygosity based on individual linkage groups is compared with whole genome genetic diversity as a predictor of grain yield in sorghum hybrids.

Materials and Methods

DNA was extracted from 29 female and 30 male lines developed in the Queensland Department of Primary Industries (QDPI) sorghum breeding program. The 59 parent lines were screened with 44 RFLP markers distributed over 6 out of 10 major linkage groups identified by Tao et al. (manuscript in preparation) in a cross between two Australian sorghum lines. The size of each linkage group in centi-Morgans is shown in Table 1. Work is continuing to screen the parents with markers on the remaining four linkage groups. Average RFLP heterozygosity was calculated for each hybrid for the six linkage groups combined and for each linkage group individually. In addition, linkage group 1 was divided into two parts (1A and 1B) at a conveniently large gap in the map and heterozygosity calculated separately for each part. Best linear unbiased estimates (BLUEs) were made of the grain yield performance of 98 hybrids based on the 59 parent lines. The BLUEs of hybrid performance were calculated using trial data from 44 environments which formed part of normal hybrid testing in the QDPI breeding program. Simple linear regressions and correlation analyses were carried out between the BLUEs and the heterozygosity estimates. Heterozygosity estimates for individual linkage groups with significant r^2 values (LG 1,2,4 and 6 see table 1) were then used as independent variables in a multiple regression.

Results

Significant positive relationships were detected between marker heterozygosity and hybrid yield (Table 1). The r^2 value calculated for the regression of yield against average heterozygosity of all the marker information is highly statistically significant, but only accounts for a relatively small proportion of the variation in yield ($r^2=0.23$). Heterozygosity showed a significant positive association with variation in yield in four of the six linkage groups observed (LG1, LG2, LG4 and LG6). The r^2 values for these linkage groups varied from 0.08 to 0.12. Heterozygosity was not associated with yield in LG3 and LG5. The multiple regression based on information only from the four linkage groups which showed significant relationships with yield produced an r^2 value of 0.30 compared with 0.23 obtained using average heterozygosity. LG1A and LG1B varied considerably in their association with yield. LG1A

showed a significant relationship with yield ($r^2=0.12$) while the heterozygosity of group LG1B was not correlated with hybrid yield.

Discussion

Average heterozygosity using all the marker information can be used to predict a significant but relatively small amount of the variation in hybrid performance. The amount of variation explained may increase when the parent lines are screened with RFLP markers located on the remaining four major linkage groups. In addition, the inbred parent lines used in this study are known to vary considerably in grain yield on a line basis. Unfortunately parental performance data is not available to allow the calculation of heterosis. It is conceivable that RFLP marker heterozygosity would explain considerably more of the variation in heterosis than hybrid yield *per se*. The relatively low r^2 values obtained in this study, are broadly comparable with those obtained in most of the maize studies. This study demonstrates that in sorghum the magnitude of the relationship between RFLP heterozygosity and performance varies between linkage groups. As in maize, this variation is probably due to differences in the location of genes which contribute to heterotic effects. By locating the relatively important regions associated with heterotic effects, it should be possible to more efficiently predict performance in untested crosses than is currently possible without this information.

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Table 1. Regression and correlation analysis of the relationship between marker heterozygosity and yield in sorghum hybrids

Linkage Group	Number of RFLP loci	Group size cM	r	r ²
Combined	44	1270	0.48	0.23 ***
LG1	16	186	0.35	0.13 ***
LG2	7	301	0.28	0.08 **
LG3	9	230	0.04	0.00
LG4	7	210	0.28	0.08 **
LG5	6	202	0.16	0.03
LG6	6	141	0.28	0.08 ***
1A	9	63	0.35	0.12 ***
1B	7	123	-0.05	0.00
LG1, 2, 4 and 6	36	838		0.30 ***

** and *** = r^2 significant at $p<0.01$ and $p<0.001$, respectively.

Genetic Diversity and Heterosis

A.E. Melchinger

Institute of Plant Breeding, Seed Science, and Population Genetics, University of Hohenheim, D- 70593 Stuttgart, Germany

This review deals with the fundamental role of genetic diversity and heterosis in different breeding categories and crops. It starts with an overview of approaches to assess the genetic diversity in germplasm of interest to breeders (cultivars, breeding populations, gene bank accessions etc.). Special attention is given to compare the usefulness of various types of molecular markers, such as RFLPs, AFLPs, and microsatellites (SSRs) for this purpose. By using examples from different crops, it is demonstrated that genetic distances based on these types of molecular markers can be used for (1) revealing genetic relationships among different germplasm, (2) assigning germplasm to groups and subgroups of similar materials, and (3) detecting pedigree relatedness between germplasm.

Theoretical and experimental results are presented on the relationship between the genetic distance of parent lines or populations and the heterosis and heterotic increase, respectively, in their crosses. Accordingly, heterosis increases with genetic distance among the parents up to a certain optimum level of divergence and decreases thereafter. An important aspect in this context is the adaptation of the parents to the target environments.

With regard to the optimum exploitation of heterosis in three breeding categories (hybrids, synthetics, and clone cultivars) theoretical arguments and experimental data are presented in support of the concept of heterotic groups and patterns. It is shown that groupings of germplasm based on molecular marker information can provide the basis for establishing new heterotic groups or broadening the genetic base of existing ones. However, this must be supplemented by evaluating the performance of crosses among these subgroups to assess their heterotic response, which is essential for identifying promising heterotic patterns.

Finally, the prospects for predicting the heterosis in single-cross hybrids by molecular data from their parents is examined. Experimental results from maize and rice show that genetic distance estimates of inbreds, based on molecular markers covering the entire genome, are closely correlated with hybrid performance and heterosis of their crosses for (a) related lines and (b) unrelated lines from the same heterotic group. However, they are not indicative of hybrid performance for crosses between lines from genetically divergent heterotic groups. It is shown that these results are in agreement with quantitative-genetic expectations.

Effect of Hybrid Breeding on Genetic Diversity in Maize

J.S.C. Smith

Pioneer HiBred International, Inc.

The availability of a broad array of useful genetic diversity is a prerequisite to achieve sustainable increases in agricultural productivity. Genetic diversity provides the potential for adaptation to meet different maturity zones, husbandry types, agroecologies, consumer and industrial demands, shifting climate, and constantly evolving pests and diseases. Farmers and consumers in the United States are blessed with the ready availability of a relatively broad base of adapted and highly productive maize diversity due to the indigenous origins of the Corn Belt Dent race from two genetically divergent parental races (the Northern Flints and the Southern Dents) with subsequent selection for adaptation over many decades.

The biology of a crop determines the application of appropriate technologies to its improvement, farming, and utilization. Nowhere is this more true than for heterosis. Heterosis is possibly the most influential attribute in all aspects of maize agriculture, affecting breeding strategies, the availability of intellectual property protection, the consequent balance of private and public sector funding for conservation, research and product development, and the extent of genetic diversity arrayed in agriculture and available over time from conserved stocks through prebreeding and product development programs. Genetic diversity can be measured by several means, including heterosis, pedigree data, and molecular methodologies. Data will be presented to show the level of genetic diversity in US maize agriculture as measured by pedigree and by isozymes; comparisons will be made to other crops. The characteristics and limitations of assessing useful genetic diversity by various methods will be outlined.

The extent and arrangement of genetic diversity in elite maize germplasm that is used in the US is broader and more complex than is traditionally recognized. Germplasm can be classified into ten heterotic groups, some of which encompass considerable diversity. Evolution continues through pyramiding of diversity among these groups. Nonetheless, there is a long-term need to introduce new useful diversity into this germplasm base and the hybrid nature of the crop determines strategies for these activities. Sources of genetic diversity for the future include both preexisting and *de novo* variation in elite and exotic germplasm. Technical abilities to utilize this germplasm will depend on access to germplasm; evaluation information (including data from molecular tools and DNA sequence data linked to biochemistry and physiological information); prebreeding or genetic enrichment programs to adapt, further evaluate and identify potentially useful germplasm; and molecular assisted or transformation technologies to more effectively select and integrate useful new germplasm into elite cultivars. Opportunities to utilize these technologies and breeder skills will depend on the continued availability of new knowledge, finances, and markets. Researchers, conservators, breeders, and farmers must remain at the forefront in melding biology and technology into the biotechnology of agriculture by making the most productive and sustainable use of genetic resource diversity so that the growing food and industrial demands of consumers can be met in an environmentally harmonious way.

Population Genetics of Increased Hybrid Performance Between Two Maize Populations Under Reciprocal Recurrent Selection

J.A. Labate, K.R. Lamkey, M. Lee and W.L. Woodman

USDA-ARS and Department of Agronomy, Iowa State University, Ames, Iowa 50011 USA

Introduction

Reciprocal recurrent selection (RRS) was originally proposed as a method to improve the performance of the interpopulation cross of two genetically divergent populations (Comstock et al. 1949). It allows gradual increases in the frequency of favorable alleles within genetically broad-based populations and genetic recombination within them, while minimizing inbreeding. Two maize populations, Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic #1 (BSCB1), are currently in their 14th cycle of RRS in the Cooperative Federal-State maize breeding program at Iowa State University. Increased grain yield of the interpopulation cross has been the primary target of selection, with reduced grain moisture at harvest and increased resistance to root and stalk lodging as secondarily selected traits. Selection has been highly successful; mean grain yield of the interpopulation cross improved 77% by cycle 11, relative to cycle 0, with concurrent favorable responses in the other traits (Keeratinijakal and Lamkey 1993).

Materials and Methods

We examined allele frequencies from three populations within BSSS(R) and BSCB1(R) representing three different stages in their selective history: Progenitors (P) (collections of inbred lines which were intermated to form the starting material), Cycle 0 (C_0) (representing populations before selection) and Cycle 12 (C_{12}) (representing populations after 12 cycles of RRS). Leaf samples were collected from 100 plants from each C_0 and C_{12} population, as well as single plants from all available inbred progenitor lines (16 and 12 lines representing BSSS and BSCB1, respectively). DNA was isolated and all 428 individuals were genotyped at 82 restriction fragment length polymorphism (RFLP) loci randomly distributed throughout the nuclear genome (Labate et al. 1997).

Results and Discussion

Frequencies of alleles within populations can be altered by mutation, migration, selection, and genetic drift. By comparing allele frequencies in P, C_0 , and C_{12} , it was found that mutation and migration exerted minimal effects at the 82 loci. The focus of the study has subsequently been on separating the effects of directional selection and genetic drift within BSSS(R) and BSCB1(R), and the nature of genetic divergence between them.

The BSSS and BSCB1 progenitor populations were initially genetically similar (NeiUs genetic distance = 0.07). After 12 cycles of selection, they had substantially diverged (NeiUs genetic distance = 0.66). Gene diversity (probability of heterozygosity under random mating) across populations was very broad for progenitors (mean gene diversity = 60%) and remained at that level to C_{12} . Within both populations gene diversity decreased from about 60% to 30% between progenitors and C_{12} , and mean allele frequency rose from approximately 29% to 45%.

A statistical test (Waples 1989) was applied to each locus to determine if any observed changes in allele frequency between C_0 and C_{12} within populations were greater than expected from drift alone. Assuming that each cycle of selection was equivalent to a single generation and that effective population size equaled the harmonic mean of the number of selected lines per cycle, the null hypothesis of drift in BSSS(R) and BSCB1(R) was rejected for 11 and 17 loci, respectively. These loci were not limited to particular chromosomes or regions but seemed to be spread rather evenly throughout the genome. They fit a pattern of fixation of complementary alleles between the two populations, because none of the loci was shared except one, and at this locus a different allele was approaching fixation in BSSS(R) and BSCB1(R). Approximately half of the non-neutral alleles in one population were present in low

frequencies (less than 0.10) in the other population at C_0 and remained low at C_{12} . We estimated mean expected heterozygosity of interpopulation crosses and found no significant difference between $BSSS(R)C_0 \times BSCB1(R)C_0$ and $BSSS(R)C_{12} \times BSCB1(R)C_{12}$ for all 82 loci. However, the 27 non-neutral loci increased in mean expected heterozygosity for the interpopulation cross between C_0 and C_{12} , whereas the 55 neutral loci did not. This implies that an intralocus mechanism could be responsible to some extent for increasing interpopulation hybrid performance. These results must be interpreted with caution because we assume that we are identifying hitchhiking loci rather than the selected loci per se.

The results from the molecular analyses correspond well with interpretations made of phenotypic data on grain yield in $BSSS(R)$ and $BSCB1(R)$ populations (Keeratinijakal and Lamkey 1993). Inbreeding depression of the interpopulation cross, as measured by selfing their F_1 , has increased with cycles of selection. Inbreeding depression for grain yield within the interpopulation cross depends on the number of segregating loci, levels of directional dominance, and allele frequencies at the loci affecting yield. The magnitude of inbreeding depression created by a particular locus depends on allelic frequencies, and is maximized at 0.5. An increase in inbreeding depression will be observed if complementary alleles at loci in each population are approaching fixation; this also results in an increase in heterozygosity of the interpopulation cross.

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Broadening the Genetic Diversity in Breeding by Use of Exotic Germplasm

M. M. Goodman

Department of Crop Science, North Carolina State University, Box 7620, Raleigh, NC 27695-7620, USA

Use of exotic germplasm in U.S. maize hybrids has increased almost 3-fold during the past twelve years, with total exotic-germplasm use increasing from about 1% in 1984 (Goodman, 1995) to almost 3% in 1996 (Table I). Use of tropical exotic germplasm in deployed U.S. hybrids is much smaller (about 0.1% in 1984; about 0.3% in 1996). Most widely-sold U.S. hybrids that contain exotic germplasm have small percentages (2 to 6% is typical) of temperate, exotic germplasm from the insect-resistant, Argentine cultivar, Maíz Amargo (mostly via B68), while a few have higher percentages of temperate, exotic germplasm, typically 12 to 25%, from the related French lines F2 or F7. U.S. hybrids containing tropical germplasm show the same pattern: widely sold hybrids with tropical maize germplasm usually contain from 1 to 5% tropical germplasm, but a few less-popular hybrids contain 25 to 50% tropical germplasm.

Maize breeding throughout the temperate parts of the world is rapidly becoming well-integrated, with phytosanitary restrictions and intellectual property rights almost the only barriers to germplasm, line, and hybrid exchange between organizations. Thus, the focus of this paper is the use of tropical germplasm in temperate areas. Five questions are considered:

1. What types of germplasm sources are most promising?
2. How can choices be made among the many possibilities within a specific type?
3. How difficult is the problem of photoperiod response?
4. Can tropical germplasm lead to yield improvement, in addition to its current role as a last-resort source of disease- and insect-resistance?
5. How can field-based selection be conducted so as to maximize any positive yield-potential available within a specific, variable, exotic accession or hybrid?

Evidence suggests that elite tropical germplasm with a proven record of inbreeding carries a better than 50-fold advantage over elite material that has had no inbreeding (Goodman, 1992). Since yield- (and most disease-) trials grown in higher latitudes cannot be reliable for topcrosses containing more than 50% tropical germplasm, choices must be made on the basis of performance under short days. Photoperiod response is mostly a cosmetic problem; it can be eliminated even from descendants of 100% tropical crosses, and is mostly an inconvenience to the uninitiated who try to grow tropical materials for crossing in summer, rather than short-day, winter nurseries. Yield-trial data (Tables 2 and 3 for example) demonstrate that at least a few 100%-tropical inbreds can be crossed with domestic materials to make hybrids that are competitive with the best available commercial hybrids. While early selection within a variable exotic source is not essential for the development of partly-exotic inbreds, variance component distributions among and within lines under development certainly suggest that early selection (within the variable F₁) is necessary if the exotic source is variable and only a small portion of the variation is desirable.

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Table 1. Use of exotic germplasm in U.S. hybrids in 1996.

Area	Average % exotic germplasm	Area	Average % exotic germplasm
Argentina	1.99		
Australia	0.03	Caribbean	0.23
Europe	0.46	Mexico	0.07
South Africa	0.08		
Temperate total	2.56	Tropical total	0.3

Table 2. Highest yielding NC line topcrosses, Clayton, Lewiston, and Plymouth, NC, USA, 1991-1994.

Pedigree	Yield (t/ha)	% H ₂ O	% EP	Ear height	Days to tassel	
NC258 X LH132	8.7	18.9	95	96	74	<i>Lines</i>
NC268 X LH150	9.3	16.6	95	116	76	<i>less</i>
NC280 X LH150	8.6	17	95	116	75	<i>than</i>
NC292 x LH150	8.7	16.7	98	117	74	<i>10%</i>
NC296 X LH132	9.6	17.1	96	107	75	<i>Lines</i>
NC298 X LH132	8.6	18	96	106	76	<i>100%</i>
NC300 X LH132	8.4	18.1	97	100	75	<i>exotic</i>
Mo17Ht x B73Ht	7.6	15.2	94	104	72	
Pioneer 3165	8.8	19	94	109	77	<i>Checks</i>
DEKALB 689	8.9	17.1	97	111	76	
LSD. 05 (ENT. xENV.)	0.14	0.4	4	4	1	
C.V. % (ENT. xENV.)	6	3	5	5	1	

¹ NC lines of largely Lancaster (NC258), B73 (NC268, NC280, NC292, NC294) Or tropical (NC296, NC298, NC300) origin were crossed to Holden tester lines (LH132 is a stiff- Stalk line; LH150 is a non-Stiff-Stalk line). The subset of lines shown here was a part of a larger experiment encompassing virtually all NC lines from NC250A through NC300 crossed to either LH132 or LH150 (both of which are all-temperate), as appropriate. 2% EP = percent erect plants at harvest.

Table 3. NC296A topcrosses vs. commercial hybrids, Clayton, Lewiston (not 1993), 1992-1994.

	Commercial hybrid					NC296A cross				
	Yield (t/ha)	% H ₂ O	% EP	So rust	GLS	Yield (t/ha)	% H ₂ O	% Ep	So rust	GLS
B73HtxMo17Ht	7.5	16.1	92	4	3	9.5	18	83	9	6.9
DEKALB 689	8.8	18.0	91	4	4.9	8.2	19.3	82	9	7.3
LH132 X LH82	7.1	16.8	97	5	5.1	9.1	18	89	9	6.7
NK N8727	9.1	18.7	95	2.5	4	9.8	19.8	90	9	6.4
Pioneer 3140	8.8	18.0	97	7.5	4.7	8.4	19.8	89	9	6.7
Pioneer 3162	8.8	18.8	97	4	3.3	9.2	20	89	9	6.7
Pioneer 3165	8.9	19.8	89	4	5.5	9.1	20.8	83	9	6.5
Pioneer 3379	7.8	15.8	97	4	3.5	9.2	18	89	9	6.8
Pioneer 3394	8.6	16.4	98	4.5	2.7	9.7	17.8	90	9	6.9
AVERAGE	8.2	17.5	95	4.4	3.9	9.2	19.1	87	9	6.8
LSD. 05 (EntxEnv)	0.7	0.7	8	1.5	1.5	0.7	0.7	8	1.5	0.7
C.V. % (EntxEnv)	8	4	9	10	10	8	4	9	10	8

NC26A is a temperate- adapted line that was derived from a cross of two tropical hybrids, Pioneer X105A from Jamaica and H5 from the Rockefeller program in Central America % EP = percent erect plants at harvest. Southern rust and gray leaf spot both rated only in 1992 at one and two locations each, respectively, both scored on a 9 = no disease 1= dead.

Mechanisms Contributing to Genetic Diversity in Maize Populations

P.A. Peterson

Departments of Agronomy and Zoology/Genetics, Iowa State University, Ames, Iowa 50011-1010, USA

Introduction

The maize plant has been manipulated by plant breeders for many centuries. The improvement in the past four decades has been most remarkable. This has been aided by the abundant polymorphism in maize as highly heterogeneous genotypes have been found in surveyed populations (Goodman and Stuber 1983a,b). This heterogeneity can be manipulated in most directions to achieve the desirable goal (Hallauer 1992). When one surveys the particular populations that have been the source of successful inbreds and, for example, the BSSS populations, one is impressed by the striking improvement in that population and a question arises as to the source of this improvement.

Certainly the accumulation and concentration of favorable alleles has most contributed to the genetic gain. The corn breeder recombines and resorts the abundant polymorphism and provides the selection protocols to augment the successful improvement in the population. However the source of these favorable alleles and the recombinant combinations has been a question in breeders' minds. Are the alleles newly generated as new variability (Peterson 1986a,b) or is this simply a re-establishment of alleles in a more favorable combination for the breeders' needs. The proposal presented here is that they are newly originated alleles that are favorably recombined with the previous established elite combinations. Thus, this report presents the contention that it is a combination of the recombination and newly originated alleles that produces this improvement, and the source of these newly established alleles will be presented.

Transposon Contribution

Transposable elements have been a major study in maize genetics for a half a century (McClintock 1948; Peterson review 1994). In the premolecular era, several systems of transposons were established which generally include two components, a functional and deficient element and the accompanying differences seen in mutable patterns. With the advent of molecular biology, many features of transposon genetics were clarified, including the molecular structure size (up to 17 kb), terminal inverted repeats (TIR), target size duplications (TSD) (Fedoroff et al. 1983; Pereira et al. 1985), and gene nucleotide alterations accompanying the excision of elements from a gene (Sachs et al. 1983), leading to a consequent change in gene products (Schwarz-Sommer et al. 1985; Wessler et al. 1986; Franken et al. 1994). More significantly, the transposon activity at gene loci was found to lead to altered nucleotide gene sequences and this has generated a discussion on the role of transposons as a force in evolution (Schwarz-Sommer et al. 1985), and the discovery of functional transposons in numerous corn populations (Friedemann and Peterson 1982; Peterson and Friedemann 1983; Peterson and Salamini 1986; Peterson 1986a; Cormack et al. 1988; Lamkey et al. 1991; Seo and Peterson 1995) has accentuated the possible role of transposon induced changes in these corn populations. The varied inserts in most genes examined in several plant species (Okagaki and Wessler 1988; Wessler 1986) have piqued the interest of investigators in the role of transposons in native populations. Despite all these indirect indications of transposons inducing variability, there is still insufficient evidence to take a firm position on their possible role. Equally important when one considers that, in maize population improvement, there is the problem of the source of the infinite variability in these populations. For example, the BSSS(C0) and BSSS(R) populations have been "closed" since their original development (Sprague 1946); the genomic content in populations has not had introductions of additional germplasm and all the selections arise from within the population (Lamkey 1992; Lamkey et al. 1991).

Intragenic Recombination Contributing to Diversity

Intragenic recombination has been known in maize. One of the first cases uncovered was that of the A1 locus line with unequal recombination occurring between alleles obtained from widely diverse locations

(Laughnan 1952). This recombination, though, occurs by *homologous pairing* and leads to a redistribution of the components of the *A1* locus and not an alteration in nucleotide sequences. This also contributes to our knowledge about the evolution of different alleles. A more significant and more thoroughly explored allelic diversity is at the *R1* locus. Here the very complicated arrangements of alleles has been examined and the changes ascribed to a transposon origin (Eggelston et al. 1995; Walker et al. 1995). However both the *A1* and the *R* can be determined to be from homologous recombination. The other type of intragenic recombination is nonhomologous and occurs at a much lower frequency, leading to altered sequences and new proteins. This intragenic exchange has been studied at several loci in maize (Brown and Sundaresan 1991; Dooner and Kermicle 1996; Dooner and Ralston 1990; Freeling 1976; Xu et al. 1995) and in other species (Dorer and Christensen 1989). These exchanges generally had a selection scheme to wild type and the rearrangement of nucleotides leading to new proteins is not apparent. What is proven is the intragenic events following transposon excisions at loci (Giroux et al. 1996; Sommer et al. 1988) and the new proteins arising from their excisions (Franken et al. 1994).

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A20 - Extent of Inter-racial Heterosis in Short Duration Maize Hybrids

K. Zada, M. Saleem and A.T. Salam

Department of Agronomy & PBG, Plant Science Building, NWFP Agricultural University, Peshawar 25120, Pakistan

Introduction

Combining ability and interracial heterosis are important in determining grain yield in maize hybrids, where Sprague (1955) defined the concept in two expressions, general combining ability (GCA) and specific combining ability (SCA). GCA and SCA have had a significant effect on inbred line evaluation and population improvement in maize breeding. Traits such as early maturity, lower ear placement on stalk, shorter plants, disease resistance affect acceptance of the varieties on small farms in Pakistan. The reduction in yield associated with earlier maturity, lower ear and plant heights, as well as the need for greater disease and insect resistance have been identified as challenges associated with the development of such materials. Hull (1945) proposed recurrent selection for specific combining ability in maize as a practical and efficient, method of improving grain yield and other traits. Specific combining ability should be emphasized from the beginning because of the dominance involved in heterosis for grain yield

Methods

Research was conducted at the Malakandher Research Farm, Northwest Frontier Province (NWFP) Agricultural University, Peshawar, during 1994-1995 to determine the GCA and SCA of locally developed inbred lines in hybrid combinations as well as to identify good combiners for commercial hybrid production. During the first season, 15 locally developed, early maturing inbred lines were crossed in all possible combinations, while in the second season, the 47 best crosses, including two improved checks, Kissan and Quaid, were tested in 7x7 simple lattice design. The plot size was 15 m².

Results

Statistically significant differences existed for the important agronomic traits studied. The highest mean yield of 6,213 kg/ha was observed for the single cross hybrid PS 170 x PS 182 (temperate x subtropical) and was 58% and 50% higher yielder than the two improved checks, Kissan and Quaid. This cross exhibited the highest heterosis for grain yield. The lowest mean yield of 1,574 kg/ha was obtained from the cross PS 941 x PS 492. The parents in this hybrid were sister lines and naturally showed practically no heterosis. The crosses PS 101 x PS 305, PS 211 x PS 101 and PS 492, x PS 181 showed good performance over checks for key agronomic traits.

Conclusions

Hybrids PS 170 x PS 181 and PS 101 x PS 181 demonstrated a high level of heterosis and were good general combiners; they should be studied for possible use in the production of commercial hybrids.

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Table 1. Yield of maize hybrids during kharif, 1994, at Malakandher farm, NWFP Agricultural University, Peshawar.

S. No.	Entry No.	Name of Hybrid					Grain yield kg/ha	S. No.	Entry No.	Name of hybrid					Grain yield kg/ha
1	17	PS	170	X	PS	181	6213	26	29	PS	239	X	PS	252	3835
2	18	PS	101	X	PS	181	6175	27	37	PS	301	X	PS	252	3790
3	24	PS	211	X	PS	181	5581	28	42	PS	492	X	PS	82	3715
4	23	PS	211	X	PS	305	5366	29	38	PS	305	X	PS	239	3715
5	21	PS	211	X	PS	252	5086	30	1	PS	23	X	PS	252	3673
6	132	PS	242	X	PS	181	5044	31	33	PS	252	X	PS	101	3503
7	25	PS	211	X	PS	82	5037	32	41	PS	491	X	PS	101	3319
8	9	PS	101	X	PS	82	4975	33	31	PS	252	X	PS	491	3308
9	11	PS	101	X	PS	305	4779	34	36	PS	301	X	PS	181	3226
10	8	PS	82	X	PS	301	4758	35	44	PS	492	X	PS	301	3163
11	15	PS	170	X	PS	492	4681	36	3	PS	23	X	PS	239	3156
12	18	PS	181	X	PS	731	4645	37	28	PS	239	X	PS	82	3099
13	19	PS	305	X	PS	161	4581	38	26	PS	239	X	PS	491	3045
14	24	PS	301	X	PS	16	4542	39	7	PS	23	X	PS	170	3037
15	22	PS	211	X	PS	101	4373	40	6	PS	23	X	PS	491	2884
16	2	PS	23	X	PS	492	435	41	45	PS	492	X	PS	101	2847
17	14	PS	170	X	PS	252	4327	42	12	PS	82	X	PS	491	2792
18	35	PS	301	X	PS	82	4399	43	19	PS	181	X	PS	491	2739
19	5	PS	23	X	PS	305	4290	44	49				Quald		2683
20	30	PS	252	X	PS	492	4285	45	27	PS	239	X	PS	301	2542
21	4	PS	23	X	PS	181	4162	46	18				Kissan		2424
22	20	PS	181	X	PS	239	4077	47	43	PS	492	X	PS	181	2113
23	13	PS	101	X	PS	301	4014	48	47	PS	731	X	PS	491	2050
24	14	PS	170	X	PS	82	3897	49	40	PS	491	X	PS	492	1574
25	46	PS	492	X	PS	305	3858								

A21 - Increasing Female Sterility and Heterosis in Maize

V. Micu and E. Partas

Maize and Sorghum Research Institute, Pascani, Criuleni, Republic of Moldova

In long-term research among collections of maize varieties and lines mutants were identified which cause various types of male, female and full sterility. Female sterility in maize is represented by five distinct morphological types and genetic mechanisms: 1) defective pistils (gene *dep*); 2) branched silkless ears (gene *bd*); 3) silkless ears; 4) absence of ears (genes *ba1- ba4*); and 5) development of fertile tassels instead of ears (gene *tb*) (Table 1). The recessive homozygous plants for genes determining female sterility (*dep*, *sk*, *bd*, *ba*, *tb*) do not differ significantly from normal plants in other traits.

In our materials we observed the absence of ears (*ba*) in 64 sources, the absence of pistils (*sk*) in 13 sources, and *bd* in 4 sources. The most interesting type of female sterility, teosinte branched with ears transformed into male fertile tassels was observed in only one source. Lateral tassels of recessive homozygous plants (*tb*) flower later than apical tassels and shed an abundant supply of pollen. These plants can be used as male parents in seed production.

To study the influence of heterosis and the possibilities of using *ba*, *sk*, and *tb* plants as a male in seed production, segregating versions of some elite lines (norm:*ba*, norm:*sk*, norm:*tb*) were developed. Using the normal and mutant plants as males, two versions of hybrids were obtained: dominant homozygous and heterozygous (for respective genes of female sterility), both phenotypically normal. These hybrids were evaluated for most important economical and biological characters, and some essential differences were revealed (Table 2). Thus, it is clear that heterozygosity for *Sk sk* affects economic characters of hybrids negatively, decreasing yield. But heterozygosity for *Ba ba* and *Tb tb* genes increases heterosis and grain yield in some hybrids (Table 2). Some segregating (norm:*tb*) analogues were used as a male in seed production. They increased seed yield as a result of the long duration of flowering of lateral male tassels. A program for breeding *tb Rf* lines has been developed, making it possible to 1) increase seed production, 2) avoid detasseling, and 3) use heterosis more efficiently.

The high frequency of different forms and types of female sterility in the natural population of maize, as well as the diversity of morphological types and genetic mechanisms conditioning them, prove the evolutionary significance of this phenomenon as a mechanism that provides heterozygosity and polymorphism in populations.

Female sterility in maize is insufficiently studied, especially the interaction of genetic mechanisms and exogenic factors in determining different types of sterility as well as the possibilities of their practical utilization.

Table 1. Genes and sources of female sterility in maize.

Phenotypes	Genes	Number of sources	
		revealed	identified
Defective pistils	<i>dep</i>	5	5
Branched silkles ears	<i>bd</i>	4	4
Silkless ears	<i>sk</i>	13	13
Absence of ears	<i>ba1-ba4</i>	64	12
Development of lateral tassels instead ears	<i>tb</i>	3	3
Total	8	89	37

Table 2. Grain yield of homozygous and heterozygous variants of maize hybrids.

Average grain yield (t/ha)					
Genes	Number of hybrids studied	Homozygous	Heterozygous	Heterozygous as % of homozygous	LSD $p < 0.05$
<i>sk</i>	22	5.27	5.08	96.4	2.47
<i>ba</i>	87	4.76	4.85	101.9	1.70
<i>tb</i>	80	6.52	6.70	102.8	2.60

A22 - Germplasm Enhancement in Hybrid Maize Breeding by Use of Tropical and Subtropical Germplasm

Zhang Shi-huang and Shi De-quan

Institute of Crop Breeding and Cultivation, Chinese Academy of Agricultural Sciences (CAAS), Beijing, 100081, P.R. China

Introduction

The first limiting factor to maize breeding activities in China is the lack of superior germplasm; the genetic background of hybrids is growing narrower in China. Only six dominant hybrids covered 57.5% of the total maize acreage in 1991. More than 65% of the total maize area is sown heavily to germplasm based on six dominant lines. Tropical and subtropical maize germplasm has been introduced and utilized to broaden the genetic base of temperate maize hybrids, prevent genetic vulnerability, and enhance heterosis. However, most of the exotics are not adapted to the long days in north China. Improvement should be done to adapt exotics to long-day conditions in temperate areas. Mass selection has usually been used for this purpose.

Methods

Pools 33 and 34 QPM (a high-lysine or "quality protein" maize) from CIMMYT were improved using bi-parental mass selection in Beijing since 1985. The improved populations were named C. Pop 13 and C. Pop 14, respectively. A five-location experiment was carried out to evaluate the effectiveness of selection on adaptation and yield performance of exotics in 1991.

Results

Four cycles of bi-parental mass selection reduced days to silking by 18 days compared with the same trait for C₀, but days to pollen shed were reduced by only 9 days under long-day conditions. This gap resulted in reduced PSSI. The adaptability of maize genotypes is associated with photoperiod sensitivity, which was calculated by the relative deviation (RD) of leaf numbers on main stem under long-day (L) and short-day (S) conditions:

$$RD(\%) = [(L-S)/S] * 100 \quad (1)$$

RD diminished from 30% in C₀ to 23.% in C. Pop 13-C₄ and from 31% to 18% in C.Pop 14. That means the photoperiod sensitivity in both populations has been reduced and their adaptation to the long-day conditions improved.

Four cycles of selection for early silking increased grain yield significantly in both populations, with average gains of 25-28% per cycle evaluated in temperate long-days, but decreased grain yield by 3.6-1.4% in short-days (Fig. 1). This suggests that most of the yield increases should be due to the genetic improvement of the populations for adaptation to long-day conditions. The increased yields as a correlated response resulted from three components; ear number per plant, grain weight per ear, and harvest index.

Conclusions

Bi-parental mass selection is effective in improving the adaptability of tropical and subtropical maize germplasm to long-day conditions in temperate areas. The improved exotic populations exhibit lower photoperiod sensitivity. Most of the yield gains appear to be due to the genetic improvement for photoperiod insensitivity. We are planning a new project to introduce 8-10 more tropical and subtropical populations from CIMMYT and improve and utilize them in hybrid maize breeding programs in China. A dozen provincial institutions are interested in participating in this activity. Two approaches will be adopted to improve and utilize exotics in this project. Bi-parental mass selection will be used as

the common method of population improvement for adaptation. We will also cross exotics with germplasm with temperate adaptation, and then select inbred lines from the semi-exotics after 2-3 cycles of bulk pollination and selection. We hope this project will broaden the genetic base of hybrid maize breeding programs in China.

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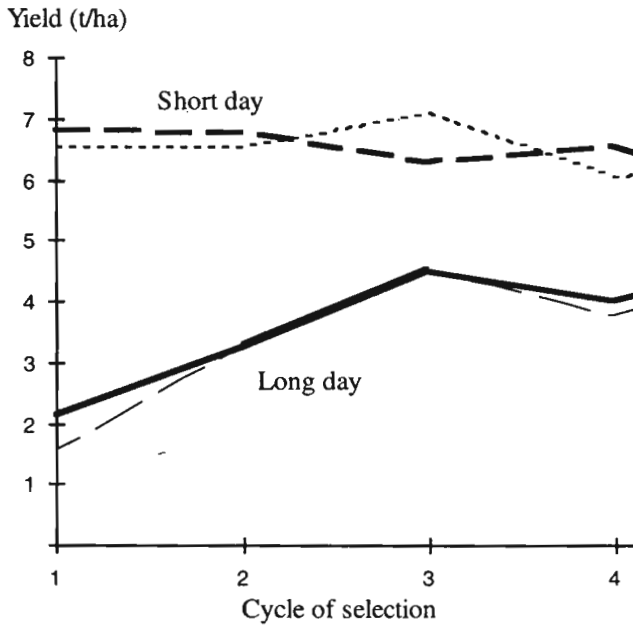


Figure 1. Results of four cycles of bi-parental selection in exotic maize germplasm for adaptation to long daylengths in China.

A23 - Use of RAPD Markers to Identify Divergent Heterotic Groups and Improve the Heterosis of Hybrid Wheat

Qixin Sun, Zhongfu Ni, Zhiyong Liu, Jianwei Gao, and Tiecheng Huang

Department of Plant Genetics and Breeding, Beijing Agricultural University, Beijing 100094, P.R. China

Introduction

Hybrid wheat has the potential to provide not only increased yields but increased stability across a range of environments. To date, though, the level of heterosis is still a major limiting factor for the commercial use of hybrid wheat. On average only 8 to 10% heterosis over mid-parent is observed in F_1 hybrids, while the parental combination with over 20% heterosis is rare among the current germplasm pool. This could be related to the relative high degree of genetic similarity among the parental lines (Sun et al. 1996). Therefore, it is necessary to identify divergent heterotic groups to improve the level of heterosis. Although morphological characters, pedigree information, and biochemical markers have been used to characterize wheat genetic diversity, molecular markers are more powerful (Plashke et al. 1995; Siedler et al. 1995), and have been used to identify heterotic groups in crop plants (Melchinger et al. 1994). The objective of this study is to use random amplified polymorphic DNAs (RAPDs) to identify divergent genotypes and improve the level of heterosis in wheat.

Materials and Method

A total of 46 genotypes, which include 7 selected accessions of the Tibetan endemic wheat, 22 common wheat (7 spring and 15 winter) and 17 spelt wheat (4 spring and 13 winter) (Table 1), were chosen for this study. Genomic DNA isolation and PCR were performed according to the method of Sun et al. (1996). Data were scored on the presence or absence of amplification products. The data matrix was then used to generate genetic similarity index (GS) (Nei 1979). A phenogram was constructed based on genetic distance ($GD=1-GS$) using the unweighted pair-group method with arithmetical average (UPMGA).

Results

The mean GDs within the Tibetan wheat (0.432) and within spelt (0.393) are relatively higher than that within common wheat (0.169). It was also found that the mean GD (0.505) between spelt and common wheat and between Tibetan wheat and common wheat GD (0.473) are much higher than that between spring and winter wheat (0.236). These results suggest that there is much more genetic variation in the spelt and Tibetan subspecies than in common wheat. Cluster analysis separated the 46 genotypes distinctly into two groups. Group 1 includes all 17 spelt genotypes, in which spring and winter spelt could also be separated into two subgroups at lower hierarchy. All 7 accessions of *T. aestivum* ssp. *tibetanum* and 23 common wheat genotypes were included in the group 2, in which all 23 common wheat genotypes were clustered into subgroup 1, subgroups 2, 3 and 4 including all accessions of the Tibetan subspecies.

Conclusions

Since the spelt and Tibetan wheats are readily crossable with common wheat and their F_1 hybrids are highly fertile, spelt and the Tibetan wheat could be used as divergent heterotic groups to improve the level of heterosis in hybrid wheat. The following heterotic groups could be employed: spring wheat x spring spelt, winter wheat x winter spelt, spring wheat x Tibetan wheat.

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Table 1. Forty-six genotypes and accessions used in this study with their origin.

Name	Origin	Categories*	Name	Origin	Categories*
PI348682	Canada	I-1	8202-69	China	II-1
PI348501	Canada	I-1	90-14	China	III-2
PI294576	Canada	I-1	90-18	China	III-2
PI348494	Canada	I-1	90-16	China	III-2
Di-1	Germany	I-2	90-12	China	III-2
Di-4	Germany	I-2	90-11	China	III-2
Ostar	Germany	I-2	90-17	China	III-2
1994WSC	Canada	I-2	90-10	China	III-2
Balmegg	Switzerland	I-2	Changyang 8850	China	II-2
Altgolt	Switzerland	I-2	BAU3320	China	II-2
Hubel	Switzerland	I-2	2410TD	China	II-2
Ostro	Switzerland	I-2	Jingshi390	China	II-2
Di-7	Germany	I-2	BAU3338	China	II-2
Okerkulmer	Switzerland	I-2	BAU3330	China	II-2
Di-8	Germany	I-2	BAU95	China	II-2
Di-9	Germany	I-2	Yuandong 8790	China	II-2
Di-13	Germany	I-2	CA9070	China	II-2
309-1	China	II-1	Jingshi404	China	II-2
Gandong442	China	II-1	Jingdong6	China	II-2
Ningchun15	China	II-1	Jinghe9331	China	II-2
NPPF	China	II-1	T0002	China	II-2
11178-3460	China	II-1	BAU92-101	China	II-2
Mian2-285	China	II-1	Zhongmai 9	China	II-2

* I-1 is for spring spelt, I-2 for winter spelt, II-1 for spring, II-2 for winter wheat, III-2 for *T. aestivum* ssp. *taibetanum*.

A24 - Pattern of Phenotypic Diversity of the Caribbean Maize Accessions

Taba, S., J. Diaz, F. Pineda E., J. Franco and J. Crossa

International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico

Introduction

West Indian maize consists largely of interracial products of hybridization, in addition to seven distinct races (Brown 1960). Two sets of a non-overlapping groups of Caribbean accessions from CIMMYT were identified and used in evaluation trials to form non-overlapping clusters and discover patterns of phenotypic diversity within clusters. Representative subsets were selected from the clusters to facilitate further evaluation and use of the accessions. Accessions from different clusters are also expected to show greater heterosis when crossed than accessions from the same cluster.

The 498 accessions used were from Antigua (4), Bahama (1), Barbados (6), British Virgin Islands (46), Cost Rica (17), Cuba (148), Grenada (17), Guadeloupe (13), Guatemala (4), Guyana (15), French Guyana (9), Haiti (35), Jamaica (3), Martinique (1), Puerto Rico (29), Panama (41), Dominican Republic (21), Saint Croix (9), Santa Lucia (2), Surinam (11), Saint Vicente (13), Tobago (14), Trinidad (39), and Uruguay (1). Trial set 1 was planted on the CIMMYT experiment stations at Poza Rica, Veracruz (60 masl), in summer cycle, 1992, and winter, 1994, and at Tlaltizapán, Morelos (940 masl), in summer, 1992, and winter, 1994. Trial set 2 was planted at Poza Rica in winter, 1993, and summer, 1993, and at Tlaltizapán in winter, 1993, and summer, 1993. (In normal years, winters are summers wet at both these Mexican sites). A 16 x 16 alpha lattice design was used with two replications. Each plot comprised two 5 m rows 76 cm apart with 32 plant hills. The combined analysis was performed using Proc Mixed in SAS (1996) using a mixed liner model. The adjusted means of plant height, ear height, senescence, ear diameter, ear length, days to silk, days to anthesis, moisture %, ease of shelling, number of kernel rows were used to cluster accessions into homogeneous groups. The cluster analysis was done using the CLUSTAN (Wishart 1987) software and employing the sequential strategy proposed by Franco et al. (1997).

The 505 entries, including seven common checks, were grouped in twelve final clusters and the number of accessions in each cluster and their morpho-agronomic characteristics are shown in Table 1. Each cluster has unique racial components. The well-known Caribbean races and a subrace (Early Caribbean, Coastal Tropical Flint, Cuban Yellow Flint, Tuson, Chandelle, Haiti Yellow) were involved in the predominant racial components in clusters 1, 2, 3, 4, 5, 6, 8, 10, 12. Since each cluster was characterized by three or more racial components, the clusters formed by the sequential clustering method are supra-racial groups of the accessions (Bretting et al. 1987). Race Cateto Nortista was the major race in cluster 7 and 9. It was introgressed with Caribbean races from Guyana, French Guyana, and Surinam (Goodman and Brown 1988). Salvadoreño was observed with higher frequency (73%) in cluster 11, which showed the clear separation of the Central American race from those of the Caribbean.

The centroids of the twelve clusters were plotted for the first three canonical variables. Phenotypic diversity of the clusters was clearly shown with respect to the variation associated with each dimension. A breeder's selection index based on yield, ear rot, erect plant, and maturity was used to select 100 accessions to represent the non-overlapping clusters for a core subset of the collection.

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Table 1. The twelve non-overlapping clusters formed by Normix after Ward (Franco et al. 1997). The number of accessions, the means of Agro-morphological traits, average Mahalanobis distances, and the numbers of selected accessions, and kernel traits are shown for each cluster.

Cluster	No. Acc		ANT	SIL	PH	EH	SE	SL	RL	SH*	Kg/ha	KRN	H2O	EL	ED	ES	ASR	D ² (ij)	Kernel	Kernel	Acc. Sel		
	Set1	Set2																			Set1	Set2	
a	9	36	71	72	226	122	45	11.6	18.9	84.2	3598	13.1	15.1	16.2	4.2	2.9	2.9	32.5	FC	BJ	4	5	
b	24	1	73	75	251	142	46	9.7	11.0	88.0	4137	12.8	16.7	16.1	4.3	2.4	2.7	34.8	FCE	B	5	0	
c	37	59	74	77	244	143	47	11.1	16.6	81.4	3823	14.6	17.4	14.9	4.9	2.9	2.7	28.5	FC	BF	7	12	
d	29	61	74	76	246	141	48	10.0	18.2	83.1	4457	13.8	18.3	17.0	4.8	2.8	2.6	26.6	FCE	BFAJ	8	10	
e	47	24	83	85	276	180	41	12.4	24.0	82.7	3629	13.2	18.8	16.5	4.5	2.9	2.9	25.2	FCE	B	12	2	
f	19	15	68	70	184	100	42	23.7	23.0	81.0	2292	13.2	15.0	14.6	4.0	2.9	3.4	56.3	FG	BJFAI	2	5	
g	3	16	83	86	242	150	39	11.5	31.6	80.0	2238	15.5	18.0	14.3	4.7	3.0	3.6	40.5	F	B	1	3	
h	2	12	76	78	251	143	47	8.6	20.0	85.7	4203	13.9	18.2	18.2	4.1	2.6	2.5	38.0	FCE	BFJ	1	2	
i	4	16	86	90	266	175	39	10.5	29.3	81.2	2361	14.6	23.4	14.5	4.7	3.0	3.5	50.8	FC	BA	3	1	
j	19	9	86	89	284	174	41	8.5	13.6	81.4	3615	12.7	20.6	15.2	4.3	2.8	2.6	38.4	F	BA	5	1	
k	41	0	77	81	270	172	42	10.4	9.5	82.4	3162	12.9	16.2	15.5	4.3	2.8	2.9	28.1	F	BF	8	0	
l	15	0	82	84	282	187	42	10.7	20.5	84.0	4025	13.0	18.6	17.5	4.5	2.4	2.6	35.8	FC	BA	3	0	
			Mean	78	79	250	152	44	11.5	18.8	82.9	3641	13.6	17.7	15.9	4.4	2.8	2.9	36.3				
			C.V. (%)	8	8	11	17	8	48.6	54.7	2.7	25	6.5	12.7	8.5	6.2	6.9	15.5	26.2				

Codes on the table: ANT=Days to anthesis, SIL=Days to silking, PH=Plant height (cm), EH=Ear height (cm), SE=Days to senescence after silking, SL=% Stalk lodging, RL=% Root lodging, SH= % shelling.

Kg/ha=Kg yield per ha, KRN=# Kernel row number, H2O=% Moisture, EL=Ear length (cm), ED=Ear diameter (cm), ES=Rating (1-5) on easiness to shell.

ASR=Rating (1-5) on agronomic performance (description of rating: 1=very good or easy to shell, 5=very poor or difficult to shell), D²(ij)=Average Mahalanobis Distance.

Acc. Sel=Accessions selected for core subset, Set1=Trials set1, and Set2=Trials set2.

* SH evaluated in cycle A and B at Tlalzapán, Mor.

** Texture: C=Dent, E=Semi-flint, F=Flint, G=Pop. Color: A=White, B=Yellow, F=Orange yellow, I=Red, J=Sun red, based on CIMMYT database.

A25 - SSR Characterization of Heterozygotic Patterns of Parents for Predicting Heterosis in Rice Breeding

Xiao C. Liu ¹, M. A. Saghai Maroof ², Jian L. Wu ¹ & Lian Pan ¹

¹ China National Rice Research Institute, Hangzhou 310006, Zhejiang P. R. China.

² Department of Crop and Soil Environmental Sciences, Virginia Polytechnic Institute and State University, Virginia, VA 24060, USA

The most important concerns of hybrid rice breeders are selection of donors to improve parents of hybrids, and prediction of hybrid performance based on the parents. In this study, SSR molecular marker technology and a half-diallel experiment of hybrid performance have been attempted to apply for those aspects. Results show that genetic diversity among the parental lines is related to heterosis, but it is not a good indicator for it. The heterozygosity of the parents pairwise is significant in the direct relation to the general combining ability, but not to the specific combining ability. A suggestion is made to hybrid rice breeders that hybrid breeding programs should be undertaken on the basis of a conventional breeding improvement in order to accumulate more favorable additive and dominant genes in hybrids. We also found that four favorable alleles and six favorable heterozygotic patterns of the parental lines significantly contribute to the heterosis of their hybrid. Meanwhile, we noted that six unfavorable alleles and six unfavorable heterozygotic patterns significantly reduce heterosis. These findings could be useful and practical for hybrid rice breeding with the SSR marker-aided selection. They may indicate that an improvement of inbred lines still has a great potential value for exploiting further heterosis in hybrid rice by removing the unfavorable alleles and patterns with the aid of SSR marker selection. In the indica/japonica hybrid breeding, it may also be important to remove the unfavorable alleles, rather than to make larger genetic diversity or heterozygosity to the parental lines.

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A26 - Development and Improvement of Heterotic Populations in Maize

B.S. Dhillon, N.S. Malhi, and V.K. Saxena

Punjab agricultural University, Ludhiana 141 004, India

Heterotic populations have been extensively used in hybrid maize breeding. In spite of their significance, maize heterotic patterns have not been systematically established. An ideal approach would be to cross all promising germplasm in series of diallel crosses and identify two or more stocks as testers. The testers should be crossed with diverse germplasm and those showing heterosis with the tester, assigned to the opposite heterotic pool. Reciprocal recurrent selection should be conducted in pools to enhance heterosis. New germplasm may be introgressed to maintain or enhance within-pool genetic variation and to rectify specific defects. The objective should be to develop heterotic populations which are broad-based, genetically diverse, highly heterotic, and have high performance per se and acceptable inbreeding tolerance.

PAU Maize Heterotic Pools

Punjab Agricultural University (PAU) has developed three pairs of heterotic pools (Khehra and Dhillon 1984; Khehra et al. 1986; Saxena et al. 1993): 1) Makki Safed x Tuxpeño, 2) Indigenous x Semi-Exotic, and 2) Ludhiana Lancaster x Ludhiana Stiff Stalk. Makki Safed x Tuxpeño and Indigenous x Semi-Exotic are adapted to the monsoon season. Makki Safed and Tuxpeño pools have long duration and high yield potential and were developed using Makki Safed 1 - Disease Resistant (MSIDR), an improved indigenous flint landrace, and Tuxpeño Planta Baja C₇ Ludhiana (Tuxpeño PBL), an improved dent Mexican race as testers. The Lancaster and Stiff Stalk germplasm was assigned to Makki Safed and Tuxpeño pools, respectively. Indigenous and Semi-Exotic pools have short duration and stress tolerance. The testers used were JS2, a composite developed from Indigenous germplasm, and CM124 x CM125, a single cross of lines derived from Pioneer H104. The Semi-Exotic pool has sub-pools A and B, which correspond to the Makki Safed and Tuxpeño pools. Ludhiana Lancaster and Ludhiana Stiff Stalk pools basically include US germplasm which has shown adaptation to the winter of northwest India. (CM202 x Mo17) # and (B73xB79) # were employed as testers to develop these pools. Modified reciprocal recurrent selection (Dhillon et al. 1986) accompanied by introgression of new germplasm was completed to improve the pools. Four cycles were carried out in the Makki Sated and Tuxpeño Pools and three cycles in the Ludhiana Lancaster and Ludhiana Stiff Stalk Pools. The materials which have contributed to the development of various pools are listed below. Inbred lines were evaluated and assigned to only one pool.

Makki Safed Pool C4: Arun, Ageti 76 x (Mo 17 x Fr13A), CM104, CM202, CM 202 x H 101, CM 202 x J632, CM600 x 95, J101, J607, J641, J663, J664, J2006, J660 x Mo17, J663 x FRVa26, Kaipur Local, Kalakh Local x MSP2, MS1DR, MS1DR x J617, MSIDR x Mo17, MSIDr Yellow x J 617, MSIDR C2, Navjot, Partap, Partap x (FR619 x FRMo17), Partap x (Mo17 x B57), Partap x (Mo17xFRI3A), Sarhad x (FR619 X FR670), Tarun x MS1, Vijay and Vijay 444 x CM20T

Tuxpeño Pool C4: CM123, Cuba 11J,, Exp. 10-5, H104, J1031, McNair hybrid (Ec103838), Suwan1, Suwan 1 x B73, Suwan 1 x H93, Suwan 2, TAD, Tuxpeño PBL, Tuxpeño PBL X Tuxpeño C16, Tuxpeño PBL x Tuxpeño C17, Tuxpeño PBL x Tuxpeño Yellow, Tuxpeño PBL C8 x B73, upeno PBL C1 x Tad, Tuxpeño C17 x Suwan 1, Jtuzpeno PBL x (Suwan 1 x B73), (Tuxpeño PBL x CM206) x Tuxpeño PBL, (Tuxpeño PBL x TAD) x Tuxpeño PBL, and Z216.

Indigenous Pool: Arun, J663, JS2, JS2 x J3022, Local 28, Local x JS2, Megha, Nagdi Local, Nasvjot and Renuka.

Semi-Exotic Pool - A: Ageli 36 x (Mo 17 x Fr 13A), Js044, Js4, Makki Safed Pool C2 and Tarun x MS1.

Semi-Exotic Pool - B: (B73xB79) x B73, Kiu 1401, Kiu 1403, Pop. 24 (Antigua - Veracruz 181) Pop. 36 (Mezcla Amarilla), Pop. 31 (Amarillo Cristalino-2), Pop. 36 (Cogollero); Sabour Selection and Tuxpeño Pool C2.

Ludhiana Lancaster Pool C3: (A670 x FRVa26) x artap, (57 X Mo17) x B57, BS1, Bs2, BS16, Bsul2, Clivc, CM111 x Mo17, Cm205 x CM202, Dhankara Local, (H98 x CM 202) x W64, H98 x H99, (H98 x H99) x H95, (H98 x H99) x H99, H99 x CM202, H99 x Sarhad, Lancaster Composite (Ludhiana), MO17 x B57, Mo17 x Fr13A, (Mo17 x F\$13a) x H99, (Mo17 x FR13A) x H101, (Mo17 x FR13A) x Partap, Mo17 x H99, Mo17 x H101, (Mo17 x B57) x (H99 x CM202), (Mo17 x H101) x H95, (Mo17 x H101) x Mo17, MSIDR, MS1dr x (A670 x FRVa26), MSP2, MSP2 x Partap and Partap 1.

Ludhiana Stiff Stalk Pool C3: (A632 x H100) x A632, B73 x B79, (B73 x B79) x B73, [(B73 X B79) X B73] x N7A, (B73 x B79) x Suwan 1, B73 x B84, B73 x Suwan 1, Bs13 (S2) C1, BSS (R) C8 x Suwan 1, CM123, FR4A x FR4C, FR632 X H100, FRK 55 x (Mo14W x Mo1W), KUI 1418, MSP1, RDBBDE and Stiff Stalk composte (Ludhiana) and Suwan 1.

Flint x dent heterotic patterns are also being exploited in the USA, Europe and Latin America; and indigenous x exotic pools in Europe, Asia and Africa (Hallauer et al. 1988; Dowsell et al. 1996).

Genetic Diversity

The expression of heterosis depends on the divergence in gene frequency of the parental stocks and dominance effect at various loci. Therefore, it is important that heterotic pools are made divergent. However, there seems to be an optimal level of diversity beyond which heterosis does not increase (Moll et al. 1962, 1965). Among various approaches, heterosis has proved to be a direct and useful measure of genetic diversity. The new molecular techniques have so far not given encouraging results for the prediction of heterosis in maize (Melchinger et al. 1992; Dhillon et al. 1993). The pools may be diversified for plant type, ear traits, kernel traits, and even for maturity, height and tassel traits within certain limits. The pools may be designated as seed parent or pollen parent with the development of hybrid breeding programs, and accordingly genes for contrasting traits may be concentrated in the pools.

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A27 - Classification of Argentine Maize Germplasm in Heterotic Groups

G.H. Eyherabide, A.S. González and G. Nestares

Estación Experimental Agropecuaria Pergamino, Instituto Nacional de Tecnología Agropecuaria (INTA), CC 31, Pergamino 2700, Argentina

Introduction

The Argentine flint x US Corn Belt dent heterotic pattern is being used for developing hybrids in Argentina. 'Reid Yellow Dent' and 'Lancaster Sure Crop' germplasm groups were first introgressed into elite flint lines (Brun and Dudley 1989) through backcrosses, and the new flinty lines crossed following Reid x Lancaster combinations. The search for alternative heterotic patterns and concerns about kernel physical quality as well as tolerance to viral diseases constitute a new scenario. This research was aimed at classifying a wide array of local flint germplasm in heterotic groups and identifying genotypes to be composited in new breeding populations to form alternative flint x flint heterotic patterns.

Methods

The testcrosses of 80 orange flint local landraces and 50 flint local inbred lines with two pairs of testers were evaluated in three and four environments, respectively. The first pair of testers represents a local flint heterotic pattern, and the second pair represents the Reid Yellow Dent vs. Lancaster Sure Crop heterotic pattern. Landrace and line testcrosses were assigned to sets, each set including testcrosses tracing to 10 landraces or lines. A two-replication-within-set design with a split-plot arrangement of entries was utilized. Main plots corresponded to landraces (lines) and subplots to landrace (line) x tester combinations.

Landrace experiment. Landrace (sets), testers, and landrace (sets) x environment sources of variation were analyzed following additive main effects and multiplicative interaction (AMMI) models (Gauch and Zobel 1988). The concept of relative grain yield (RY) was used to give equal weights to sets and environments (Yau and Hamblin 1994). The landrace x tester interaction sum of squares for relative yield was partitioned into principal component axes, and the singular value, landrace eigenvector and tester eigenvector for each axis were determined. A hierarchical cluster analysis was performed on the group of landraces with relative grain yields across environments and testers above the overall mean. Variables used for this analysis were the landrace eigenvectors for the significant principal component axes multiplied by the square root of the corresponding eigenvalues (referred to hereafter as 'scores').

Inbred line experiment. The general combining ability effects of each line and tester, and the specific combining ability effects for grain yield were calculated. The mean grain yield of each set in each replication and environment was used as a covariate to remove the effect due to sets and environments. The specific combining ability effects underwent principal component analysis, and the resulting line scores for the three principal components used as variables for a non-hierarchical cluster analysis.

Results and Conclusions

Landrace experiment. The first two significant principal components accounted for 74% of the landrace x tester interaction. Both local flint testers had positive scores while both US dent testers had negative scores for the first axis. These results were consistent with the major heterotic pattern, Argentine flint x US Corn Belt dent. For the second axis, the two largest scores (absolute values) with opposite signs corresponded to flint testers. Both dent testers had negative and almost equal scores. The second axis could be interpreted as a contrast within the local flint heterotic pattern. Landraces could be classified on the basis of the sign and magnitude of their respective interaction with flint or dent testers. This classification and the performance of the landraces for other important agronomic traits, such as standability, were considered to identify 10 landraces to be used as parents of two divergent populations (Fig. 1)

Inbred line experiment. The line x tester interaction was significant. The cluster analysis defined 4 groups of lines with a particular pattern of interaction with the testers (Fig. 2). The lines within each group with positive general combining ability effects were recombined and the resulting four synthetics are being evaluated in a diallel cross that also includes a BS13-derived populations.

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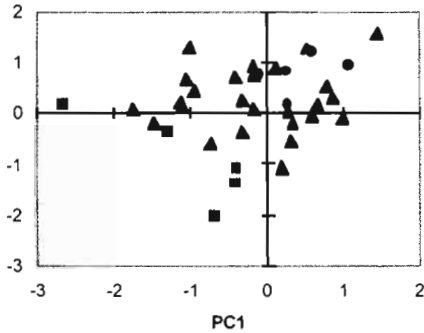


Figure 1. Score arrangements for 37 selected landraces and four testers for the first two principal components axes for relative grain yield across environments. Scores for flint testers are HP3 (1.90, 5.99) and P5L2 (5.36,-3.70); scores for dent testers are SB73 (-2.30,-1.14) and Smo17 (-4.96, -1.16). Squares and circles indicate the landraces to be composited in two different populations.

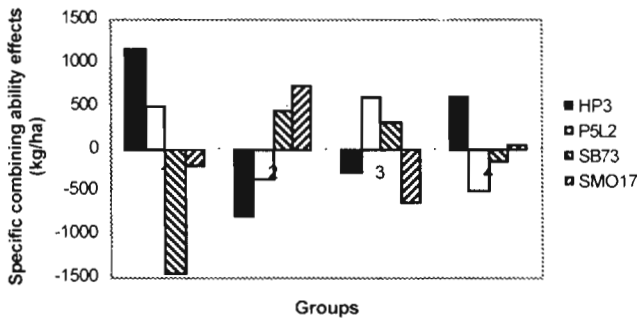


Figure 2. Average specific combining ability effect of lines assigned to each group with local flint (HP3, P5L2), and U.S. dent (SB73, Smo17) testers.

A28 - Enhancement of Yield Heterosis for Sustenance of Hybrid Rice Technology in India

M. Ilyas Ahmed*, K. Krishnaiah and E.A. Siddiq

Directorate of Research, Rajendranagar, Hyderabad-500 030, India

Exploitation of hybrid vigour has been identified as the potential technological option for raising the genetic yield ceiling in rice. Acceleration of heterosis breeding research since 1990 through the ICAR-UNDP supported project on "Development and Use of Hybrid Rice Technology" has led to the development of seven public bred hybrids (Table 1) and marketing of another 6-7 hybrids by the private sector, for commercial cultivation. Simultaneously a seed production package has been standardised, resulting in seed yields of 1.5-2.0 t/ha. A yield advantage of at least 1 t/ha or more over the highest yielding conventional variety has been the reason for planting of rice hybrids on 60,000 ha during last year in India. Improving the yield advantage of hybrids by another 10-15% and the production and supply of quality seed at affordable prices are the keys to large-scale adoption of the technology. The following are breeding strategies being pursued with this aim in India.

Use of Diverse Parental Lines

All rice hybrids released in India have the same female line, IR58025A, developed at the International Rice Research Institute (IRRI), Philippines, and most of male (restorer) parents (again IRRI bred) are of closely related lineage. The impact of excessive dependence on a single CMS line (IR58025A) and single source of sterility inducing cytoplasm (wild abortive) and limited diversity among restorer lines has resulted in no appreciable change in mean and range of yield potential of rice hybrids over the last five years. During the past two years, many promising CMS and restorer lines have been developed from native germplasm. Experimental hybrids among them as well as between India and IRRI bred lines have been found which show 5-10% higher standard heterosis than presently available hybrids. Work is underway to improve the parental line by isocyttoplasmic restorer development, $R \times R$ crosses, a convergent breeding programme, $B \times B$ crosses, and genetic male sterility facilitated recurrent selection. This has led to the identification of second generation restorer and maintainers, which are presently undergoing combining ability evaluation.

Hybrids with Better Grain Quality and Pest and Disease Resistance

A widely used CMS line, IR58025A, suffers from a mild *basmati* aroma and stickiness; qualities disliked by consumers in southern and eastern India. Another CMS line viz., IR62829A, often results in hybrids which have very poor head rice recovery in milling. Special efforts are being made to improve cooking and eating quality characteristics to ensure consumer acceptance and market demand for hybrid rice on one hand and to enhance the economic attractiveness of the technology on the other. Most test entries in the National Hybrid Rice Trial are of desirable quality. In addition, all promising parental lines have been screened for resistance to major pests and diseases and only those possessing resistance to at least one major pest or disease of the target area are used.

Development of Inter-Sub-Specific Hybrids

Another promising approach for enhancement of heterosis is development of inter-sub-specific *indica* \times tropical *japonica* hybrids, which are reported to give 15-20% higher yields than *indica* \times *indica* hybrids. Inter-varietal sterility characteristics of *indica* \times *japonica* crosses, the need for fertility restorers common to both varietal group, and asynchrony of flowering due to differences in photo- and thermo-sensitivity are problems to be overcome. Significant progress has been made in recent years in recombining wide compatibility (WC) genes in some of the A and R lines. The search is in progress for universal restorer genes for the WA and WU 10 cytoplasm, especially among the ecotypes believed to constitute the point of inter-specific differentiation. Preliminary study of some of the *indica* \times tropical *japonica* hybrids

indicates the possibility of raising heterosis for yield by 10-15% over that of *indica x indica* hybrids. Both two- and three-line approaches are being used.

Development of Two-Line Heterosis Breeding

The scope for unrestricted choice of male parent, a less cumbersome system of seed production, and the relatively easy exploitation of inter-sub-specific hybrid vigour are unique advantages of two-line heterosis breeding. Several thermo-sensitive genic male sterile (TGMS) lines of spontaneous and induced origin have been identified, characterised with respect to the critical sterility point (CSP) and critical fertility point (CFP), and used in experimental two-line hybrids. Preliminary evaluation of two-line hybrids, based on the stable TGMS lines viz., TGMS-1 and TGMS-2, has indicated that a heterosis in some of 15-20% over three-line hybrids. Efforts have intensified recently and a promising two-line hybrids is likely to be released for commercial cultivation soon.

Table 1. Salient features of released hybrids.

Hybrids/ Year	Parentage	Duration (days)	Yield in OFT (t/ha)		Adv. over check	
			Hybrid	Check	(t/ha)	%
APHR-1 (1994)	IR58025A/ VAJRAM	130-135	7.14	5.27 (Chaitanya)	1.87	35.4
APHR-2 (1994)	IR62829A/ MTU 9992	120-125	7.52	5.21 (Chaitanya)	2.31	44.2
MGR-1 (1994)	IR62829A/ IR10198	110-115	6.08	5.23 (IR 50)	0.85	16.2
KRH-1 (1994)	IR58025A/ IR9761	120-125	6.02	4.58 (Mangala)	1.44	31.4
CNRH-3 (1995)	IR 62829A/ AJAYA R	125-130	7.49	5.45 (Khitish)	2.04	37.4
DRRH-1 (1996)	IR 58025A/ IR 40750	125-130	7.30	5.50 (Tella hamsa)	1.80	32.7
KRH-2 (1996)	IR 58025A/ KMR 3R	130-135	7.40	6.10 (Jaya)	1.70	21.3

A29 - New CMS Lines with Diversified CMS Sources and Better Outcrossing Traits in Rice

M.S. Ramesha, M. Ilyas Ahmed*, B.C. Viraktamath, C.H.M. Vijayakumar and S. Singh

Hybrid Rice Programme, Directorate of Rice Research (DRR), Rajendranagar, Hyderabad-500 030, India

Introduction

Most of the commercial hybrids of indica rice are based on wild abortive (WA) source of cytoplasmic genetic male sterility (CMS). About 95% of the total area of hybrid rice in China, and elsewhere in the tropics are based on WA type of cyto-sterility system. This excessive reliance on a single source of sterility may lead to genetic vulnerability of hybrids to sudden out break of diseases and insect pests. Another drawback of the WA system is poor panicle exertion and undesirable flowering behaviour leading to low seed yield in hybrid seed production plots. There is thus urgent need for cytoplasmic diversification of the male sterility source for hybrid rice breeding. Shinjyo (1969) transferred cytoplasm of *indica* cv Chinsurah boro into *japonica* cultivar Taichung 65 and developed a BT type CMS source. Since then CMS lines with different CMS sources have been developed (Virmani and Shnjo 1988; Dalmacio et al. 1995). Three new and diversified CMS sources, i.e., one from *O. rufipogon* and two from *O. nivara* have been identified (Hoan 1993). In this paper, we report the pollen stainability and spikelet sterility characteristics of the three new CMS sources (Hoan 1993) in the advanced backcross generations (BC5 to BC8) and their desirable outcrossing traits which will be of value in commercial hybrid rice seed production.

Methods

The material consisted of four advanced backcross generations (BC5-BC8) of CMS lines viz., RPMS 1-1 and RPMS 1-3 having *O. rufipogon* CMS source and RPMS-2 and RPMS-4 possessing *O. nivara* source (Hoan 1993). Pollen stainability was determined in 40-50 plants of each of the lines in BC5, BC6, BC7 and BC8 generations. The pollen stainability characteristics of the lines were determined by staining pollen grains in 1.5% potassium iodide-iodine (IKI) solution. Based on iodine and starch interaction, pollen grains were classified into Typical Abortive (TA), Round Sterile (RS) and Partially Stained (PS) types and microscopic count was taken and expressed in terms of percentage. Two to three panicles of each plant were bagged and mean spikelet sterility was recorded after harvest. Apart from this, the new CMS lines were grown along immense with CMS lines belonging to WA, IR 64A and MS577A source, during wet season 1994 and dry season 1994-95 at Directorate of Rice Research farm, Hyderabad, India. The observations on panicle exertion, stigma exertion and per cent seed set on sterile plants were recorded on five random and competitive plants in each replication and expressed in terms of percentage.

Results

The CMS lines viz., RPMS1-1, RPMS1-3 and RPMS-2 showed very high proportion of round sterile type of pollen grains. However, the line RPMS-4 showed very high proportion of typical abortive sterile pollen grains. The new CMS lines possess very high panicle exertion (93-97%), stigma exertion (50-58%) and outcrossing percentage (sterility 40-48%) as compared to CMS lines belonging to other sources.

Conclusion

Based on pollen stainability and maintenance of sterility with restorers of WA source, all the lines were found to possess new source of cytoplasmic genetic male sterility, thus ensuring cytoplasmic diversification. The lines viz., RPMS1-1, RPMS1-3, and RPMS-2 were found to possess gametophytic type of male sterility. However, the pollen stainability pattern of RPMS-4 indicates the sporophytic nature of male sterility. Besides stable male the new CMS lines possess very high panicle and stigma exertion and high outcrossing ability as compared that of WA and other CMS sources. The use of good hybrid combinations involving new CMS lines can pave the way for maximising the hybrid seed yield

without the use of GA3, a costly input in hybrid rice production. Reduction in the cost of hybrid seed and the nuclear and cytoplasmic diversification of hybrids will help in large scale adoption and sustenance of hybrid rice technology in India, in the years ahead.

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A30 - Heterosis and Genetic Diversity in Crosses of Adapted East African Maize Composites

B. Tolessa, K. Mulatu, L. Wolde, G. Bogale, M. Worku and G. Keneni

Bako Agricultural Research Center, P.O.Box 3, Bako, Ethiopia

Introduction

Diallel cross analysis for a fixed set of populations provides a basis for preliminary determination of heterotic groups. This heterosis information serves as a measure of genetic diversity (Bridges and Gardener 1987, Moll et al. 1962). A high level of heterosis in a cross indicates that the parents are more genetically diverse than those of crosses which show little or no heterosis (Miranda and Vencovsky 1984, Mungoma and Pollak 1988). Several studies have established the need for the use of genetically diverse materials in developing high-yielding hybrids (Crossa and Gardener 1987, Lonquist and Gardener 1961). The Ethiopian maize breeding program has attempted to use parental stocks from diverse sources in its population improvement work. However, the genetic similarity or diversity of the adapted East African maize composites is not well known. Therefore this study was designed to determine genetic divergence in a diallel cross among eight locally adapted maize composites based on F_1 heterosis.

Methods

Eight maize composites and their 28 possible F_1 crosses, excluding reciprocals, were evaluated in a randomized complete block design in 1985 and 1986 at Bako and Didesa research centers. The two years and two locations were assumed to represent four random environments. In each environment the study had three replications. Each plot comprised four rows, each 3m long. A spacing of 75 cm was used between rows and 30 cm within rows. The middle two rows were used for recording data on grain yield, days to 50% silk emergence, plant height, and ear height. Data over the four environments were pooled by considering the environments as random variables. Mid- and better-parent heterosis for yield was computed for each of the two environments and used to analyze genetic diversity.

Results

The heterotic response of F_1 crosses among the hybrids was with few exceptions, not high (Table 1). The superiority of F_1 hybrids over parents was better expressed under a high-yielding environment of Bako. This suggests the need for introgressing additional germplasm from diverse genetic sources into the locally available well-adapted population to synthesize superior composite varieties for extensive exploitation through a systematic breeding program involving evaluation in selected diverse environments in the country. Better parent percentage of heterosis of UCA x KCB is too low to justify the formation of a heterotic group and commercial exploitation of hybrid vigor (Table 1).

Conclusion

A few F_1 hybrids gave higher grain yields than the better parental composites, but only at Bako, which was a better yield location than Didesa. Frequency of F_1 hybrids having negative heterosis was much higher at Didesa. Mid-parent percentage of heterosis based on combined data from the two environments indicated that UCA and KCB were the most divergent composites. Alemaya composite was found to be related to Awasa-Jima (c4), EAH-75, and Bako composite II. Based on better parent heterosis, genetic divergence was interpreted to exist only between UCA and KCC. This indicates most of the composites included in the study lack distinct genetic difference.

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Table 1. Percent heterosis in relation to the mid parent (MP) and better parent (BP) for yield in 28 maize crosses tested at Bako and Didesa.

Cross	Bako MP	1986 BP	Didesa MP	1985 BP	Grain yield (t/ha)
UCA x Bako Composite II	-11.7	-16.6	-16.7	-18.0	5.8
UCA x EAH-75	16.3	1.3	-21.5	-24.4	6.5
UCA x Awasa Jima (C4)	15.8	5.8	2.4	1.8	6.5
UCA x KCB	35.2	24.4	-7.4	-22.4	6.2
UCA x KCC	-10.7	-17.9	-31.1	14.5	6.6
UCA x Bako Composite (C2)	1.9	1.6	-1.9	-7.9	6.4
UCA x Alemaya Composite	-2.7	-2.2	-31.9	-37.3	6.1
Bako Composite II x EAH-75	-2.7	-4.5	-6.7	-11.4	6.5
Bako Composite II x Awasa Jima (C4)	7.0	-7.1	-7.2	-8.0	6.4
Bako Composite II x KCB	11.3	-2.8	-23.7	-35.3	6.5
Bako Composite II x KCC	-23.0	-25.1	-11.0	-21.3	6.0
Bako Composite II x Bako Composite (C2)	-10.5	-15.8	-16.9	-20.8	5.6
Bako Composite II x Alemaya Composite	5.9	-4.5	-48.4	-53.1	5.9
EAH-75 x Awasa Jima (C4)	3.3	-8.8	-26.6	-29.7	5.7
EAH-75 x KCB	10.0	3.8	18.0	-33.4	6.2
EAH-75 x KCC	8.0	3.2	-48.6	-56.5	6.2
EAH-75 x Bako Composite (C2)	-8.1	-12.0	-24.2	-31.3	5.7
EAH-75 x Alemaya Composite	-5.0	-12.8	-43.5	-46.1	5.7
Awasa Jima (C4) x KCB	33.3	32.5	-60.4	-66.7	5.2
Awasa Jima (C4) x KCC	-3.0	-17.6	-33.2	-41.3	6.2
Awasa Jima (C4) x Bako Composite (C2)	-1.6	-9.6	-10.6	-15.6	6.5
Awasa Jima (C4) x Alemaya Composite	4.6	0.4	-42.7	-47.6	5.6
KCB x KCC	10.6	-5.6	-31.5	-34.7	5.9
KCB x Bako Composite (C2)	5.2	-2.9	-29.9	-38.0	5.6
KCB x Alemaya Composite	18.9	14.8	-18.1	-35.8	6.6
KCC x Bako Composite (C2)	-2.6	-10.7	-5.4	-12.5	5.5
KCC x Alemaya Composite	6.4	-6.4	-5.2	-22.9	7.2
Bako Composite (C2) x Alemaya Composite	35.1	29.1	-29.5	-38.7	6.2

A31 - Combining Ability of Corn Belt and Tropical Maize

R.C. Pratt and M.A. Casey

Department of Horticulture and Crop Sciences, Ohio Agricultural Research and Development Center, The Ohio State University, Wooster, OH, 44491, USA.

Introduction

The 'Reid Yellow Dent' and 'Lancaster Surecrop' heterotic pattern accounts for most US maize hybrids. However, interest exists in further broadening the US maize gene pool to reduce genetic vulnerability, increase productivity, and identify new value-added traits. The success or failure of a germplasm enhancement project depends on the degree of heterosis expressed between the elite and donor germplasm. The breeder must also decide whether or not exotic germplasm must first be crossed with adapted germplasm. Wellhausen (1966) advocated creation of multi-racial germplasm pools by crossing a tropical pool by a Corn Belt dent composite and backcrossing to Corn Belt Dent, followed by several generations of random-mating. Before developing new populations and breeding lines, however, information is needed on heterotic patterns. Diallel analysis for a fixed set of populations provides a basis for preliminary analysis of heterotic patterns among populations crosses.

Methods

An 8 X 8 diallel was produced by crossing all combinations of populations OhS3(C5) (Pratt et al. 1991), OhS10(C1) (Pratt et al. 1993), OhS3267LAN (Pratt 1995), BS28, BS29, and BS30 with single crosses B73 X B94 and Mo17 X Va58. The latter hybrids were intended to represent 'Reid Yellow Dent' via the Iowa Stiff Stalk Synthetic (BSSS) and 'Lancaster Sure Crop' heterotic patterns of US Corn Belt maize. The Ohio breeding populations represented 1) diverse populations of undefined heterotic responses [OhS3(C5) and OhS3267LAN] and 2) OhS10(C1), composed primarily of Reid Yellow Dent-derived inbreds crossed with a Tuxpeño population. Other populations included contributions from Tuxpeño (BS28), Caribbean Flint (Suwan 1 derived BS29), and US Corn Belt 'Iodent' (BS30) released by Iowa State University. Hybrids were planted in two-row plots at three locations during 1995-96 according to conventional production practices recommended for Ohio. Plots were mechanically harvested and yield was adjusted to 15.0% moisture. Data from each location were analyzed using the SAS Macro "GRIFFING" obtained from Dr. S. Linda (IFAS Dept. of Statistics) to perform analyses of the diallel crosses. Griffing (1956) Model 1 (fixed) Method 4 was used.

Results

The BSSS derived single cross (B73 X B94) manifested the highest level of GCA, followed by the Lancaster Sure Crop derived cross (Mo17 X Va58), and BS29. BS30 (Iodent derived) showed the poorest general combining ability (Table 1). F values for GCA exceeded those for SCA by magnitudes of 3 to 10 fold. The highest positive SCA values were obtained for the crosses (Mo17 X Va58) X OhS3267LAN and (B73 X B94) X BS28. Interestingly, these values exceeded those of established heterotic patterns such as BSSS X Lancaster Sure Crop and Tuxpeño X Suwan 1. BS28 displayed high yield in combination with the BSSS hybrid and BS29 showed promising yield and SCA with OhS3267LAN and Mo17 X Va58 (Table 2). Population BS30 displayed both low yield and GCA. Ohio synthetic populations OhS3(C5) and OhS10(C1) displayed average-to-low yield and combining ability. Mungoma and Pollak (1988) also showed BSSS had the highest combining ability with Tuxpeño germplasm. Specific combining ability of OhS3267LAN (which is comprised approximately 50% of Lancaster Sure Crop derived inbreds) with Mo17 X Va58 was not expected.

Conclusions

The data for GCA were consistent with well established knowledge regarding the broad combining ability of BSSS and Lancaster Sure Crop derived US Corn Belt germplasm. The high GCA of Suwan 1 derived BS29 was noted as were high SCA and yield values for Tuxpeño in certain combinations.

Combination of germplasm from distinct heterotic patterns likely reduced the opportunity for heterotic responses with the Ohio synthetics tested in this study. High SCA of OhS3267LAN X (Mo17 X Va58) and BS29 was not expected and this heterotic patterns may offer opportunity for further development through recurrent selection.

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Table 1. General combining ability (Mg ha⁻¹) of Corn Belt and tropical maize germplasm populations at three locations in Ohio, 1995-1996.

Genotype	Custar 1995	S. Charleston 1995	Guerne 1996
Mo17 X Va58	0.158	0.420	0.443
B73 X B94	0.700	0.507	1.010
OhS3267LAN	0.272	0.028	-0.234
OhS3(C5)	-0.075	-0.020	0.280
OhS10(C1)	-0.050	-0.063	-0.407
BS28	-0.292	-0.518	-0.459
BS29	0.237	0.312	0.453
BS30	-0.950	-0.705	-1.085

Table 2. Average yield (Mg ha⁻¹) of Corn Belt and tropical maize germplasm populations in diallel intercrosses at three locations in Ohio, 1995-1996.

Genotype	Yield 1995 (avg. 2 loc.)	1995 Rank	Yield 1996	1996 Rank
Mo17 X Va58	4.94	2	5.76	3
B73 X B94	5.21	1	6.10	1
OhS3267LAN	4.82	4	5.18	5
OhS3(C5)	4.67	5	5.62	4
OhS10(C1)	4.64	6	5.03	6
BS28	4.35	7	4.98	7
BS29	4.93	3	5.81	2
BS30	4.03	8	4.70	8

A33 - Heterotic Potential of Germplasm from the Highland-Andean Region

R. Sevilla, A. Manrique, H. Sanchez, and J. Nakaodo

Maize Program, National Agriculture University La Molina (UNALM), Apdo. 456, Lima, Perú.

Introduction

orregrosa (1975) and Barandiarán (1993) have published studies on heterosis in Highland-Andean flourey maize varieties. Torregrosa presented a summary of heterosis research conducted in Colombia. Mid-parent heterosis gains varied from 26.8 to 11.9%, whereas high-parent heterosis varied from 17.9 to 3.3%. Chillos, a landrace from Ecuador, performed very well in different studies. When Chillos was crossed to Rocamex V I Syn 4 (ZM II), a selection of Mexican origin, the cross yielded 9.0 Mg ha⁻¹. In other study, Chillos and Harinoso Mosquera 1(R) Sin 7 (ZM VI) were the best performing populations and gave the best yield in crosses. Correlation between productivity of the parents and the crosses was 0.81. In general, populations improved by recurrent selection produced the best yielding crosses. Barandiarán made all crosses among 10 landraces from Latinoamerica adapted to cold climates. Cacao, a landrace from Colombia, performed the lowest yield but the highest heterotic variety effect. INIAP 153 from Ecuador and Blanco Urubamba from Perú (Cuzco Gigante landrace) showed the main variety effect, but negative estimates of variety heterosis. In relation to earliness, negative values of mid-parent heterosis indicate that the F₁ is similar to the earliest parent. Most of the values (87%) for mid-parent heterosis were negative. High-parent heterosis for plant height was generally negative. In heterosis for ear volume and kernel depth, two mechanisms of cold tolerance, most of the variation was due to cultivar effect, but the specific heterosis was the more important component.

Methods

For programming the use of heterosis in the Highland Andean-region, all the inter-variety crosses made on the 1960s in the highlands of Perú were reanalyzed. Crosses were placed in five groups: 1) crosses among accessions of nine different landraces by five varieties of wide distribution; 2) crosses among flourey white cultivars "Chocleros"; 3) crosses of flourey white cultivars by hard whites; 4) crosses of national accessions by exotic hard yellow cultivars; 5) crosses of accessions and national varieties by varieties and synthetics from U.S.A.. In all cases, the crosses were tested at two locations of contrasting altitude. The experimental methodology is described in detail in Sevilla et al. (1977).

Results

Table 1 shows composite data from 189 crosses among accessions of 9 landraces from the Peruvian highlands crossed with 5 varieties from that region. Percentage of heterosis varied from 30.1% for a cross between Blanco Urubamba by an accession from the same race, to 201.3% for a cross by San Geronimo. Yields were high because agronomic conditions were very good. Some Peruvian races such as Ancashino and Cuzco Amarillo Flint combined very well. Table 2 shows the frequency distribution in heterosis of more than 110 crosses among white cultivars, with flourey and hard endosperm. The more frequent heterosis was found in the range of 91 to 120%. Heterosis over 130% with high yield corresponded to crosses where Arizona, a landrace from the north coast of Perú, was one of the parents. Table 3 shows the good heterosis expressed by two american cultivars: Lancaster x Ferguson Yellow Dent. Both American and Guatemalan germplasm were found to be good sources to improve yield in Peruvian germplasm. Table 4 confirms the excellent heterosis obtained when Peruvian improved germplasm (Morochu Ayacucho, Amarillo Calca, Lib. 42 and Amarillo Ancash Morochu) is crossed to improved germplasm from U.S.A. (Hays Golden, A_{III} Syn 4, K_{II}A Syn 3, SSS_{III} Syn 3 and K_{III} x Caribe). It is evident that improved germplasm is more heterotic.

Conclusions

Studies on the potential of maize landraces will continue to help plant breeders better utilize this germplasm. Even though some studies have been conducted so far, much information is yet to be

obtained on the potential and performance of the hundreds of landraces of maize accessions that comprise the world collection of this species.

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Table 1. Average yield (Kg/ha) and percentage of average heterosis of accessions crossed by five varieties from the high land of Perú. (Carhuaz 1963).

	Yellow of Ancash	White Urubamba	Morocho Ayacuchano	Yellow of gold	San Geronimo
Number of crosses	49	45	28	45	22
Average yield of all crosses	8,977	8,156	8,038	8,163	8,630
<i>Percentage of average heterosis:</i>					
over average of the parents	114.0	112.4	110.2	116.17	133.4
range	83.3-181.4	30.1-147.9	86.2-125.4	92.7-139.8	92.7-201.3
over the superior parent	101.7	105.6	104.9	106.5	117.3
range	74.8-146.9	29.4-145.3	82.1-123.4	82.4-126.1	78.2-160.4
over the tester variety	101.8	109.3	111.0	122.6	151.7

Table 2. Frequency distribution of the yield heterosis (average of 117 crosses: 4198 Kg/ha) from white maize (average of two locations: Junín: 3,300 masl, Ayacucho: 2,500 masl).

% heterosis	71-80	81-90	91-100	101-110	111-120	121-130	131-140	141-150	151-160	Total crosses
Parents' average	3	7	20	30	13	4	3	4	84	
Superior parent	5	16	33	26	16	8	3	2	2	111

Table 3. Yield heterosis of crosses among germplasm from three different geographic origin (average of two locations: Junín: 3300 masl, San Miguel: 2300 masl).

	Nº of Crosses	Yield (Mg ha ⁻¹)	% heterosis (average)	% heterosis (superior parent)
Peruano x Peruano	1	5565	103.3	99.1
Peruano x Guatemala	4	6079	114.2	105.4
Peruano x Norteamericano	4	6153	116.2	113.7
Guatemala x Norteamericano	4	5936	113.0	103.8
Guatemala x Guatemala	1	6066	113.5	93.4
Norteamericano x Norteamericano	1	6344	121.8	116.4

Table 4. Average yield (Kg/ha) and heterosis of crosses from Peruvian x USA germplasm (Caraz: 2300 masl).

Crosses	No. crosses of or parents	Yield	% heterosis	
			Parents' average	Superior parent
Peruano x Peruano	9	2650	92	76
Peruano x Norteamericano	18	5207	160	139
Peruanos	4	3200		
Norteamericanos	5	3376		

A34 - Yield Improvement of Two Maize Populations

J. Ininda and W.K. Mmatta

National Agricultural Research Centre, Muguga, Kenya

Introduction

Two unrelated maize populations Muguga A (MgA), and Muguga B (MgB) were developed in Muguga Kenya (2,100 masl) to initiate a reciprocal recurrent selection scheme for the midaltitude areas of Kenya (1500-2100 masl). MgA was formed with at least 75% local Kenyan germplasm, while MgB consisted of less than 25% local populations. In order to maintain the heterotic patterns, Kitale Synthetic II (KSII) made up approximately 25% of MgA and Ecuador 573 (Ec573) 25% of MgB. Earlier studies had shown that populations MgA x MgB did not exhibit significant high parent heterosis, probably because the genetic base of the two parents was too wide. The objective of this study was to test whether there was any heterosis and/or enhancement in yield levels to either MgA or MgB by use of populations of a narrower genetic base.

Methods

Reciprocal crosses were made between MgA and two exotic populations, SR52 and SC13; and between MgA and two local populations, LFM Zack and Mg 12. Reciprocal crosses were also made between MgB and six local populations (Mg7, Em3, Mg32, Mg12, MgA465, and MgA614). Crosses were evaluated together with their parents (MgA and MgB) and three popular local checks (H511, H613 and H625) in a completely randomized-block design in two replications at two locations of Kenya. Data was collected for yield (kg/plot) and other agronomic traits, but only yield will be reported in this paper.

Results

Table 1 shows the percentage yield enhancement or decline obtained in either MgA or MgB. Crosses involving SR52 to MgA showed yield increases of up to 246%. There was very little increase in yield in the cross involving SC13. On the other hand, most crosses involving MgB (except MgB x Mg12) showed a negative decline in yield when compared to that of MgB. All crosses had significantly lower yield than the checks.

Conclusions

The yield increase in crosses involving MgA warrant improvement of the population. MgA showed heterosis with SR52, LFM Zack, SC13, and Mg12, all of which have a narrower genetic base than MgB. It would be interesting to know whether MgA populations enhanced for yield could now show any heterosis with MgB. MgA has the added advantage of containing maize streak virus resistant germplasm. Improvement of this populations could therefore be of economic benefit to Kenya.

Table 1: Percent yield increase in kg/plot in crosses involving MgA and MgB.

Cross	% yield	Cross	% yield
MgA x SR52-100	140**	MgB x Mg7	- 0.20
MgA x SR52-73	246**	MgB x Em3	- 0.05
MgA x SR52-72	166**	MgB x Mg32	- 0.05
MgA x LFM Zack	113**	MgB x Mg12	15.00*
MgA x SC13	140**	MgB x MgA65	0.00
MgA x Mg32	113**	MgB x MgA614	0.00

* Significant at 5% level.

** Significant at 1% level.

A35 - Introgression of Exotic Germplasm to Enhance Heterosis and per se Performance in Medium Maturity Maize Populations in Kenya

D.T. Kirubi, S.K. Gathama, and Z. Muthamia

Kenya Agricultural Research Institute, Regional Research Centre, EMBU. P.O. Box 27. EMBU. KENYA

Introduction

Observations in the late 1980s on midaltitude maize cultivars of intermediate maturity revealed that the performance of the recommended varieties was very low. H511 and H512 are the main commercial hybrids grown in midaltitude agro-ecological zones. This was attributed to genetic and non-genetic factors, especially genetic shift in the maize populations Embu 11 and Embu 12 used in the production of the commercial hybrids. Agronomic problems associated with the source populations are tallness, lateness, lodging and susceptibility to diseases, especially maize streak virus. Lines extracted from these populations produced late and tall hybrids.

Methods

In order to augment the current populations by broadening their genetic base, elite populations were obtained from CIMMYT and screened. Data on heterosis studies using Embu 11 and Embu 12 as testers were used to select six elite populations from CIMMYT-Harare. Three dent maize streak virus (MSV) resistant populations EV 8549SR, Pool 20SR, and SNSYNF2(N3/TUX-A-90) were crossed to Embu 11 synthetic to form Pool A. The procedure used was first to make single crosses with Embu 11, then make all possible double crosses and eight-way crosses. Three flint MSV resistant populations Across 8530SR, EV 8725SR and SNSYNF2(SC/ETO-B-90) were crossed to Embu 12 synthetic using the same procedure as explained to form Pool B. The resulting populations were then random mated twice. These pools are composed of 50% local germplasm and 50% exotic maize streak resistant germplasm. During all the crossing work and random mating, selection was made for resistance to maize streak virus, *Exserohilum turcicum*, lodging, low ear placement, and earliness. Further improvement was done within each pool for agronomic characters such as plant type, husk cover and prolificacy.

Results

Pool A and Pool B are tolerant to maize streak virus and have good stalk strength, low ear placement, and low levels of lodging. A cross between the two pools resulted in a varietal hybrid with the same maturity and a higher yield potential than the check H511, which is a product of Embu 11 crossed to Embu 12. The varietal cross from the two pools also has shorter plants, lower ear placement, and hence less tendency to lodge (Table 1). It has a yield potential similar to that of H512 but more stable across locations. Other positive aspects include tolerance to maize streak virus, good husk cover, and prolificacy.

Conclusions

Introgression of elite, exotic germplasm into the midaltitude maize breeding populations resulted in improved pools, earliness, and better plant aspect than the existing materials -- all with a stable yield potential. Pool A and Pool B are being improved for better performance against major diseases, for standability, and for earliness, to increase their yield potentials.

Table 1. Performance of a varietal cross between Pool A and Pool B.

Variety	4 Sites (1995)			6 Sites (1996)		
	Yield (t/ha)	Days to 50% pollen shed	Ear height (cm)	Yield (t/ha)	Days to 50% pollen shed	Ear height (cm)
Pool A x Pool B	4.9	70.1	141.0	4.98	68.0	122.0
H511	5.27	71.6	162.9	4.85	72.0	140.0
H512	5.62	75.4	162.2	5.29	76.0	146
LSD 5%	0.62	1.2	11.2	0.45	3.15	6.43

A36 - Evaluation of Heterotic Patterns to Develop Maize Hybrids for Midaltitude Regions of Mexico

H. de-León-Castillo, E. Ramírez-Rodríguez, G. Martínez-Zambrano and A. Oyervides-García.

Instituto Mexicano del Maíz "Dr. Mario E. Castro Gil", Universidad Agraria Antonio Narro, Buenavista 25315, Coahuila, México

Introduction

Classification of maize lines and prediction of crosses from specific heterotic patterns facilitates the development of high yielding hybrids for a region or environment. The present study sought to evaluate and characterize several heterotic patterns for developing hybrids for the Bajío region in Mexico, based on the performance of experimental crosses, estimation of the type of gene action within each heterotic pattern, and the identification of high yielding hybrids for midaltitude regions of Mexico.

Methods

The genetic material evaluated included three heterotic groups: Tropical \times Bajío (T \times B); Dwarf \times Normal (D \times N), and Early \times Late (E \times L), 20 hybrids in each category and two commercial checks recommended for the region. Hybrids were obtained using a nested mating design (Comstock and Robinson 1948), each of five males were crossed with four females. Hybrids were considered as full-sibs, and then, utilized for the genetic characterization of the groups or heterotic patterns. Data was recorded for ear yield at 15.5% moisture content, days to anthesis, days to silking and plant height. Hybrid evaluation was conducted in two representative locations of midaltitude (1100 to 1900 masl) regions during the spring-summer seasons of 1995 at Celaya, Gto., and Sandia el Grande, N.L.

Results

Results showed that the additive variance was more significant than nonadditive variance for the five traits studied for the three heterotic groups (Table 1). This suggests that reasonable heterotic expression can be obtained without a reciprocal recurrent selection scheme among contrasting populations within the heterotic pattern. The E \times L pattern produced hybrids with the highest genetic variance (Table 1) and the best agronomic traits; nevertheless D \times N and T \times B produced better ear yield (Table 2). Use of the E \times L would result in practical difficulties because of the intrinsic asynchrony of flowering in parents. D \times N, on the other hand, has synchronous flowering and offers good pollination among parents by using dwarf as female progenitor. In addition, D \times N was similar to E \times L for plant and ear height (Table 2).

Conclusions

The E \times L pattern produced hybrids with superior agronomic characteristics and higher genetic variance. Nevertheless, considering their intrinsic asynchrony difficulties, it was concluded that the D \times L pattern is the best strategy for developing hybrids for the midaltitude regions of Mexico.

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Table 1. Genetic variation components of five traits for three heterotic patterns of maize evaluated in two representative locations in midaltitude regions of Mexico, 1995.

Component	DMF	DFF	PH	EH	EY
<i>Bajio x Tropical</i>					
σ^2_A	7.61	7.65	59.91	-34.47	1.82
σ^2_D	-2.54	-3.10	2.16	216.15	-4.45
CVG(%)	1.92	1.82	2.91	7.30	5.90
<i>Dwarf x Normal</i>					
σ^2_A	43.56	48.66	82.29	-6.33	3.06
σ^2_D	-23.60	-23.90	-198.90	-54.92	-2.98
CVG(%)	4.27	4.42	2.57	0.00	7.73
<i>Early x Late</i>					
σ^2_A	18.44	58.83	61.38	229.84	0.95
σ^2_D	4.53	-31.88	284.03	-177.30	4.23
CVG(%)	3.64	5.03	5.61	9.69	11.72

σ^2_A = Additive Variance; σ^2_D = Dominance Variance; CVG = Coefficient of Genetic Variance.

DMF, DFF = Days to male and female flowering; PH and EH = Plant and ear Height; EY = Ear yield at 15.5% moisture content.

Table 2. Means of five traits for three heterotic patterns of maize evaluated in two representative locations of midaltitude regions of Mexico, 1995.

<i>BxT</i>	92.4a ¹	95.7a	188.9a	92.3a	11.4a
<i>DxN</i>	93.2a	96.8a	176.1b	84.5b	11.3a
<i>ExL</i>	88.3b	92.0b	179.8b	86.7b	10.6b

BxT = Bajio x Tropical; *DxN* = Dwarf x Normal; *ExL* = Early x Late.

DMF, DFF = Days to male and female flowering; PH and EH = Plant and ear height; EY = Ear yield at 15.5% moisture content.

¹Means with the same letter within columns are not different at the 0.05 level of probability.

A37 - Genetic Diversity for Molecular Markers and Prediction of Heterosis in Maize

S. Mladenovic- Drinic and K. Konstantinov

Maize Research Institute "Zemun Polje", 11080 Zemun - Belgrade, Serbia

Introduction

Development of a suitable method to predict heterosis before field evaluation could increase the efficiency of maize breeding programs. One possibility is use of molecular marker technology better understand the genetic and molecular bases of heterosis. If marker loci provide a reliable sample of the genome, then the distance between parents calculated on the basis of marker analyses would be correlated with heterosis (Charcosset 1992).

Material and methods

A diallel set of five maize inbred lines, F2, ZPL120, ZPI203, W401 and EP1, excluding reciprocal crosses, was studied at two locations in a random block with four replications. Gene effects were estimated from generation means by ordinary diallel analyses and by the Eberhart-Gardner model (1966). The five parental inbreds underwent isozyme, RFLP and SSR analysis. In addition, the polymorphism of salt soluble protein was analyzed in embryo tissue of inbred lines and hybrids. Based on the number of protein bands, we calculated their distribution according to the molecular weights and presence or absence index of similarity.

Results

In all hybrid combinations, significant positive heterosis was obtained for grain yield. To correlate grain yield, heterosis, and salt soluble proteins in embryo tissue, two hybrids expressing high and two hybrids expressing low heterosis for grain yield were selected for high resolution PAGE electrophoresis of embryo salt soluble protein. More hybrid specific protein bands were identified in crosses with higher heterotic effect for yield as compared to crosses with lower heterosis. Indices of similarity between lines ranged from 79.2 (highest heterosis) to 88.5 (lowest heterosis). Estimated correlation coefficients between isozyme diversity and grain yield and heterosis for grain yield were low and non-significant. Analyses of DNA markers revealed polymorphism of inbreds (Fig. 1). Genetic distance (RD) between lines, estimated from DNA marker data, averaged 0.52, ranging from 0.37 to 0.68.

Conclusions

Parameters derived from the variability of genome expression could be used as markers for different phenotypes including heterosis (Tsaftaris 1994). Comparison of heterosis for grain yield with an index of similarity suggests that inbreds with the lowest level of salt soluble protein similarity expressed the highest heterosis for grain yield. Correlation of RD and heterosis for yield were positive but relatively small (0.66) to be of practical predictive value (Melchinger et al. 1990).

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Figure 1. SSR marker analysis of five inbred line. F2 (line 1,6,11,16); ZP120 (line 2,7,12,17); ZP203 (line 3,8,13,18); W401 (line 4,9,14,19); EP1 (line 5,10,15,20).

A38 - Practical Use of Heterosis in Sorghum x Sudangrass Hybrids

C.G.S. Valdés-Lozano¹, I. Gómez-Rodríguez², J.A. Pedroza-Flores³

¹ Professor, ² Agricultural Science Doctorate Graduate Student, ³ Research Assistant, Facultad de Agronomía UANL, Apdo. Postal 358, San Nicolás de los Garza N. L., CP 66420, México.

Introduction

Interspecific forage sorghum (*Sorghum bicolor* L. Moench x *S. sudanense* Piper.) hybrids (IFOSHs) are planted in Northeast Mexico to produce forage for meat and milk production during the dry and winter seasons. All are currently imported from the USA. The Maize, Bean and Sorghum Improvement Project at the Agronomy Faculty of the Universidad Autónoma de Nuevo León (FAUANL) began an IFOSH breeding program in 1988 to teach plant breeding and develop new IFOSHs for Northeast Mexico, focusing among other things on use of intra- and interspecific hybrid vigour .

Materials and Methods

Since 1977 many sets of crosses between A1 x R1 lines have been made to develop grain sorghum hybrids. A1 and R1 lines were introduced from different sources and many R1 were developed in situ. In 1987 a Sudangrass accession from Central America was introduced and discarded for high susceptibility to *Helminthosporium turcicum*. In 1988 two Sudangrass varieties, Piper and Green Leaf (GL), were introduced from Texas. GL was selected to be used as a male parent to form two-way IFOSHs in crosses with A1 lines. Looking for a complementation for associated forage yield traits, the line A2TX632 was crossed with tropical R1 lines to form male sterile F₁s which, crossed to GL, might enhance green forage yield in three-way IFOSHs. Practical heterosis (PH) was considered as the improvement in an F₁ over the best commercial hybrid check for a given trait. We used Fisher's protected LSD (0.05) test to rank PH and form three selection groups: higher (a), none significant (b), and lower (c) PH. This approach avoids having several, overlapping significance groups and was used to group female F₁s for heterosis for high seed yield (HSY). Finally, IFOSHs that combined acceptable PH for forage grain yield (FGY), total number of leaves (TNL), leaf area index (LAI), and stem perimeter (SP), as well as high HSY female parents were identified to be suitable for commercial production.

Results and Discussion

Three IFOSHs showed statistical significance for PH for GFY in at least one of three years against two different checks (Table 1); two three-way IFOSHs and one was a single cross. A2TX632 x 10351, a three way, was made using a female single-cross hybrid that showed outstanding heterosis for seed yield under favorable environments. The high seed yield heterosis of A2TX632 x 10351 was a result of the lower rate of night respiration at warm temperatures (250°C). Because of the balance between a high heterosis for green forage yield and seed yield of the female parent, (A2TX632 x 10351) GL was tested in demonstration plots with two popular IFOSHs, Pioneer 855F and Dine A Mite. (A2TX632 x 10351)GL was not statistically different to Pioneer 855 F but had significantly higher GFY than Dine A Mite as well as two checks for TLN, LAI and SP. This IFOSH, now named Potro F 93, is ear-marked for release.

Conclusions

To enhance PH for GFY and other associated traits in IFOSHs as well as for HSY in F₁ female parents, it is useful to select within materials of complementary genetic background and parental line traits. Three-way rather than two-way hybrids allow the development of IFOSHs with a high GFY and associated traits, as well as a high potential for hybrid seed production. Use of % PH LSD ranks facilitated preliminary selection of experimental genotypes.

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Table 1. GFY PH in three test (1990, 1991 and 1992) for six IFOSH out of fourteen tested. FAUANL, Spring-Summer, Marin, N. L. , Mexico.

IFOSHs	1990	1991	1992
2A x GL*	124b	139a	79c
11A x GL	115b	124b	75c
ATX627 x GL	142b	120b	-
A2TX632 x GL	94b	108b	65c
(A2TX632 x BTX631)GL*	-	167a	106b
(A2TX632 x 10351)GL*	-	124b	127a
Cow Hand	100b	100b	74 c
Pioneer 855F	-	-	100b
% PHLSD Rank (0.05)	51-149	63-137	82-118
Best Check GFY t ha ⁻¹	35	30	14
CV%	24	22	-

* Significant in at least one year

A39 - The Improvement of Forage Yield Heterosis by Selection in Sorghum x Sudangrass Hybrids

C. G. Valdés-Lozano¹ and I. Gómez-Rodríguez²

¹ Professor, ² PhD Student., Facultad de Agronomía UANL. Apdo. Postal 358. San Nicolás de los Garza N. L., México. CP66420. Phone Fax (52) (824) 80022 and 80101

Introduction

The Maize, Bean and Sorghum Improvement Project at the Agronomy Faculty of the Universidad Autónoma de Nuevo León (FAUANL) began grain sorghum breeding in 1977 and, in 1988, a forage sorghum breeding program began to develop interespecific forage sorghum hybrids (IFOSH). Several sets of A grain sorghum lines have been used to cross to Green Leaf (GL) sudangrass cv. to obtain two-way IFOSHs. Using A2 male sterile cytoplasm grain sorghum lines crossed to R1 lines, we also obtained high-grain-yield, male sterile hybrids that produce high-hybrid-seed-yield, three-way IFOSHs via crosses with GL. The aim of this work was to evaluate the variability and select within GL to breed synthetics with higher heterosis for GFY than that of IFOSHs from crosses to male sterile A lines or A2 x R1 hybrids.

Materials and methods

In northeast Mexico there are two planting seasons for sorghum: spring to summer (SS) and summer to autumn (SA). In SA 1993, GL was planted to begin a semiannual phenotypic family (among, a) and combined (among and within, c) selection (1) under full watering (r) and a single irrigation (pr). For SA 1994, the same number of seeds of 99 half sib families, 50, 6 and 60 selected plants were mixed and in SA 1995 recombined under isolation to obtain 10 synthetics: 6 with open pollination seed (op) and 4 with selfing seed (sf): S0(a99Famop), S1(c50plrop), S2(c6plrsf), S3(c6plrop), S4(c6plprsf), S5(c60plprop), S6(c60plrsf), S7(c60plrop), S8(c60plprsf), and S9(c60plprop). In SA 1995, GL and synthetics were crossed to five A lines and to a female F₁, respectively: ATX623, ATX629, ATX631, A2TX632, N96A and A2TX632x10351(2). Seed of 41 out of the 60 possible IFOSHs was obtained. In SS 1996, under a split plot design with three replications, full watering and a single irrigation were applied within main plots and 10 synthetics were placed in subplots. An experimental unit of three 5 x 0.8 m rows was used to measure GFY in t/ha. Similarly, in SA 1996, the 41 IFOSHs were planted under the same experimental design.

Results and Discussion

In the experiment with 10 synthetics, a CV of 13.97% was obtained. There was a significant (0.05) difference among treatments and for interactions. By using a protected Fisher's LSD test, (LSD = 4.5 t/ha) under full watering only S₇ (32.0 t/ha) was higher in GFY than GL (22.5 t/ha), and S₃ (26.0 ton/ha), S₀ (22.0 t/ha), and S₉ (t/ha) were similar to GL, while the other seven synthetics were lower in GFY than GL.

The GFY of GL was compared to the average of the six open pollinated synthetics (23.6 t/ha) and to the average of the four selfed synthetics (13.1 t/ha). There was significant difference between GL and the average of the four selfed synthetics, apparently an effect of GFY inbreeding depression. Under only one irrigation GFY was depressed and GL showed a GFY of 17.0 t/ha, being statistically no different to S₀ (13.5 t/ha) or S₉ (13.0 t/ha); the other synthetics were lower in GFY than GL. No inbreeding depression was detected for GFY under only one irrigation.

In the 41-IFOSH experiment, there was a significant difference for GFY between the levels of watering among the IFOSHs and for the interaction, and an LSD_{0.05} = 2.7 t/ha indicated that full watering (41.3 t/ha) and only one irrigation (31.7 t/ha) were different for GFY. By using LSD_{0.05} = 12.4 t/ha, the six highest IFOSHs for GFY made by crossing each male sterile parent to synthetics were compared to the

six IFOSHs made with the male sterile parents crossed to GL to determine if there was improvement in GFY heterosis by selection under full watering and only one irrigation. Under this last condition, only N96A x S7(c60plprop) presented a GFY of 36.7 t/ha that compared to the 23.0 t/ha GFY of N96A x GL. This gives a significant GFY genetic gain of 12.8 t/ha by selection, the other five IFOSHs made with synthetics did not differ statistically from those containing GL. However, ATX629 x S9(c60plprop) showed the highest GFY of 43.2 t/ha but did not significantly outyield ATX629 x GL (40.8 t/ha). Under full irrigation, three IFOSHs did not show improved heterosis through selection, but the others [ATX629 x S9(c60plprop) (60.2 t/ha), A2TX632 x S3(c6plprop) (59.4 t/ha), and N96A x S8(c60plprsf)] had gains in GFY of 31.6, 21.8 and 17.6 t/ha, respectively. The greater gains under full irrigation may be explained by the depression of GFY under only one irrigation; however, the highest yielders under either treatment were IFOSHs made with selected synthetics rather than with GL without selection.

Conclusion

There was genetic variability in GL and it was possible to improve heterotic response for GFY through selection in three out of six male sterile parents when crossed to improved GL synthetics. There is no evidence that selection within GL is not successful at increasing heterosis genetic gain for GFY in IFOSHs made with the male sterile parents that did not produce a heterotic response in crosses with GL selected synthetics in this experiment. Nor can it be concluded that there is a lack of specific combining ability (SCA) for these female parents with GL, until further individual selection work for SCA in these female parents is conducted.

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A41 - Hybrid Maize and Wheat for Developing Countries: Opportunity or Challenge for Sustainable Production?

J.W. White and L. Harrington

Natural Resources Group, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico

Introduction

Increased use of hybrid maize or wheat cultivars in developing countries must affect the natural resource base for production. Possible consequences of increased use of hybrids include 1) shifts in the nutrient and water balance due to changes in uptake or losses due to runoff and leaching; 2) decreased stability of hybrid cultivars to pests, diseases or abiotic stresses due to a narrower genetic base; 3) shifts in farm economies due to increased seed cost or input requirements vs. increased farm revenue; and 4) shifts in regional economies due to increased productivity and decreased grain costs. This paper examines expected primary effects of introducing hybrids and possible consequences. Loss of crop biodiversity due to displacement of traditional cultivars and reduced *in situ* evolution of cultivars are not discussed here, since they do not affect the potential productivity of a region *per se*.

Increased Crop Vigor

Increased grain production with hybrids is usually accompanied by increased vigor that is also reflected in increased straw production. This has multiple implications.

Nutrient uptake: For stable grain and straw nutrient concentrations, a 30% grain yield increase similarly increases nutrient and water demand. To sustain yields, the nutrient balance must be positive or zero:

$$\text{Balance} = \text{Inputs} - (\text{Runoff} + \text{Leaching} + \text{Volatilization} + \text{Harvested}) .$$

With increased harvested products (grain plus straw), inputs must increase or other losses reduced. Strategies for increasing use of organic and inorganic inputs in developing countries are well known. Scope for reducing non-harvest losses of nutrients and water is less but merits study. Increased early vigor also might reduce runoff, since greater canopy cover reduces direct impact of raindrops on soil. Greater straw production can make residue conservation and zero-tillage more attractive, leading both to greater direct protection of the soil surface and long-term improvements in aggregate stability.

Farm income: Increased use of hybrids will most often increase farm income, which may have several results: 1) increased fertilizer use can restore nutrients but increase ground-water contamination or soil acidification.; 2) a shift from livestock to tractors can facilitate retention of crop residues, increasing soil organic matter, but it may also lead to increased residue burning; 3) purchase of equipment and herbicides for zero-tillage may lead to conservation of soil moisture and reductions in erosion, but may also result in evolution of new weed or pest complexes and in agrochemical misuse; 4) investments in erosion control structures will help conserve soil, but land clearing may increase degradation.

Reduced grain prices: For constant grain demand, increased yields will cause prices to decline, potentially making production on fragile lands uneconomical. Hybrids thus may allow concentration of production on less-fragile, intensively managed farmlands. Conversely, low grain prices can stimulate area expansion onto fragile lands.

Higher Seed Costs

If faced with higher seed costs for hybrids, farmers may reduce sowing rates. Lower plant stands means less early-season canopy cover, thus increasing potential for soil erosion.

Decreased Crop Genetic Diversity

The hypothesis that genetic diversity increases yield stability is frequently invoked as an argument against use of hybrids, especially for resource-poor farmers in marginal environments. Yield studies that appear to support this view exist both for temperate (Rowe and Andrew 1964) and tropical

(Ristanovic and Mungoma 1989) maize environments. However, comparing mean yields in stability indices (e.g., linear regression coefficient (b) and deviation from regression [S^2d]) often reveals that the indices are confounded with yield. In Zambia at four locations over three years, Ristanovic and Mungoma (1989) found that OPVs yielded less than hybrids in all environments, even with mean yields of trials as low as 2,900 kg/ha. For losses due to pests and diseases, a susceptible hybrid may perform worse than an OPV containing necessary resistances. Resistance genes with dominant inheritance should be easier to introduce into hybrids than OPVs. Furthermore, releasing mixtures of hybrids (Funk and Anderson 1964) can reduce the risk of resistance breaking down.

Possible Interventions

Possible consequences of the increased use of hybrids have known agronomic solutions (Table 1).

Previous research on sustainable farming systems suggests the following approaches:

- Farmer participatory research to determine, early on, possible farmer responses to use of hybrids.
- On-farm monitoring and long-term experiments to obtain hard data on consequences of adoption.
- Simulation models and GIS to examine potential consequences over longer periods and over regions and to understand better biophysical processes that affect sustainability.

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Table 1. Possible effects of use of hybrids. "+" indicates an increase, and "-" indicates a decrease.

Primary effect	Immediate implication	Secondary implication	Natural resource consequences	Interventions needed
Increased vigor	+ grain yield	+ nutrient uptake	+ soil fertility decline	runoff, erosion controls nutrient inputs
		+ farm income	+ fertilizer use	fertilizer management
			+ pesticide use	IPM, IDM
		+ machinery use	reduced/zero tillage	
	- grain prices	- marginal lands in production	alternative employment	
		+ land in production	land use planning	
		+ nutrient uptake	+ soil fertility decline	runoff & erosion controls nutrient inputs
+ crop residues	+ residue as feed	+ soil fertility decline	use of manures	
	+ residue as ground cover	- soil loss	reduced/zero tillage	
	- seed rate	- early ground cover	+ soil erosion	runoff, erosion controls nutrient inputs
Higher seed cost	+ disease and pest susceptibility	- yield instability	+ risk	IPM, IDM genetic resistance
			+ pesticide use	IPM, IDM genetic resistance

A42 - Patterns of Heterosis in South African Maize Breeding

H.O. Gevers

Quality Seed CC, P.O.Box 100881, Scottsville 3209, Republic of South Africa

Introduction

The development of hybrid maize in South Africa commenced in 1945 and continued in public and private maize breeding programmes thereafter. Following the great success of hybrid maize in the USA, the local open-pollinated maize varieties (OPVs) and numerous other introductions, mainly from the United States (US), provided the most important sources of inbred lines in public research programmes. This sector released the first maize hybrids in South Africa while subsequent releases of inbred lines during 1960-1990 continued to play an important part in the development of commercial hybrids (Gevers 1989). During this period superior heterotic combinations emerged which provided a reliable and highly successful formula for the exploitation of yield heterosis in the years to come. (Cowie 1997).

Sources of Maize Germplasm

The first inbred lines were derived from local OPVs (Van Schaik et al. 1958). Among others, the local yellow OPVs Teko Yellow (TY), Sahara (SAH) and Natal Yellow Horsetooth (NYHT) and the white OPV Potchefstroom Pearl (PP, NPP), mostly of earlier Corn Belt origin (Saunders 1942), played a significant part in the development of useful breeding sources for the future. In retrospect, however, all local germplasm showed optimal heterosis for yield only in combination with introductions from other countries, mainly the USA but, surprisingly, also from Australia. In a large introduction of germplasm from the USA in the 1950s, the Kansas inbred K64 was described by Laubscher (1970) as "a diamond in a pile of gravel". Similarly, a solitary inbred of Australian origin, namely 21A, in combination with the US OPV Jellicorse, gave rise to the outstanding breeding source M37W (heterotic group M). In the course of time local maize breeding sources, introductions from other countries, and introgressions of various genetic backgrounds resulted in heterotic groups which for many years have provided important sources of elite and widely used inbred lines.

Results and Conclusions

A review of the most important heterotic groups indicates that a limited number of local and introduced maize breeding sources were used in the development of conventional and quality protein maize (QPM) hybrids in southern Africa (Gevers and Whyte 1987) (Table 1). For instance, some 30 years after their release, a survey showed that the yellow inbred lines F2834T (F group), used in both normal maize and QPM, and I137TN (I group), were still being used in commercial products by all respondents in 1993. Similarly, the white inbreds M162W, a K64R type, remained an important contributor, while the use of M37W (M group) was declining in commercial hybrids. Furthermore, the production of hybrid seed involving one or more public lines, although declining, still stood at 80% in 1993 (Cowie 1997). Inbred K64R (K group) has also made a profound impact in white hybrids both in southern and sub-Saharan Africa, the latter due to its widespread use in Zimbabwean hybrids. QPM has been developed mainly around the heterotic groups F, M, and P in high combining conversions of normal breeding material. Finally, the contribution of Corn Belt maize germplasm, notably from the Reid (R) and Lancaster (L) groups, have maximised heterosis for yield in yellow hybrids. The elite yellow inbred I137TN (from the OPV cross TY × NYHT), was particularly successful in combination with Reid- and Lancaster-type inbreds B73 and MO17, respectively. These heterotic groups have all made a considerable impact in southern African maize hybrids but have no doubt been subjected to widespread sub-selection and modification. The impact of the increased use of hybrid maize seed in South Africa, since its inception in 1949-50, has been directly associated with the phenomenal maize production trends in the period 1950-1980 (Gevers 1997).

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Table 1. Main heterotic groups (HG), their origin, and typical use in South African maize hybrids.

HG	Source/Inbred type	Source origin	Heterotic use
P	PP, NPP/NAW5867*	Local OPV	PxK ₁ ,PxP,F,PxM**
K	K64*/K64R*, M162W*	Kansas, USA	KxP**,KxF,KxI
F	TY/F2834T*	Local OPV	FxM**,FxP,FxR
M	21A ² . Jelllicorse/M37W*	Australia/USA	MxF**,MxP,MxL
I	TY x NYHT/I137TN*	OPV cross	IxR,IxL,IxM,IxP**
R	Reid/B37*, B73*	USA OPV/Inbred	RxI,RxF,RxP
L	Lancaster/MO17*	USA OPV/Inbred	LxI,LxF,LxM,

* Representative inbred line derived from source.

** QPM and normal hybrids.

A44 - Yield Potential of Hybrids Developed from Tropical Semi-Prolific Populations

D. Beck, J. Betrán, C. Sánchez, G.O. Edmeades, M. Bänzinger, M. Sierra, O. Cano, and A. Ortega

Maize Program, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F.; and Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP), Mexico.

Introduction

The growing demand for maize in the tropics is often not met due to yield losses caused by poor plant stands, high weed incidence, competition from intercrops, drought, low fertilizer inputs, etc. Prolific plant types with the ability to produce more than one ear under low densities or high input conditions and to produce one ear more consistently under stressed conditions may provide farmers with more stable and higher yields across a range of environments (Maita and Coors 1996; Subandi 1990). For this reason the CIMMYT maize physiology subprogram began work on developing semi-prolific populations and hybrids.

Materials and Methods

In 1986 two tropical, semi-prolific, white-grained populations were formed. An early fraction (Semi-Prolific Early, SPE) and a late fraction (Semi-Prolific Late, SPL) comprised a wide variety of elite, white tropical materials which showed moderate prolificacy at normal plant densities (Edmeades et al. 1995). Selection was based on high grain yield and lodging resistance at high densities, and on a high number of ears per plant (EPP) and lodging resistance at low densities. Half-sib selection was used initially, then S_1 selection. Early generation inbred lines from the S_1 recurrent selection program were both recombined to form a new selection cycle and further inbred in a separate nursery. Initial combining ability evaluations were conducted with S_3 lines from SPE and S_2 lines from SPL in combination with the CIMMYT tropical tester lines, CML247 and CML254. Topcross hybrids were evaluated in separate trials for SPE and SPL in Mexico in 1995 and 1996 under drought and non-stressed conditions. Lines selected from these evaluations were further inbred and crossed to a broader range of tropical tester lines. In the 1996 summer cycle, a 50-entry trial of SPE hybrids and a 90 entry trial of SPL hybrids were tested in 3-4 non-stressed Mexican environments.

Results

The initial topcross trials with SPE and SPL lines show the same pattern. Mean yield for topcrosses to CML254 were approximately 1.5 t/ha higher than topcrosses to CML247 (Figure 1). In this and subsequent trials we consistently observed more prolificacy in crosses with CML254. Both SPE and SPL lines have mainly flint grain and show the best heterotic response with the Tuxpeño A type dent tester, CML254. In the 1996 winter/spring evaluations in non-stressed and water-stressed environments in Mexico, mean grain yields ranged from 3.0 to 8.7 t/ha (data not shown). Few SPE and SPL hybrids showed good performance over the range of environments tested. Mean yields for the trials conducted in Obregón under well-watered conditions were only 3.5 t/ha. Temperatures exceeding 40°C were common at this location, thus heat stress may have accounted for the low yields. In the 1996 summer season evaluation under non-stressed conditions, five of the six best SPE hybrids for yield were in combination with CML254 (Table 1). The superior hybrid was SPEC6F74-1-5-1-1-1/CML254, yielding 9.3 t/ha with 1.4 EPP, using 58 days to male flowering, with essentially no lodging, and a harvest moisture of 22.6%. This hybrid out-yielded all late-maturing check entries, including CML247 × CML254 which produced 8.1 t/ha, using 61 days to male flower, and with a harvest moisture of 32.5%. Results from the 90 entry trial of SPL hybrids evaluated in four non-stressed Mexican locations show the high yield potential of this material (Table 2). Among the various lines showing significant promise is SPLC7F254-1-2-3-2, which in combination with CMLs 258, 254, 264, and 273 ranked number 1, 2, 4, and 6 for yield. SPLC7F254-1-2-3-2 × CML258 yielded 10.2 t/ha across four environments with good standability. This hybrid had taller plant height, similar ear height, less lodging, less harvest moisture, and 29% more yield than the check hybrid CML247 × CML254.

Conclusions

Development of semi-prolific tropical populations from elite source germplasm appears to have provided a unique source of inbred lines. Most lines from these populations have flint grain type and combine well with Tuxpeño A type, largely dent testers. Improved sink strength through prolificacy along with a fairly clear heterotic pattern may partially explain the high yield potential of this material. Under drought stress, hybrids from the semi-prolific populations appear to perform average at best although they seem to be above average in susceptibility to heat stress. Evaluations in additional environments should help us further clarify the utility of the prolific characteristic and the yield potential of the semi-prolific germplasm in hybrid combinations.

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Table 1. Best Semi-prolific early (SPE) hybrids with CML254 and CML258 across locations in 1996B.

Ent	Pedigree	MF	PH	EH	RL	SL	YD	EPP	MS
4	SPEC6F74-1-5-1-1-1/CML 254	58.2	238	142	4	1	9.32	1.4	22.6
10	SPEC6F271-1-1-1-1-1/CML 254	59.8	255	141	28	6	9.01	1.2	26.9
31	SPEC6F23-1-3-1-2-1/CML258	58.4	243	135	22	1	8.97	1.0	25.7
16	SPEC6F23-1-3-1-2-1/CML 254	58.8	245	134	16	1	8.88	1.1	26.4
11	SPEC6F271-1-1-1-2-1/CML 254	60.3	245	131	22	1	8.88	1.3	27.0
	Check CML247 x CML254	60.7	226	123	8	1	8.11	1.0	32.5
	Mean, hybrids	58.0	233	128	23	2	7.5	1.1	24.9

Table 2. Best semi-prolific late (SPL) hybrids with CMLS 254, 273, 264 and 258 across locations, 1996B.

Ent	Pedigree	MF	PH	EH	RL	SL	YD	EPP	MS
55	SPLC7F254-1-2-3-2/CML258	62.3	241	130	4	2	10.2	1.2	24.1
1	SPLC7F254-1-2-3-2/CML 254	62.6	240	141	12	1	9.7	1.6	22.2
73	SPLC7F210-2-3/CML 254	64.2	256	153	19	1	9.6	1.5	24.2
38	SPLC7F254-1-2-3-2/CML264	62.7	244	121	14	0	9.5	1.4	23.3
74	SPLC7F183-1-2/CML 254	64.1	256	143	19	2	9.3	1.2	23.9
20	SPLC7F254-1-2-3-2/CML273	61.8	241	133	16	1	9.1	1.4	21.1
	Check CML247xCML254	64.7	229	133	11	2	7.9	1.0	26.7
	Mean, hybrids	63.0	238	133	18	2	7.8	1.1	23.1

MF: male flowering date (d). PH: plant height (cm). EH: ear height (cm). RL: % of plants affected by root lodging. SL: % of plants affected by stalk lodging. YD: grain yield adjusted to 15.5% moisture content (t/ha). EPP: Ears per plant MS: % moisture content.

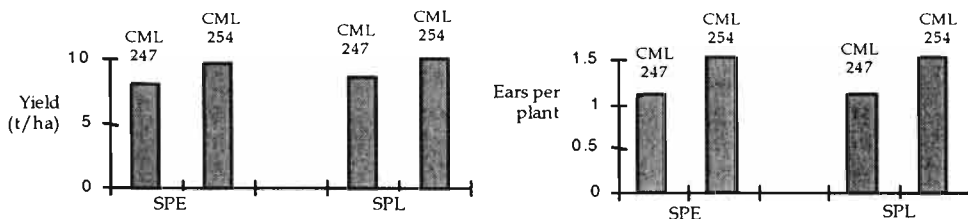


Figure. 1 Yield and ears per plant for SPE and SPL topcrosses evaluated at three locations, 1995B.

Transgressive Variability of Productivity Characters of Triticale Plants Developed in vitro and in vivo from Heterotic F₁ Hybrids

L.N. Kaminskaya, K.V. Khotyljova, S.N. Matveenکو

Institute of Genetics and Cytology of Belarus Academy of Sciences,
220072, Minsk, Belarus

Introduction

An important application of in vitro culture techniques in triticale breeding programs concerns anther culture to produce homozygous lines from F₁ hybrids in the shortest possible time. Androgenesis by anther culture offers a way to develop haploid regenerants that carry new gene combinations and rapidly produce homozygous lines by artificial or spontaneous chromosomes doubling. The technique avoids the time consuming process of conventional methods that require several selfing generations after hybridization to develop homozygous lines. It was observed that there was a high level of variability within populations of dihaploid plants which allows to select desirable genotypes (Borojevic and Sesek 1989). A combination of conventional and biotechnological techniques was the most useful and effective approach to achieve the best results in plant breeding programs (Pauk et al. 1995, Arzani and Darvey 1996). The objective of this study was to compare quantitative characters and their transgressive variability in triticale dihaploid plants R₂, R₃ produced in vitro by anther culture from heterotic F₁ hybrids with those of segregated generation F₂ and F₃ plants on the same hybrid combinations.

Methods

Ten F₁ hybrids were developed from 5 dihaploid lines (Kaminskaya, Khotyljova, Matveenکو 1996). The F₁ hybrid crosses were used to produce dihaploid plant generations R₁, R₂ and R₃ using segregating generations. F₂ and F₃ plants were obtained from the same hybrid combinations. Selection of the most productive plants was carried out within R₂ and F₂ populations. The selected plants formed populations R₃ and F₃. Thus, five groups of plants: R₂, R₃ (designated as "variant I") and F₂, F₃ (designated as variant II") and the parental dihaploid lines were studied during 1995 and 1996 under field conditions to compare quantitative characters of R₂, R₃ and F₂ and F₂ F₃ populations and their rate and frequency of transgressive variability according to Vosresenskaya's and Shpota's method (1967). Field experiments included five groups of plants in randomized complete design blocks with five replications. The experiment was planted in 10 m in length with 20 x 5 cm between plants. At harvest, quantitative traits of 20 plants in each replication were measured for each entry. Border plants were excluded. Five traits (spike length, spikelet and grain number, yield per spike and per plant) were evaluated. The results for hybrid N1 (Rosner x 6TA471), N4 (6TA471 x Rosner), N5 (6TA471 x T441), N7 (T441 x Rosner), N8 (T441 x Armadillo), N9 (T441 x 6TA471) with high productivity and N3 (Rosner x GL17), N10 (T441 x GL17), N11 (GL17 x Rosner), N14 (GL17 x T441) with low productivity (Matveenکو, Khotyljova, Kaminskaya 1994) are presented in Table 1.

Results

It was shown that there were segregations of positive transgressions in populations R₂ developed on the basis of hybrids F₁ with high productivity (Table 1). Rate and frequency of positive transgression for grain yield per plant in R₂ populations derived from F₁ hybrids with high levels of heterosis N4, N7 and N8 were higher compared with those obtained from F₁ hybrids with low heterosis (Table 1). The same result was observed in R₃ populations, but the magnitude of the character expressions was lower compared with R₂. A comparison of variant I (R₂, R₃) and variant II (F₂, F₃) populations revealed a higher frequency of favorable segregants in R₂ and R₃ populations.

Conclusion

It can be concluded that *in vitro* culture techniques in combination with conventional field selection of desirable plants may be an effective procedure in triticale breeding. The use of F_1 triticale hybrids with high levels of heterosis may increase the probability of selecting desirable homozygous lines from R_2 , R_3 populations. This research project was sponsored by The Foundation for Fundamental Research of the Republic of Belarus (Project Number B96-089).

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Table I. Rate and frequency (*) of positive transgressions of triticale plants in R_2 , R_3 (variant I) and F_2 , F_3 (variant II) populations, %.

Sample	Variant	Spike length		Spikelet number		Transgressions		Yield per spike		Yield per plant	
		R	F	R	F	Grain per spike		R	F	R	F
1	I	19.2	30.0	17.9	43.4	104.4	46.7	90.9	40.0	170.0	56.7
	II	16.7	46.0	4.4	6.0	65.5	80.0	22.7	10.0	23.6	15.1
4	I	2.5	8.3	6.7	25.0	43.1	66.7	27.3	58.3	112.5	75.0
	II	-5.8		-15.8		6.3	6.0	-4.5		-12.8	
5	I	2.3	3.3	13.5	56.7	62.8	66.7	60.9	46.7	192.5	50.0
	II	-5.4		-9.1		23.3	36.0	26.1	16.0	33.8	18.0
7	I	0		8.6	25.0	98.5	65.0	117.4	70.0	191.2	80.0
	II	-15.4		0		24.1	20.6	-4.3		28.4	13.1
8	I	0		12.4	69.2	74.4	100.0	39.1	100.0	155.9	100.0
	II	-17.7		-6.4		2.2	16.7	-43.5		-10.0	
9	I	10.0	18.5	11.1	48.1	56.5	59.3	60.9	48.1	127.5	63.0
	II	-2.3		-9.1		2.1	7.7	-26.1		-16.5	
3	I	-4.9		-1.1		-3.0		-42.1		-6.3	
	II	-10.6		-15.8		-30.9		-47.4		-29.3	
10	I	5.4	6.7	16.1	60.0	15.5	6.7	10.5	6.7	54.2	23.3
	II	0		1.5	4.0	-4.4		-31.6		-8.9	
11	I	-2.4		-1.1		-25.1		-36.8		60.4	21.4
	II	-2.4		-3.7		-9.1		-42.1		-12.5	
14	I	7.7	16.7	16.1	50.0	15.9	13.3	2.6	10.0	75.0	33.3
	II	2.3	5.3	3.7	10.5	5.4	5.3	-39.5		-13.1	

R = Transgression rate.

F = Transgression frequency.

* Frequency of negative transgressions was not calculated.

The Biology and Physiology of Heterosis

C.W. Stuber

US Department of Agriculture, Agricultural Research Service, and Department of Genetics, North Carolina State University, Raleigh, NC, 27695-7614, USA

Introduction

The manifestations of heterosis abound in hundreds of millions of hectares of field and vegetable crops. Although this phenomenon is one of the primary reasons for the success of the commercial maize industry as well as the success of plant breeding endeavors in many other crop and horticultural plants, the causal factors for heterosis at the physiological, biochemical, and molecular levels are today almost as obscure as they were at the time of the Conference on Heterosis held in 1950 (Stuber 1994). Genetic theories for heterosis are 1) dominance, including linked dominant favorable factors; 2) true overdominance, which is nearly impossible to distinguish from pseudo-overdominance (i.e., nearby loci at which alleles having dominant or partially dominant advantageous effects are in repulsion phase linkage; and 3) certain types of epistasis. Although the elucidation of these theories remains as a major challenge, several studies using biochemical, molecular, or physiological approaches provide some limited insights into a better understanding of heterosis. Even though the biochemical and/or physiological responses reported may only represent manifestations of heterosis at a level other than at the overall mature plant stage (as measured in the field), these responses should be closer to the gene level and may ultimately help to elucidate the genetic basis of heterosis.

Review and Perspective

Hepburn et al. (1987) studied DNA methylation in plants and reported several observations in the literature that offered evidence for a relationship between methylation and suppression of gene activity. Extrapolations of these observations lead to the hypothesis that provides for a gradual accumulation of methylation during selfing, which is released and/or repatterned when hybrid crosses are made. Tsafaris et al. (1996) also implicated DNA methylation as a mechanism for controlling gene regulation in maize. They reported that environments which cause stress (such as high density planting) increased the level of methylation, which, in turn, suppressed genetic expression throughout the genome. They suggested that an epigenetic DNA modification such as this (which may alter gene expression) could be heritable because such a change can occur in a plant cell that may become a gamete.

The role of the phytohormone gibberellin (GA) has been studied with respect to the regulation of hybrid vigor. Rood et al. (1988) studied shoot growth in maize and reported that hybrids contained higher concentrations of endogenous GAs than their parental inbreds, which could provide a phytohormonal basis for heterosis. They also showed that a deficiency of endogenous GA limited the growth of the inbreds, which could cause inbreeding depression. In a more recent study, Rood et al. (1992) found that endogenous GAs are probably involved in heterosis in sorghum, but the effects are not as dramatic as in maize. Rood (1995) stated that the correlation between GA content, GA metabolism and growth rate in inbreds versus hybrids suggests that the phenomenon of heterosis for rapid shoot growth rate in sorghum is partially mediated by GA. Although rare, examples of heterosis associated with a specific form of an enzyme attributed to a single genetic locus have been reported. However, it is generally recognized that overall plant response involves the interactions of many enzymes associated with numerous genetic loci.

Environmental variability may have an effect on the relationships of specific physiological components to heterosis. However, in a study of the influence of temperature on heterosis for several seedling traits, Rood et al. (1988) found that the level of heterosis for these traits could not be explained simply by the ability of hybrids to better tolerate cool temperature stress. We have mapped QTLs affecting heterosis for grain yield and several other traits in maize under eight combinations of stress and non-stress

related variables. The variables were drought and optimum moisture, deficient and optimum nitrogen, and low and high planting density. Even though the yield level of the least stressful combination of variables was 10 times greater than that of the most stressful combination, the QTL mapping pattern changed very little. Veldboom and Lee (1996) likewise found similar QTLs in a maize study grown in two different environments, though without the severity of stress applied in our studies.

Conclusions

Even though there is a dearth of information regarding the biochemical, physiological, molecular, and genetic factors involved in the expression of heterosis, plant breeders will continue to use this phenomenon to produce more productive hybrids. As new technology at all levels (molecular, cellular, tissue, organismal) unfolds, exciting new methodologies should become available to make plant breeding more efficient and more precise.

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Towards Understanding and Manipulating Heterosis in Crops - Can Molecular Genetics Help?

M. Lee

Department of Agronomy, Iowa State University, Ames, Iowa 50011-1010, U.S.A.

Introduction

Plants are exceedingly complex and unusual biological systems. Their genomes typically contain large-scale duplications indicative of polyploidization events, localized duplications (gene families), a high proportion of mobile elements (DNA and RNA transposable elements) and other systems of DNA modification which confer considerable fluidity and much raw genetic material for adaptation and selection. In the simplest terms, the final phenotype reflects the expression and interactions of tens of thousands of genes in the genome during a complete cycle of plant growth and development.

Expression of each gene may be regulated by several other gene products (e.g., transcription factors), chromatin status and environmental cues at various stages of development and at several points along the path from DNA to the final product(s) and phenotype(s). Often, the metabolic and signal pathways within the plant intermingle, interact and overlap such that complex networks mediate much of the flux among genes, environments and phenotypes.

When the primary goal of a crop breeding program is improved grain yield, it is a certainty that most of the genome contributes to the ultimate aggregate phenotype. This is especially true in dynamic and stressful production environments which challenge the production as well as the protection of biomass (yield). In hybrid breeding programs, higher and/or more stable yield is achieved by systematically improving and combining interactive genomes and exploiting heterosis. This presentation will examine areas of molecular genetics and technologies as potential tools for understanding heterosis and for facilitating crop improvement.

Perspectives and Prospects

Genome projects have become important engines of awareness and change in the biological sciences. The projects have generated much basic information and have stimulated the development of new technologies relevant to crop improvement. The first generation of technologies included DNA markers such as RFLPs. DNA markers have improved or expanded our abilities to discriminate among genotypes, understand the genetic architecture of phenotypes, isolate genes, conduct indirect selection, and connect plant breeding to plant biology. DNA markers have become another tool for plant breeding programs. Concurrently, new high-capacity DNA sequencing facilities have been used to determine the DNA sequence of entire genomes (e.g., yeast) and thousands of cDNA clones of plants (e.g., *Arabidopsis*, rice and maize). Most of the sequenced genes have no known function and many others merely have an inferred function.

The next generation of activities involves characterization of the cDNA clones, their genes, functions, and interactions. Obviously that is an enormous task which requires several phases and approaches, such as high density hybridization arrays (i.e., DNA chips). No doubt each approach will have its logical limitations but they will gradually reveal for the first time the components (genes) of complex biological systems (plants).

Questions and Conclusions

What do we really know about the biological basis and mechanisms underlying heterosis? Very little. Will new information and technology enhance our understanding of heterosis, hybrid breeding programs and crop productivity? Are they compatible with the magnitude and holistic nature of plant breeding? Plant breeding has achieved much with limited knowledge of basic plant biology. How long can we expect that to continue? Initially, the new information and technology will have the problems of any new expedition - no track record, competition for resources, and great expectations. However, given the predictions for human population growth, such efforts are needed because a greater burden will be placed on plant genetics as a management tool to sustain crop production. Knowledge will become a more important source of variation for crop improvement.

Epigenetic Changes in Maize DNA and Heterosis

A.S. Tsaftaris, M. Kafka, A. Polidoros* , E. Tani

Department of Genetics and Plant Breeding, Aristotle University of Thessaloniki, Thessaloniki, Greece

* Present address: Dept. of Genetics, North Carolina State University, Raleigh, NC, USA

Introduction

Although the biological basis of heterosis remains unknown, plant breeders have made wide use of this phenomenon and it is generally believed that the understanding of the mechanisms underlying heterosis will enhance our ability to form new genotypes which may be used directly as F₁ hybrids or form the basis for future selection programs. While the original data concerning the phenomenon came out of studies at the phenotypic level, they were followed by physiological and later by biochemical data (Srivastava 1981; Rhodes et al. 1992). More recently efforts have been made at the molecular level and the results suggest the significance of both the regulatory proteins (and their encoding genes) and the mechanisms of regulation of gene activity in manifestation of complicated phenomena such as heterosis (Leonardi et al. 1991; Tsaftaris 1995; Tsaftaris and Polidoros 1993). One such mechanism involved in regulating the amount of expression output of genes is methylation of cytosines residues in its DNA (Cedar 1984). The extent and distribution of genomic DNA methylation was found to be significantly correlated with the rate of expression of many genes examined not only in plants but in all higher organisms as well.

The goal of this work was to study the extent of cytosine methylation in maize genomic DNA, its variation among different genotypes (parental inbred lines and hybrids), and developmental stages. The role of maize growth conditions in the field on the extent of genomic DNA methylation under stressful or more favorable conditions was also examined.

Methods

DNA methylation was measured following different approaches and at different levels, namely as percent methylation of the whole genomic DNA and at random regions of the regions of the genome. The plant material used was grown at the Experimental Farm of Aristotle University of Thessaloniki using the honeycomb experimental design (Fasoulas 1995) and it consisted of different maize inbreds and their hybrids. All maize plants were sown in two different plant densities: 1.5m (spaced) and 25cm (dense) distance between individual plants, with a density of 0.513 plants/m² and 18.5 plants/m² respectively. DNA was extracted as described by Karlinsky et al. (1989) with minor modifications from leaves of plants grown for 20 (stage 1), 32 (stage 2), 47 (stage 3), and 66 (stage 4) days in the field. DNA after alkaline hydrolysis was hydrolysed with 99% HCOOH at 170° C for 30 minutes, the bases were then lyophilized for 4-5 hours and, finally, were separated using high performance liquid chromatography (HPLC). The molecular concentrations of cytosine and 5-methylcytosine were estimated according to Patel and Gopinathan (1986).

Methylation of random regions of maize genome was studied using methylation sensitive enzymatic digestion (HpaII) followed by Polymerase Chain Reaction (PCR) where a number of different random primers were used. Furthermore methylation status of maize genotypes was correlated with their performance in the field.

Results

Maize DNA methylation was found to be genotype, tissue and developmental stage specific as well as to be affected by the environmental conditions. The average methylation for all genotypes (excluding those from the dense planting) was 27,6%, a number which is very close to the 27,2% estimated by Amasino et al. (1990). In general, hybrids were less methylated than inbreds and between inbreds there was a variation in their methylation status: improved lines were less methylated than with old low yielding lines.

In addition, our results indicate that environmental conditions can induce epigenetic changes by altering maize DNA methylation. Random regions of maize genome were methylated at the dense planting whereas at the spaced less or no methylation was observed for both inbreds and hybrids .

However changes of methylation status seemed to be more significant for inbreds than for hybrids. Total genome methylation of inbreds at the dense planting at stage 4 was 29.19% versus 27.54% at the spaced whereas hybrids showed similar percentage of methylation (26.45% at the dense versus 26.15% at the spaced).

Conclusions

Significant differences exist in maize DNA methylation among maize parental inbred lines and hybrids and between inbreds and hybrids. These epigenetic modifications in maize DNA are highly affected by the growing conditions of the plant.

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Potential Heterosis Associated with Developmental and Metabolic Processes in Sorghum and Maize

J. D. Eastin¹, F. Zavala-Garcia, A. M. Dhopte, V. B. Ogunlela, C. Petersen, M. W. Witt, P. K. Verma, V. Gonzales-Hernandez, M. Livera-Munoz, L. Mendoza-Onofre.

1 University of Nebraska, Agronomy Dept., Lincoln, NE 68583-0817, USA

Introduction

Grain yield gains attributable to heterosis in maize and sorghum have been substantial despite the fact that "...we actually understand relatively little about the genetics, physiology, biochemistry, or molecular bases of hybrid vigor" (quote from this symposium announcement). At times it appears that we know more about the methodologies by which traits are manipulated than about which yield limiting traits we should be manipulating. Therefore, let us begin to consider ways to improve our understanding of the order of yield limiting factors in any environment of choice to provide a sound framework within which to best utilize the advantages of hybrid vigor and related genetic manipulations as they apply.

Approach

Developmental physiology was popular several decades ago (prior to the advent of fancy physiological research toys), even before hybrid vigor in maize and associated cultural practice changes shook up production levels. Unfortunately, developmental physiology receives little attention now apart from the recognition of "critical stages" and general maturities required for the environments in question. Critical stage oriented research, even in the absence of yield component analyses, has and is serving breeders and production scientists well in increasing crop production. However, progress could increase if vagaries in climate over short intervals (weekly) during all of inflorescence development were related to fluctuations in the seed number component of yield. Also climate fluctuations during all of grain fill need to be related to changes in the seed size component of yield. One might then compare current year fluctuations in yield and yield components to long-term yield and component of yield averages for specific locations. Relating fluctuations in climate to yield and yield component fluctuations allows one to pinpoint developmental stages when yield reductions are most commonly climate forced. This narrows the stages at which biochemical strengths and weaknesses in essential mechanisms need to be investigated and subsequently manipulated using modern molecular techniques to complement traditional breeding techniques. Research on how to sharpen selection techniques for yield limiting mechanisms (apart from pest and herbicide resistances and crop quality enhancements) to amplify gains from heterosis and other genetic manipulations merits very high priority.

Results

Eastin (1983) compared sorghum hybrids (RS610, RS626, RS625, RS671 and Redlan x TX415) and parents for duration of preanthesis panicle development (growth stage two-GS2) and grain fill duration (GS3). All hybrids yielded significantly more than their parent means except Redlan x Tx415. RS671 had only a 2.5% longer GS3 than its parent mean and accomplished its 18.8% higher yield mostly through a GS3 grain fill rate 16.4% faster than the parent mean. By contrast the other RS hybrids showed 10 to 15% faster grain fill rates sustained over 10 to 12% longer GS3 periods giving a mean yield increase of 24.8% over parent means. These simple types of analyses seem not to have been used extensively in hybrid improvement programs and appear useful. Unfortunately yield components were not measured.

Understanding yield-limiting stress/high yield mechanisms begins with pinpointing the times the yield limitation is induced. Ogunlela and Eastin 1984, 1984, and Eastin et al. 1990 determined that near microsporogenesis is the most stress sensitive preanthesis stage in sorghum and the nature of the damage is reduction in seed number. Data were used by Eastin, et al. (1988) to fashion a successful

preanthesis field stress screening technique for the U.S. Great Plains. Hybrids using R lines from these field stress screenings usually are near or at the top of the US Regional Research Dryland tests conducted at Lubbock, TX by D. T. Rosenow (Tx A&M) demonstrating that they are competitive with hybrids from breeding programs several times the size of our germplasm manipulation. The screening technique works well in traditional plant breeding programs but does not help in molecular genetics programs. However, field data upon which the technique is based are being used to develop a potentially useful metabolic mechanism screening approach as follows. Ogunlela and Eastin 1984, determined developmental stage sensitivities by regulating night temperature 5°C and 10°C above ambient in the field and also determined that this did not inhibit photosynthesis (PS) (Ogunlela and Eastin 1985). Therefore, night effects were of a higher limiting order than day effects, implicating respiration (RS) and energy requiring RS-coupled syntheses as more limiting than PS. Therefore, mitochondrial RS studies have just been initiated on stress sensitive and stress resistant sorghums. Stress resistant genotypes seem to maintain greater oxidative coupling at higher temperatures which appears to be related to production of 22 Kd heat shock proteins. The potential utility of metabolic research seems sound but couching the research within sound field frameworks is challenging.

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A45 - Genetic Analysis of Chromosomes of a Wheat R-line for Fertility Restoring (Rf) Genes

M.A. Samad, J.D. Franckowiak and S.S. Maan

Wheat Research Centre, Bangladesh Agricultural Research Institute, Joydebpur, Gazipur, Bangladesh and Department of Crop and Weed Sciences, NDSU, Fargo, ND 58105, USA

Introduction

Production of commercial hybrid seed of wheat requires a system where a male sterile female parent is cross-pollinated efficiently under field conditions by the male parent and the hybrids are fully self fertile. To produce fully fertile F₁ hybrids having *T. timopheevii* cytoplasm, male sterile A-lines are crossed with R-lines. B-lines which have *T. aestivum* cytoplasm and the A-line nuclear genes are used to produce seed of A-lines. The R-lines have fertility restoring (*Rf*) genes, which produce fertility in the F₁ hybrids. Unfortunately, expression of *Rf* genes is not effective in all A-line genotypes and is a major obstacle in breeding parental lines for production of hybrid cultivars. Genetic and cytogenetic analyses of R-lines have indicated that one or two major *Rf* genes, one or two minor *Rf* genes, and several positive and negative factors modify conditions of the *T. timopheevii* sterility-fertility restoration system of wheat hybrids (Robertson and Curtis 1967; Talaat 1969; Maan et al. 1984; Bahl and Maan 1973; Zeven 1970; Du 1988). Expression of major *Rf* genes on chromosomes 1A, 6B and 1B in different R-lines are modified by genes located on other 18 chromosomes. Studies of R113, a wheat R-line to locate *Rf* genes in specific chromosomes indicated that major *Rf* genes are located on chromosomes 1A and 6B (Maan et al. 1984; Maan 1985). The interrelationship of other nuclear genes in R113 and individual *Rf* genes has not been investigated. Individual chromosomes of R113 were studied by developing chromosome substitution lines for each of the 21 chromosomes of R113. The objectives of the experiments were designed to: 1) evaluate individual chromosomes of R113 in substituted lines for their effect on fertility restoration and 2) determine the chromosomal location of inhibitors which suppress *Rf* genes present in R113.

Methods

To analyze the 21 chromosomes of a wheat R-lines, R-113 for the effect of the fertility restoring (*Rf*) genes, genetic materials developed at the North Dakota Agricultural Experiment Station, North Dakota State University, were used. A set of 381 R113 chromosome substitution (R-sub) lines were developed via SSD (single seed descent F₇ lines, 2A lines at F₄) from crosses between the 21 monosomic Chris stocks and R113. Twenty-four F₄ lines (control-1) were developed via SSD from crosses of euplastic Chris and R113. Two male sterile lines (A-lines) having *T. timopheevii* cytoplasm -- mst-Chris and mst-Era -- were used as male sterile testers. Normal Chris, Era and alloplasmic R113 served as a fertility control (control 2). R-sub lines having a specific R113 chromosome, were crossed to mst-Chris and mst-Era. To make the test crosses, 100 seeds of each of mst-Chris and mst-Era were planted in rows twice with a seven-day interval in a greenhouse soilbed. Four seeds of each of 381 R-sub line were planted in continuous rows with 5 cm between seeds. Test crosses of mst-Chris and mst-Era to R-sub lines and control 1 lines were made in three greenhouse nurseries: 1986 Spring, 1987 Spring, and 1987 Fall. The testcross F₁ (TCF₁) progenies were planted during the subsequent greenhouse nursery to examine male-fertility. A total of 335 test crosses with mst-Chris and 327 with mst-Era were made, and 301 R-sub lines were crossed to both male sterile female testers. A total of 662 TCF₁ progenies from crosses to R-sub lines 48 TCF₁ progenies from crosses to control (Chris/R113) lines, and two TCF₁ progenies from R113 crosses were evaluated during the four greenhouse nurseries 1986 Fall, 1987 Spring, 1987 Fall and 1988 Spring. Male-fertility was estimated from self-fertility determined by seed set in bagged spikes. Seed set in TCF₁ plants was estimated on spikes which were placed in a glassine paper bag prior to anthesis. The primary and a secondary tiller of each plant were bagged. The seed set estimate was based on an average of two bagged spikes from each of four plants. Total seed and spikelets from bagged spikes were recorded and seed set was expressed as seed/spikelet.

Results

Two *Rf* genes, probably *Rf*₆ located on 3A and *Rf*₁ on 1A chromosome of R113, had weaker restoring effects than *Rf*₄ on 6B. R-sub lines of chromosomes 2A and 6A produced more male sterile TCF₁ plants and appeared to have dominant fertility restoration inhibitor genes. R-sub lines of chromosome 5D produced no male sterile TCF₁ plants in mst-Era crosses suggesting that mst-Era has a fertility restoring factor on 5D, which is not present in mst-Chris.

Conclusions

Presence of inhibitor factors on chromosome 2A and 6A of R113 expressed in TCF₁ progenies produced dominant effects in heterozygotes. Thus, these inhibitor factors are different than those observed by Du (1988). Only the sterility pattern produced by chromosome 5D R-sub lines in their TCF₁ progenies could be caused by recessive inhibitors present in Chris and not in Era. Du (1988) reported that chromosomes of group 1 and 7 of Chris had inhibitors which produced monosomic F₁ hybrids with higher fertility in hemizygous conditions. In this study, R113 chromosomes of group 1 and 7 did not reduce fertility in the respective TCF₁ progenies. Du (1988) reported that chromosome group 3 and 6 of Chris are essential for fertility of F₁ hybrids. Genetic analysis of chromosomes of R113 chromosome 3A carried an *Rf* gene which may be ineffective in hemizygous conditions. He also reported that a single hemizygous *Rf*₄ gene on chromosome 6B was not expressed in F₁ mono-6B, but the *Rf*₁ gene on 1A was better expressed in F₁ mono-1A or a backcross mono-1A. Genetic analysis of 21 chromosomes of R113 in this study confirmed that chromosome 6B of R113 had a restoration effect and chromosome 6A produced an inhibitory effect. Robertson and Curtis (1967) identified only one critical chromosome in R3 for having *Rf* gene but could not analyse chromosome 3A. The same R-line is reported to have two *Rf* genes (Livers 1964). They speculated that the second *Rf* gene might be located on 3A of R3. Analysis of R113 chromosomes identified an *Rf* gene on chromosome 3A. Thus, *Rf*₆ gene may be on chromosome 3A and come from *T. timopheevii* genome.

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A46 - A System for Study of the Biochemical and Molecular Basis of Heterosis in Maize

N.W. Widstrom,¹ P.F. Byrne,² M.D. McMullen,³ and M.E. Snook⁴

¹ USDA-ARS, Plant Resistance/Germplasm Enhancement Research Unit, Tifton, GA 31794

² Dept. of Agronomy, Colorado State University, Fort Collins, CO 80523

³ USDA-ARS, Plant Genetics Research Unit, Columbia, MO 65211

⁴ USDA-ARS, Phytochemical Research Unit, Athens, GA 30613 (retired)

Introduction

Enzyme polymorphism and protein electrophoresis have been proposed as tools for research on hybrid vigor in maize (Drinic et al. 1996; Konstantinov et al 1996). The study of regulation and expression in flavonoid biosynthesis also has been suggested as a potentially useful framework for studying heterosis mechanisms (Bowen 1996). Numerous genes that control anthocyanin and plant pigment production in maize have been identified and catalogued during the last 60-80 years. Neuffer et al. (1968) published a convenient summary of these genes and their effects, but research on the chemistry of flavonoids and its control by these genes was delayed until the 1970s (Styles and Ceska 1977, 1981, 1989). The identification of a flavone glycoside that inhibits growth of the corn earworm, *Helicoverpa zea* Boddie (Waiss et al. 1979) initiated research that revealed a host of other related compounds with similar effects (Gueldner et al. 1991; Snook et al. 1994, 1995; Widstrom and Snook 1997). Specific genetic control of the biosynthesis of these compounds and how previously identified genes are involved has also been the subject of recent studies (McMullen et al. 1996; Byrne et al. 1996a, 1996b, 1996c, 1996d). The involvement of some enzymes in the biosynthetic pathway has also been reported (Deboo et al. 1995; Marrs et al. 1995; Matsuki 1996).

Methods

We first examined relevant literature for interrelationships among pathways, particularly for the flavones, which elicit inhibitory responses in corn earworm and fall armyworm, *Spodoptera frugiperda* J. E. Smith. We then established a framework for the synthesis of the compounds using known and proposed pathways, including enzymes and genes that regulate segments of the pathway or encode for enzymes for specific steps in the biosynthesis. Genes and quantitative trait loci (QTLs) have been identified which are associated with synthesis of the primary antibiotic flavones found in maize silks; maysin, apimaysin, 3'-methoxymaysin and isoorientin (Fig. 1). Several crosses manifesting heterosis for these compounds (Table 1) have been identified.

Results

We have established a framework for synthesis of several biologically active compounds found in corn silks. The proposed pathway for flavonoids and plant pigments includes more than twenty known chemical steps -- 10-12 that are hypothesized or not well characterized -- and some 20 genes and associated enzymes. Most pathway entities are involved with the synthesis of compounds that are biologically active against the corn earworm. Using RFLPs we have located QTLs on chromosomes 1, 2, and 9 for maysin and chromosome 5 for apimaysin and have implicated several known plant pigment genes as pathway regulators or as elements controlling specific pathway reactions.

Conclusions

Several compounds, including maysin, have been isolated from corn silks and identified as having inhibitory effects on growth of the corn earworm. Genes and QTLs have been identified on at least three chromosomes that are associated with synthesis of these compounds. We now have several crosses expressing heterosis for maysin production; and the study of interrelationships among alternative genes, enzymes, and pathway reactions leading to the production of maysin and its analogues can be expected to give us new insight for understanding heterosis and its mechanisms.

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Table 1. Summary of chemical concentrations in silks of 12 corn inbreds and their 66 possible single crosses.

	Chlorogenic acid	Maysin	Apimaysin + 3'-methoxymaysin
Range of inbreds (% dry wt)	0.03-0.40	1.14-6.43	0.11-0.64
Range of hybrids (% dry wt)	0.06-0.48	0.41-7.60	0.08-0.58
# of hybrids exceeding high parent	8 [†]	12 [‡]	3 [§]

[†] Three exceeded the high parent by more than 0.1%; [‡] Seven exceeded the high parent by more than 0.5%; [§] One exceeded the high parent by more than 0.1%.

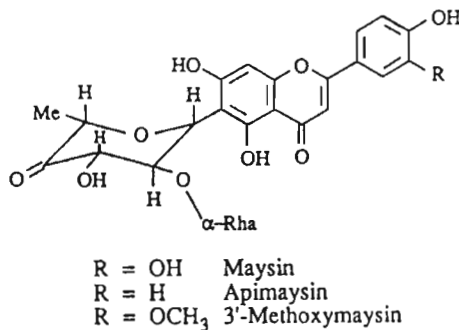


Figure 1. Structures of three frequently occurring corn silk compounds which inhibit corn earworm growth.

A47 - *Enarthrocarpus lyratus* Cytoplasm Causes Male Sterility in Oilseed Rape

S.S. Banga and Shashi K. Banga

Department of Plant Breeding, Punjab Agricultural University, Ludhiana-141004, India

Introduction

Current F₁ hybrids of oilseed rape (*Brassica napus* L.) are based on two sources of cytoplasmic male sterility namely *polima* and *tournefortii* (Banga 1996). In spite of the commercial status of these sources, identification of new and functionally superior CMS systems remains the major concern of *Brassica* breeders. Such a need arises due to environment sensitive expression of male sterility (*pol*) and the biological penalty associated with these systems. This report describes the development of a new cytoplasmic male sterility - fertility restoration system for oilseed rape that is based on *Enarthrocarpus lyratus* cytoplasm.

Material and Methods

BC₁ seeds of an intergeneric cross (*Enarthrocarpus lyratus* x *B. campestris*) x *B. campestris* (Gundimeda et al. 1992), provided by Prof K.R. Shivanna, Delhi University, New Delhi, comprised the basic material. BC₁ plants were observed to have varied degree of pollen fertility. One plant having almost normal fertility was selected to be crossed and backcrossed with *B. napus* so as to develop *napus* alloplasmic line with *lyratus* cytoplasm. In each cycle of backcrossing alloplasmic male-fertile plants were used as female. Most of the plants in each generation of backcrossing were either sterile or partially sterile. Cytological analysis of one almost fertile plant in BC₃ generation revealed presence of extra chromosome (2n=39). Further meiotic analysis (19 II + 1 I) confirmed addition of alien chromosome from *E. lyratus*. This plant was again backcrossed with *B. napus* recurrent parent wherein conscious attempts were made to select normal (2n=38) male sterile as well as male fertile plants. Both these objectives were achieved in BC₅ generation.

Results

Alloplasmic male sterile *B. napus* plants closely resembled the recurrent parent in morphology and plant vigour. These had slight leaf yellowing (due to high carotenoid content), reduced plant height and were late to flower and mature as compared to the recurrent parent. The male sterile flowers possessed normal-sized nectaries but narrow petals and reduced anthers which contained very low number of unstained pollen grains. The meiosis was normal as revealed by normal diakinesis and separation during anaphase I and II.

Alloplasmic male fertile plants were indistinguishable in morphology from the recurrent parent. Pollen fertility was normal although some PMC's showed meiotic deviations like two univalents during diakinesis or aberrant separation of one chromosome pair during anaphase I.

The F₁ between alloplasmic male sterile (*lyr* CMS) and alloplasmic male fertile plant was fertile with an average pollen fertility of about 80%. However, pollen fertility in individual F₁ plants varied from 38 to 92%. The F₂ derived from a perfectly fertile plant (92% pollen fertility) segregated in 26 fertile : 5 sterile fashion. This revealed a good fit with the expected 3:1 ratio of monogenic dominant inheritance.

Discussion

Cytoplasmic male sterility in alloplasmic lines is a common manifestation of lack of harmony between endogenous nucleus and alien cytoplasmic genome. Wild crucifers have proved to be excellent sources of cytoplasmic male sterility in crop brassicas (Prakash et al. 1995; Banga 1996). *Enarthrocarpus lyratus* (2n=20 EnEn), a weedy crucifer endemic to Mediterranean region, has been demonstrated to be cytogenetically diverse (Gundimeda et al. 1992) from crop brassicas. Successful induction of CMS in *B. napus* also proves its cytoplasmic diversity from *B. napus*. *E. lyratus* (*lyr*) male sterility appears to possess

commercial potential due to stable expression of male sterility, absence of serious morphological aberrations and complete development of floral nectaries. It was also possible for us to simultaneously introgress the gene(s) for fertility restoration from *E. lyratus* to *B. napus* genome. However, variation for pollen fertility in F₁ (38 to 92%) and meiotic abnormalities, albeit at low frequency, in PMC's of fertile plant with *lyr* cytoplasm suggest that introgression of gene(s) for fertility restoration is yet to be stabilized. Further selection will be needed to achieve meiotic stability and uniform fertility restoration. It is expected that *lyr* CMS systems will aid in the development of better hybrids in this crop of global importance.

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A48 - Standardization of Row Ratios and GA₃ Application in Hybrid Rice Seed Production in India

M. Ilyas Ahmed*, Sukhpal Singh, C.H.M. Vijayakumar and M.S. Ramesha

Hybrid Rice Programme, Directorate of Rice Research, Rajendranagar, Hyderabad-500 030, India.

Introduction

For economic feasibility and commercial viability of hybrid rice technology, development of an efficient seed production package is a pre-requisite. Seed yield in a seed production plot depends, among other factors, on proportional area under female parent and extent of seed set on it. Seed yield of female parent was proportional to increase in its area between 16% and 78%, after which it declined (Virmani, 1996). The proportion of female parent in seed production plot is determined by number of rows of seed parent to pollen parent. Therefore the row ratios assume special significance in seed production. All the commercially useable CMS lines in India, have the wild abortive (WA) cytoplasm. Panicle exertion in these CMS lines is incomplete and Gibberellic Acid (GA₃) is needed to be applied for complete exertion of panicle. The extent of outcrossing and consequently the per cent seed set depends on application of appropriate dosage of GA₃. The objective of the present study was to standardize the row ratios and GA₃ application, for hybrid rice seed production under Indian conditions.

Methods

During wet seasons 1993, 1994, 1995 and dry season 1994-95 experiments were conducted following a ratio of 2 rows of male and 16 rows of female parent with six replications at 26 locations in wet season and 6 locations in dry season across the country for CMS multiplication and hybrid seed production to ascertain the optimum row ratio for obtaining higher seed yields. Similarly during wet seasons 1994, 1995 and dry season 1994-95 experiments on GA₃ application with doses ranging from 0 to 200 g/ha were conducted at 11 locations with four replications to find out the appropriate dosage of GA₃ to increase seed yield. GA₃ was applied on two consecutive days with 40% of the dosage given on first day and the remaining 60% on next day. Data were recorded on seed yield (kg/ha) and seed set (%).

Results

In row ratio experiments based on mean calculated over locations and seasons the highest seed yield of 1348 kg/ha was obtained with a ratio of 2 male : 10 female in CMS multiplication; but it was not significantly different from 2 : 6 and 2:8 ratio. Considering the seed requirement of A line and its cost, a ratio of 2:6/2:8 was considered optimum (Fig. 1). Similarly based on the results obtained, a ratio of 2 male : 10 female was considered optimum for hybrid seed production (Fig. 2). The seed set (%) was highest at 2:2 ratio both in CMS multiplication (32.8) as well as in hybrid seed production (34.4) which gradually declined to 23.5 and 28.1 respectively in 2:16 ratio. The results from the experiment on GA₃ application indicated that the seed yield obtained was highest (1499 kg/ha) at 45 g/ha beyond which there was no significant increase.

Conclusion

Based on the exhaustive studies conducted over the past four years on row ratio and GA₃ application the following conclusions have been drawn. A seed rate of 15 kg of female and 5 kg of male parent for CMS multiplication and 16.5 kg of female and 3.5 kg of male parent per hectare for hybrid seed production has been suggested. With presently available parental lines and under prevailing cultural practices the optimum row ratios were found to be 2 male : 6 or 8 female and 2 male : 10 female for CMS multiplication and hybrid seed production respectively. A GA₃ dosage of 45 g/ha in two splits (40 and 60%) on consecutive days at 5% heading resulted in higher seed yields. These findings have been incorporated into the package developed for hybrid rice seed production in India.

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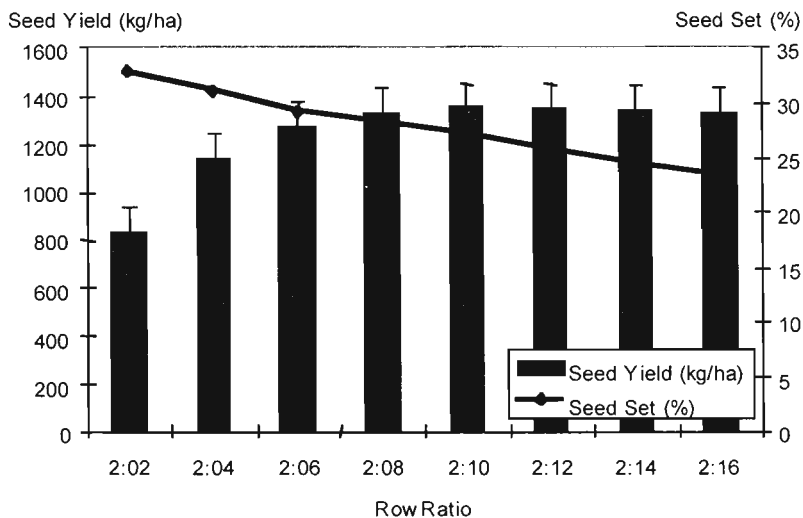


Figure 1. Effect of row ratio on seed yield in CMS multiplication.

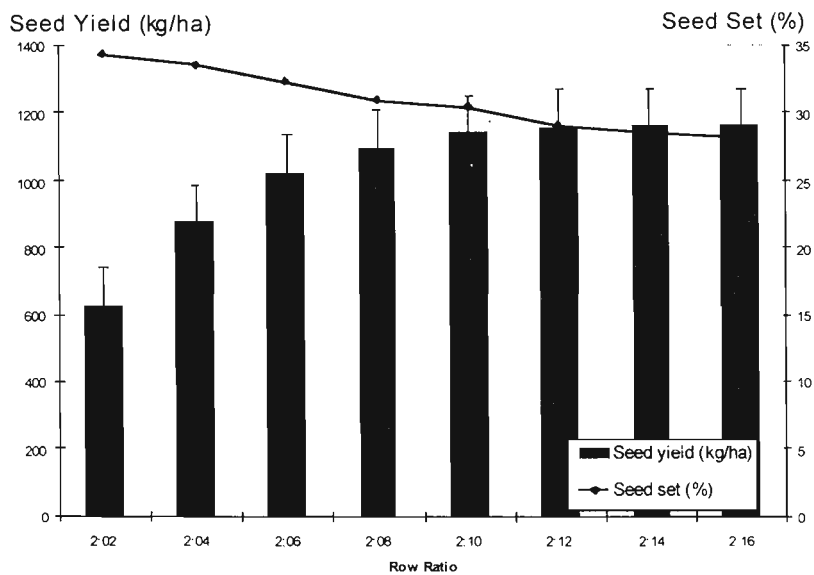


Figure 2. Effect of row ratio on seed yield in hybrid seed production.

A49 - Heterosis Under Normal and Stressed Conditions and the Possibilities for Combining High Productivity and Stress Resistance in Tomatoes

Zh. P. Danailov

Institute of Genetics "Acad. D. Kostoff" BAS, Sofia - Bulgaria

Introduction

Temperature resistance studies and elaboration of methods for general improvement of adaptability in tomatoes are the subject of intensive scientific work (e.g., Bruggeman et al. 1994; Cannon et al. 1973; DeVos et al. 1981; Marshall 1982;). The absence of suitable methods for evaluation as well as the complex genetic nature of cold tolerance appear to be the greatest constraints on improvement. Of great interest in the elaboration of methods for tomato adaptive breeding is research to achieve enhanced heterosis in F_1 hybrids. The present study concerns cold stress tolerance in tomato genotypes at early growth stages, its inheritance in F_1 under normal, stressed, and recovery conditions, and the extent to which quality differences in parental seed lines affect heterosis.

Materials and methods

Seed germination tests of tomato lines and F_1 hybrids were conducted at 12°C and 22°C in a thermostat controlled chamber. Seed germination and its inheritance in F_1 were determined on the basis of the mean scores for U-statistics (Scott and Jones 1982) at 12°C. Experiments on initial stages of vegetative growth, carried out in phytocabinets, determined relative growth rate (RGR) of plant height and biomass weight in three treatments -- control (at 3-4 true leaf stage, grown at 26°C/18°C - day/night), stress (20 days at 12°C/8°C - day/night), recovery (15 days at the conditions of the control). The variability and inheritance of the traits analyzed in F_1 . To study environmental effects on heterosis, parental lines of F_1 hybrids were grown in three different regions and the plants obtained were crossed in a diallel in the hybrid breeding range. Comparative yield trials of parental lines and F_1 hybrids were then conducted in the same region.

Results

Tomato genotypes analyzed at germination differed in cold tolerance. The more negative the U score, the more intensive the seed germination and the greater the tolerance. Definite patterns in the degree of dominance in F_1 are not established when contrasting and similar tomato parental lines for tolerance are crossed. There was no correlation between tolerance at germination and at early vegetative growth: r (to 50% germination, RGR of plant height) = 0.29; r (to 50% germination, RGR of biomass weight) = 0.32. The RGR and its inheritance in F_1 under normal, stressed, and recovery conditions differed according to the specific norm of genotype response for each environment. The genotype variability of growth reaction under recovery is significantly wider than under stress (Fig. 1); analogous to the variability for biomass accumulation. Thus, recovery response gives the best opportunity to identify cold tolerance in tomato genotypes during early vegetative growth stages. Regarding environmental effects on heterosis, in most hybrid combinations some 0.7 to 28.0% was observed, depending on the combination and the crossing location.

Conclusion

Seed germination of tomato genotypes under low temperatures is not correlated with tolerance in early vegetative stages and cannot be used as a criterion for tolerance in subsequent growth stages. The degree of recovery for plant height and biomass accumulation at early stages, based on RGR, could be used to select and develop tomato genotypes that possess cold tolerance. Differences in the type of inheritance in F_1 under normal, cold, and recovery conditions at early growth stages are determined by different genetic mechanisms. Tolerant tomato genotypes at seed germination and early vegetative stages were identified and it was established that the degree of environmental effects on heterosis for yield depends on the environment of seed formation of parental lines -- but the relationship is not

linear. Increased environmentally related heterosis is observed when the mother line is grown in the same environment as that where the hybrid cross occurs.

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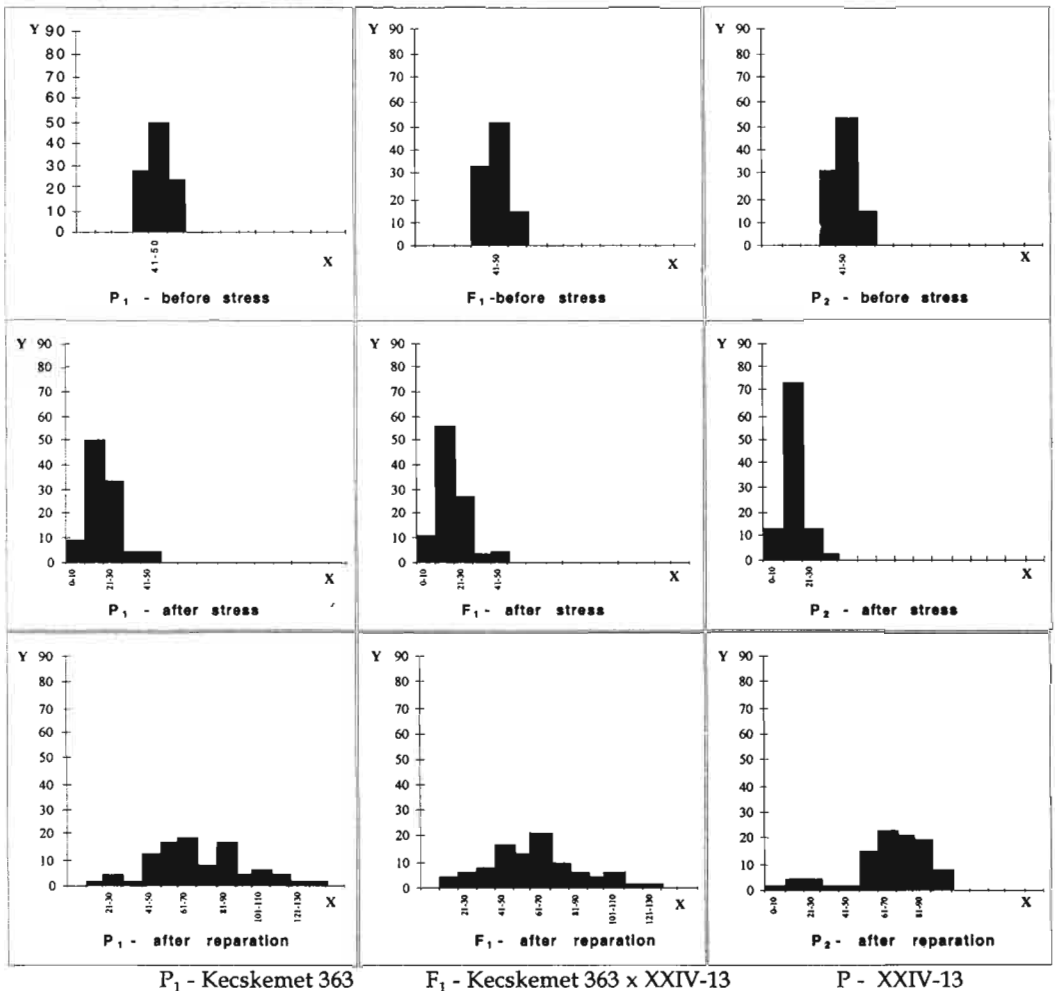


Figure 1. Influence of low temperature stress on the genotypic variability of plant height (x = height; y = % frequency).

A50 - Physiological Basis of Heterosis: Gibberellins and Heterosis in Eggplant

M.A. Rashid

Horticulture Research Center, Bangladesh Agricultural Research Institute, Gazipur 1701, Bangladesh

Introduction

There has long been interest in the physiological or biochemical mechanisms which underlie genetic differences in growth, including differences associated with hybrid vigour. The stimulus to growth that results in hybrid vigour remains a biological phenomenon that has not been fully explained either physiologically or genetically. The possible involvement of gibberellins (GA's) in heterosis was originally suggested by Nickerson and Embley (1960). They suggested that genetically determined changes in indigenous hormone could have measurable phenotypic effects. In recent years Rood and colleagues (Rood *et al.* 1983, 1988, 1990, 1992; Rood 1986). demonstrated in maize and sorghum that hybrids possessed greater concentrations of GAs. They observed greater promotion of shoot growth in maize and sorghum inbreds when sprayed with gibberellic acid (GA₃) which suggested that a deficiency of endogenous GA limited the growth of inbreds. Although hybrid vigour has repeatedly been observed in eggplant, no such studies have been made. Therefore, an experiment was made to study the involvement of GA in hybrid vigour in eggplant (*Solanum melongena* L).

Methods

Three eggplant inbreds P₁, P₂ and P₅ and their two heterotic hybrids P₁×P₂ and P₁×P₅ were included in this study. Seedlings were grown in 9cm (dia.) plastic pot. Following an initial harvest, three concentrations of GA₃: 20, 65 and 200ppm (w/v) were applied on the stem apex and young expanding leaves, starting with two weeks old seedling and spraying was carried out at 2-day interval for two weeks. The experiment was conducted in glass house following a factorial design. Data were collected on different growth parameters eg., shoot dry weight (g), Leaf area, leaf dry weight, stem height and stem dry weight. Relative growth rates (RGR) were calculated using the standard formula as in Radford (1967).

Results

The analysis of variance for all the characters measured are shown in Table 1. All the shoot characters showed significant differences between genotypes and between GA₃ treatments, except for leaf area and leaf dry weight. However, all the characters showed non-significant genotype x treatment interactions except for stem height which showed a linear trend: the genotypes which were shorter at the beginning responded most to GA₃ irrespective of whether they are inbreds or hybrids.

Significant genotypic differences were observed for Ln shoot dry weight at the initial harvest prior to GA₃ application (Table 2). The hybrid plants were larger with greater shoot dry weights than their parents, an indication of hybrid vigour in these crosses. Although the in shoot dry weight showed significant differences between genotypes and treatments but the genotype x treatment interaction was not significant. The two hybrids P₁×P₂ and P₁×P₅ produced the highest dry weights and maintained their advantage consistently across all GA treatments. GA₃ application increased the RGR of all genotypes equally so that there were highly significant genotype and GA treatment effects but no genotype x treatment interaction.

Conclusions

Exogenous GA₃ applications showed significant modifications of the shoot growth of both inbreds and hybrids. The shoot growth was similarly influenced in all the five genotypes including inbreds and their hybrids. The two hybrid P₁×P₂ and P₁×P₅ had already produced greater dry weights than their parents at the initial harvest and their superiority was maintained consistently across all GA treatments including control. Thus the results clearly suggest that the mechanism of hybrid vigour in eggplant is

quite different from that demonstrated in maize and sorghum. Hybrid vigour in this material was expressed at a very early stage of development. Further research should therefore be concentrated on development of enzyme and/or hormone activities in early seedling growth.

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Table 1. Mean squares and their significance for different growth parameters from the analysis of variance.

Source	Df.	Ln shoot dry wt.	Ln leaf area	Ln leaf dry wt.	Ln stem ht.	Ln stem dry wt.
Rep	2	0.053*	0.082**	0.017 ns	0.088***	0.289
Geno	4	0.417***	0.270***	0.267***	0.591***	1.008***
Gibb	3	0.199***	0.021 ns	0.003 ns	2.081***	1.732***
Gen x Gibb	12	0.009 ns	0.007 ns	0.006 ns	0.011**	0.017 ns
Residual	38	0.015	0.012	0.015	0.004	0.020

NS = Non significant; ** = Significant at P < 0.01 *** = Significant at P < 0.001.

Table 2. Ln shoot dry weights (g) as affected by exogenous GA₃ application.

Genotypes	Initial harvest	GA ₃ Concentration			
		00 (Control)	20	65	200
P ₁	-2.583	-0.470	-0.102	-0.065	-0.146
P ₁ xP ₂	-2.526	-0.275	-0.043	-0.027	-0.036
P ₂	-3.372	-0.673	-0.465	-0.434	-0.426
P ₁ xP ₃	-2.422	-0.107	-0.011	-0.024	-0.036
P ₃	-2.601	-0.297	-0.224	-0.129	-0.099

LSD (P<05)

Genotype = 0.101 Gibberellin = 0.089

Geno x Gibb = 0.201

A51 - Microsatellite and RAPD Polymorphism in Rice Cytoplasmic Male-Sterile Lines

E.D. Redoña, L. R. Hipolito, T.D. Ocampo, L.S. Sebastian

Plant Breeding and Biotechnology Division, Philippine Rice Research Institute (PhilRice), Maligaya, Muñoz, Nueva Ecija 3119, Philippines

Introduction

Maintaining genetic diversity among cytoplasmic-genetic male sterility (CMS) system rice germplasm would reduce risks associated with genetic uniformity and could also facilitate the development of heterotic gene pools and combinations. This study assessed the nuclear genome diversity of CMS lines at PhilRice using microsatellite and random amplified polymorphic DNA (RAPDs) markers.

Methods

Twenty-two CMS lines were studied, including 16 developed at or introduced through the International Rice Research Institute (IRRI) and provided by Dr. S.S. Virmani, four from Yunnan Agricultural University (YAU), China provided by Professor Li Zhengyou, and two from PhilRice. DNA extraction from 8-week old plants followed the CTAB procedure. PCR reactions were run on a PTC-100 thermocycler (MJ Research, Inc., Watertown, MA) using 22 microsatellite primers (RM pairs, Research Genetics, Hansville, AL) and 30 random decamers (Operon Technologies, Alameda, CA). To widen the genomic coverage of marker assays, RAPD primers and RM pairs that produced bands mapping to different rice chromosomes (Redoña and Mackill, 1996; Panaud et al., 1996) were used. RAPD products were electrophoresed on 2% agarose gels and visualized under UV light after ethidium bromide-staining. PCR products for microsatellite analysis were run on 6% (w/v) polyacrylamide denaturing gels and visualized using Silver Sequence™ DNA staining reagents (Promega, Madison, WI). Binary scoring was based on presence, '1' or absence, '0' of bands. Similarity coefficients, derived through Nei's method (Nei and Li, 1979) were used for cluster analysis and a dendrogram was made using the UPGMA procedure and NTSYS-PC computer software (Rohlf, 1990).

Results

Seventy-seven of the 79 microsatellite alleles (97%) amplified by the 22 primers were polymorphic among the CMS lines, with the number of alleles ranging from 2 to 7. Seventeen of the 77 polymorphic alleles (22%) were unique to a CMS line. The 30 RAPD primers amplified 83 polymorphic bands ranging from 1 to 9 and averaging 2.7 bands per primer. Only two RAPD bands (2%) were unique to a CMS line. With the exception of IR69627A, CMS lines from IRRI had at least 50% of their microsatellite alleles in common with those of IR58025A, a line that has been used extensively to develop hybrids in the tropics (Table 1). Allele comparisons with IR62829A, another popular CMS line, showed similar results, although the percentage genomic similarities were generally lower. CMS lines from YAU and PhilRice had fewer alleles in common with either IR58025A or IR62829A; but PR2A was the most similar line to IR62829A. Cluster analysis also revealed a major grouping of 10 IRRI CMS lines and the differentiation of other lines into separate groups (Fig. 1), though several IIRI lines clustered together with lines from YAU and PhilRice. PR1A, PR2A, IR62829A, 28A, and Jinante A were the most genetically dissimilar from the rest of the CMS lines assayed.

Conclusions

Although RAPDs provide wider genomic coverage, microsatellite markers were more effective in detecting unique alleles among the CMS lines. The use of CMS lines from various sources appeared to have widened the genetic resource base for hybrid breeding in the Philippines. There appeared to be sufficient diversity that could be useful in facilitating testcrossing activities through the use only of representative CMS lines from each major cluster. The impact on genetic diversity of the transfer of the CMS character from introduced CMS lines into more suitable genetic backgrounds, however, is still

unclear. Furthermore, molecular characterization of the cytoplasmic genome would be required if both nuclear and cytoplasmic diversity in our hybrid rice breeding materials is to be ensured.

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Table 1. Percent common microsatellite alleles between IR58025A or IR62829A and CMS lines.

CMS Line	Source	Alleles shared w/ IR58025A (%)	Alleles shared w/ IR62829A (%)	CMS Line	Source	Alleles shared w/ IR58025A (%)	Alleles shared w/ IR62829A (%)
28A	YAU	45.5	45.5	IR70960A	IRRI	77.3	54.5
IR58025A	IRRI	100.0	54.5	IR70963A	IRRI	50.0	54.5
IR62829A	IRRI	54.5	100.0	IR78371A	IRRI	68.2	50.0
IR68280A	IRRI	59.1	59.1	913A	YAU	50.0	50.0
IR68886A	IRRI	81.0	54.5	JinanteA	YAU	50.0	40.9
IR68896A	IRRI	77.3	54.5	LianA	YAU	52.4	45.5
IR68901A	IRRI	63.6	59.1	PMS8A	IRRI	54.5	50.0
IR68902A	IRRI	68.2	50.0	PMS10A	IRRI	68.2	54.5
IR69622A	IRRI	72.7	50.0	PR1A	PhilRice	27.3	31.8
IR69626A	IRRI	59.1	50.0	PR2A	PhilRice	50.0	63.6
IR69627A	IRRI	40.9	45.5	PragathiA	IRRI	59.1	40.9

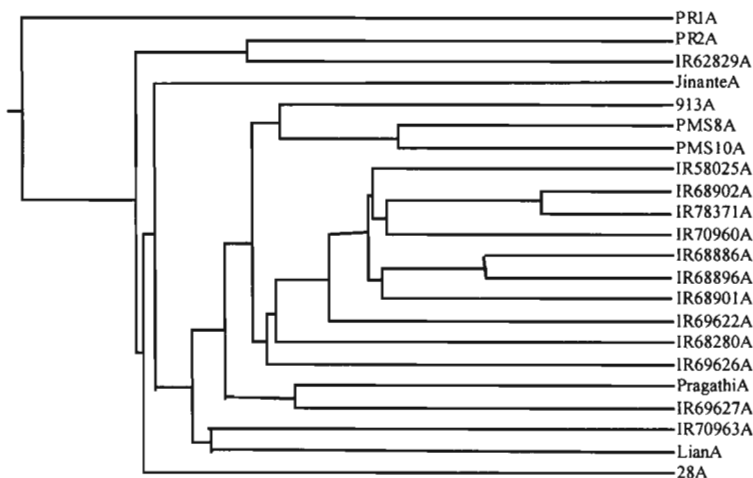


Figure 1. Cluster diagram for the 22 CMS lines classified by banding patterns produced by 22 microsatellite and 30 RAPD primers.

A52 - Development of a Transposon Based Strategy to Analyze the Genetics of Apomixis

E. Perotti, O. Leblanc, D. Grimanelli, D. Hoisington and Y. Savidan

Institut Francais de Recherche Scientifique pour le Developpement en Cooperation (ORSTOM) and the International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F. Mexico

Introduction

Apomixis in higher plants can be defined as asexual reproduction through seeds (Nogler 1984). It is a process usually restricted to polyploid plants that bypasses meiosis and fertilization of the egg cell, producing by parthenogenesis offspring which are clones of the mother plant. Typically it is a facultative phenomenon as apomictic plants normally produce both reduced and non reduced megagametophytes. Although the apomictic process seems complex, it has been shown in a wide variety of species to segregate as a Mendelian factor (Asker and Jerlings 1992). Recently Grimanelli et al. (1997) working on *Tripsacum dactyloides* showed that the genomic segment carrying apomixis was characterized by a strong restriction to recombination. This result does not exclude a monogenic control of apomixis but it suggests that there could be a cluster of genes involved in the process. Due to its characteristics, apomixis would permit the fixation of hybrid vigor, simplify hybrid production and allow for niche-breeding. Therefore we are trying to isolate the genetic system responsible for apomixis and transfer it to maize.

An important step in achieving this objective is to determine the number of genes controlling apomixis as well as to isolate the corresponding alleles. One option for this is to dissect the process by knocking out its components and study the phenotypes produced. As transposons seem to be the best tool available to achieve that goal we have initiated a transposon tagging experiment (Walbot 1992).

Methods

In *Tripsacum* ($x=18$) the closest apomictic relative of corn, polyploids reproduce through the diplosporic type of apomixis. Diplospory results from meiotic failure in megasporocytes that directly develop into mature unreduced female gametophytes through three or more mitoses. As no transposable elements have been found in *Tripsacum*, the facultativeness of apomixis was utilized to introduce transposons into a maize-*Tripsacum* apomictic background. Provided maize transposable elements activity occurs in an ameiotic *Tripsacum* environment, three types of possible results are envisioned: First, the apomictic process could be totally or partially disrupted. This should give us information on the number of genes involved. Secondly, while the plant remains apomictic, the level of expression of the trait (level of facultativeness) may vary. This would show the existence of regulatory activities. Finally the transposon tagging experiment will enable us to clone the genes implicated in the control of apomixis.

Results and Discussion

Apomictic maize-*Tripsacum* dihaploid plants combining 10 and 18 chromosomes from maize and *Tripsacum* respectively (Leblanc et al. 1996) were crossed with maize stocks containing a high number of transposable elements of the Mutator family (provided by M. Freeling, Berkeley, California). 20 % (about 7500 plants) of the progeny were 38 chromosome plants (18 of *Tripsacum* and 20 of Mutator-maize) resulting from the fertilization of unreduced gametes. From this population 100,000 seeds were produced. In a preliminary analysis, we showed by Southern blot using Mutator elements as probes that transposons are active in absence of meiosis. Therefore the population we have developed promises to be an interesting tool for the analysis of the genetic factors contributing to the expression of apomixis.

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A53 - Synthesis of Alloplasmic Male Sterile Systems and Introgression of Fertility Restoration Genes in Mustard

S. Prakash and P.B. Kirti

National Research Centre on Plant Biotechnology, Indian Agricultural Research Institute, New Delhi-110 012, INDIA

Introduction

Mustard (*Brassica juncea*) is a major crucifer oil crop in India with a total annual production of around 6 million tons. Exploitation of heterosis is a relevant strategy for enhancing productivity but has been hindered commercially due to non-availability of suitable cytoplasmic male sterility (CMS) - fertility restoration system. CMS arise spontaneously as mitochondrial mutants, and can also be induced by cytoplasm substitutions from alien species - the alloplasmics. The wild and weedy germplasm related to crop Brassicas (collectively called *Brassica coenospecies*) is a source of diverse cytoplasm as revealed by mitochondrial and chloroplast DNA RFLPs (Warwick & Black, 1991) and has potential for inducing cytoplasmic male sterility.

We have synthesized cytoplasmic male steriles in *Brassica juncea* based on 6 cytoplasms. Fertility restoration genes have been introgressed in two of these systems.

Methods

Wild species were combined either sexually or through protoplast fusion and the synthetic allopolyploids were repeatedly backcrossed to *B. juncea*. Cytoplasmic substitution lines were obtained in BC₃/BC₄ generations. Nuclear genes for fertility restoration were introgressed for the two systems from *Trachystoma* and *Moricandia* by different approaches. In *Moricandia* system, chromosome carrying Fr gene was added to CMS *B. juncea* and introgression occurred following allosyndesis in the monosomic addition line. In *Trachystoma* CMS, the forced recombination between *Trachystoma* and *B. juncea* chromosomes in the hybrid *B. juncea* + *Trachystoma* allowed introgression (Kirti *et al.*, 1997).

Results

Male sterility was completely stable in all the CMS and no developmental or floral abnormalities were observed. However, leaf chlorosis was observed in CMS (*Oxyrrhina*) and (*Moricandia*) *B. juncea* and was rectified following protoplast fusion. Intergenomic chloroplast recombination or chloroplast substitution was the mechanism of rectification. Flowers were normal with anthers either slender and non-dehiscent or petaloid. Nectaries were excellent. Meiosis proceeded normally and pollen abortion in all systems occurred just prior to microgametogenesis. An important feature was the normal female fertility. Restorers for CMS (*Moricandia*) and (*Trachystoma*) have normal female fertility and the restored hybrids exhibit more than 90% seed fertility. Genetical studies of Fr genes show that it is a single dominant gene.

Conclusion

This research demonstrates the importance of wild germplasm for inducing maternally inherited male sterility. A large number of CMS of diverse cytoplasmic origin have been obtained. Molecular analysis of mitochondrial genomes in these CMS revealed that those originating from somatic hybrids have restructured mitochondria arising out of intergenomic recombinations. Such plants have less floral abnormalities and are easily restored. Where the cytoplasm was unaltered, fertility restoration could not be achieved due to multilocus incompatibility between alien mitochondria and nuclei of the crop species. As a result of these investigations, two functional 3-line systems have become available in *B. juncea* for the first time.

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A54 - Lethal Genes Associated with Grain Yield in Inbred Lines of Maize

J.C. Salerno,¹ D. Díaz,¹ C. Robredo,¹ R. Ríos,¹ A. Reid,¹ R. Boggio Ronceros,² and O. Sorraín²

¹ Instituto de Genética "Ewald A. Favret", INTA- CICA, Castelar

² Cátedra de Estadística y Biometría, Facultad de Ciencias Agrarias y Forestales, U.N. La Plata. C.C. 25-1712, Castelar, Pcia. Bs. As., ARGENTINA

Introduction

To increase the crop production efficiency we need high-yielding, more efficient plant types with low production costs. Crumpacker, Burnham, and other authors have made a review of genetic load, showing that the frequency of recessive mutations is very high in different populations (wild and domesticated) and also in human beings. We are interested in the problem of the existence of a few linkage groups in which lethal genes associated with yield factors should be useful for manipulating these inherited traits. This hypothesis is supported by the finding of natural balanced lethal systems which keep a short heterotic chromosome segment. Such balanced lethal systems maintain heterozygosity in a short chromosome segment in an otherwise homozygous line, which promotes higher grain yield in maize. In addition, the development of statistical inference was studied for the estimation of the number of generations that a balanced lethal system maintains its linkage, in order to get permanent heterozygosity without any problem of recombination.

Methods

The "BLS1" Argentine Flint line regulated by a balanced lethal system located in the pericentric region of chromosome 6 with two lethals was evaluated in a grain yield trial against the same line with one lethal using B73, MO17, B14 and N28 inbred lines as controls during four years at the same location. A randomized block design was used, with three replications. The number of tassel branches was evaluated last year. At the same time, B73, MO17, B14 and N28 lines were crossed to different inbred lines regulated by a balanced lethal system to transfer the short heterotic chromosome segment by two continuous backcrosses. In this way, grain yield trials were made for backcrosses one and two, with three replications. The theory of absorbing Markov chains, discrete in space and time (Boggio et al.) was used to estimate the number of generations that a balanced lethal system maintains its linkage.

Results

The "BLS1" Argentine line showed significantly higher grain yield than the opposite one and the controls (Table 1). At the same time, the number of tassel branches of BLS1 was significantly different from the opposite one (Table 2). Grain yields of backcrosses one and two were significantly higher than the original lines. (Table 3). The balanced lethal system associated with yield factors was maintained during six generations, according to the absorbing Markov chains model.

Conclusions

Lines regulated by a linked balanced lethal system, where important yield genes exist in the heterozygous segment, may provide the higher level of grain yield seen in single-cross hybrids, with low production costs, for at least six generations.

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Table 1. Grain yield of the "BLS1" lines during four years.

	1993	1994	1995	1996
BLS1 1:1	2625 A	3697 A	3747 A	3243 A
BLS1 3:1	1285 A	2517 B	2713 A	2116 B
N28	2473 A	2017 C	2240 B	1709 C
B73	701 A	1793 C,D	2060 B	853 D
MO17	2471 A	1623 D	2007 B	1503 C
B14	443 A	1544 D	1860 B	811 D
C.V.(%)		4.18	16.45	5,88
msd (Kg/ha.)		366	1100	400

Table 2. Number of tassel branches in the BLS 1 line (1:1) and (3:1)

BLS1	Number of tassel branches
1:1	6.6
3:1	3.6**
X2 (p<0.001)	16.531

Table 3. Grain yield of BC₁ and BC₂ between dent and balanced lethal lines.

Backcross 1				
	(4373) BLS1	(3967) BLS14	BLS 6	BLS 12
B73 (2060)	4607 *	3583 *		
MO17 (2007)		5040 *	44807 *	4200 *
B14 (1860)		4140 *	3913 *	
N28 (2240)		3653 *	4533 *	3193

The value between parenthesis is the grain yield per-se of each line.

C.V.= 10.18% msd= 1114 kg/ha.

Backcross 2

	(4155) BLS1	(3351) BLS14	BLS 6
B73 (1823)	2860 *	3863 *	
MO17 (2262)		4346 *	4287 *
B14 (2159)		2871	3775 *
N28 (2131)		3482 *	4497 *

CV= 7,45%msd= 972 kg/ha.

A55 - Heterosis for Growth Rate to Low Temperature Stress in Rice Callus, *Oryza sativa* L.

S. Kuroda

Dep. Rice Research, Hokuriku Nat. Agr. Exp. Stn, Inada, Joetsu, Niigata 943-01, Japan

Introduction

In tissue cultures of major crops, the culture relationship between heterozygosity and *in vitro* callus growth has already been studied. Because not all reports calculated the intrinsic growth rate of the callus after a fixed duration of culture by starting from the induced callus instead of explants, we still do not understand the genetic properties of the callus growth rate and cell division rate in the *in vitro* culture of plant cells. From a previous study in rice callus, *Oryza sativa* L., the genetic information and the relationship between *in vitro* genetic traits and heterosis for plant growth in the field has been defined (Kuroda et al. 1995). The present experiments were undertaken to elucidate the heterosis for the growth rates in the callus culture of rice at different temperatures, especially low temperature stress.

Materials and Methods

A 14x14 diallel crossing scheme including parents and without reciprocals was set up with 14 cultivars of rice, including different subspecies, i.e., 4 *japonica*, 4 *javanica* (the tropical type of *japonica*), and 6 *indica* cultivars. Each sterilized seed was placed a culture tube containing N6 induction medium with 2,4-D. After fully induced calli were isolated from original seeds, each of them was spread out in a Petri dish containing the N6 medium for callus proliferation. For preparation of callus growth measurement in each line, following 4 weeks of culture in the dark at 28°C, small pieces from each of the proliferated calli were picked up until between 240 to 280 mg in the total fresh weight with repeatedly 8 times. Each callus was exactly weighed (primary weight), and put into a Petri dish containing the modified fresh culture medium. They were equally divided into 4 groups and placed in 4 culture rooms in dark kept at 20, 28, 35, and 40°C individually. After 4 weeks of culture, fresh callus (final) weight per Petri dish was measured. The callus growth rate (times) after 4 weeks of culture in each line was calculated as a final weight/primary weight. Calculation of the diallel analysis was performed using a microcomputer program (DIALL) developed by Ukai (1989).

Results and Conclusions

As shown in Table 1, among the temperatures tested, the highest callus growth rates were obtained at 28°C without exception ($P < 0.01$), followed by 35°C, for the genotypes used. At 40°C, there were very little growth. At 28°C, the rates were tended to be high in *javanica* parents ($P < 0.05$) and *japonica* parents. In comparison with parental subspecies and their F_1 crosses, all crosses between subspecies had significantly ($P < 0.01$) higher rates than parental subspecies at 20 to 35°C, and the average rates of the F_1 crosses at 20, 28 and 35°C were 86%, 57% and 56% higher ($P < 0.01$) for those of parents, respectively. On the other hand, in a relative cell division rates (%) of 20/28°C (Table 2), the average rate of the F_1 crosses was similarly 19% higher ($P < 0.05$) for that of parents. Especially, *javanica* x *javanica* cross had higher relative rate, i.e., tolerance for 20°C, than other subspecies combinations. While *japonica* x *japonica* cross had the lowest relative rate among all subspecies combinations. It has proved, therefore, that the F_1 crosses showed a hybrid vigor on the callus growth rate and tolerance for low temperature compared to parents. However, nonsignificant ($P < 0.05$) difference between parents and the F_1 crosses was observed in the average relative rates of 35/28°C. Means of midparent heterosis (%) of crosses among subspecies at 20 to 35°C were positive, indicating an overdominance on callus growth. The effects of heterosis on the callus growth rate were generally lower at 28 than 20 or 35°C; i.e., F_1 hybrids had superior adaptability to extreme culture temperatures than their parents.

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Table 1. Means of the callus growth rate (times) for 4 weeks culture at each temperature in a diallel cross.

Subspecies /cross	N	Temperature (°C) of culture			
		20	28	35	40
<i>Parent</i>					
Jap	4	2.43	5.08	3.33	1.33
Jav	4	2.78	5.93	4.13	1.30
Ind	6	2.87	4.48	4.10	1.33
Total	14	2.71	5.06	3.89	1.32
<i>Hybrid</i>					
Jap x Jap	6	4.53	6.93	3.68	1.38
Jap x Jav	16	5.23	8.80	5.44	1.23
Jap x Ind	24	4.81	8.66	7.70	1.40
Jav x Jav	6	7.17	8.22	7.35	1.13
Jav x Ind	24	5.23	7.69	6.30	1.37
Ind x Ind	15	4.09	6.67	6.09	1.25
Total	91	5.03	7.96	6.08	1.30

Table 2. Relative callus growth rate of 20°C and 35/28°C.

Subspecies /cross	N	Temperature (°C) of culture	
		20	35
<i>Parent</i>			
Jap	4	48.5	67.5
Jav	4	47.8	68.8
Ind	6	65.5	98.0
Total	14	56.8	80.9
<i>Hybrid</i>			
Jap x Jap	6	65.7	56.5
Jap x Jav	16	63.7	70.1
Jap x Ind	24	62.0	82.0
Jav x Jav	6	88.0	89.3
Jav x Ind	24	71.4	91.2
Ind x Ind	15	63.9	92.5
Total	91	67.5	82.6

A56 - The Photosynthesis Rate of Lines, Hybrids and Open-Pollinated Varieties of Tropical Maize

A. Elings and G.O. Edmeades

Maize Program, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico, D.F., Mexico; aelings@cimmyt.mx

Introduction

It is often believed that maize hybrids are characterised by a greater photosynthesis rate (PhR, $\text{mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) than their parent lines. A comparison between genotypes, however, must take into account leaf nitrogen content (LNC, %), as PhR is positively related to LNC (van Keulen and Seligman 1987; Watanabe et al. 1995), and a greater PhR may simply be the result of a better extraction of soil N by the hybrid, instead of a greater PhR itself. Other reported causes of variation are leaf age and leaf position (Dwyer et al. 1989). Verheul et al. (1995) have measured a greater oxygen evolution rate in a temperate inbred line than in a tropical line. This research compares PhR of several tropical maize lines, their hybrids and open-pollinated varieties, using LNC as a covariate.

Materials and Methods

Eighteen genotypes (Table 1) classified as inbred line, hybrid, or open-pollinated variety (OPV) were sown on July 25, 1996 at the CIMMYT experimental station at Tlaltizapán, Mexico, in a RCB design with 3 replications, in single-row plots of 5.25 m. Within and between-row plant distances were 0.25 and 0.75 m, respectively. Photosynthesis rates were measured with the LI-COR 6200 at the centre of the uppermost expanded leaf (Dwyer and Stewart 1986; Dwyer et al. 1989) on 4 to 5 plants per plot, between 11 AM and 2 PM under generally cloud-free conditions on August 27 and 28, when plants were at the 7-9 leaf stage. Area and weight of the measured leaf section were determined, and specific leaf weight (SLW; g m^{-2}) was computed. A chlorophyll-related measure was obtained with the SPAD-502 (Minolta). LNC was computed as: $\text{LNC} = -0.62 + 3.32 \cdot \text{SPAD-reading}$ (Chapman, pers. comm.). Only observations taken at quantum flux densities greater than $1800 \text{ mmol m}^{-2} \text{ s}^{-1}$ were used in analysis. Significance of the effects by genotype class and genotype on LNC was tested through analysis of variance (ANOVA). Significance of the effects by genotype class and genotype on PhR were tested through analysis of covariance (ANCOVA) with LNC as covariate. Least significant differences (LSD) were calculated on the basis of studentized range Q-value.

Results

ANOVA of LNC with genotype class as main effect resulted in a significant ($p < 0.01$) genotype class effect. Average LNCs for lines, hybrids and OPVs were 1.78, 2.09 and 2.17 %, respectively ($se = 0.07$; $LSD = 0.19$). LNC was highest for the OPVs DTP1 RU C₀, TLRUE+, PR 8330, Tuxpeño Sequía C₀ and TBF C₂, and lowest for the lines CL00331 and CML287 (Table 1). Data scatter of PhR was large. PhR and LNC could be mathematically related as $\text{PhR} = 18.62 + 9.33 \text{ LNC}$ ($r^2 = 0.27$). ANCOVA of PhR with genotype class as main effect and LNC as covariate, indicated that PhRs adjusted for LNC differed ($F = 5.25 > F_{2,198} = 4.71$ at $p < 0.01$). This was caused by the significantly lower average PhR of lines in comparison with OPVs: adjusted PhR of lines, hybrids and OPVs were 34.5, 37.2 and 38.2 $\text{mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$ ($se = 1.2$; $LSD = 3.5$), respectively. ANCOVA of all individual genotypes showed significant ($p < 0.05$) genotype effects (Table 1).

Discussion

OPVs and hybrids are characterised by significantly greater average LNC and PhR than lines. The greater LNC may be the consequence of a greater nitrogen uptake from the soil due to a larger root system, which in itself could be called a heterotic response. Data regarding this were not available. The greater adjusted PhR of OPVs and hybrids in comparison with lines suggests fundamental differences in one or more of the factors that determine PhR. These may be morphological (e.g., stomata density) or

biochemical (e.g. diffusion resistance, enzymatic processes). The wide data scatter is partly the consequence of the small leaf area that is measured by the LI-COR 6200, and may be further explained by non-saturating irradiance levels, which are greater than 2000 mmol m⁻² s⁻¹ for young maize leaves (Dwyer and Stewart 1986). Further experiments will be conducted to increase precision; this may enable non-linear covariance adjustment, instead of the linear adjustments that are assumed with ANCOVA.

Conclusions

OPV and hybrids were characterised by a significantly greater average leaf nitrogen content and photosynthesis rate than lines. This may be caused by differences in nitrogen uptake or partitioning, or by one or more of the morphological or biochemical factors that determine photosynthesis rate.

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Table 1. Adjusted means of leaf nitrogen concentration (LNC, %) and photosynthesis rate (PhR, mmol CO₂ m⁻² s⁻¹) of 18 lines, hybrids and open-pollinated varieties (OPV). All entries, except #11, have been developed for lowland tropical environments.

#	Genotype	Description	LNC	PhR
1	La Posta Sequia C ₅	OPV selected under drought	2.22	39.13
2	Across 8328 BN C ₆	OPV selected under low N	2.07	36.66
3	PR 8330	OPV	2.30	37.44
4	Pool 16 C ₂₀	OPV	1.96	40.02
5	CML247 x CML254	Hybrid with high yield stability (white)	1.98	38.38
6	CML247	Inbred line	1.96	33.54
7	CML254	Inbred line	1.96	35.36
8	CML287 x CL00331	hybrid (yellow)	1.83	41.05
9	CML287	Inbred line	1.57	32.28
10	CL00331	Inbred line	1.62	32.92
11	FRB73 x FRMo17	Temperate hybrid	2.22	32.44
12	LPSC3H297-2-1-1-2-1-# x CML254	Drought tolerant hybrid (white)	2.24	38.48
13	LPSC3H297-2-1-1-2-1-##	Inbred line derived from La Posta Sequia	1.77	34.07
14	TBF C ₂	OPV selected under low iron conditions	2.26	39.88
15	Tuxpeno Sequia C ₀	OPV	2.27	36.77
16	TS6 C ₄	OPV selected under drought (10 cycles after #15)	2.08	35.82
17	DTP1 RU C ₀ TLRUE+	OPV selected for high radiation use efficiency	2.31	39.16
18	DTP1 RU C ₀ TLRUE-	OPV selected for low radiation use efficiency	2.02	37.29
		Mean	2.04	36.96
		Standard error of differences of mean	0.17	2.67
		Degrees of freedom	17, 34	17, 183
		F-value	10.15	2.05
		5% F-value	1.94	1.68
		1% F-value	2.55	2.07

A57 - Phenotypic Plasticity, Heterosis, and Environmental Stress: A Concise Review

M.S. Kang

Agronomy Department, Louisiana State University Agricultural Center, Baton Rouge, LA 70803-2110, USA

Phenotypic plasticity is "...the amount by which the expressions of individual characters of a genotype are changed by different environments" (Bradshaw 1965). Genotype-environment interaction is equivalent to genetic variation in phenotypic plasticity (Via and Lande 1985). Phenotypic plasticity is extremely common in plants, and is often expressed in stressful environments; for example, production of cleistogamous flowers (that do not open and ensure self-fertilization) in dry periods compared to open flowers in other periods, and the loss of leaves under climatic stress (Bradshaw 1965). Phenotypic plasticity encompasses short-term reversible responses, acclimation responses, and irreversible changes during development (Hoffmann and Parsons 1991). High levels of phenotypic plasticity for physiological traits occur in species from habitats experiencing environmental fluctuations, whereas levels of plasticity for morphological traits are relatively low in species from stressed environments (Hoffmann and Parsons 1991). The degree of expression of phenotypic plasticity is under genetic control; populations and species show different levels of plasticity for the same character in response to the same environmental variables (Bradshaw 1965; Schlichting 1986). Mazer and Schick (1991) demonstrated, by examining norms of reaction, that genetic variation (additive genetic variance) existed for phenotypic plasticity. Therefore, phenotypic plasticity can be manipulated through breeding (Kang 1997). The amount of phenotypic plasticity of a species would be inversely related to its genic heterozygosity (Marshall and Jain 1968). Adaptation to variable environments may be accomplished either by means of genetic variation or phenotypic plasticity and the least heterozygosity should be the most plastic (Schlichting and Levin 1984).

In *Arabidopsis thaliana*, the degree of heterozygote advantage (heterosis) for growth increased with stress for all environmental variables (temperature, light intensity, mannitol concentration) except nutrient concentration (Pederson 1968). The following explanations were proposed to account for changes in heterosis with stress (Hoffmann and Parsons 1991):

- Parental lines are highly inbred, and heterosis largely represents a recovery from inbreeding depression. Heterosis will increase with stress if inbreeding depression is more pronounced in adverse environments than in favorable ones. This explanation does not account for heterosis in the many crosses where parental strains are not inbred.
- A second possibility is that parental lines reach their optimal performance at different levels of a single environmental variable or a combination of variables (Knight 1973). Hybrid genotypes are assumed to have an intermediate optimum between the two parents (additive gene action). The hybrid will perform better than or equal to the mid-parental value across environments, and there will be heterosis x environment interactions because the hybrid will outperform its parents at some levels of the environmental variable. One environmental variable is not enough to generate increased heterosis in stress environments. Knight (1973) considered different levels of a second environmental variable that interacts with the first. Different levels of the first and second environmental variables can result in heterosis under extreme conditions, or heterosis under optimum conditions, or cases where hybrid performance increases or decreases relative to mid-parental value.
- Heterozygotes have an advantage under stressful conditions but not in favorable environments. Heterozygote advantage may, therefore, be due to the fact that these genotypes are more successful at countering fluctuating conditions (greater homeostasis) (Lerner 1954), which may relate to

agricultural studies in which stressful conditions cause decreased productivity. Environmental variability may increase as conditions for agricultural productivity deteriorate (Blum 1988).

- Heat-sensitive enzymes were the most common consequences of mutations that do not inactivate the enzyme, and some of the mutations were expressed only at high temperatures with complete dominance in the heterozygote (Langridge, 1968).

An F₁ hybrid of two maize inbred lines exhibited an increased activity of two antioxidant enzymes (SOD and glutathione reductase) (Malan et al. 1990); improved protection from oxidative stress was observed. Singly, neither enzyme effectively resulted in stress resistance; a balanced increase in antioxidants was needed. Maize hybrids contain higher concentrations of gibberellins than their homozygous parents, suggesting that heterosis has a phytohormonal basis (Rood and Larsen 1988; King and Stansfield 1997). A correlation was also observed between the concentration of endogenous GA-like activity and hybrid vigor for height growth and shoot dry weight in poplar (Bate et al. 1988).

A hypothesis that sorghum hybrids sustained a higher carbon exchange rate (CER) over a wider temperature range than their parents was tested (Blum et al. 1990). Significant heterosis was found for biomass, grain yield/plant, and grain number/panicle. No heterosis was found for harvest index, indicating that heterosis in grain yield was due to heterosis in biomass. CER and stomatal conductance for hybrid 378/430 were greater than for both its parents at leaf temperatures above 38°C. Hybrid 378/434 manifested heterosis only under drought stress when it yielded more biomass and grain than 378/430. The relative advantage of 378/434 under drought stress was also well reflected in its higher grain number/panicle and sustained leaf area duration. Parental line 434 maintained significantly higher leaf water potential under stress and conferred a yield advantage under drought stress to its hybrid indicating the importance of genetic background (Blum et al. 1990). In maize, the Y_y heterozygote showed a heterotic effect for plant and ear height and cob weight (Kang and Zuber 1990).

A positive correlation between individual heterozygosity and fitness-related traits is expected under a range of models which fit in two classes: those treating the observed genetic variants as agents of the correlation (selection hypothesis) and those treating these variants as markers of genetic conditions responsible for the correlation (associative overdominance hypothesis) (Zouros and Pogson 1994). A controlled-nutrient (CN) experiment was conducted to test three heterosis hypotheses for tomato yield (Griffing 1990): 1) heterosis is a consequence of a more efficient hybrid metabolic system that can produce more with equal input; 2) heterosis results from the somatic multiplication of additive component traits; and 3) heterosis results from a faster hybrid growth rate. Neither hypothesis was rejected by field data, but CN experimental data rebuffed the first two. The first hypothesis would be tremendously important for agricultural productivity. It was speculated that the indeterminate pattern of plant development responsible for yield and its components was due to two major gene systems: those that relate to morphogenesis, and those that determine growth rate (Griffing 1990). The CN technique permitted separation of responses due to these two gene systems.

The importance and role of genome organization relative to heterosis have been discussed (Pontecorvo 1955; Mino and Inoue 1989; Rayburn et al. 1993; Biradar and Rayburn 1993). DNA content was higher in the F₁ hybrid than in parental lines of maize (Mino and Inoue 1989). Hybrids from somewhat distantly related parents were able to organize nuclear DNA with no deletion or amplification, whereas hybrids from closely related parents had difficulties in organizing the two parental genomes and DNA amplification occurred (Biradar and Rayburn 1993). Normal inheritance of nuclear DNA content was associated with a high heterotic response and DNA amplification was associated with low heterosis (Biradar and Rayburn 1993). Use of isozymes and molecular markers in studying heterosis has received impetus during the 1980s and 1990s (Strauss 1986; Trehan and Gill 1987; Chakraborty 1989; Smith et al. 1990; Stuber et al. 1992; Mechinger 1993; Lee 1993). Ruebenbauer (1962) proposed that the yield of an F₁ hybrid was a function of both the genome and the cytoplasm.

(over)

Extrachromosomal cell components also play an important role in heterosis. Current knowledge on the physiological, biochemical, and genetic bases of heterosis and the implication of mitochondrial and chloroplast activities were discussed by Srivastava (1991), and statistical aspects by several authors (Jinks 1983; Wricke and Weber 1986; Hallauer and Miranda 1988; Schnell and Cockerham, 1992; Comstock 1996). Heterosis for the one-locus, two-allele model is a function of the square of the difference in gene frequency multiplied by the dominance deviation (Willham and Pollak 1985; Kang 1994). Heterosis for a two-loci, two-allele model contains an additive x additive epistatic term (Willham and Pollak 1985). Complementary and duplicate epistases suppressed heterosis even when parents showed gene dispersion (Pooni and Treharne 1994). Extensive literature on heterosis due to multiplicative effects between characters was reviewed by Schnell and Cockerham (1992), as was the earlier work on the genetic description of heterosis.

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A58 - The Effect of Ethephon and Uniconazol Applied on Two Local Rice Varieties

M.T.Karbalai, A. Hashemi- Dezfuli and S. Farahi - Ashtiani

Iran Rice Research Institute, P.O. Box 1658, Rasht, Iran

Introduction

Local rice varieties are usually preferred over high-yielding cultivars due to their grain quality. However, almost all local varieties are tall and face the problem of lodging. This in turn limits the use of nitrogen fertilizer. This study determined the plant height and grain yield responses of rice plants to the application of two growth inhibitors used at two different growth stages.

Material and methods

The study was conducted in 1994 in a field near Babol City. The design of the experiment was split plot with three replications. Main plots consisted of two growth stages of rice plants: the beginning of stem elongation and appearance of the flag leaf. Sub-plots were allocated to two local varieties (Tarom and Rashti) and two growth inhibitors (ethephon and uniconazol) which were factorially combined.

Results

Uniconazol and ethephon both reduced plant height by 16 and 8 cm, respectively, compared with control plants. However, the reduction caused by ethephon was not enough to prevent plants from lodging. The application of uniconazol reduced the lodging index from 6.2 to 2.7. The reduction was mainly attributed the reduction of the rice of the flag internode and the node just beneath the flag leaf. The two varieties were significantly different in plant height. However, the difference between application times was not significant. The interactive effect of the growth inhibitor and the time of chemical application on length of flag internode were statistically significant. Reducing lodging by using uniconazol caused a significant reduction in percentage of unfilled grains. Thus this increased grain yield to as much as 250 kg/ha compared with the control.

Conclusion

Results of this experiment indicated that both uniconazol and ethephon have considerable effects on plant height, but that ethephon has an insignificant effect on the lodging index. One of the main problems in producing hybrid seed through CMS lines of our local cultivars is the plant height. This is because the local CMS lines (Domsia and Gharib) are taller than their affiliated restorer lines. Naturally, pollination does not occur. To cope with his problem, there are two possible solutions: one could change plant architecture through breeding or apply the uniconazol hormone to reduce plant height.

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Table 1. The result of variance analysis indicating plant height lodging index, and grain yield.

Source of variation	df	Mean square		
		Height	Lodging index	Grain yield
Replication	2	16.74	1.44	365.95
Stages	1	1.40	1.78	1171.89
Error (a)	2	6.31	0.11	303.05
Hormons	2	670.69***	54.11**	2675.19**
Varieties	1	12.33	1.78	201.55
HXS	2	19.44**	1.44	20.93
VXS	1	10.13	0.44	130.56
HXV	2	4.72	1.44	447.91
HXVXS	2	4.45	0.78	10.20
Error (b)	20	2.67	1.44	319.07

*, **, ***, are equal with $p=5\%$, $p=1\%$, and $p=0.01\%$, respectively

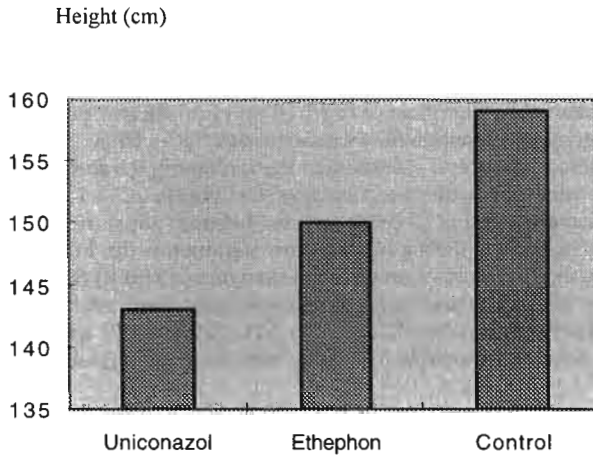


Figure 1. Comparison of the effect of different growth inhibitors on rice plant height.

A60 - Nonallelic Interactions and Heterosis in Corn

L.V. Khotyleva and L.A. Tarutina

Institute of Genetics and Cytology, Academy of Sciences of Belarus, Pr. Skorina 66, 220072, Minsk, Belarus

Introduction

Nonallelic interaction (epistasis) ranks high among different types of gene action inducing heterosis in plants. They can be one of the causes of high heterotic effect, give rise to additional heterogeneity in average hybrids with the participation of one parent and, in consequence, result in shifting estimation of other types of gene action (Stuber and Moll 1977; Gallais 1988). Absence of information on the corn hybrids adapted to Belarus made us study the role of epistasis in genetic determination of heterosis for ear length in F_1 hybrids.

Methods

Seven early maturing inbred corn lines adapted to Belarus conditions, F_1 , F_2 , and backcrosses B_1 and B_2 were sown in a randomized complete block design with 3 replications. The spacing between rows was 70 cm and each row contained 30 plants at 35 cm intervals. Ear length was recorded. Nonallelic interactions and heterosis were measured by estimating the magnitude of m , $[d]$, $[h]$, $[i]$, $[j]$ and $[l]$ parameters calculated on the basis of 6 the generations by means of a least square technique (Mather and Jinks 1982; Jinks 1983).

Results

Table 1 lists values of heterosis and interaction parameters only for those hybrids with $F_1 > P1$; $P1$ being the parent with the greater mean value. Significance of $[i]$, $[j]$ and $[l]$ indicates presence of a certain type of epistasis. Estimates of interaction parameters for three hybrids -- L25 x 018a, L25 x L15, and L15 x 024a -- are insignificant, indicating absence of epistasis. In the remaining 9 hybrids estimates of at least one of three parameters are considerably different from zero. In hybrids L25 x L21 and 018a x L15 the parameters $[i]$ (homozygous-homozygous) or $[j]$ (homozygous-heterozygous), respectively, make a basic contribution to the interaction; in hybrids 018a x L21 all three parameters do; in the remaining six hybrids two are responsible, with the combination of the parameters $[i]$ and $[l]$ (homozygous-homozygous and heterozygous-heterozygous) being the most frequent and interpreted as a duplicate type of epistasis. There are some hybrids (L25 x 024a, L25 x L21, 018a x L15) where parameters $[h]$ and $[l]$ are insignificant. In these cases it is impossible to classify nonallelic interaction.

Conclusions

Our results show that epistasis was of the duplicate type (parameters $[h]$ and $[l]$ were of different sign) for ear length in those cases where positive heterosis existed in the presence of epistasis. No complementary type of epistasis was observed in the hybrids studied. Such results are very uncommon (Vazquez and Sanchez-Monge 1987) in the literature, even when the relationship between high and positive heterosis and epistasis is observed, epistasis is normally complementary type where $[h]$ and $[l]$ are significant and of the same sign (Pooni and Jinks 1981; Ivanovic and Pooni 1988). Thus, the level of heterosis observed in various hybrids does not always directly depend on the value and behavior of gene action. For instance, high estimates of dominance, as well as the presence of epistasis, are not always accompanied by higher heterosis.

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Table 1. Heterosis components for ear length in F₁ corn hybrids.

Hybrid	<i>m</i>	[<i>d</i>]	[<i>h</i>]	[<i>i</i>]	[<i>j</i>]	[<i>l</i>]	Heterosis: [<i>h</i>]+[<i>l</i>]-([<i>d</i>]+[<i>i</i>])	Epistasis type
L25x024a	12.8*	0.10	9.4*	3.4*	-3.6*	-0.8	5.1	Unknown
L25x018a	14.3*	0.05	7.0	1.8	0.5	-1.5	3.7	No
L25xL15	18.0*	0.30	0.5	-1.6	1.4	3.0	4.8	No
L25xL21	11.1*	0	9.8*	5.0*	0.2	-1.6	3.2	Unknown
L25xL20	5.8*	0.10	24.9*	10.2*	1.2	-12.2*	2.4	Duplicate
018axL15	17.6*	0.25	-0.2	-1.2	-4.1*	2.1	2.9	Unknown
018ax024a	12.4*	0.05	11.1*	3.8*	2.9*	-3.5	3.7	Duplicate
018axL20	3.3*	0.15	30.9*	12.8*	0.1	-15.1*	2.8	Duplicate
018axL21	9.2*	0.05	18.4*	7.0*	2.1*	-9.3*	2.0	Duplicate
L15x024a	15.1*	0.20	6.0	1.4	-0.2	-1.2	3.2	No
024axL20	7.5	0.20	23.1*	8.6*	1.8	-11.8*	2.5	Duplicate
024axL21	9.0*	0.10	17.6*	7.2*	-0.6	-6.0*	4.3	Duplicate

* Significant at the 5% level.

A61 - Development of Heterotic Pools, Inbred Lines, and Hybrids: A Comprehensive Breeding Approach

S.J. Patil¹ and N.N. Singh²

¹ Special Officer (Seeds) UAS Dharwad-580 005 Karnataka, India

² Project Director (Maize) IARI, New Delhi-110 0121, India

Introduction

Since genetic divergence is the basic factor in heterosis, it is worthwhile to develop heterotic pools based on divergent heterotic patterns. Extraction of elite inbred lines and their evaluation and utilisation in hybrids would certainly constitute a successful comprehensive breeding approach in developing superior high yielding hybrids. This method would serve as an efficient alternative to conventional breeding approaches. A well thought out, comprehensive strategy was implemented in the all India Coordinated Maize Improvement Project, with Dharwad as leading center.

Methods

CM-202 (a yellow Dent derivative of us line) x cm-111 (a yellow flint derivative of Cuban source) is the best single cross in the Indian Maize Improvement Programme. These two lines have opposite heterotic patterns and were chosen as the testers. The elite genotypes available in the country were topcrossed and the selected topcrosses were evaluated over locations. The selected nine lines with 17.61 to 51.49% yield superiority over per se in topcross performance with CM-202 and the opposite tester cm-111 formed the basic material for X1(Y) Pool. Similarly, seven lines with 11.12 to 42.62% yield superiority over per se in topcross performance with CM-111 and the opposite tester CM-202 formed the basic material for the X2(Y) pool. Four cycles of recombinations through half-sib nurseries in isolation for both Pools were made after the first cycle of diallel matings. The half-sib nurseries were given 400 kg N, 100 kg P205, and 200 kg K20 per ha to increase the frequency of alleles responsive to high fertility. At least 250 to 300 half sibs were obtained from female rows each cycle. A population based on seeds from the fourth recombination cycle was grown to initiate inbreeding. As many as 807 (X1,Y) 578 (X2Y) lines from each pool were subjected to screening for stalk rot at Dhaulakuan, for sorghum downy mildew at Mandya, for *turicum* blight at Nagingalli, an nitrogen response at Delhi. As many as 712, 375 and 115 in X1(Y) and 510, 174 and 70 in X2(Y) lines were advanced from S₂ to S₃ and to S₄ respectively. The S₄ lines were topcrossed to opposite pools as testers and 106 and 41 topcrosses respectively were tested at 3 locations. From this evaluation 5 lines from X1(Y) with 16.11 to 26.24 and 5 lines from X2(Y) with 7.0 to 78.5 % yield increase over testers were finally chosen for a diallel crossing programme.

Results

The single crosses were tested at seven locations in rainy and winter seasons. The field performance of the top 15 double cross hybrid which were selected based on predications ranged from 8.9 to 15.77% yield superiority over the best check. The yield superiority of some of the best double top crosses ranged from 10.3 to 51.74% and two had 23.6 and 23.74% yield increases over the best hybrid checks, Deccan-103 and 105 (Table 1). An elite double top cross hybrid (KDMI-4 x KDMI-10) CM-501 was released in the state of Karnataka during 1996 for commercial cultivation (Table 2).

Conclusions

Several elite inbred lines, superior single, double and double top cross hybrids which are fairly tolerant to major pests and diseases besides being high yielding and responsive to high productivity conditions, both season-specific and across seasons, were obtained. The maintenance and strengthening of the basic pools with new elite germplasm through intergression, improvement through suitable selection schemes, extraction of new inbreds, their evaluation, use of new inbreds among themselves and in combination with other inbreds are some of the proposed activities.

Table 1. Performance of genotypes developed by using inbred lines obtained through a comprehensive breeding approach.

Genotypes	Pedigree	Yield (quintals/ha)	% increase over best check		Environments
Single Cross	KDMI-4 x KDMI-10	59.28	12.44	(D-103)	Winter, 1991
"	KDMI-7 x KDMI-8	61.49	45.64	(D-103)	Rainy, 1991
"	KDMI-3 x KDMI-9	51.28	21.46	(D-103)	Rainy, 1991
"	KDMi-3 X KDMI-9	54.62	3.6	(D-103)	Winter, 1991-92
"	Pop.28-C6-HS-B x KDMI-10	90.92	14.42	(D-105)	Winter, 1992-93
	Pop.28-C6-HS-B x KDMI-10	82.57	42.78	(D-105)	Rainy, 1992
Double cross hybrid	(KDMI-1 x KDMI-9) x (KDMI-4 x KDMI-10)	54.64	15.77	(D-105)	Over 3 locations Winter 1991-92
"	(DKMI-1 x KDMI-10) x (DKMI-8 x KDMI-9)	73.55	8.9	(Trishulata)	Rainy, 1992
Double top cross hybrid	(KDMI-4 x KDMI-7) x Prabha	64.70	23.74	(D-103)	Over 3 seasons & 3 locations
"	(DKMI-4 x KDMI-10) x CM-501	60.10	23.60	(D-103)	Over 3 seasons & 3 locations

Table 2. Performance of Dharwad Maize Hybrid-1, DMH-1 [(KDMI-4 x KDMI-10) CM-501] (double topcross hybrid).

	DMH-1	Percent increase over Deccan-103
Mean grain yield (q/ha)		
Kharif	52.85	13.6
Rabi	52.00	20.9
Farm trial yield (quintal/ha)	37.73	11.7
% downy mildew incidence	15	73

A62 - Genetic Diversity and Combining Ability of Inbred lines Derived from Heterotic Maize Populations

L.B. Chaudhari and P.K. Singh

Rajendra Agricultural University, Bihar, T.C.A., Dholi (Muzaffarpur), India - 843121

Introduction

Hybrid development is an evolutionary process emphasizing development and identification of simple hybrid types as a short-term objective with a gradual shift towards producing more diversified types to cater to various specialised uses. Success depends on the availability of genetically superior source germplasm to develop hybrids. Genetically diverse and productive lines play vital role in a successful breeding program (Ahloowalia and Dhawan 1963; Moll et al. 1965; Utkhede 1977).

Methods

Fifty-five inbred lines derived from broad-based heterotic populations were evaluated to assess genetic divergence. Each plot consisted of two 5 m rows and row to row and plant to plant distances were maintained at 75 cm and 25 cm respectively. Eight genetically diverse inbred lines selected for per se performance and D2 values were planted in a breeding nursery at Dholi during kharif 1994 to make all possible crosses, excluding reciprocals. Twenty-eight F₁ hybrids developed were evaluated along with 8 parental lines and 4 released hybrids as checks during winter 1994-95. Multivariate analysis by means of Mahalanobis' D2 statistics was performed to quantify divergence in the inbreds. Means of quantitative traits for each entry for all the replications were measured. The graphical analysis was performed based on the variance and covariance values following the procedures given by Jinks and Hayman (1953) and Hayman (1954). Variance components were calculated as per Hayman (1954). Combining ability analysis followed Griffing's (1956) Method-2, Model-1.

Results

All the inbred lines were grouped into five clusters. Clusters were not formed according to geographical distribution/origin of the source genotypes. The clustering pattern reflected the presence of genetic diversity in the inbred lines and also revealed that there was no correlation between genetic diversity and geographical diversity. Hence, crossing among selected inbred lines from different clusters was suggested to produce hybrids for exploitation of heterosis. The graphic and variance components analyses generally agreed for all eight traits studied. The genetic system controlling these traits showed the major role of dominance in the inheritance of all these traits (Table I). The magnitude of additive (D) variance was smaller than H1 and H2 for all the traits.

Conclusions

Clustering patterns of the inbred lines revealed that selection of inbreds for hybridization should be based on genetic diversity rather than geographical distribution. The high x high and high x low general combining ability crosses involving diverse parents also showed greater heterosis, suggesting that parents with genetically diverse origin should be used for heterosis breeding. The significance of the variances due to GCA and SCA indicated that both additive and non-additive gene effects are important for these traits. The degree of dominance both by geographical and components analysis revealed the presence of dominance for all the traits studied.

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Table 1. Comparative evaluation of the results on gene action and average degree of dominance.

Character	Graphic analysis	Variance component analysis			Combining ability analysis		Average degree of dominance	
		D	H1	H2	GCA	SCA	Wr-Vr	(H1/D) ^{1/2}
Days to 75% tassel	NA	NS	HS	HS	HS	HS	OD	OD
Days to 75% silk	NA	NS	HS	HS	HS	HS	OD	OD
Days to maturity	NA	NS	HS	HS	HS	HS	OD	OD
Plant height	NA	NS	HS	HS	HS	HS	OD	OD
Ear length	NA	HS	HS	HS	HS	HS	OD	OD
ear diameter	NA	HS	HS	HS	HS	HS	OD	OD
Kernel rows per ear	NA	NS	HS	HS	HS	HS	OD	OD
Yield per plant	NA	NS	HS	HS	HS	HS	OD	OD

NA = Non allelic

NS = Non significant

OD = Overdominance

HS = Highly significant

A63 - Development of TGMS Lines with Diversified Sources of Sterility

H.T. Minh, T.D. Quy, N.T. Nhan, and L.Q. Du

Plant Cytogenetics and Wide Hybridization Division, Institute of Agricultural Genetics, Hanoi, Viet Nam

Introduction

The commercial success of hybrid rice in China has clearly demonstrated the potential of this technology to meet the ever increasing global demands for rice. Efforts to develop and use hybrid rice in Vietnam began in 1990. Research on two-line heterosis breeding and development of inter-subspecific *Indica* x *Japonica* hybrids was also initiated.

Methods

The TGMS lines received from IRRI, as well as from mutated populations isolated from germplasm collections selected from differential progenies of inter-specific hybrid rice were evaluated under controlled temperature conditions in a growth chamber and the field. Some TGMS lines have been characterized with respect to their critical sterility point (CPS) and fertility point (CFP). Under suitable temperate condition TGMS lines showed almost normal fertility, and can be multiplied by selfing.

Results

Newly obtained TGMS lines have been used in differential testing crosses as well as in trials for TGMS breeder seed production. VN-01, VN-02 and TG-162 had stable CFP values and showed high outcrossing percentages (Table 1). The yields of their F₁ hybrids were superior to those of checks and other three-line hybrids by some 15% (Table 2).

Conclusion

Development of TGMS lines by selection from segregated progenies of differential generations of crosses is most effective method in rice breeding. Newly created TGMS lines had many advantageous characteristics especially sterility and good out-crossing ability.

Table 1: Desirable characteristics of TGMS lines.

Lines	Number of male sterile plant (%)	Critical fertility point (°C)	Abortive pollen grain (%)	Duration of sterile period (Consecutive days)	Out-crossing during sterile phase (%)
VN-01	100	<24	99.5	34	45
VN-02	100	24.5	99.7	32	47
TG-162	100	99.7	99.7	37	45

Table 2. Preliminary evaluation of two-line hybrids.

Cross	Yield potential (kg/ha)	Heterosis (%)	Panicle length (cm)	Plant height (cm)
NV - 01/D -18	13,973.9	162.0	24.4	98.02
VN -01/212	11,089.3	107.9	23.2	110.90
TG-162/321	9,237.8	73.9	24.6	107.60
CR - 203(Check)	5,332.6	-	19.1	92.40

A64 - Heterosis for Diversity among Locally-Developed Maize Inbred Lines in Malaysia

G. Saleh and S. Sujiprihati

Department of Agronomy and Horticulture, Universiti Putra Malaysia, 43400 UPM, Serdang, Malaysia

Introduction

Although maize and maize products are important import items in Malaysia (Dep. Statistics, Malaysia 1995), the cultivation of the crop has not received much attention because of its low productivity and consequent low profitability. One cause is the lack of high-yielding varieties adapted to local conditions (Lee 1987). To increase productivity, for the past 10 years the University Putra Malaysia has conducted a hybrid development programme using locally-developed inbred lines (Saleh et al. 1994). The objectives were mainly to develop inbred lines from the locally-available open-pollinated varieties and test their combining abilities. Since the inbred lines were developed from various source populations, we also sought to compare heterosis and performance of the hybrids produced from inbreds among different source populations.

Materials and Methods

Inbred lines were developed independently from four diverse Southeast Asian source populations, through pedigree selection and tests of general combining ability (GCA). At homozygosity, the inbred lines were evaluated for per se performance. Twelve inbred lines from different population sources were selected as parents for a diallel cross. The performance of the single-crosses between inbred lines between and within populations was then evaluated at two locations for yield and estimation of heterosis. In the succeeding planting season, selected double crosses were also evaluated.

Results

There were significant differences in grain yield among the single-crosses, parental lines and check varieties. Three hybrids -- Hy-58, Hy-59, and Hy-60 -- gave consistently high grain yields at both locations (Table 1). Most single-crosses gave high heterosis for yield. Heterosis over better parent for grain yield ranged from 72.3 to 383.1% at Field 2, and from 16.8 to 333.1% at Share Farm. Two double-crosses, -- DC-26 and DC-34 -- gave consistently excellent yields at both locations (Table 2).

Conclusions

Most top ten hybrids (based on their per se performance, heterosis estimates, or SCA effects) had parents from diverse population sources. This was also confirmed by the distribution of the inbreds plotted using graphical analysis of the diallel (Sujiprihati 1996). The highest yielding crosses were not necessarily the ones with highest heterosis, although they had high heterosis as well. The four inbred parents involved in both the superior double crosses, DC-26 and DC-34, were from different population sources, again indicating that diversity among them is a factor contributing to the high heterosis and performance of the hybrids. Predicted yields of the double crosses based on non-parental single cross means (Jenkins 1934) were lower than the actual, although the relative trends were in good agreement.

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Table 1. Ten top-yielding hybrids, their yields and heterosis, and combining abilities of the respective inbreds from a 12X12 diallel cross evaluated at two locations. BP, MP: better-parent, mid-parent; *, **: sig. at $p \leq 0.05$, $p \leq 0.01$.

Hybrid (and inbreds $P_1 \times P_2$)	Grain yield (kg/ha)	Heterosis(%)		SCA effects		GCA effects (kg/ha)
		BP	MP	P_1	P_2	
At Field 2:						
Hy-51 (S-9 x SM5-5)	4763	383	255	1855.6**	1934.0**	-40.1
Hy-59 (M-13 x SM5-4)	3941	436	288	304.9**	-138.6*	71.0
Hy-20 (SM7-6 x TW-12)	3867	54	117	962.5*	1319.7**	-166.6**
Hy-76 (S-9 x S-2)	3800	131	165	264.6*	253.4**	8.1
Hy-57 (S-2 x SM5-4)	3741	66	237	1050.8**	1374.7**	71.0
Hy-44 (M-13 x SM5-9)	3733	122	303	339.8**	131.8*	-397.3**
Hy-43 (S-9 x SM5-9)	3719	277	198	844.5*	1582.1**	-397.3**
Hy-58 (S-9 x SM5-4)	3704	289	240	304.9**	-138.6*	71.0
Hy-79 (M-13 x S-9)	3644	271	314	1019.1**	1395.4**	304.9**
Hy-60 (M-5 x SM5-4)	3452	289	344	8.0	131.8*	71.0
At Share Farm:						
Hy-60 (M-5 x SM5-4)	5948	134	187	1223.3**	970.0**	130.2*
Hy-59 (M-13 x SM5-4)	5730	277	187	1168.3**	1100.0**	130.2*
Hy-58 (S-9 x SM5-4)	5659	313	260	304.9**	131.8*	130.2*
Hy-45 (M-5 x SM5-9)	5511	276	215	885.2*	1503.3**	45.0
Hy-73 (S-9 x SM7-11)	5393	289	244	304.9**	-138.6*	-161.9**
Hy-79 (M-13 x S-9)	5378	42	333	432.3	1400.1**	131.8*
Hy-43 (S-9 x SM5-9)	5296	111	372	264.6*	-108.5	45.0
Hy-53 (M-5 x SM5-5)	5259	276	71	858.2*	1934.0**	-132.8*
Hy-23 (S-2 x TW-12)	5259	295	135	120.0	-138.6*	-55.0
Hy-66 (M-5 x SM7-6)	5244					200.0**

Table 2. Grain yield and plant height of ten double-cross hybrids and check varieties evaluated at two locations.

Double-cross/ Check variety	Grain yield (kg/ha)		Plant height (cm)	
	At Field 2	At Share Farm	At Field 2	At Share Farm
DC-26	6125	5649	188	177
DC-27	4505	4470	179	165
DC-28	5135	5022	180	181
DC-29	5803	4971	172	171
DC-30	4449	4626	154	160
DC-31	5438	5455	195	190
DC-32	5433	5410	179	184
DC-33	5193	5108	185	177
DC-34	5918	5676	180	191
DC-35	5422	5134	178	157
Suwan-1	5342	4862	193	186
Suwan-3	4885	4869	181	185
Metro	4985	4585	226	203
LSD (0.05)	747	887	26	28

A65 - Improvement of Soybean Yield via Crosses, Mutation and Heterosis

Tran Van Lai, Nguyen Ngoc Thanh, and Mai Quang Vinh

Research Institute of Fruit and Vegetables, Trau Qui, Gia Lam, Hanoi, Vietnam

Introduction

Soybean cultivation has existed in Vietnam for a long time, but cultivated area per year has not surpassed 200,000 ha, and gross output is below 120,000 t, with average yields of only 0.8 t/ha). Improving soybean yield is quite urgent in Vietnam.

Materials and Methods

During 1990-1995, two varieties -- V74 and AKO4 -- were mutated by Co 60 with 5, 10, 20, 30 and 40 kr and A93, A94 and A96 lines were selected. During 1992-1996, the combination of AKO4x 43DL27, AKO4 x VMK, and AKO4 X V74 were evaluated for studies of heterosis in soybean. The soybean breeding program at the Vietnam Agricultural Science Institute started in 1997 with a set of crosses between Vietnamese and Chinese varieties: DH4 X Santamaria; V74 X Santamaria and VMK x Santamaria.

Results

AKO4 was selected from the crosses Santamaria x DH4. It is a promising early duration variety, allowing three crops in northern Vietnam. It has high yield, large seeds, high chlorophyll content, and high photosynthesis (Table 1). But it has green seeds, so it is less marketable and is still being improved. Out of the mutation from V74 and AKO4, we have selected some soybean varieties for intensive farming regions in spring and summer seasons with yield of 2.8-3.1 t/ha. Six promising soybean varieties are also being multiplied and released for production (Table 2). Mid-parent heterosis (HMP%), heterosis over the better parent (HBP), and heterosis over the check variety (Table 3) were estimated and highly significant differences were observed among varieties (lines) in number of pods/plants, number of seeds/plant, 1000-seed weight, seed weight/plant, and yield (Tables 4 and 5).

Conclusions

Selection and mutation have been carried out and 10 cultivars have been introduced on a large scale : AKO4, SO5,S31, S50,S52, Ag3, Ag4, Ag6, D48, D46, D92 and D90. From above - mentioned results yield has increased to between 15 - 25%. All results indicate that heterosis differs with cross combination and characters.

Table 1. Yield and yield components of some promising soybean varieties.

Crosses and Parents	Duration (day)	No pods/plant	No seeds/pod	1000 seed weight (gr)	Yield (t/ha)
Santamaria x DH ₄ (AK ₀₄)	94	131.6	1.95	180	2.85
Santamaria x DH ₄ (AS ₃)	96	96.2	1.75	156	2.50
Santamaria x DH ₄ (AS ₄)	98	131.5	1.65	154	2.40
Santamaria	97	76.9	1.42	146	2.30
DH ₄	92	52.8	1.37	166	2.45
V ₇₄	102	45.5	1.67	132	1.96
VMK	98	49.5	1.48	142	1.67
Mean	98	72.5	1.52	152	2.3
CV%	0.7	12.0	0.75	24	14
LSD (5%)	1.9	11.9	0.83	21	0.6

Table 2. Yield and yield components of mutation lines of soybean.

Line		No pods/plant	1000 seed weight (gr)	Protein (%)	Yield t/ha
Mutation	V ₇₄	27 + 2	139	39.5	2.25
From V ₇₄	S ₂₅	32 + 1	170	40.5	2.45
	S ₃₁	33 + 2	165	41.2	2.62
	S ₅₀	30 + 2	152	42.5	2.71
	S ₅₂	29 + 2	169	41.5	2.57
Mutation	AK ₀₄	27 + 2	186	40.5	2.75
	A ₉₃	35 + 2	205	42.0	3.04
	A ₉₄	34 + 3	210	41.8	3.15
	AK ₉₆	30 + 2	198	40.9	2.95

Table 3. Heterosis of characteristics in F₁ of soybean.

Crosses	HMP %	HBP %	HS %
	Number of pod/plant		
VMK x AK ₀₄	173.0	166.7	173.1
43DL ₂₇ x AK ₀₄	186.4	164.0	157.7
Cuc x AK ₀₄	143.4	135.7	135.7
	Seed weight/plant		
VMK x AK ₀₄	151.3	125.5	187.3
43DL ₂₇ x AK ₀₄	192.0	153.2	228.6
Cuc x AK ₀₄	130.7	88.3	251.5

Table 4. Yield and yield components of F₁ generation.

Crosses/parent	Duration (day)	No pods/plant	No Seeds/pod	1000 seed weight (gr)	P seed/plant
VMK x AK ₀₄	87 + 3	45 + 3	1.9 + 0.5	142 + 2	11.8 + 1.5
43DL ₂₇ x AK ₀₄	101 + 4	41 + 4	2.1 + 0.4	166 + 3	14.4 + 1.8
Cuc x AK ₀₄	80 + 3	38 + 5	1.9 + 0.6	118 + 2	8.3 + 1.7
VMK	85 + 2	27 + 3	1.8 + 0.7	130 + 3	6.2 + 1.2
AK ₀₄	96 + 3	25 + 4	2.1 + 0.8	181 + 2	9.4 + 1.1
43DL ₂₇	110 + 2	19 + 3	2.0 + 0.9	151 + 3	5.6 + 1.3
Cuc	74 + 3	28 + 2	1.7 + 0.8	72 + 2	3.3 + 1.4
V ₇₄	98 + 4	26 + 3	1.9 + 0.7	131 + 2	6.3 + 1.5

Table 5. Yield and yield components of some promising soybean lines.

Crosses/parent	No pods/plant	P ₁₀₀₀ seed weight (gr)	P seed/plant	Yield (t/ha)
D ₄₈ (43DL ₂₇ x AK ₀₄)	26.1	152.2	6.1	2.3
D ₄₆ (43DL ₂₇ x AK ₀₄)	27.1	164.5	7.2	3.0
D ₉₂ (43DL ₂₇ x AK ₀₄)	22.6	137.6	5.9	2.9
D ₉₀ (43DL ₂₇ x AK ₀₄)	22.2	142.3	5.2	2.9
V ₇₄	21.1	132.7	4.7	2.4
AK ₀₄	20.1	170.5	6.3	2.8
VMK	22.8	132.8	4.6	2.4
43DL ₂₇	19.7	137.2	4.3	2.4
CV%	5.8	1.7	3.3	3.5
LSD 5%	3.0	5.8	0.4	1.1
LSD 1%	4.4	8.6	0.6	1.2

A66 - Physiological Aspects of Tomato Heterosis Under *in vitro* Culture

V.V. Titok, S.I. Yurenkova, and V.A. Lemesh

Institute of Genetics and Cytology, Academy of Sciences of Belarus, Skorina St. , 27, 220072 Minsk, Belarus

Introduction

Cell bioenergy is a promising system for studying heterosis mechanisms. Efficient biosynthetic processes that can ensure high plant productivity depend on potential power of energy-generating systems and mechanism perfection of their regulation (Tsaftaris 1995). In our research, attention was concentrated on investigating individual stages of energetic metabolism (glycolysis, pentose phosphate pathway, electron transport chain of mitochondria) in green leaves of plants taking into consideration their interactions by using values of key enzyme activity and estimating the content of chlorophylls, adenine, oxidized and reduced forms of nicotinamide nucleotides in leaves of parental forms and F_1 hybrids of tomato, differing in heterosis effect.

Methods

We used tomato plants of the following selection forms: Tropson, Premier, Son, Kar and Sokrat. F_1 hybrids were produced by crossing Tropson x Son, Son x Kar, Premier x Son, Tropson x Premier, Premier x Sokrat. To preserve the unique genetic features and to exclude the influence of growth conditions on plant material, we used a method of tomato propagation in a meristematic *in vitro* tissue culture (Titok et al. 1994). Biochemical analysis was carried out in 36-40-d green plants with five leaves. Adenine nucleotides and recovered and oxidized forms of nicotinamide coenzymes were determined using the method of the reversed-phase ion pair DPLC (Titok et al 1995). The activities of glucose-6-phosphatodehydrogenase (G6PDH), phosphofructokinase (PFK) and cytochrome-c-oxidase (Cyt-c-oxidase) were determined by spectrophotometric methods. (Ashihara and Komamine 1976; Stamp 1981; Bergman et al. 1980).

Results and Discussion

The means of F_1 -hybrid combinations for this character significantly surpasses parents. The experimental results show higher activity of G6PDH in leaves of tomato parental forms in comparison with hybrids (Table 1). Activity of PFK in parents is also high, but the ATP content is much higher in hybrids. Probably in green cells of hybrid organisms, ATP is produced mainly in the course of mitochondrial respiration and photosynthetic phosphorylation, as indicated by the high energy values. High-heterotic hybrid (Tropson x Son) is intermediate among parental varieties in PFK activity. On comparing results obtained for Cyt-c-oxidase activity in parental forms and their hybrids, in particular heterotic ones, a significant increase in this value for the latter was noted. The contribution of photosynthesis and individual respiration stages to the total energy pool were determined by genotype. Pentose phosphate cycle is suppressed in green leaf of heterotic hybrids in contrast to nonheterotic ones, glycolysis and electron transport chain of mitochondria are not inhibited. This may indicate that photosynthesis, glycolysis and mitochondrial respiration are the major sources of supplying macroergic compounds and reduction equivalents in the heterotic forms. Heterotic hybrids in comparison with parents had more powerful bioenergetic potential, which ensured their superiority in productivity. In parental forms reactions of glycolysis, the pentose phosphate cycle and electron transport chain of mitochondria are not inhibited in green leaves; however, in the latter the available level of energetic metabolites are. They are possibly not used completely to form organic substances in the cell, a supposition supported by the productivity analysis of these forms. Thus, the results indicate the modification of energy metabolism in green leaves of heterotic hybrids. This is perhaps expressed as the optimization of functional relationships between bioenergetic pathways.

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Table 1. Glucose-6-phosphatedehydrogenase (G6PDH), phosphofructokinase (PFK), cytochrome-c-oxidase (Cyt-c-oxidase) activities, ATP content and adenylate energy charge (AEC) in tomato leaves of parents and F₁-hybrids . Student's t-test represents significance of difference between parents and hybrids means at the * -P ≤ 0.05, ** -P ≤ 0.01. Means from 8-9 experiments are given.

Parents, hybrids	G6PDH [μmol (NADPH) mg ⁻¹ (protein) min ⁻¹]	PFK [MMOL (nadh)mg ⁻¹ (protein min ⁻¹)]	ATP [nmolg ⁻¹ (f.m.)]	AEC ratio	Cyt-c-oxidase [mkmol (Cyt-c/oxidazed)mg ⁻¹ (protein) min ⁻¹]
Tropson	0.043	0.045	73.51	0.602	0.0389
Premier	0.027	0.037	48.93	0.576	0.0600
Son	0.032	0.014	69.58	0.562	0.0951
Kar	0.033	0.031	85.44	0.524	0.553
Sokrat	0.041	0.042	110.39	0.659	0.0756
Tropson x Son	0.027	0.036	95.24	0.689	0.0991
Son x Kar	0.024	0.012	54.39	0.578	0.0626
Premier x Son	0.019	0.017	89.97	0.567	0.0645
Tropson x Premier	0.026	0.011	112.44	0.661	0.0596
Premier x Sokrat	0.015	0.011	112.70	0.664	0.0842
Mean of parents	0.035**	0.034**	77.11*	0.582**	0.0650*
Mean of hybrids	0.022**	0.017**	93.43*	0.633**	0.0738*
LSD ₀₅	0.003	0.005	14.69	0.042	0.0098

Adenylate energy charge = $[ATP] + 0.5 [ADP] / [ATP] + [ADP] + [AMP]$ (Atkinson and Walton 1967)

A67 - Using the Thin Layer Cell Culture Technique for Multiplication of TGMS Lines In Rice

N.T. Nhan, H.T. Minh, N.T. Hoai, and V.T. Thuy

Plant Cytogenetics and Wide Hybridization Division, Institute of Agricultural Genetics. Hanoi, Vietnam

Introduction

Hybrid rice research in Vietnam began in 1990. Researchers have created several new TGMS lines. The question is how to rapidly purify and multiply these new lines. The application of biotechnology (in-vitro propagation, in particular) may be used to solve this problem. We carried out experiments to find suitable culture media for obtaining high frequency of callus as well as soma embryo callus induction and green plantlet differentiation, to increase plantlet survival when transferred to the soil.

Methods

Lines VN-01, VN-02 and TG-162 were used for thin layer cells culture. Vigorous seedlings and tillers of these lines were cut and cleaned with distilled water several times and immersed in 70% ethyl alcohol for 20 min. Before being cut into small pieces they were washed with sterile distilled water. Very thin layers of cells were inoculated directly into callus induction mediums which contained different combinations of 2,4 D + BAP and put in a darkroom at $25 \pm 1^\circ\text{C}$. After 20 days, induced calli were transferred to a plant regeneration medium. Plantlet formation took about 20 days under 10 h light/ 14h dark at room temperatures. Green plantlets can be cultured continuously in the same medium to multiply them or transferred to LS medium with a certain amount of NAA for root formation. After 14 days, all plantlet with good root systems can be transferred to a nutrient solution or the soil.

Results

We obtained many young plants after 60 days. The frequency of callus induction and plant regeneration was 50 and 100%. Plant survival was more than 90% and transferred plants grow normally in the field.

Conclusion

Thin layer cell culture is one of the most advantageous techniques for multiplication of sterile lines, especially TGMS lines, in rice. The frequency of both callus formation and plant regeneration were high. The CFP and CPS values of the TGMS lines were stable after many generations of culture.

Table 1. Callus formation frequency.

Varieties	Number inoculated	Peak callus forming period (d)	Callus (No.)	Induction frequency (%)
VN - 01	70	16	42	60
VN - 02	70	20	36	51.4
TG - 162	70	18	35	50

Table 2. Redifferentiation of green plantlets from callus.

Varieties	Green plantlet formation period (d)	Callus (No.)	Green plantlets (No.)	Redifferentiation frequency (%)
VN - 01	12	43	42	100
VN - 02	14	36	32	88.8
TG - 162	12	35	32	94.2

A68 - Artificial and Natural Parameters Influencing Outcrossing of Cyto-sterile Lines in Rice

R. Singh and S.K. Sahoo

Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, B.H.U., Varanasi - 221 005

Introduction

Since rice (*Oryza sativa* L.) is strictly a self-pollinated crop, heterosis breeding must involve the use of an effective male sterility system to produce bulk quantities of hybrid seed. Any mechanism that would improve the outcrossing potential of rice would increase success in composite breeding and hybrid development. To determine the factors affecting the outcrossing of cyto-sterile line IR 58025A, we standardized natural parameters to screen the maintainers/restorers having floral traits which may enhance outcrossing. Artificial parameters were used to evaluate the available hybrid seed production technology along with a new growth hormone, Mangiferin.

Materials and Methods

1. *Artificial Parameters.* Twenty-five treatments including GA₃, Boric Acid, Urea Solution and a new growth hormone Mangiferin, and Glycine, were applied on cyto-sterile line seed production of IR 58025A/B, either singly or in combination at different concentrations. Leaf clipping and rope pulling were practiced in all the treatments. We measured floral traits related to outcrossing (duration of opening of spikelets, percentage of exerted stigma, angle of florets opening, panicle exertion percentage, length of spikelet, grain yield per hectare and plant height). The analysis of variance was carried out separately for each of the traits following Panse and Sukhatme (1954).

2. *Natural Parameters.* Seventy-five restorers and maintainers were studied for variability parameters according to Burton (1952) in floral traits associated with outcrossing in rice (duration of opening of spikelets, percentage of exerted stigma, angle of florets opening, panicle exertion percentage, length of spikelet, grain yield per hectare, plant height, anther length and stigma length).. Heritability, genetic advance, and correlation among the floral traits were also evaluated.

Results

GA₃ and Mangiferin affected important floral and associated traits equally, but GA₃ had a greater effect on grain yield (Table 1). Flag leaf clipping and rope pulling contributed to an increased seed set.

Glycine improved seed yield 26% to 39% over the control. The evaluation of variability led to screening of genotypes like Aditya, VD Dhan-63, IET-10111, IET-10115, VL Dhan-8, Pratibha, Kunti, Surajmukhi, and Vikas, all possessing multiple floral traits which facilitate outcrossing (Table 2)..

Positive and significant correlations were observed between duration of opening of spikelet and angle of opened spikelets; percentage of exerted stigma and duration of opened spikelet; angle of opened florets and spikelet length; etc. (Fig. 1).

Conclusions

The essential factors to develop cyto-sterile lines with good outcrossing potential are present in rice germplasm. Maintainers with these traits can be converted into cyto-sterile lines with high outcrossing potential. GA₃, Mangiferin, and to some extent Glycine affect seed yield and important floral traits of cyto-sterile lines (Singh and Sahoo 1996).. *Mangiferin* improves seed production in cyto-sterile lines, but additional comparative studies, particularly on economics of *Mangiferin* vs GA₃, are required.

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Table 1. On the basis of effectiveness with respect to grain yield, some of the promising treatment combination have been ranked as follows.

Rank	Treat no.	Treatment	Yield (kg/ha*)
1.	T1	60 ppm GA ₃ + FLC + RP	1417 (100.14%)
2.	T4	40 ppm GA ₃ + FLC + RP	1230 (73.72%)
3.	T9	60 ppm GA ₃ + BA+U+FLC+RP	1081 (52.68%)
4.	T21	60 ppm GA ₃ + 60 ppm Mangiferin + U + FLC + RP	1043 (47.31%)
5.	T2	60 ppm Glycine + FLC+RP	984 (38.98%)
6.	T5	40 ppm Glycine + FLC+RP	984 (38.70%)
7.	T15	80 ppm Glycine+BA+U+FLC+RP	890 (25.70%)
8.	T17	40 ppm GA ₃ +40 ppm Glycine + FLC + RP	868 (22.60%)
9.	T3	40 ppm Mangiferin+ FLC+RP	859 (21.32%)
10.	T25	Control	708

* Values in parenthesis are percentage increase over control

FLC- Flag leafclipping, RP-Rope pulling, BA - Boric acid and U-Urea.

Table 2. Based on *per se* performance and variability studies, it was found that following were the outstanding genotypes with respect to each trait and may be explored in future crossing programme for hybrid breeding in rice.

Characteristic	Genotypes
Duration of florets opening	Aditya, IET-101102, IET-10307, IET-10311, Vibhava, IET-10322
Angle of opened florets	VL Dhan 63, VL Dhan 8, IET-101111, IET-101112, IET-101115, IET-101116
Percentage of exerted stigma	IET-10317, IET-10319, IET-101114, IET-101119, Vibhava, Pratibha
Anther length	IET-101110, IET-101113, Ravi, IET-10315, BK-190
Spikelet length	IET-101115, IET-101116, IET-101104, IET-101117, IET-101106
Stigma length	IET-101115, Iet-101104, IET-101107, IET-101111, IET-101114

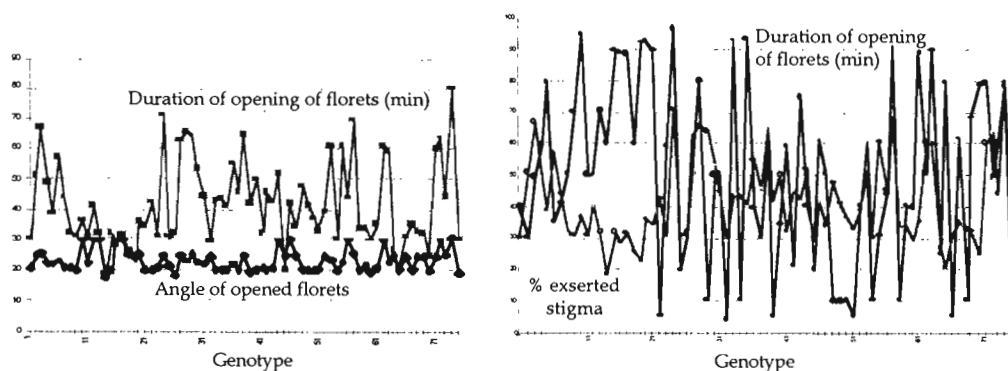


Figure 1. Genotype to genotype correlations between several key traits relating to outcrossing in 75 rice genotypes.

A69 - Studies on Heterosis for Certain Physiological and Biochemical Parameters in Rice

R. Singh

Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, B.H.U., Varanasi - 221 005

Introduction

Growth and yield are the result of phenotypic expression of biochemical and physiological reactions under genetic control. Heterosis can influence the size of source as well as of sink. The study of certain physiological/biochemical traits is essential to understanding sink and source relationships. The superiority of F₁ hybrids for photosynthetic area, chlorophyll content per unit area, photosynthetic efficiency, mitochondrial activity, root activity, embryo development, etc., has been reported by Lin and Yuan (1980) and McDonal et al. (1971), and much work has been done on the genetic behaviour of similar traits in conventional rices. This study addresses hybrid rice (*Oryza sativa* L.).

Methods

The extent of average heterosis and heterobeltiosis were estimated in thirteen hybrids and 10 parents for various physiological and biochemical traits.

Photosynthetic Rate and Stomatal Conductance. Measured using an infrared gas analyser (IRGA) and a portable closed gas exchange photosynthetic system (LI-COR-6000, Lincoln, Nebraska) under ambient oxygen and CO₂ concentrations and naturally occurring solar radiation at 25 and 50% flowering.

Chlorophyll. Total chlorophyll and its fractions (chlorophyll a and chlorophyll b) were determined accordingly to Mackinney (1941) in mg. chlorophyll per gm. fresh weight.

Soluble Protein. Estimated using folin catachol reagent (Lowery et al. 1951) and expressed in mg. per gm. of fresh weight of plant material.

Peroxidase Enzyme Activity. Assayed according to Mallick and Singh (1980).

Seed Protein. Nitrogen was estimated as per Braddstreet (1965) and multiplied by 6.25.

Flag Leaf Area. Area of two randomly selected flag leaves were estimated using a leaf area meter.

Results and Conclusions

Heterosis differs from character to character depending upon the hybrid combinations (Table 1). Most hybrids showed significant and positive relative hererosis and heterobeltiosis for the flag leaf area, chlorophyll, seed protein, peroxidase activity and stomatal conductance (Fig. 1). Hybrids IR54752A x Narendra 118, V20A x Narendra 80, V20A x Saket 4 and ES18A x Saket 4, which exhibited high relative and better parent heterosis for grain yield, also showed strong heterosis for the above-mentioned traits, suggesting a positive relationship of these characters with grain yield. Most hybrids expressed low heterosis for soluble protein and chlorophyll ratio. No specific relationship between photosynthetic rate and grain yield existed, as some hybrids having high grain yield heterosis expressed positive as well as negative heterosis for photosynthetic rate.

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Table -1: Relative heterosis for certain biochemical-physiological parameters in rice.

I - Flag Leaf Area, II - Chlorophyll (a), III - Total Chlorophyll, IV - Chlorophyll Ratio (a/b), V - Soluble Protein, VI - Seed Protein, VII - Peroxidase Activity, VIII - Photosynthetic Rate, IX - Stomatal Conductance.

Hybrid	I	II	III	IV	V	VI	VII	VIII	IX
IR 54752 A x Narendra 118	22.81**	11.76**	-6.45**	-21.84**	-1.31	54.96	14.30**	6.78**	3.08**
IR 54752 A x Narendra 80	64.53**	-19.32**	-15.71**	19.90**	-4.41**	70.07*	8.57**	47.25**	-35.80**
IR 54752 A x Saket 4	31.54**	-11.77**	-12.27**	-12.44**	1.37	38.00	62.95**	-3.32**	-22.77**
IR 54752 A x Saket 1	65.32**	-58.18**	48.40**	-8.25**	-55.96**	45.64	40.33**	2.83**	14.53**
V 20 A x Narendra 118	-10.28**	39.46**	38.30**	-5.23**	-18.98**	168.99**	112.17**	4.96**	32.52**
V 20 A x Narendra 80	12.84**	54.62**	53.82**	-0.86	29.75**	63.96	54.87**	33.06**	27.74**
V 20 A x IR 24	53.80**	-13.01**	10.56**	-24.77**	-30.16**	73.20	14.32**	29.62**	49.33**
V 20 A x Saket 4	15.75**	30.00**	30.42**	-2.33*	-16.47**	103.99*	57.12**	1.43	20.44**
V 20 A x Saket 1	-17.79**	-11.09**	10.24**	-4.54**	-36.59**	113.23**	23.57**	38.84**	59.44**
IR 46830 A x IR 24	-10.65**	11.81**	14.61**	10.11**	-45.66**	53.49	13.01**	35.53**	30.96**
IR 46830 A x Saket 1	2.45**	52.85**	50.44**	4.67**	-21.80**	65.31*	23.62**	-13.74**	-4.93**
ES 18 A x Saket 4	78.29**	24.65**	-39.70**	82.49**	7.72**	79.79*	158.46**	-37.97**	-11.04**
Madhu A x Narendra 118	-18.36**	5.29**	31.83**	17.15**	3.23**	92.47*	130.80**	-24.43**	12.56**
Mean heterosis	22.33	8.97	18.84	4.16	-14.55	78.70	54.93	9.25	14.01
Number of hybrids with positive heterosis	9(9)	8(8)	9(9)	5(5)	4(3)	13(7)	13(13)	9(8)	10(10)
Number of hybrids with negative heterosis	4(4)	5(5)	4(4)	8(7)	9(8)	0(0)	0(0)	4(4)	3(3)

*,** - Significant at P-0.05 and P-0.01. Figure in parenthesis indicate significant deviation.

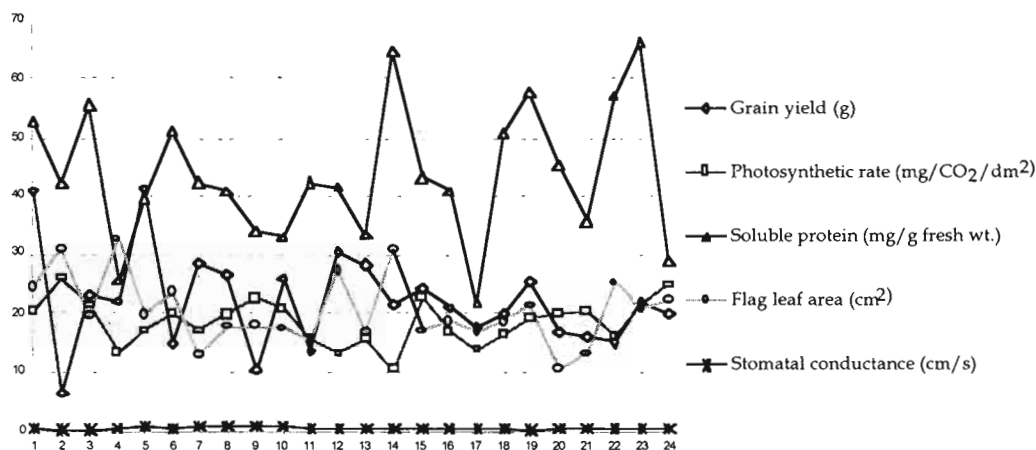


Figure 1. Relationships between grain yield and biochemical/physiological traits in rice hybrids (1-13) and their parents (14-24).

A70 - Novel Heritable Source of Genetic Modifications in Wheat: Production of Colchiploids

L. Hassan

Department of Genetics & Plant Breeding, Bangladesh Agricultural University, Mymensingh - 2202, Bangladesh

Colchicine induced heritable variation was demonstrated by Lockett (1989) in cotton. Variations in important agronomic characters due to colchicine induction was demonstrated by several authors (Francis and Jones 1989; Hassan *et al.* 1989; Hassan 1997) in ryegrasses; Hassan *et al.* 1993 in rice plants. Heritable modifications at cellular levels were demonstrated by Hassan *et al.* 1991 in ryegrasses and Hassan 1997 in wheat. This genetic variations was also observed in some important cytological parameters in ryegrasses (Hassan *et al.* 1992; Hassan & Jones 1994 and 1995). They also concluded that the induced changes are heritable in nature and transmitted undiminished through a self-seed generation. The aim of the present work was to test the hypothesis in 10 wheat varieties/advanced lines and genotypes in five important agronomic characters and create heritable nature of genetic variability in the breeding population.

Materials and Methods

In 1995 seedlings from wheat varieties (Aghrani, Kanchon, DSN-61, DSN-72, MD-2329, Ad-66-1, Anza, SA-36, Sonalika and YC-17) from the wheat research project, department of Genetics and Plant Breeding, Bangladesh Agricultural University were treated with colchicine and grown to flowering and self pollinated. Seeds from the selfed plants were grown again without further treatment and a selection of agronomic and other traits were measured.

Results and Discussion

In the comparison of means \bar{X} for the treated and control plants the analyses were performed using all the values for individual plants and show a highly significant ($P < 0.001$) difference in fresh weight and significant ($P < 0.01$) differences in dry weight, straw/plant and grain yield/plant (Table 1). Only the character days to flowering shows non-significant variation. Colchicine treatments given to the young seedlings of wheat varieties appear to change development significantly, often improving key agronomic characters, and the changes in most cases are transmitted through at least one selfed generation. The mechanisms underlying these changes in plant growth and development remain speculative. One possibility is that of genome re-organization in the form of DNA amplification of certain DNA sequences of the kind described in some flax genotrophs (Walbot & Cullis 1985; Cullis 1986). Another possibility is that the changes are epigenetic, without any alteration in sequences, and that they result from reprogramming of genes through processes of DNA methylation. In any event these results pose new questions about the optimum dosage of colchicine for induction processes, and for exploring the underlying causes of the effects. One useful approach could be AFLP molecular marker analysis to detect sequences alterations. However, the colchiploids obtained with novel heritable genetic modifications may be utilized for the exploitation of heterosis in wheat.

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Table 1. Mean values per line for fresh weight, dry weight, days to flowering, straw/plant and grain yield/plant. In the comparison of means, the analyses were performed using all the values for individual plants, rather than means per line.

	<u>Fresh weight (g)</u>		<u>Dry weight (g)</u>		<u>Days to flowering</u>		<u>Straw/plant</u>		<u>Grain yield/plant</u>	
	Control	Treated	Control	Treated	Control	Treated	Control	Treated	Control	Treated
Aghrani	8.54	13.65***	5.93	7.53***	7.53	6.97n.s	16.66	17.13n.s	11.06	16.05***
Kanchon	10.79	12.24***	7.94	9.78***	17.73	14.90***	11.31	16.46***	8.87	13.22***
DSN-61	8.27	9.65**	5.34	7.05***	26.50	24.53n.s	15.18	18.88***	14.91	21.89***
DSN-72	6.88	8.30	4.55	5.09n.s	35.63	34.37n.s	15.37	19.49***	9.36	12.08*
MD-2329	10.63	12.56***	7.27	9.70***	10.70	10.73n.s.	10.08	13.06**	9.41	14.38***
Ad-66-1	10.12	13.42	6.81	10.47***	29.90	27.13**	16.34	15.25n.s	8.81	12.02***
Anza	12.40	15.13***	9.24	11.93***	21.53	10.03*	16.48	21.51***	11.09	15.90***
SA-36	12.18	15.42***	8.54	9.93*	34.63	29.77***	20.05	25.14***	17.37	20.80*
Sonalika	11.86	12.81*	8.82	9.67*	10.20	10.33n.s	15.39	19.31***	12.02	12.98n.s
YC-17	10.36	10.76n.s	7.54	8.61**	38.07	37.30n.s	20.07	25.23***	10.16	14.45**
Mean	10.20	12.39***	7.20	8.98**	23.24	21.61n.s	15.69**	19.15**	11.31	15.38**

NS Not Significant For line, n=30; For mean, n=300

*P<0.05

**P<0.01

***P<0.001.

A72 - Genetics and Physiology of Heterosis in Soft Wheat

R.A. Urazaliev, M.A. Yessimbekova and O.I. Sidorenko

Kazakh Scientific Research Institute of Agriculture, Almalybak, Kaskelen District, Almaty Region, 483133, Kazakhstan

Introduction

Yield increases in many crops are based on the widespread use of heterosis. Heterosis makes it possible to easily combine desired traits, to reduce growing periods of varieties and hybrids, simultaneously increasing their productivity by 20-30%, and to control pest and disease infestations resulting from long-term reseeding of similar genetic material. Research on hybrid wheat in Kazakhstan has been conducted at the Kazakh Scientific Research Institute of Agriculture under the program "Heterosis and its use in agriculture". The effect of soft wheat (winter, spring) heterosis on fertile and sterile basis (cyt. *T. timopheevi*) types of heritability of economically-valuable traits (grain quality, the dynamics of their change over F_1 - F_4) were studied in a diallel trial. Photosynthesis mechanisms in highly productive heterosis hybrids of winter wheat were considered.

Methods

The experimental work was done at the foot of the Zailiiski Alatau mountain range (40-44 ° N; 72-78 ° E; 740 m above sea level; light chestnut soils; heat units/season 2,500-2,700°C; yearly average precipitation 433 mm supplemented by irrigation). F_1 - F_4 hybrid populations were received on a fertile and sterile basis (*T. timopheevi*) with the use of soft wheat, short stature cultivars, resistant to rust and high combining ability. The heterosis effect of the best and average parent was recorded and diallel analysis was made. Traits measured included leaf area and photosynthetic potential, photosynthesis pure efficiency, daily dry biomass increment, leaf and head photosynthetic intensity, economic efficiency coefficient, and biological and economic yield. Seeding, crop tending and phenological observance were performed by generally accepted techniques in selection.

Results

The study of heterosis in F_1 hybrids on a fertile and sterile basis has shown discrete heterosis effectiveness by degree and frequency, depending on genetic peculiarities of parental varieties, crossing combinations, cytoplasmic basis and vegetation conditions. The degree of heterosis effectiveness in F_1 hybrids on a fertile basis for tillering, 1000-kernel weight, and head length was as high as 50%; for grain yield it varied from 4 to 25%, and by crop it varied from 18% to 43%. Fertility restoration through CMS in F_1 hybrids predetermined the degree of heterosis for grain yield and crop. Heterosis was observed in combinations with practically complete restoration. Trait heritability varied from epistasis to overdominance. Dominance was found for secondary traits such as plant height, number of head spikes, and 1000-kernel weight. By such traits as head length, number of head kernels dominance is directed to the increase of trait levels. Grain quality was inherited by the type of maternal parent (in the year of crossing) and by an intermediate type in F_1 - F_2 (Fig. 1). Wheat hybrids were characterized by higher rates of formation and low rates of leaf necrosis, which increased leaf photosynthesis and, along with a larger leaf area, significantly increased photosynthesis pure efficiency, daily growth rate, and accumulated dry biomass during grain formation (Fig. 2).

Conclusions

Wheat hybrids displayed a high degree of heterosis (up to 50%) for productive traits and crop. Hybrids preserving the advantage of economically important traits in F_3 - F_4 (established by selection) have practical significance for selection work. Hybrids of high quality parents inherit high grain quality. Grain yield is determined by level of photosynthesis. The heterosis effect on photosynthesis parameters is displayed during reproduction, which is the most important period for grain formation. The use of the genetic system A-lines, B-lines, R-lines, is limited by the difficulties of creation and insufficient stability of fertility restorers (R-lines), low level of seed setting during cross pollination, and by the cost of hybrid seed.

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Distribution of plants

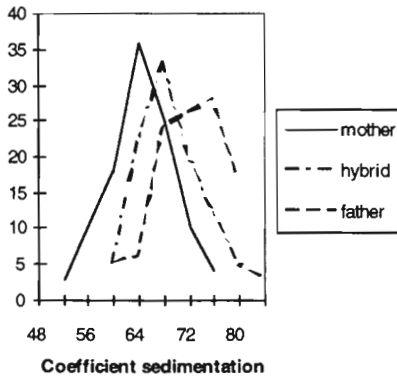


Figure 1. Variational curve distributions of plants of hybrids F1 on coefficient sedimentation

Accumulation of dry biomass, g/tiller

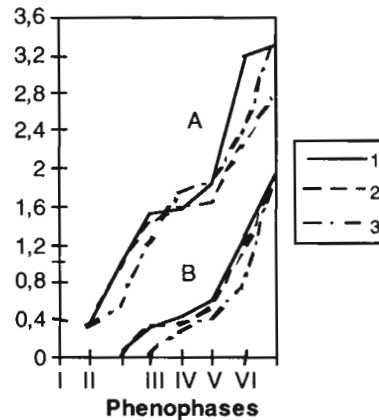


Figure 2. Accumulation of dry biomass of heterosis hybrids (1) and parents (2 - mother, 3 - father) : A - tiller, B - head.

Selection Methodologies and Heterosis

J.G. Coors

Department of Agronomy, University of Wisconsin-Madison, Madison, WI 53706, U.S.A.

The genetic mechanisms underlying heterosis are largely unknown. Competing genetic theories differ on the relative importance of overdominance, epistasis, and linkage and how they contribute to hybrid performance. In a practical sense, though, knowledge of the genetics of heterosis has not been essential for maize improvement. In the early part of this century, the commercial potential of maize hybrids increased interest and funding for breeding far beyond the level of other crops, and this led to one of the most highly acclaimed genetic success stories of modern times. The ample financial and intellectual resources of hybrid seed companies have been primarily dedicated to insuring high selection intensities, extensive wide-area testing, improvements in mechanization, efficient data collection, and elaborate data analysis. However, there is nothing unique to the hybrid breeding system in this allocation of resources. High selection intensities and accurate, efficient testing strategies are required for breeders of all crop species. In fact, several well-run, long-term population improvement programs in maize have produced genetic gains equal to or greater than the 60 kg ha⁻¹ yr⁻¹ average of the hybrid seed industry.

This presentation will summarize a compilation of the many long-term (more than three cycles) intra- and interpopulation improvement programs in maize and compare the annual improvement in yield to those achieved by the U.S. hybrid seed industry over the last six decades. To date, a partial compilation (96 studies) has been completed. On an annual basis, the mean increases in grain yield of populations improved by mass, modified ear-to-row, full-sib, and S₁ family selection have been approximately 40, 94, 51, and 63 kg ha⁻¹ yr⁻¹ (corresponding to percentage increases of 0.8, 2.6, 2.0 and 4% cycle⁻¹, respectively). The greatest annual gain, though, has been achieved in crosses of populations improved through reciprocal recurrent selection, 109 kg ha⁻¹ yr⁻¹ (or 4.5% cycle⁻¹). These data are particularly notable because selection intensities used in population improvement programs are much less than those typically applied in hybrid development programs. The results certainly support the notion that breeders should utilize heterosis for developing productive varieties, but they also suggest that the gains realized by commercial hybrid programs are less than expected.

There are several possible reasons why hybrid gains have lagged behind those seen in selection trials involving populations. First, productive inbred parents are required for efficient hybrid seed production, and this may slow long-term progress. Second, source populations for inbred development (often F₂ or backcross populations) tend to be less variable genetically, which may reduce rate of gain. Third, reports for yield gain in hybrids incorporate results from suboptimal as well as optimal environments, whereas published recurrent selection results are primarily from optimal environments. These issues will be addressed by reviewing particular results from appropriate selection studies and yield trial databases.

Recurrent Selection and Heterosis

C. L. Souza Jr.

Department of Genetics, Escola Superior de Agricultura Luiz de Queiroz, University of São Paulo, P.O. Box 83, 13.400-970- Piracicaba, São Paulo, Brazil

Populations improved by recurrent selection have been successfully used as sources of improved inbred lines and hybrids in maize breeding programs. Recurrent selection methods are grouped into two main categories: intra- (IRS) and interpopulation (RRS) selection, where the former emphasizes the improvement of populations for *per se* performance and the latter emphasizes the improvement of population crosses. The objective of this study was to compare these recurrent selection approaches for their effectiveness in improving the performance of hybrids from inbred lines. Two populations were assumed to be simultaneously under intra- and interpopulation recurrent selection with half-sib and S_1 progenies as selection and recombination units, respectively. A theoretical approach followed by numerical evaluation was used. The results showed that hybrid improvement is heavily dependent on initial heterosis and on its improvement. If interpopulation genetic variance is much lower than intrapopulation genetic variance, the importance of heterosis in hybrids improvement will be reduced. However, there is no evidence of a large difference.

The changes in heterosis with recurrent selection depend on the difference between the rates of improvement of the populations *per se* and of the population crosses; RRS leads to greater population cross improvement than of the populations *per se*, resulting in increased heterosis. Conversely, IRS leads to greater *per se* population improvement reducing heterosis. Thus, it seems that RRS should be the choice for hybrid improvement. However, RRS will improve only one of the base populations and not the other, at least at reasonable rates. Therefore, neither IRS nor RRS can improve at reasonable rates the population crosses and the populations *per se* simultaneously, which are required to improve the performance of both the hybrids and the inbred lines *per se*. A further analysis of the contribution of each population to hybrid and inbred line improvement showed that a modified recurrent selection method that uses one of the populations as a tester for both populations could be used to fulfill these requirements.

Molecular Markers and Heterosis

J. Moreno-Gonzalez

Centro de Investigaciones Agrarias de Mabegondo, Apartado 10, 15080 La Coruña, Spain.

Introduction

The efficiency of marker-assisted selection (MAS) was studied by Lande and Thompson (1990). Knowledge about MAS in breeding programs which exploit heterosis is needed. The use of molecular markers to identify quantitative trait loci (QTLs) responsible for heterosis may help to improve the genetic gain in some selection breeding schemes. The objectives of this work were to study the effect of the degree of dominance (d), the linkage disequilibrium between markers and QTLs, and the heritability (h^2) on the detection of marker-associated QTLs with heterotic and additive effects in the test-cross selection of an F_2 population, in the modified reciprocal recurrent selection (Russell and Eberhart 1975) and diallel crossing systems.

Methods

Genetic models included those developed by Moreno-Gonzalez (1992, 1993), and Charcosset and Essioux (1994) in a theoretical study. Several stages in the selection procedure were considered. First, breeding germplasm was assigned to heterotic groups based on genetic distance, heterozygosity, and performance. Second, marker-associated QTLs were identified and located in the genome and their additive and heterotic effects were estimated using stepwise regression techniques. Third, a selection index which combines the performance of the trait under selection and the effects of marker-associated QTLs was used as a criterion for selection. Simulation studies with random locations of crossovers were performed for different heritability values, number of progenies, degree of linkage disequilibrium and type of progeny.

Results

The theory and the simulation study confirmed that increasing the number of progenies used for field evaluation and marker laboratory assessment was an important factor not only for increasing selection intensity but also for detecting QTLs with smaller additive and heterotic effects. Some degree of linkage disequilibrium is needed for locating QTLs and constructing the combined selection index. The heritability of the trait affects both the probability of finding QTLs and the genetic gain. A higher genetic gain can be attained if significant multiple correlations between field evaluations and markers are found.

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Best Linear Unbiased Predictor Analysis

R. Bernardo

Department of Agronomy, Purdue University, 1150 Lilly Hall of Life Sciences, West Lafayette, IN 47907-1150, USA

Introduction

Breeders constantly have to decide which experimental single crosses to test, which advanced hybrids to recommend for further testing or commercialization, and which inbred parents to cross to form new base populations for inbred development. Suppose a breeder has 100 inbreds from Heterotic Group A and 100 inbreds from Heterotic Group B. There are (i) 10,000 possible (A x B) single crosses, (ii) 495,000 possible (Group A F₂) x (Group B tester) combinations, and (iii) 495,000 possible (Group B F₂) x (Group A tester) combinations. Obviously breeders can evaluate only a subset of the above single crosses and F₂ populations. Best linear unbiased prediction (BLUP) has been found useful for routine prediction of the performance of maize (*Zea mays* L.) single crosses prior to field testing (Bernardo 1996). My objective is to describe the theory and application of BLUP in a hybrid breeding program.

Theory and Methods

The BLUP procedure utilizes information from relatives. A classic illustration of using information from relatives is the prediction of milk yield performance of a dairy bull. If data are available on a bull's mother and paternal half-sister, the predicted milk yield of the bull is $h^2[0.50(\text{milk yield of mother}) + 0.25(\text{milk yield of paternal half-sister})]$ (Falconer 1989). The bull is more closely related to its mother than to its half sister, and more weight is placed on the mother's performance. Similarly, yield data may be available for hybrids X₁ and X₂, but not for hybrid Y. The performance of Y can be predicted by BLUP if Y is related genetically to X₁ and X₂. Details of BLUP for single crosses were given by Bernardo (1996) and will be reviewed during the presentation. The performance of three-way crosses, F₂ x tester crosses, and double crosses can be predicted if epistasis is negligible.

The BLUP procedure was applied in the North American maize breeding program of Limagrain Genetics. Multilocation data from 1990 to 1995 for 4,775 advanced single crosses were obtained. The usefulness of BLUP was evaluated with a cross-validation procedure. Grain yield, moisture, stalk lodging, and root lodging of each single cross were predicted from the performance of other single crosses in each of 16 heterotic patterns. The correlations between predicted and observed performance served as a measure of the effectiveness of BLUP.

Results

Correlations between predicted and observed performance ranged from 0.463 to 0.770 for yield, 0.868 to 0.936 for moisture, 0.466 to 0.685 for stalk lodging, and 0.164 to 0.518 for root lodging. The correlations increased as greater numbers of tested single crosses were available. These correlations, while not perfect, seem sufficiently high to "pick the winner" in hybrid selection programs.

(over)

Conclusions

The BLUP procedure is now being used routinely by some maize breeders in the USA, not only for selecting single crosses but also for choosing F_2 populations for inbred development. An attractive feature of BLUP is that no special experiments are needed for obtaining the predictions. Rather, BLUP exploits the massive amounts of data generated yearly in a commercial breeding program. The use of both trait and marker data in BLUP is currently being studied. But even without marker information, the BLUP procedure has vast potential for increasing the efficiency of present-day hybrid breeding programs.

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Prediction of Single-Cross Performance

O.S. Smith

Pioneer HiBred International, Inc

Research development costs for commercial maize hybrids have increased logarithmically since the 1980s, whereas performance has increased linearly at about 0.09 t/ha in this same period. These increased cost have led commercial maize breeding companies to seek methods of increasing the efficiency of commercial breeding programs would be to increase the efficiency of identifying which newly developed inbred lines have commercial potential in hybrid combination and as parents in breeding crosses. At Pioneer HiBred International, Inc., we have developed a 'hybrid prediction system' based on Best Linear Unbiased Estimation (BLUE) and Best Linear Unbiased Prediction (BLUP) methods (Henderson 1952, Bernardo 1994, Smith 1996). Currently more than 700 newly coded inbreds are tested in combination with inbreds in commercial and pre-commercial hybrids, as well as in very limited combinations with each other. This generates more than 6,000 potential single crosses which are only a sample of the number of possible single crosses that could be tested. These single crosses are grown in wide area tests that consist of single replication tests, at 15-20 locations, in the areas where the potential hybrids are adapted. The goals of the 'hybrid prediction system' are to help breeders identify which of the potential single crosses should be advanced to pre-commercial status; to predict new untested combinations among the advanced lines that may have commercial potential; and, to identify which of the lines to use in new breeding crosses. This system has been evaluated by comparing actual and predicted performance for grain yield of hybrids grown in two years and by comparing actual and predicted performance of hybrids predicted from previous year's data. The system appears to predict performance better than a previously used system that was based on adjunted General Combining Ability (adj. GCA).

B1 - Heterosis for Grain Yield and Protein in Hybrid Wheat and Relationships to Tissue Fructan and Nitrogen Levels and Carbon Isotope Discrimination

Wanchun Zhao^{1,2}, D.G. Bonnett², L. O'Brien², and R.A. Richards³

¹Visiting scholar, Wheat Research Centre of Shaanxi Province, Yangling, Shaanxi, 712100, P. R. China;

²The University of Sydney, Plant Breeding Institute, Narrabri, NSW, 2390, Australia. ³CSIRO Division of Plant Industry, Canberra, ACT, 2601, Australia.

Abstract

Grain yield, grain protein concentration (%), carbon isotope discrimination and contents (g/m²) and concentrations (%) of tissue fructan and nitrogen and were examined in six wheat hybrids, their seven parents and two control varieties in a field trial conducted at the University of Sydney, Plant Breeding Institute, Narrabri in 1996 with 200 kg/ha of added nitrogen fertiliser.

Hybrids exhibited positive mid-parent heterosis for nitrogen content and concentration whereas heterosis for fructan content and concentration were positive in some hybrids and negative in others. Mid-parent heterosis for grain yield varied markedly from -10.9% for Apollo to 17.6% for H51 (Table 1). None of the hybrids had a significantly greater yield than the mean of the checks and four were significantly lower yielding (Table 1). Grain protein concentrations in four of the six hybrids were greater than the mean of the controls. The grain protein concentration of H35 was significantly lower than the controls while Mercury did not differ significantly. The greatest increase over the checks was 17.1% in Apollo which also achieved the highest mid-parent heterosis for grain protein percentage (8.4%). No significant differences were identified among genotypes for carbon isotope discrimination.

Among the hybrids, no correlations were identified between grain yield and fructan content, fructan concentration or heterosis for these traits. Fructan content, concentration and their levels of heterosis were negatively correlated with tissue nitrogen concentration and content and with grain protein concentration.

Tissue nitrogen concentration, nitrogen content and levels of heterosis for these traits were positively correlated with grain protein concentration and heterosis for grain protein. Tissue nitrogen content and heterosis for tissue nitrogen content were negatively correlated with grain yield and grain yield heterosis. Tissue nitrogen concentration and heterosis for tissue nitrogen concentration were not significantly correlated with grain yield or grain yield heterosis.

These results show that good levels of heterosis for grain yield and protein concentration can be achieved in wheat but that achieving them simultaneously is likely to be difficult. Heterosis for fructan concentration and content did not translate into grain yield heterosis.

Table 1. Grain yield and protein percentages of hybrids and check varieties and levels of heterosis for grain yield and protein.

<u>Line</u>	<u>Yield</u>		<u>Grain protein</u>	
	t/ha	% heterosis	% protein	% heterosis
<i>Hybrids</i>				
H35	3.84	6.22	12.75	-5.87
H51	4.22	17.64	13.91	-2.27
H. Apollo	3.08	-10.91	15.24	8.41
H. Gemini	3.70	-6.25	14.72	3.48
H. Mercury	4.40	9.57	13.05	-8.73
H. Meteor	3.29	-2.61	14.59	-0.43
<i>Checks</i>				
Cunningham	4.58		13.65	
Janz	4.07		12.40	
LSD (p<0.05)	1.71		0.36	

B3 - Heterosis for Resistance to Virus, Phytoplasmas, and Spiroplasmas in Maize

T.P. Narro-León¹ and J.B. Miranda Filho²

¹ Post-doctoral Fellow, Department of Genetics, Escola Superior de Agricultura Luiz de Queiroz-ESALQ/USP

² Professor, Department of Genetics, ESALQ/USP, C.P. 83, 13400-970 Piracicaba, SP, Brazil.

Introduction

Maize diseases produced by viruses, phytoplasmas, and spiroplasmas are widely distributed in tropical, subtropical, and temperate regions at elevations from 0 to 3,200 meters above sea level, and damage occurs in all kinds of maize. Grain yield losses as a consequence of these diseases vary from 10 to 15% (Castillo 1976) and can ruin entire crops (Games 1976; Niblett and Claflin 1978). This project was intended to develop maize genotypes resistant to viruses, phytoplasmas, and spiroplasmas, as well as to generate information on the genetic basis of heterosis for the resistance to these diseases and their relationships with heterosis for grain yield and other important agronomic traits in a maize breeding program.

Methods

We evaluated 1,273 maize collections from CENARGEN-EMBRAPA and 140 populations from CNPMS-EMBRAPA, the University of Sao Paulo-ESALQ, the Agronomic Institute of Campinas (IAC), and the Agronomic Institute of Paraná (IAPAR) during 1994-1995 at four locations in Brazil: Araçatuba (PR), Guaira (SP), Riberão Preto (SP), and Anhembi Experimental Station-ESALQ (SP). Twenty-four maize collections and 10 populations representing early, intermediate, and late maturities were selected for their resistance to the above pathogens.

Topcrosses were generated during 1995-1996 using five hybrids as testers: one single-cross (Cargill 909), two three-way cross (Agroceres 122 and Agromen 2012), and two double-crosses (Cargill 701, and Germinal 550). Topcross evaluations, including parents and crosses, were carried out in 1997 and analyzed according to Miranda Filho and Geraldi (1984).

Results

Large negative variety effects corresponded to resistant materials: -0.40, -0.38, -0.44, and -0.57 for BR-106, Suwan DMR, PE-001, and MG-099, respectively. For hybrids, these effects were smaller: -0.27 (Agromen 2012) and -0.21 (Germinal 550). There were large negative variety heterosis effects for susceptible materials: -0.13, -0.38, -0.40, and -0.41 for CMS-57 N.F., BR-105 III, SE-032, and Maya XVIII, respectively. Larger negative specific effects were obtained for CMS-57 N.F. x Agroceres 122 (-0.40), República Dominicana 300 x Cargill 701 (-0.47), SE-032 x Germinal 550 (-0.66), and BA-187 x Germinal 550 (-0.56). Similar results were reported by Josephson and Naidu (1971) and Naidu and Josephson (1976). The largest negative mid-parent heterosis was obtained for BR-105 x Cargill 701 (-12.80%), CNS-24 x Germinal 550 (-21.71%), SE-032 x Germinal 550 (-19.05%), and Maya XVIII x Germinal 550 (-22.94%). These values are larger than those obtained by Grogan and Rosenkranz (1968), Johnson (1971), and Josephson and Naidu (1971).

Conclusions

According to the variety effects, populations and accessions contribute greater resistance than hybrids. The highest estimates of variety heterosis for resistance were obtained from susceptible materials showing a negative relationship between variety effects and heterosis effects. High heterosis was obtained in crosses between susceptible genotypes and the hybrids Cargill 701 and Germinal 550, suggesting that heterosis for resistance to these diseases is not so important in a maize breeding program.

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B4 - Studies on the Selection of Semi-dwarfing Wheat Hybrids

Zhao Yinhuai, Zhou Wenchun, Wang Su and Wang Shuwen

Food Crops Research Institute, Jiangsu Academy of Agricultural Sciences, Nanjing, Jiangsu 210014, P. R. China

Studies on selections of wheat hybrids by cytoplasmic sterile lines with *Triticum timopheevii* cytoplasm were started at Jiangsu province in 1967. Based on studies comparing genetic effects of the *Rht1*, *Rht2*, *Rht3*, *Rht8*, and *Rht10*, the *Rht3* gene, a partially dominant dwarfing gene from a local variety "Tom Thumb" of China's Tibet, was selected for use in developing semidwarf wheat hybrids as of 1975. Genetic effects of *Rht3* on agronomic characters and the genetic model of plant height of *Rht3* dwarf lines are reported in this paper.

Breeding research involving *Rht3* dwarf lines can be divided into three periods: 1) breeding dwarf lines isogenic for *Rht3* in local varieties of Jiangsu province; 2) improving *Rht3* dwarf lines by multiple crosses and polymerizing backcross methods; 3) transferring modifying genes into dwarf lines to increase their plant height. After continuous selection for more than 20 years, a series of *Rht3* dwarf lines with good agronomic characters and good adaptability and their sterile lines have been successfully bred. R16, a restorer line with very a strong, consistent, and stable restoring ability for different types of sterile lines, was bred by accumulating restoring genes from derivative lines of T808 and other restoring lines, such as Primepi. A series of new restorer lines with similar restoring ability have been bred by improving the agronomic characters and disease-resistance of R16. As a result of efforts to develop dwarf lines and their sterile lines and restorers, several semidwarf wheat hybrids with high yield potential were selected. The yield expression of two in different places and in several years, Maiyou No.1 (CMS hybrid) and Maiyou No. 4 (CHA hybrid), are reported in the paper. The obstacles of using semidwarf hybrids in commercial wheat production are low reproduction yields and difficulties in keeping high purity of sterile lines. Methods for solving these problems are also discussed in the paper.

B5 - A Breeding Scheme to Exploit Heterosis in Apomicts

J.W. Miles

Centro Internacional de Agricultura Tropical (CIAT), Apartado Aéreo 6713, Cali, Colombia

Introduction

Apomixis, asexual reproduction through seed, offers a potent mechanism for the exploitation of heterosis. Apomixis occurs naturally in several tropical forage grasses. Attempts are underway to develop apomictic grain crops (Savidan 1992). Apomictic species of *Brachiaria*, the most important forage plants in tropical America, are sown on approximately 75 million ha in Brazil alone (Santos Filho 1996). Existing commercial cultivars have been developed directly from natural germplasm collected in East Africa (Keller-Grein et al. 1996). Sustained *Brachiaria* breeding programs began in the late 1980's in Brazil and Colombia (Miles and Valle 1996). Breeding methods for sexual crops will need to be modified to maximize genetic gain and expression of heterosis in apomicts. Recurrent selection for specific combining ability (RS-SCA) was first proposed for the improvement of hybrid maize (Hull 1945). A modified RS-SCA scheme is being developed and implemented for apomictic *Brachiaria*.

Methods

The commercial species *B. decumbens* and *B. brizantha* are natural tetraploid, aposporous apomicts (Valle 1986). Apomixis can be identified by microscopic examination of cleared embryo sacs (Young et al. 1979). A cross-compatible, tetraploid sexual biotype was developed from the diploid sexual *B. ruziziensis* (Swenne et al. 1981). Apomicts produce functional pollen and hybridize readily with the tetraploidized sexual (Miles and Valle 1996). Apomixis is conferred by a single, dominant gene (or closely linked genes) (Pessino et al. 1997; Valle and Savidan 1996). Natural apomicts are simplex (Aaaa). Sexuals are homozygous recessive (aaaa) (Valle et al. 1994; Valle and Savidan 1996; Miles and Escandón 1997). All three species are perennial. Clones can be maintained indefinitely by vegetative propagation. The proposed breeding scheme is based upon an allogamous, heterogeneous, breeding population and a cross-compatible, apomictic tester clone. The breeding cycle comprises three generations: 1) formation of testcross progenies; 2) evaluation of testcross progenies; 3) recombination of selected sexual clones (Fig. 1). The merit of a sexual individual is assessed by its testcross performance. A set of apomictic hybrids is produced and evaluated each selection cycle. Any apomictic individual in the testcross progenies can be advanced to further testing and development to a new hybrid apomictic cultivar. A sexual breeding population has been developed at CIAT by intercrossing 30 sexual clones selected from F_1 hybrid populations formed by crossing the sexual tetraploid *B. ruziziensis* with natural apomicts (Miles and Escandón 1997). This population has undergone one cycle of selection based on per se, rather than testcross, performance. Eleven selected clones have been recombined. We are attempting to identify a suitable apomictic tester clone and find a reliable molecular marker tightly linked to the apomixis locus. The proposed scheme could readily be applied to annual species. Sexual S_0 individuals would be selfed as well as crossed to the apomictic tester, and the recombination block would be established with S_1 seed of selected sexuals.

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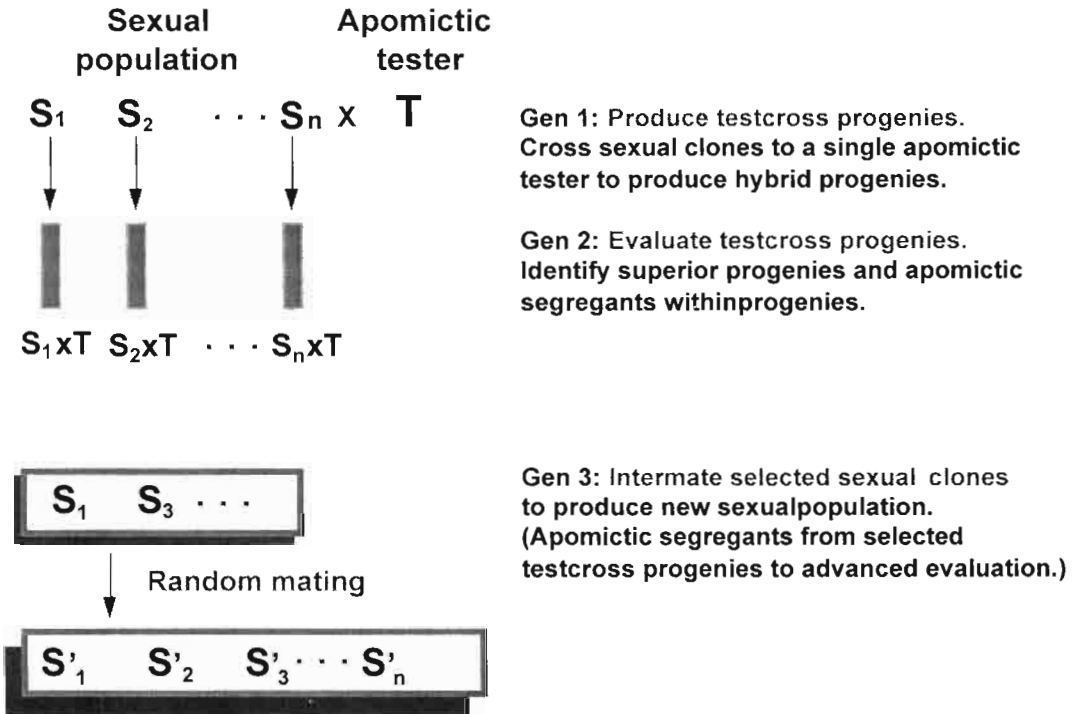


Figure 1. Outline of RS-SCA as applied to apomictic *Brachiaria*.

B6 - Combining Ability for Resistance/Tolerance to *Striga hermonthica* in Maize

A.O. Diallo¹, J.K. Ransom², and B. Badu-Apraku¹

¹ CIMMYT/IITA Regional office, 01 BP 2551 Bouaké 01, Côte d'Ivoire.

² Regional maize Agronomist, CIMMYT, P.O. Box 25171, Nairobi, Kenya, Fax(254-2) 631499.

Introduction

Striga hermonthica (Sel). Bent. is one of the major constraints to maize production and productivity in West and Central Africa and particularly affects fields of smallholders who often cannot afford recommended production inputs. Genetic variability for resistance/tolerance to *Striga* in maize has been reported (Ransom et al. 1990, Kim 1994, Reda et al. 1994, Diallo et al. 1996). Better understanding of the genetics resistance/tolerance to *Striga* in various maize germplasm sources will provide a rational basis for effective selection and help in designing appropriate breeding strategies to develop tolerant/resistant cultivars. This study was conducted to estimate the general and specific combining abilities (GCA and SCA) of new maize inbred lines for grain yield and *Striga* emergence counts under artificial *Striga* infestation.

Material and methods

Screening for *Striga hermonthica* resistance/tolerance under artificial field infestation was initiated in 1992 with 98 S₃ lines from 6 different maize populations. The *Striga* seed was mixed with fine sieved sand at the ratio of 1:99 by weight (Kim 1991). The field was inoculated the same day maize was planted by placing 5 g of inoculum mixture 8-10 cm deep in each planting hole, thus ensuring approximately 5,000 germinable *Striga* seeds per/hill. A split-plot design (maize genotypes as main plots and *Striga* level as sub-plots) with 4 replications was used. A plot consisted of 2 rows (one row artificially infested, while the other row was non-infested). Grain yield under infested and noninfested field conditions and *Striga* emergence counts were the selection criteria. After 3 cycles of inbreeding followed by evaluation under *Striga*, 4 lines (3 resistant and 1 susceptible) were identified. In 1995, the 4 lines plus 3 checks from the International Institute of Tropical Agriculture (IITA) -- making 5 resistant and 2 susceptible lines -- were crossed in a diallel excluding reciprocals to obtain 21 F₁ hybrids. The hybrids were evaluated in 5 sites in 4 countries (Côte d'Ivoire, Ghana, Cameroon and Kenya). In Côte d'Ivoire, the same method as described for line development was used. But the trial was replicated 6 times. In the other sites the trial was planted under natural infestation with *Striga hermonthica*, using a randomized complete block design with the same plot size and number of replications as the trials planted in Côte d'Ivoire. The data reported here are from only one site where artificial infestation was used.

Results

Both GCA and SCA effects for yield were statistically significant. In general tolerant lines had larger positive GCAs for grain yield, while the susceptible lines had larger negative GCA effects under both infested and noninfested conditions (Table 1). The mean grain yield of the top 10 resistant x resistant crosses under artificial infestation across locations was 20% and 83% higher than the mean yield of the best 10 resistant X susceptible and susceptible X susceptible crosses, respectively. The cross of the most resistant lines had the lowest *Striga* emergence counts (20 plants/m²), while one of the highest *Striga* emergence counts (65 plants/m²) was detected in the susceptible X susceptible cross.

Conclusions

The positive significant GCA effects for yield under *Striga* infestation indicated a uniform transmission of *Striga* resistance/tolerance by parents to their offsprings and confirms the existence of genetic variability for resistance to *Striga* in the inbred lines studied. However, the grain yield of a single-cross hybrid under *Striga* infestation cannot be predicted on the basis of GCA alone. Good progress could be expected from a pedigree breeding program by exploiting resistant parents in crosses to generate F₂

populations. With this breeding scheme, inbred lines with good GCA under infested and noninfested conditions could be recombined to develop hybrids and synthetics.

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Table 1. GCA of lines and SCA effects for grain yield (kg/ha) and their crosses tested under artificial *Striga hermonthica* infestation at Ferkessedougou, Côte d'Ivoire, 1996B.

Line name	Pedigree	SCA							GCA effect	Line mean
		1	2	3	4	5	6	7		
LI963047-STR	E25SR-6-3-2sb-#-#- #-#1 (R)	-							1064	5219
LI963065-STR	P22SR-9-1-2sb-#-#- #-# (R)	-507	-						20	4349
LI963069-STR	P22SR-54-1-1sb-#- #-#-# (R)	-207	-170	-					76	4395
LI963073-STS	P43SRC9FS52-1-#- #-#-#-# (S)	208	-201	-208	-				-508	3908
5057 (IITA S.)	-	446	-237	533	-595	-			-640	3798
STR TZi 12 9030 (IITA R.)	-	80	1058	-295	-3	121	-		-332	4055
ETR TZi 3 1368 (IITA R.)	-	0	59	348	799	-267	-939	-	321	4600
									GRAND MEAN	4332
									Standard error estimate	
									GCA	154
									SCA	303

B7 - Studies on Combining ability and Heterosis for Yield and Yield Components under Different Environments in Maize

V.P. Ahuja, N.P. Mondal, B.K. Mukherjee and N.N. Sing

Maize Programme, Division of Genetics, Indian Agricultural Research Institute, New Delhi-110 012, India.

Introduction

The present investigation provides information on the performance of new inbred lines, single cross hybrids, GCA and SCA effects and magnitude of heterosis under different environments. This will lead to the identification of promising parents and hybrids which could be grown successfully over large number of ecologically different locations.

Methods

Eight newly developed S_7 inbred lines derived from two pairs of heterotic populations namely, A 64, A 604; AD 609 and DMR 1; were mated in all possible ways excluding reciprocals. The F_3 s along with the parents were planted at four locations using a randomized block design with 3 replications. Each experimental plot consisted of 2 rows of 5 m length with a distance between the rows 75 cm and plant to plant 25 cm respectively. The experimental area was bordered on all sides by planting four rows of a composite variety to minimise the border effect. Recommended cultural practices were followed. Traits measured included yield and yield components. Combining ability analysis for individual environments was performed as per Griffing 1956 (a) Model I, Method 2. The degree of heterosis averaged over environments was estimated as per Turner (1953).

Results

The correlation coefficients between the per se performance and GCAs of parents were significant for all traits. Individual analysis showed fluctuations in correlation coefficient values for all the traits except ear girth (Table 1). Variances due to GCA, SCA and GCAXL and SCAXL were significant for most of the yield traits except ear girth (Table 2). Stable average heterosis was found for grain yield, kernels per row, and 100-kernel weight. The highest yielding parents of the top 3 heterotic crosses possessed the highest GCA effects, whereas the highest yielding cross possessed the highest SCA effects (Table 3).

Conclusions

Except for ear girth, per se performance of parents provides a crude estimate of general combining ability. The significance of GCA \times environment interaction suggests that additive gene effects are influenced by environment for all traits except ear girth. This also suggests the ear girth is stable over the environments and that seed production of these lines cannot be done in all the environments. Highly significant SCA \times environment variance indicates the instability of the non-additive components for all traits and points up the need for extensive sampling of environments for testing high yielding inbreds and hybrids. The high performance per se of the inbred lines coupled with a significant high-parent heterosis will indicate feasibility for use in commercially viable, single-cross hybrids. Cross (2 \times 4), the most promising hybrid for grain yield in this study, showed significant heterosis and high per se performance for components such as ear length, ear girth, kernels per row and 100-kernel weight. The present study reveals a good relationship between performance per se and GCA effects and between SCA effects of crosses and heterosis.

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Table 1. Correlation of performance per se and GCA effects of the parents for yield and yield components.

		Environments				Combined
		1	2	3	4	
1.	Grain yield	0.89**	0.87**	0.80*	0.24	0.88**
2.	100-kernel wt.	0.80*	0.68	0.65	0.78*	0.94**
3.	Number of Kernel per row	0.63	0.46	0.84**	0.83**	0.76*
4.	Number of Kernel rows per ear	0.96**	0.96**	0.70	0.74*	0.96**
5.	Ear girth	0.85**	0.77*	0.90**	0.91**	0.92**
6.	Ear length	0.69	0.56	0.88**	0.94*	0.79*

*, ** Significant at 5 and 1% level respectively

Table 2. Combining ability analysis pooled over environments.

Source	df.	Ear length	Ear girth	No. of Kernels rows/ear	No. of Kernels per row	100 Kernel wt.	Grain Yield
Environment (L)	3	34.64**	2.24**	3.66**	509.94**	15.49**	527.06**
GCA	7	5.16**	1.10**	6.09**	19.71**	16.28**	321.02**
SCA	28	6.58**	1.09**	1.09**	40.62**	7.84**	343.07**
GCA x L	21	1.31	0.15	0.41**	3.95**	2.21**	55.69**
SCA x L	84	0.69**	0.11	0.28**	3.71**	1.25**	41.75**
Error	280	0.28	0.08	0.14	1.91	0.81	12.66

*, ** Significant at 5 and 1% level respectively

Table 3. List of promising inbred lines and single cross hybrids based on combined analysis over four environments.

Character	Performance per se of top three inbred lines	Inbreds with desirable GCA effects	Performance of top three hybrids	Hybrids with desirable SCA effects	Top three heterotic hybrids
Grain yield	P2, P4, P1	P2, P4, P1	2x4, 5x7, 1x2	2x4, 5x7, 1x5	2x4, 5x7, 5x8
Ear length	P2, P1, P3	P2, P1	2x4, 2x8, 2x7	2x4, 2x8, 4x6	7x8, 2x4, 4x7
Ear girth	P1, P5, P6	P1, P5	5x7, 1x5, 1x2	5x7, 2x7, 3x4	3x4, 4x7, 2x8
Number of kernal rows per ear	P5, P6, P1	P5, P6, P1, P8	5x6, 5x7, 4x5	5x7, 1x7, 1x2, 4x5	4x8, 6x8, 1x2
Number of kernels per row	P1, P7, P2	P2, P1	2x4, 1x7, 1x8	2x4, 3x6, 1x8	2x4, 3x6, 6x8
100-kernel weight	P2, P4, P1	P4, P2, P1	1x4, 1x2, 2x4	1x2, 1x4, 4x8	1x4, 1x2, 1x3

B8 - Combining Ability Analysis of Local Indian Maize Varieties

S. Banerjee, M.Z.K. Warsi,¹ and N.N. Singh²

¹ Department of Genetics and Plan Breeding, College of Agriculture, G.B. Pant University of Agriculture and Technology, Pantnagar 263145, India

² Directorate of Maize Research, Cummings Lab, IARI, New Delhi

Introduction

Maize productivity in developing countries can be increased significantly by increasing the area under hybrids. The major constraint to this is the high cost of developing and testing inbred lines. Varietal hybrids offer a less expensive, faster approach. The heterosis expressed by genetically diverse varietal crosses can be exploited, and knowledge about heterotic patterns among varieties will increase the efficiency with which superior crosses are identified. India has a diverse collection of indigenous varieties; by utilizing local varietal crosses, problems of adaptability and, to some extent, disease and insect resistance, will be more easily overcome.

Methods

Nine local maize varieties and their 36 intervarietal crosses were produced in a half diallel scheme. Variety cross diallel analysis was performed following the Gardner and Eberhart (1966) analysis II model (when parents and their $P(P-1)/2$ crosses are grown). In this analysis the total sum of squares for entries are subdivided as V_i (variation due to additive effects) and h_{ij} (variation due to heterosis). Again h_{ij} was subdivided into variation due to average (h), variety (h_i) and specific heterosis (S_{ij}). Heterosis was also estimated as the percentage increase or decrease in the mean value of F_1 hybrids over the mid-parent value (relative heterosis) and the better parent (heterobeltiosis). The experimental material was evaluated in a randomized complete block design with three replications.

Results

Entry mean squares were significant ($P < 0.01$) for all traits -- as were their subdivisions into differences among varieties -- and for effects due to heterosis, except for plant height and ear length. A further division of heterosis due to average heterosis, variety heterosis, and specific heterosis revealed that specific heterosis variation was significant for ear height, 100-grain weight, and grain yield only. Variation due to variety heterosis was significant only for ear height. Average heterosis variation was significant for ear height, 100-grain weight and grain yield only. For all traits, more than 60% of the sum of squares could be attributed to specific heterosis. Few crosses showed good heterosis for grain yield; the best high-parent heterosis (38.02%) was observed in crosses 3 x 7, 5 x 6 (36.10%), 6 x 7 (34.57%), 4 x 7 (32.38%) and 2 x 4 (30.96%).

Conclusions

Combining ability studies provide useful information for the selection of superior parents for hybrid breeding. Good performance by varieties may give an idea of their relative superiority but not necessarily their ability to produce better combinations when crossed. If the combining ability effects are largely additive, selection becomes easy and more effective. It was observed that both V_i and h_{ij} (except for plant height and ear height) variances were significant for all characters, which indicates the importance of both additive and non-additive gene effects.

In order to select two varieties as initial populations for a reciprocal recurrent selection (RRS) program, the best choice is usually based on the yield of varieties themselves and on the average of their crosses, without special attention being given to specific (S_{ij}) effects. In the present study mean squares due to S_{ij} effects for grain yield were not only significant but also a major contributor (53%) to the total entries sum of squares. Other significant contributors for grain yield were V_i (22%) and h (13%) effects.

Only one variety – Sundernagar – showed consistent performance in variety effects (V_i) for all characters studied, making it a worthwhile selection. The S_{ij} effect for grain yield indicated that none of the crosses showed significant effects. But the top three S_{ij} values for grain yield were obtained for cross 5 × 6 (0.6100). Cross 2 × 9 showed positive and significant S_{ij} effects for ear height and 100-grain weight, making it a promising candidate for selection.

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Table 1. Variety effect heterosis of 9 parents for all characters.

Parents	Plant height	Ear height	Ear length	100-grain weight	Grain yield/plot
	(cm)	(cm)	(cm)	(g)	(g)
Chakrata local	8.82	6.29	-1.49	1.40	0.01
Farrukhabad local (a)	-11.51	-10.70	0.19	-3.32	0.01
Farrukhabad local (b)	-4.85	-3.37	0.63	-0.42	-0.25
Sundernagar local	33.82	19.96	0.76	4.20	0.14
Jaunpur Yellow	-17.85	-7.70	-2.18	1.13	0.10
Bahraich local	-2.85	2.30	-1.26	0.33	-0.24
Meerut local	-3.85	-0.37	1.90	-2.03	-0.34
Jaunpur local (KT-41)	-4.51	-2.37	-0.54	0.38	0.30
Jaunpur local (B)	2.82	-4.04	1.97	-1.02	0.26

B9- The Potential of Hybrid Wheat under Irrigated Conditions in Mexico

B. Cukadar ¹, R. J. Peña¹, D. Dunphy ², and M. van Ginkel ¹

¹Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6- 641, 06600 Mexico D.F., Mexico

²Monsanto, Agricultural Consultant, 6404 Wea Woodland Dr., Lafayette IN 47905 USA

Introduction

The challenge of wheat scientists is to achieve a 2.5% increase in annual production to keep up with increasing world population. To reach this goal, breeders need to exploit new technologies, including new ways of producing hybrid wheat. About a 12-17% advantage in yield over the leading check cultivars has been reported for hybrid wheat (Edwards 1995; Monsanto 1997, personal communication). However, there are other advantages reported with hybrid wheat, such as yield stability of hybrids vs. pure lines (Peterson et al. 1997; Jordaan 1996; Monsanto 1997, personal communication). With the interest from advanced national programs such as China and India, CIMMYT re-initiated its hybrid wheat program in 1996. The main objectives of the program are to develop a practical hybrid seed production scheme and to identify hybrids with high yield potential under irrigated conditions for the Yaqui Valley in northwestern Mexico. Varieties from CIMMYT origin released from the Yaqui Valley often show wide adaptation in similar environments.

Materials and Methods

In collaboration with Monsanto, a chemical hybridizing agent was used to develop wheat hybrids in El Batán in 1996. High yielding, widely adapted advanced CIMMYT lines and "Buitre" lines with very large spikes were utilized as female parents in crosses with one very high yielding male parent. Twelve advanced line wheat hybrids and six Buitre hybrids were included in four yield trials under irrigated basin and bed conditions at Obregon, Sonora, Mexico during the 1996-97 winter cycle. In addition to three commercial cultivars, female and male parents of the hybrids were also included in the experiments. The experimental design was alpha-lattice with two replications. The plots in basins included eight 5 m rows whereas plots on beds consisted of two 5 m beds. Seeding density was 90 kg ha⁻¹. Quality traits measured were grain hardness and protein (NIR analysis), SDS-sedimentation, Alveograph's strength value, and bread loaf volume.

Results

In general, most of the hybrids yielded about 7-16% higher than the leading commercial cultivar, Rayon. The highest yielding hybrid on beds had a 15.9% yield advantage over Rayon (Table 1). However, the yield difference between this hybrid and its female parent was not significant and best parent heterosis was only 2%. Hybrids among advanced CIMMYT lines were either intermediate or closer to the earlier parent for heading date and maturity. Buitre hybrids, on the other hand, headed one to two days earlier than the earlier parent (Fig. 1). Maturity differences were generally not significant between Buitre hybrids and their parental lines. About half the advanced line wheat hybrids showed positive heterosis for plant height (Fig. 1). However, Buitre hybrids were generally intermediate between the two parental lines. Protein levels of the hybrids were intermediate but closer to those of the female parents (Fig. 1). Female lines in this study had higher protein content than the male parent. Grain hardness of hybrids was in general intermediate. However, in some cases it was similar to the harder parent or harder than either parent. SDS-sedimentation values were also mainly intermediate but it appeared that the values were closer to those of females.

Conclusions

These preliminary results indicate heterosis for grain yield in CIMMYT wheat lines under irrigated conditions. The level of heterosis depends on parental line combinations. Grain and bread-making quality traits were generally not adversely affected in the hybrid background. Bread-making quality of a hybrid depends on the parental material.

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Table 1. Comparison of hybrid yields with those of their male and female parents and check cultivars, Cd. Obregón, Mexico, 1996-97.

Yield						Yield							
Hybrid (kg/ha)	On beds - % difference over					Rayon	Hybrid (kg/ha)	On basins - % difference over					Rayon
	Female	Male	MP	BCN	Advanced line hybrids			Female	Male	MP	BCN	Advanced line hybrids	
1	9150	2.0	6.9	4.4	17.2	15.9	8	7781	5.5	24.4	14.2	3.0	13.5
2	8845	9.1	3.3	6.1	13.3	12.0	2	7670	10.0	22.6	16.0	1.5	11.9
3	8821	9.9	3.0	6.3	13.0	11.7	7	7369	13.1	17.8	15.4	-2.5	7.5
4	8596	6.7	0.4	3.4	10.1	8.9	9	7332	5.2	17.2	10.9	-3.0	7.0
5	8575	0.0	0.0	0.0	9.8	8.6	10	7329	5.2	17.2	10.9	-3.0	6.9
6	8508	8.9	0.0	3.9	9.0	7.8	11	7006	8.1	12.0	10.0	-7.3	2.2
7	8461	8.4	-1.2	3.4	8.3	7.2	12	6950	-3.2	11.1	3.5	-8.0	1.4
CV (%)	2.4						CV (%)	3.9					
LSD (0.05)	421						LSD (0.05)	355					
		Buitre		Hybrids					Buitre		Hybrids		
13	8432	16.7	1.5	8.6	3.2	6.9	16	8484	10.0	18.0	13.9	10.1	11.5
14	7925	22.3	-4.6	7.2	-3.0	0.5	17	8025	22.0	11.6	16.6	4.2	5.5
15	6218	25.2	-25.2	-6.3	-23.9	-21.1	18	7193	6.6	0.0	3.2	-6.6	-5.4
CV (%)	2.0						CV (%)	2.1					
LSD (0.05)	328						LSD (0.05)	351					

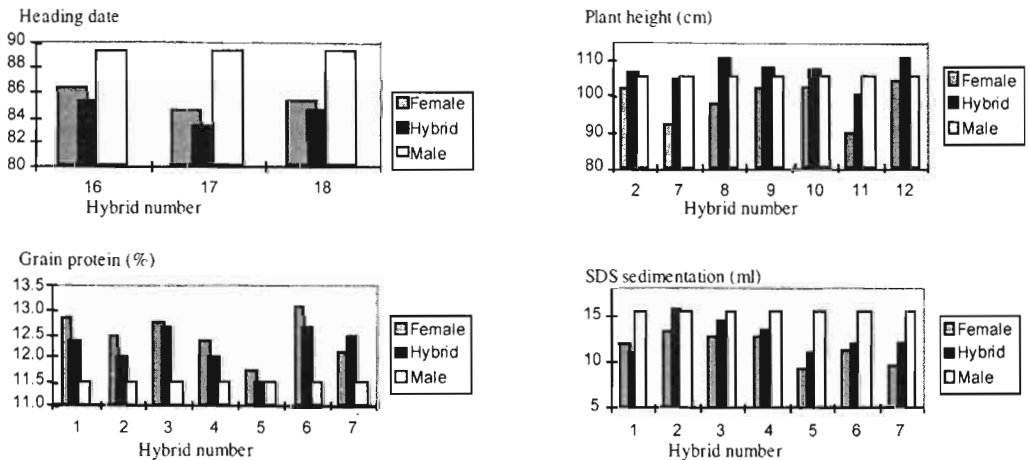


Figure 1. Comparison of hybrid wheats with their parental lines for selected traits.

B10 - Identification of Heterotic Pattern in Tropical Inbred Maize Lines using Broad Based Synthetic Testers

A.R. Hede¹, G. Srinivasan², O. Stoelen¹, and S.K. Vasal²

¹The Royal Veterinary and Agricultural University. Department of Crop Science. Thorvaldsensvej 40, 1871 Frederiksberg C, Denmark. ²Maize Program, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico.

Introduction

Much work has been done on determine the combining ability and heterotic patterns among CIMMYT's maize populations and pools (Beck et al. 1991; Vasal et al. 1992a). The next step is to obtain information on combining ability and heterotic patterns of the lines derived from these pools and populations (Han et al. 1992; Vasal et al. 1992b, 1992c). Top-cross hybrids – crosses between an inbred line and a non-inbred parent – are ideal for countries and institutions which have just initiated hybrid programs and where the seed industry is less developed. The objectives of this study were to 1) characterize the combining ability of 23 CIMMYT inbred lines and 2) identify superior top-cross hybrids.

Methods

A line x tester analysis was performed using 23 partially inbred lines (S_2 to S_4) from seven late white CIMMYT populations and pools crossed to four broad-based synthetics. The 92 crosses were evaluated for grain yield in six environments in Mexico (M1-M4), Colombia (CO), and Venezuela (VE). Checks included the four synthetics (testers), two experimental hybrids (a three-way cross, TWC; and a double cross, DC), and two local checks. Each plot consisted of one 5 m row with 21 hills per row. The experimental design was a split-plot with lines as main plots and testers as subplots and three replications in each environment. Analysis of variance (ANOVA) and general combining ability (GCA) and specific combining ability (SCA) effects were computed for each environment and combined over the six environments. Only the combined data are shown.

Results and Discussion

Mean grain yield across environments was 5.66 Mg ha⁻¹, ranging from 3.67 Mg ha⁻¹ (M1) to 7.75 Mg ha⁻¹ (CO). The ANOVA for grain yield combined over the six environments showed significant GCA effects for both lines and testers, and significant SCA effects. Across environments Line 11 (L11) and Line 23 (L23) were showing significant positive GCA effects (Table 1). Other outstanding lines were L1, L9, L12, and L17. All except L9 are CIMMYT maize lines (CMLs) which have been selected through rigorous testing and made available to the center's research partners worldwide. Across environments, ten crosses were identified with significant positive SCA effects. All are interpopulation crosses and the four with highest SCA effects are all flint x dent crosses. The best performing top-cross hybrids were higher yielding than the checks in all environments and across environments (Table 2). The highest yielding top-cross hybrid across environments was L23 x T1, a flint x dent cross with significant positive SCA effects. Superior inbred lines were identified; most were CMLs, but a new high yielding line (L9) was also found. The highest yielding hybrid was L23 x T1, confirming the heterotic pattern between ETO (CIMMYT Population 32) and Tuxpeño (CIMMYT Population 21) (Miranda and Venkovsky 1986).

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Table 1. GCA and mean grain yield (Mg ha⁻¹) across six environments and four testers for twenty-three inbred lines and four testers.

Line	Pedigree	Yield	GCA
L1	Pop. 21 C5 FS218 S3 (CML 8)	5.87	0.21
L2	Pop. 21 C5 FS57 S3 (CML 1)	5.82	0.15
L3	Pop. 21 C5 FS78 S3 (CML 2)	5.61	-0.06
L4	Pop. 21 C5 FS241 S4 (CML 13)	5.83	0.16
L5	Pop. 21 C5 FS229 S4 (CML 12)	5.62	-0.05
L6	Pop. 21 C5 FS219 S4	5.60	-0.07
L7	Pop. 21 C5 FS129 S2	5.48	-0.19
L8	Pop. 21 C5 FS109 S4	5.20	-0.46**
L9	Pop. 21 C5 FS195 S4	5.88	0.21
L10	ACR 7421 S3	5.81	0.15
L11	Pop. 21 C5 FS133 S2 (CML 5)	6.17	0.50**
L12	ACR 7522 S3	5.99	0.32
L13	Pop. 29 C5 FS172 S3 (CML 34)	5.51	-0.06
L14	ACR 7643 S2 (CML 42)	5.68	0.02
L15	ACR 7843 S3 (CML 46)	5.13	-0.54**
L16	Pool 24 TSR S3 (CML 55)	5.69	0.02
L17	Sta. Rosa 8073 S3 (CML 49)	5.94	0.27
L18	Porillo 8073 S3 (CML 48)	5.48	-0.19
L19	Pop. 25 C5 FS218 S3 (CML 8)	5.78	0.11
L20	Pop. 25 C5 FS57 S3 (CML 1)	5.42	-0.25
L21	Pop. 25 C5 FS78 S3 (CML 2)	5.21	-0.45**
L22	Pop. 32 C5 FS241 S4 (CML 13)	5.60	-0.06
L23	Pop. 32 C5 FS241 S4 (CML 13)	6.05	0.38*

Testers: T1 - Pop. 21 (STE) C1; T2 - Pop. 22 (STE) C1; T3 - Pop. 43 (STE) C1; T4 - Pop. 25 (STE) C1
 *, **: sig. GCA at P<0.01, P<0.05.

Table 2. Grain yield (Mg ha⁻¹) of the best line x tester crosses across six environments compared to best check hybrid and check OPV.

Best line x tester combinations	Grain yield		
	Mg ha ⁻¹	% of best check hybrid	% of best check OPV
L23 x T1 (CML 36)	6.53	102.8	112.2
L9 x T2	6.50	102.4	111.7
L11 x T3 (CML 5)	6.48	102.0	111.3
L11 x T2 (CML 5)	6.43	101.3	110.5
L17 x T2 (CML 49)	6.38	100.5	109.6
L1 x T2 (CML8)	6.36	100.2	109.3
L19 x T2	6.33	99.7	108.8
L3 x T2 (CML 2)	6.32	99.5	108.6
L4 x T2 (CML 13)	6.31	99.4	108.4
L12 x T1 (CML 15)	6.28	98.9	107.9
Best check OPV (T1)	5.82		
Best check hybrid (TWC)	6.35		
LSD (0.05)	0.53		

B12 - Heterotic Patterns of Early-Maturing Highland Maize Germplasm

S. Rodríguez-Herrera, N. Vergara-Avila, G. Srinivasan, J.L. Torres-Flores

Universidad Autonoma Agraria Antonio Narro (UAAAN), Buenavista, Saltillo, Coah. México. CP 25315. International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 México D.F.

Introduction

Maize (*Zea mays* L.) is grown on more than 6.2 million ha under highland conditions in the developing world (CIMMYT 1988). Mexico has the largest area of 2.8 million ha. More than 74% of this is planted to unimproved local varieties (criollos), 11% to improved open pollinated varieties (OPVs), and 15% to hybrids (CIMMYT 1990). Little information is available on the heterosis and combining ability of highland maize germplasm. In Kenya two heterotic groups, Kitale-II and EC573, have been identified (Darrah et al. 1972). In Mexico, Michoacan-21 and V-23 (Huamantla) were reported by Valdivia (1990), and Pool 10 A x Pool 12 A was identified by Vasal et al. (1995). The maize program at the Antonio Narro Autonomous Agrarian University (UAAAN), Coahuila, Mexico, has been working with highland maize populations to measure heterosis and combining ability.

Methods

Fourteen highland maize populations (6 from CIMMYT, 5 from the UAAAN, and three from the University of Nebraska) were used to form a 14 x 14 diallel at Tepalcingo, Morelos, during 1993. Seed from each cross and reciprocal were bulked to represent a particular cross. Fourteen parents and 91 crosses between them constituted a total of 105 entries. The trials were planted at 3 locations during 1994: Cheran, Michoacán; Nochistlán, Zacatecas; and Texcoco, State of Mexico. Analyses of variance were computed for each locations separately and combined across locations. General (GCA) and Specific (SCA) combining ability effects for grain yield were calculated according to the Method IV of Griffing (1956).

Results

Pop. 901 and Chihuahua had the highest *per-se* yield performance (Table 1). The highest GCA effects were recorded for Pop. 901 and Batan 8986 (Table 2). Batan 8986 x Chihuahua was the top-yielding cross, whereas Pop. 800 x VS-201 and Batan 8986 x VS-201xAN's had the highest SCA effects. Pop. 845 x VS-201 showed the highest heterosis (28.3%). Based on the SCA information for yield, the cross Pop. 800 x VS-201 was used to form two highland heterotic groups. The combination had a high, positive SCA, showing that the parents belong to opposite heterotic groups (Vasal et al. 1992a,b); Pop. 800 was assigned to group "A" and VS-201 to "B". Group "A" includes Pops. 86, 901, 800, and 845, as well as Batan 8986, Nebraska Brachytic, SD-16, and SD-17. Group "B" includes Pop. 85, VS-201, Composite Norteño, Composite Precoz, VS-201xAN's, and Chihuahua.

Conclusions

Most CIMMYT populations showed positive and significant GCA effects and good *per se* and cross yield performance. Crosses involving Pop. 901 showed high yield and positive SCA effects, indicating its potential for use in a reciprocal recurrent selection program. Chihuahua was only population from the UAAAN with a positive GCA effect. All populations from the USA showed negative GCA effects and low *per se* yield performance.

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Table 1. Grain yield (t/ha) across environments of fourteen highland maize populations as parents per-se and in crosses.

Populations	Origin	Per se grain yield (t/ha)	Grain yield in crosses* (t/ha)	Days to silking	GCA for grain yield
1.- Pop.85 C4	CIMMYT	7.23	7.01	93.3	-0.152
2.- Pop.86 C4	CIMMYT	7.62	7.57	99.1	0.409
3.- Pop.901 C3	CIMMYT	8.08	7.90	94.5	0.741
4.- Batan 8986	CIMMYT	7.45	7.83	93.6	0.672
5.- Pop.800 C5	CIMMYT	7.50	7.39	91.5	0.230
6.- Pop.845 C4	CIMMYT	5.35	7.23	94.1	0.071
7.- VS-201 C2	UAAAN	5.60	7.15	96.8	-0.008
8.- Compuesto Norteño C2	UAAAN	6.42	7.05	94.5	-0.108
9.- Compuesto Precoz	UAAAN	5.85	7.27	99.1	0.113
10.- VS-201 x AN's	UAAAN	6.51	6.94	94.0	-0.217
11.- Chihuahua	UAAAN	8.06	7.57	102.1	0.411
12.- Nebraska Brachitic	USA-Nebraska	5.88	6.88	93.3	-0.281
13.- SD-16	USA-Nebraska	4.85	6.44	94.1	-0.725
14.- SD-17	USA-Nebraska	4.52	6.01	101.1	-1.153

* Mean yield of all the crosses involving that particular parent.

Table 2. Top yielding crosses and their contributions of GCA/SCA, and heterosis over top parent.

Crosses	Grain yield (t/ha)	Parent 1 (gi)	Parent 2 (gj)	(gi+gj)	SCA (Sij)	Better parent heterosis (%)
Batan 8986 x Chihuahua	9.08	0.672	0.411	1.083	0.834	12.6
Pop.901 C3 x Chihuahua	8.75	0.741	0.411	1.152	0.435	8.3
Batan 8986 x VS-201xAN's	8.74	0.672	-0.217	0.455	1.125	17.3
Pop.800 C5 x VS-201 C2	8.56	0.230	-0.008	0.222	1.182	14.2
Pop.901 C3 x VS-201 C2	8.56	0.741	-0.008	0.733	0.664	5.9
Pop.86 C4 x VS-201 C2	8.53	0.409	-0.008	0.401	0.969	11.9
Batan 8986 x Compuesto precoz	8.41	0.672	0.113	0.785	0.465	12.9
Pop.86 C4 x Chihuahua	8.38	0.409	0.411	0.82	0.403	4.0
Pop.800 C5 x Compuesto precoz	8.38	0.230	0.113	0.343	0.877	11.7
Pop.845 C4 x VS-201 C2	7.18	0.071	-0.008	0.063	-0.040	28.3
Overall mean	7.16					

B13 - Use of Testers in Selecting Inbred Lines to Form Hybrids of Maize

M. Sierra, F. Marquez, R. Valdivia, F. Rodriguez, and O. Cano

Programa de Maíz, Campo Experimental Cotaxtla, INIFAP, Apdo. Postal 429, Veracruz, Ver. Mexico, 91700.

Introduction

In the humid tropics of Mexico, 3 million ha are planted with maize annually; one million located in good production environments and 100,000 ha under irrigated conditions. In this area is possible to use single-, three-way and double-cross hybrids. Use of testers in selecting inbred lines allows their relatively rapid classification in heterotic groups to make crosses and form hybrids. The objectives of the present study were to measure the yield and agronomic characteristics of testcrosses and their lines; gauge general and specific combining ability effects; define heterotic groups for the inbred lines; and identify the best tester.

Materials and Methods

We were formed and evaluated testcrosses at the Cotaxtla experiment station of the National Institute of Forestry, Agricultural and Livestock Research (INIFAP), México, during the spring-summer season of 1996 and fall-winter season of 1996-97. Elite lines were crossed with testers LT-154 and LT-155, which are the parental lines of the single cross hybrid H-513, and CML247 × CML254, a heterotic pattern defined by CIMMYT for the tropics. The evaluation of the testcrosses was made in four experiments in an alpha lattice design with 2 replications, with 1-row plots 5 m long and 80 cm wide (Table 1). The inbred line plantings were similar except that the rows were 3m long.

Results

Highly significant differences between treatments for yield and agronomic characteristics were found. Particularly, in the experiments of testcrosses, it was found that some of them had yields higher than 9 t/ha and were better than the checks H-513 (8.4 t/ha) and CML247 × CML254 (7.7 t/ha). Most selected testcrosses had short plants, good husk cover, and good plant and ear aspects. The inbred lines used in these testcrosses also had good yields. Table 2 shows the yield of the selected testcrosses with testers. There were heterotic groups with testers 1 (LT-154) and 2 (LT-155) and with the testers 3 (CML-247) and 4 (CML-254). Thus, while the recycled lines from the F₂ of H-513 × VS-536 had the highest yields mainly with testers 2, 3, and 4, lines derived from a broadly based composite (CABG3) had the best testcrosses with the testers 1 and 2.

Conclusions

High yielding inbred lines with good specific combining ability were identified. In testcrosses, the best yields were obtained with testers 2 and 4. Heterotic groups of inbred lines were formed. The elite lines and CMLs had the best yields per se.

Table 1. Description of the germplasm used to select inbred lines to form maize hybrids, Cotaxtla, Mexico, 1997.

No. exp.	Description	Alpha lattice	No. entries
1	Testcrosses of recycled inbred lines	13x10	130
2	Testcrosses of inbred lines derived from a compound of wide genetic base.	8x8	64
3	Testcrosses of elite inbred lines	8x8	64
4	Testcrosses of CMLs lines	9x9	81
5	Evaluation of inbred lines	14x10	140

Table 2.-Grain yield (t/ha) of lines and their crosses with four testers, Cotaxtla, Mexico, 1997.

Genealogy	Lines	Tester 1	Tester 2	Tester 3	Tester 4
<i>Recycled lines of (H-513xVS-536)F₂</i>					
FAM31XFAM30-4-3-1	2930	6203	10234*	7592	10060*
FAM4XFAM3-5-2-1	3106	8330	7173	7935	9532*
FAM49XFAM48-4-2-1	2069			8167	9325*
FAM4XFAM3-1-1-1	2126			9122*	8347
FAM5XFAM4-5-1-1	3624	7741	7237	9039*	9120*
<i>lines from CABG3</i>					
CABG3-12-2-1-2-1-1	1909	7992	10237*		8727*
CABG3-10-1-7-2-2-1	3860*	8392	9235*	9897*	7912
CABG3-10-1-7-1-2-1	2284	7436	9720*		8240
CABG3-10-1-2-1-4-1	4553*	8155	9294*		7992
CABG3-10-1-7-1-1-1	1406	9050*	8730*		
CABG3-75-2-3-1-3-1	4359*	9048*	7856		
CABG3-40-2-1-1-3-1	2900	8939*			8984*
CABG3-47-3-2-2-2-1	3163	8897*	5673		
CABG3-3-4-2-1-3-1	3917*	7028	8829*		
<i>Elite lines from Cotaxtla</i>					
POB INT DENT-5-1-1-2-1-1	3171	8463	10104*	8173	6965
POB22TSR-S2-21-2#-1-1-1	4435*	9223*	8951*		
POB23TSR40-2_3-2	5607*			9038*	8024
ST-549	2920	8205	7962	8597*	8894*
AC-7421-46-2-1-2-1	4303*	8864*	8806*		
POB22TSR-S2-21-2#-1-1-3	5007*		8844*		
POB21C5HC28-1-33	3186	7497	8706*		8721*
POB32C4HC20-3-2-2-1-1	4658*	8708*	6884	8310	8211
PABG ST-477-2-1-1-1	5463*	8695*	8060		
D-471	4904*			8564*	8644*
<i>CIMMYT maize lines</i>					
CML55	4953*	5521	9629*		
CML15	3000		7950	7846	9525*
CML13	3047	8714*	9426*		
CML2	2769	7326	9085*		
CML3	2249	8080	8244	8883*	
CML1	3610*	8822*	8255	8305	
CML270	2926	8727*	8059		
<i>Checks (testers)</i>					
LT-154	3082		Checks		
LT-155	4137		Crosses		
CML247	3104			8399	
CML254	2151		H-513	7663	
			247X254		

*Best lines and specific combining ability

B14 - Heterosis and Combining Ability Among Long and Short-Ear Maize Inbred Lines

N. Vergara A., S.K. Vasal, S.D. McLean, G. Srinivasan and S. Rodríguez H.

Universidad Autonoma Agraria Antonio Narro (UAAAN), Buenavista Saltillo Coah. México. CP 25315. International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 México D.F.

Introduction

Maize is grown on more than 55 million ha under lowland conditions in the developing world, 2.8 million in Mexico. Hybrid maize research at CIMMYT was re-established in 1984 to integrate population improvement and hybrid development programs. Thousand of inbred lines have been developed and improved, and some of them have proved to be good hybrid parents (Vasal et al. 1993). In a hybrid program, information on the combining ability of germplasm sources is very important. The sources should belong to opposite heterotic groups for maximum expression of heterosis. The objectives of this study were to examine the heterosis and combining ability effects of 24 lines and to provide information on heterotic patterns of CIMMYT maize germplasm.

Materials and Methods

Twenty-four tropical white inbred lines at S_6 - S_{12} levels of inbreeding derived from eight CIMMYT maize pools and populations were selected based on their *per-se* performance and separated in two groups of twelve lines each. The lines from the first group with generally long ears (L) were crossed with the lines from the second group with broad ears (G). A total 144 single cross hybrids were developed. The yield trials were planted with four replications using a 12x12 lattice design during 1996 at Poza Rica, Cardel, and Cotaxtla, in the state of Veracruz; Tlaltzapán, Morelos; and Gómez Farías, Jalisco (all locations were in Mexico). Analyses of variance were computed for each location separately and combined across environments. Line (group 1) x tester (group 2) analyses for grain yield were conducted for each site and across locations using adjusted means (Kempthorne 1957). General (GCA) and specific (SCA) combining ability effects for grain yield were calculated according to the line x tester model. High parent and mid-parent heterosis were also calculated.

Results

The lines L8, L7 and G11, G3 had the highest *per se* yield performance. The highest GCA effects for yield were recorded for line L4 and G7 (Table 1). The lines L3 and G3 had the longest ears and showed good GCA effects for this trait, whereas lines L4, L11 and G2 had the most rows and showed good GCA effects. The highest heterosis from yield was recorded for hybrid L11 x G10 (Pop.21 x Pop.32) which is a well known heterotic pattern (Vasal et al. 1992). The highest heterosis for ear length was recorded for hybrid L9 x G8 (Pop.21 x Pop.25) and the highest heterosis for number of rows was for hybrid L2 x G4 (Pop.21 "CML10" x Tuxp. Seq. "CML254").

Conclusions

The F_1 hybrids involving the high-yielding parents showed the least heterosis and those involving the lowest-yielding parents showed the highest heterosis. Similar results were found for ear length, ear diameter, and number of rows. The lines with long ears and lines with more rows generally had good GCA effects for these traits. Most of hybrids involving lines from Populations 21 (Tuxpeño) and 32 (Eto) showed high heterosis for yield and good yield performance.

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Table 1. GCA effects for yield, ear length and number of rows of twenty-four maize inbred lines.

Lines with long and thin ears (group 1) Line code	Yield (t/ha)	Length (cm)	Rows (no.)	GCA yield	GCA length (cm)	GCA rows (no.)
L1 Pop.21 C5 FS219-S ₇ (CML9)	3.97	12.3	13.4	2.1	-0.6	0.3
L2 Pop.21 C5 FS219-S ₁₀ (CML10)	3.45	15.6	10.1	-121.8	1.2	-1.3
L3 Pop.21 C5 FS219-S ₇	3.85	16.9	10.4	138.1	1.4	-0.9
L4 (Pop.21xPop.43)-S ₆	3.14	15.0	14.1	576.5	0.4	1.2
L5 (Pop.21xPop.21)-S ₈	2.80	17.9	11.3	30.9	0.7	-1.1
L6 (Ac7643xPop.43)-S ₁₂	3.57	12.9	13.4	-51.8	-0.6	0.7
L7 (Ac7643xPop.43)-S ₇ (CML273)	4.13	12.4	14.4	172.4	-0.5	0.6
L8 Pop.43 STE C1 FS ₁₀ -S ₁₂	4.35	14.6	12.1	-277.1	-0.3	-0.2
L9 Pop.21 C5 FS219-S ₁₀ (CML264)	2.68	10.8	14.7	314.9	-1.2	0.8
L10 Ac7643-16-S ₇	3.51	15.1	10.9	-696.9	0.1	-1.1
L11 Pop.21 C6 S1 HS226-S ₈	2.76	11.1	16.0	18.1	-0.4	1.2
L12 Pop.21 C5 FS84-S ₈	3.28	12.6	12.0	-105.4	-0.1	-0.4
mean	3.47	13.9	12.7			
Lines with thick ears (group 2)						
G1 (P24xP24)-S ₇ (CML247)	3.49	11.5	14.5	-245.4	-0.7	-0.2
G2 (P24xP24)-S ₁₀	3.21	11.9	18.2	-10.7	-0.3	1.6
G3 Pool 24-S ₇	4.02	14.6	13.8	-80.0	1.7	-0.1
G4 Tuxp. Seq.149-S ₁₀ (CML254)	2.73	11.5	10.5	280.8	0.3	-1.7
G5 Tuxp. Seq.219-S ₁₄	2.52	10.2	12.8	-380.5	-0.8	-0.8
G6 Pop.22 TSR-S ₈ (CML267)	2.61	12.2	14.2	-205.5	0.1	0.2
G7 Pop.25 C9 HS5-S ₁₀	2.91	10.0	15.0	475.2	-0.1	0.6
G8 Pop.25 STE C1 HS5-S ₁₀	2.34	8.5	16.8	78.2	-0.9	0.9
G9 Pop.32 C4 FS242-S ₇ (CML39)	3.27	12.3	15.8	-714.7	-0.7	0.6
G10 Pop.32 (MRRS) C1-S ₉	2.27	13.2	12.3	272.6	1.0	-0.5
G11 Syn.TSR-S ₁₂	4.36	13.3	12.7	298.2	0.3	-0.3
G12 Pop.21 C5 FS109-S ₁₄	3.23	10.8	12.7	231.8	0.1	-0.4
mean	3.08	11.7	14.1			

Table 2. High-parent and mid-parent (in parenthesis) heterosis (%) between lines selected for different ear length.

Ear size (cm)	17.9	14.6	10.8
14.6	2.2 (10.4)	22.6(22.6)	15.1 (32.3)
11.5	-7.8 (12.2)	4.8 (16.8)	21.7 (25.0)
8.5	-12.3 (18.9)	2.1 (28.4)	32.4 (47.4)

Table 3. High-parent and mid-parent (in parenthesis) heterosis (%) between lines selected for different number of rows.

Rows (no.)	16.0	13.4	10.1
18.2	-3.9(2.3)	-6.6(7.6)	-17.6(6.0)
14.2	3.1(9.3)	9.2(12.3)	-11.9(2.9)
10.5	-15.6(1.9)	4.5(17.2)	14.3(16.5)

B15 - Heterotic Pattern Stability Analysis of Diallel Crosses in Quality Protein Maize

T. Hohls, P.E. Shanahan, G.P.Y. Clarke, and H.O. Gevers

Department of Genetics, University of Natal, P. Bag X01, Scottsville, 3209, South Africa

Introduction

The genetic model for the analysis of half diallel crosses proposed by Gardner and Eberhart (1966) provides information on the contributions of lines towards the heterosis of crosses in which they are involved. This model does not, however, relate the ancestry of the lines to the heterotic patterns obtained. Addition of a term that relates to the ancestry of the lines being crossed enables tests of significance of the deviation of the heterotic patterns of the lines, from that expected on the basis of the heterotic group to which the lines belong. A combination of a stability analysis and the cross-over test of Gail and Simon (1985) has been shown to be useful in identifying genotypes with good stability across environments without changes in rank order (Hohls et al. 1995).

Methods

The heterotic pattern model for the analysis across environments (Hohls et al. 1994) was modified to a joint regression model. The methodology is illustrated by application to a 7 x 7 half diallel cross of white modified opaque-2 maize inbreds conducted across six environments. The data was obtained by considering diallel entries common to a 12 x 12 diallel experiment conducted across two sites in the 1991/92 breeding season, and a 10 x 10 diallel experiment conducted across four sites in the 1992/93 breeding season. The seven inbred lines are representative of three heterotic groups used in the South African quality protein maize breeding programme. The weighted heterotic pattern analysis was carried out through the method of fitting constants by least squares, as described by Hohls et al. 1994. The test for cross-over interactions was carried out according to the method of Gail and Simon (1985).

Results

The heterotic performance of the inbred lines was generally representative of the mean heterosis displayed by the heterotic groups. The line heterosis (h_i) of SO507W(M) was significantly higher ($p < 0.01$) than that of the other inbreds (h_j , Table 1). SO507W(M) also had good stability across the six sites, responding favourably to improved environmental conditions ($b = 0.34$, Table 1). There were significant interactions ($p < 0.05$) of the mean heterosis displayed by the heterotic groups with environments. These interactions could be accounted for by a linear regression of the pedigree heterosis terms (p_w) on the environmental indices (e_m). Some pedigree groups therefore have their own characteristic linear responses to environmental change. The M heterotic group, represented by SO507W(M), clearly had the best heterosis and stability across environments (Table 1). The Gail and Simon (1985) c^2 test revealed that there were significant interactions between the P and M, and M and F groups across environments. The cross between SO713W(P) and RO558W(F) resulted in the highest specific interaction effect across environments (s_{26}). However, the specific heterosis obtained in this cross showed below average stability across environments ($b = -0.16$).

Conclusions

The heterotic pattern analysis of the 7 x 7 diallels provided useful information on the heterotic behaviour of the seven inbred lines. The heterotic behaviour of the inbred lines was generally representative of their heterotic groups. Seasonal variation was shown to affect the heterotic patterns of the inbreds more than site variation. Inbreds from the P and M heterotic groups were shown to have similar frequencies of the genes responsible for an improvement in yield. SO507W(M) had the highest mean contribution to heterosis on crossing, and the best linear response to environmental change, responding favourably to improved environmental conditions.

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Table 1. Heterosis effects for the separate environments, and the stability parameters obtained from regression of the effects on the environmental indices (excluding specific heterosis), for the 7x7 diallel analysis of yield (t ha⁻¹).

	91U	92P	92U	92C	91C	92B	Intercept	Slope
f ₁	0.13	-0.36	-0.18	0.01	0.43	-0.29	-0.11	0.15
f ₂	-0.28	-0.30	0.03	-0.49	-0.08	-0.06	-0.15	-0.01
f ₃	0.02	-0.31	-0.36	-0.29	-0.22	-0.02	-0.23	0.12
f ₄	0.36	0.48	0.37	-0.12	0.08	0.46	0.30	-0.15
f ₅	-0.29	0.22	0.45	0.28	0.37	0.18	0.27	0.02
f ₆	-0.60	0.04	-0.29	0.13	-0.22	-0.79 ^{**}	-0.28 [*]	-0.19
f ₇	0.65	0.23	-0.01	0.48	-0.37	0.50	0.21	0.04
h ₁	0.51	0.43 [*]	0.24	0.26	-0.05	0.24	0.26 ^{**}	-0.17
h ₂	0.10	0.30	-0.20	0.06	-0.07	-0.37	-0.07	-0.20
h ₃	0.43	0.85 ^{**}	0.91 ^{**}	0.61 ^{**}	1.52 ^{**}	1.30 ^{**}	0.97 ^{**}	0.34
h ₄	-0.69 [*]	-0.36	-0.21	0.10	-0.36	-0.42 [*]	-0.28 ^{**}	0.04
h ₅	0.14	-0.51 [*]	-0.26	-0.23	-0.94 ^{**}	-0.67 ^{**}	-0.43 ^{**}	-0.29
h ₆	-0.09	-0.50 [*]	-0.24	-0.38	-0.13	-0.00	-0.24 ^{**}	0.17
h ₇	-0.41	-0.22	-0.24	-0.42	0.04	-0.08	-0.21 [*]	0.12
p _P	0.29	0.19	-0.42	-0.04	-0.86 [*]	-0.76 ^{**}	-0.33 ^{**}	-0.48
p _M	0.55	1.15 ^{**}	1.36 ^{**}	0.86 ^{**}	2.31 ^{**}	1.98 ^{**}	1.43 ^{**}	0.57
p _F	-0.84	-1.34 ^{**}	-0.94 ^{**}	-0.82 ^{**}	-1.44 ^{**}	-1.22 ^{**}	-1.10 ^{**}	-0.09
d _{1P}	0.21	0.06	0.22	0.10	0.01	0.30	0.16 [*]	0.02
d _{2P}	-0.21	-0.06	-0.22	-0.10	-0.01	-0.30	-0.16 [*]	-0.02
d _{1M}	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
d _{1F}	-0.43	0.04	0.03	0.33	-0.01	-0.13	0.04	0.03
d _{2F}	0.40	-0.11	-0.02	0.01	-0.59 ^{**}	-0.37 [*]	-0.18 [*]	-0.12
d _{3F}	0.17	-0.10	0.00	-0.15	0.22	0.29	0.06	0.16
d _{4F}	-0.15	0.18	-0.01	-0.19	0.39	0.21	0.08	0.11
e _m	-0.72 ^{**}	-0.69 ^{**}	-0.40 ^{**}	0.40 ^{**}	0.68 ^{**}	0.75 ^{**}		
SE(f _i)	0.55	0.32	0.24	0.34	0.38	0.30	0.13	
SE(p _w)	0.46	0.29	0.22	0.31	0.34	0.27	0.12	
SE(h _i)	0.34	0.21	0.16	0.23	0.25	0.20	0.09	
SE(d _{iw})	0.28	0.17	0.13	0.19	0.21	0.16	0.07	

f_i = parental effect, h_i = line heterosis, p_w = pedigree heterosis, d_{iw} = deviation effect, and e_m = environment.

Numbers 1-7 refer to the seven inbred lines used in the diallel cross, in the following order: FO215W(P), SO713W(P), SO507W(M), RO550W(F), KO54W(F), RO558W(F), and RO504W(F).

Letters P, M and F refer to the three heterotic groups to which the inbred lines belong.

SE(e_m) = 0.14

B16 - Hybrid Rice Breeding for the Mekong Delta of Vietnam

Bui Ba Bong and Nguyen Van Luat

Cuu Long Delta Rice Research Institute, Omon, Cantho, Vietnam

Introduction

The Mekong Delta (called Cuu Long) is the largest rice-producing region in Vietnam, accounting for more than half the national production. The increased productivity of high-yielding varieties planted annually on about 2 million ha in the Mekong Delta has contributed significantly to the increase in rice production in Vietnam, resulting in exportable surpluses in recent years. However, the yields of existing semidwarf varieties are approaching a plateau in large areas, particularly under intensive cultivation. We have implemented a hybrid rice breeding program to increase the crop's productivity.

Methods

Work includes 1) evaluation of CMS lines to identify adapted lines for hybrid rice development; 2) identification of adapted maintainer and restorer lines; and 3) evaluation of hybrid rice varieties. The CMS lines were grown in the field and measured for pollen sterility, spikelet sterility (bagged panicles), and agronomic characters. Selected CMS lines were crossed with elite lines in the germplasm, and the F_1 s were evaluated for seed set. When seed set in an F_1 was below 5%, the male parent was a prospective maintainer for the corresponding female parent (CMS line) and when it was above 80%, the male parent was a prospective restorer. To evaluate the performance of hybrid varieties, field trials were conducted following a completely random block design with three replications. Each trial consisted of around 30 hybrid varieties plus two conventional semidwarf varieties as checks. Recommended cultural practices were followed.

Results

During 1992-1996, 50 CMS lines were evaluated. The promising CMS lines included IR58025A, IR62829A, IR64608A, IR 68275A, IR68888A, IR68891A, IR66897A and PMS10A. These lines had complete and stable male sterility over seasons and acceptable agronomic characters. From the evaluation of hundreds of F_1 test crosses, the maintainers and restorers for some promising CMS lines were identified. They included varieties well adapted to the region or elite lines (Table 1). Eleven yield trials of hybrid rice varieties were conducted over 1992-1996. In 6 trials, the best hybrid varieties significantly increased yield by 10.9-46.8% over the check variety (Table 2). In 5 trials, there was no significant difference in yield between the best hybrid varieties and the check variety. Over 11 trials, the best hybrid varieties yielded 6.49 t/ha as compared to 5.56 t/ha for conventional varieties (increased 0.93 t/ha or 14.3%). Hybrid rice in China is reported to increase yield by about 20% (Yuan and Fu 1995). The hybrids we have evaluated so far all were of *indica* x *indica* type. A new generation of hybrid rice varieties are expected from crossing *indica* and "tropical japonica" (a new plant type) (Khush, 1995); these would provide greater heterosis.

Conclusions

With the breeding materials available, it is possible to develop hybrid rice varieties for the Mekong Delta of Vietnam with estimated yield increase of around 15%. However, additional aspects such as hybrid seed supply and seed cost should be considered to make hybrid rice technology economically feasible.

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Table 1. Adapted varieties/lines identified as prospective maintainers or restorers, 1992-1996.

CMS line	Maintainer	Restorer
IR50825A	IR50404, IR44595	OM269, IR64, IR62032, OM997
IR62829A	DM16, OM1270, OM1305	IR59606, OM1630, OM1590
IR64608A	MTL98, OM1327, OM1633	IR54622, IR54765
PMS10A	OM1270	OM1630, OM916, IR44675, IR72

Table 2. Yield of hybrid rice varieties vs conventional semidwarf varieties, 1992-1996.

Location	Year	Best hybrid variety		Conventional variety		% yield increased by hybrid variety ^b
		Name ^a	Yield (t/ha)	Name	Yield (t/ha)	
Cantho	1992-93	29A/IR47310	5.80	OM90-9	5.27	10.0
Kiengiang	1992-93	29A/IR47310	7.29	IR64	6.57	10.9*
Angiang	1992-93	25A/IR54742	7.50	IR64	7.80	-0.03
Tiengiang	1992-93	29A/IR35366	6.40	IR64	5.94	7.7
Kiengiang	1993	29A/IR21567	6.17	IR64	5.04	22.4*
Angiang	1993	29A/IR29723	5.30	IR64	4.50	17.8*
Cantho	1994	25A/IR25912	7.80	OM269	6.93	12.5
Cantho	1995	PMS10A/IR48725	5.96	OM1706	4.06	46.8*
Cantho	1995	25A/RP1057	5.67	OM1706	3.87	46.5*
Cantho	1995-96	25A/IR65516	6.80	OM1706	6.30	7.9
Cantho	1996	29A/IR65517	6.73	OM997	4.89	27.3*
Average			6.49		5.56	14.3

(a) 29A= IR62829A, 25A=IR58025A.

(b)* indicates significance at 5% level.

B17 - Comparative Response to Selection of Two Reciprocal Recurrent Procedures in BS21 and BS22 Maize Populations

M.A. Menz, A.R. Hallauer, W.A. Russell

Department of Agronomy, Iowa State Univ., Ames, IA 50011

Introduction

Reciprocal Recurrent Selection (RRS) proposed by Comstock et al. (1949) has proven to be a successful method to improve the performance of a cross population and to increase the heterosis between populations. However, RRS has not been widely adopted by commercial breeders because RRS is not as efficient to recover inbred lines as other methods of inbred development (Russell and Eberhart 1975). To overcome this limitation Russell and Eberhart (1975) introduced a modification in the RRS procedure. They suggested the use of two inbred lines as testers instead of the opposite population as reciprocal testers in an RRS scheme. Line 1 is the tester for population A and line 2 is the tester for population B. The lines must be unrelated to the population which are under selection but they may be related to the opposite population (1 unrelated to A but related to B). Reports by Horner et al. (1973; 1989) and by Russell et al. (1973) showed that inbred line testers were effective for improving general as well as specific combining ability. These studies also showed greater genetic variance among the testcrosses when using an inbred line instead of a broad genetic base population as testers. The authors suggested that greater genetic gains also are expected. Use of an inbred line as a tester also reduces the problem of sampling in a heterogeneous tester. Another potential advantage of the modification proposed by Russell and Eberhart (1975) is that lines derived from the improved populations using elite inbred lines as testers could be used in hybrid combinations with the testers.

Methods

Russell initiated a breeding research program in 1974 at Iowa State University to evaluate the modified RRS procedure. He applied RRS in BS21 and BS22, two synthetic populations adapted to North and North Central Iowa for maturity. Simultaneously he used the modification (MRRS), suggested by Russell and Eberhart (1975) in the same two populations using inbred line A632 as tester for BS21 and inbred line H99 as tester for BS22. A632 and H99 were elite inbred lines with above average combining ability at the time selection was started. The H99 and A632 testcrosses were producing crossing each of ~200-300 S_0 plants of each of these two synthetics with three plants of the corresponding inbred tester, obtaining ~200-250 full-sib progenies (S_0 plants \times inbred tester) for evaluation in replicated yield trials in the next season. At the same time, each S_0 plant that was used as male to produce the full-sib testcrosses, was selfed to obtain S_1 seed. This seed was advanced to the S_2 generation and used for recombination, if its full sib progeny was selected in the yield trial, to develop the next cycle of selection (Russell 1975).

In 1993 six cycles of selection were completed in BS21 and BS22 using both methodologies, and an experiment was conducted to evaluate the response to selection. In this experiment the populations per se [BS21(R) C_{0-n} and BS22(R) C_{0-n} for RRS; BS21(HI) C_{0-n} and BS22(HI) C_{0-n} for MRRS], testcrosses to inbred testers [BS21(R) $C_{0-n} \times$ A632, BS22(R) $C_{0-n} \times$ H99, BS21(HI) $C_{0-n} \times$ A632 and BS22(HI) $C_{0-n} \times$ H99], and crosses between cycle populations of RRS and MRRS [BS21(R) $C_{0-n} \times$ BS22(R) C_{0-n} and BS21(HI) $C_{0-n} \times$ BS22(HI) C_{0-n}] were evaluated in replicated yield trials conducted in eight environments.

Results and Discussion

There were significant and linear increases in grain yield in all the six cross populations as a consequence of selection. However, the rate of direct response, expressed as %/cycle was significantly greater for the RRS procedure than for the MRRS (4.5, 1.8, and 2.9% cycle⁻¹ for BS21(R) \times BS22(R), H99 \times BS22(HI), and A632 \times BS21(HI), respectively) (Table 1). The indirect response in the cross populations also show a linear, positive, and significant response. RRS was as efficient as MRRS to improve the grain yield of the populations in crosses with the inbred lines.

With the populations included in this study and using A632 and H99 inbred lines as testers, there is no evidence that the genetic variance among TC for yield was greater when using inbred lines as testers than when using a population as tester. In this study the traditional RRS procedure was more efficient than MRRS to improve grain yield in the cross population BS21xBS22.

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Table 1. Linear regression coefficients (b), response to selection(R), and heterosis (H) for grain yield in Mg ha⁻¹ for six cross populations after six cycles of recurrent selection.

Cross population	b	R	H	
			C ₀	C ₆
	Mg ha ⁻¹	% cycle ⁻¹	-----%-----	
BS21(HI) x A632	0.19** " 0.02	2.9	11.4	37.8
BS21(R) x A632	0.15** " 0.02	2.4	11.4	26.5
BS22(HI) x H99	0.10** " 0.03	1.4	17.4	37.5
BS22(R) x H99	0.12** " 0.05	1.8	17.4	23.8
BS21(HI) x BS22(HI)	0.08** " 0.02	1.2	1.0	17.2
BS21(R) x BS22(R)	0.27** " 0.02	4.5	1.0	25.4

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

Commercial Strategies for Exploiting Heterosis

D.N. Duvick

Department of Agronomy, Iowa State University, Ames, IA 50011 (USA)

Introduction

Commercial application of heterosis – breeding, production, and sale of hybrid seed – can be successful if it meets certain criteria, to wit: 1) The hybrids must satisfy the needs of the customer for all important traits. 2) The price of hybrid seed must be low enough so that expected extra profits are at least three times the extra cost of seed. 3) The price of hybrid seed must be high enough that the seed company can make about 10-15% return on equity while investing in research in amounts equivalent to 5-10% of sales. Two other criteria underpin all other requirements: 1) Farmers must have sufficient financial resources to be able to risk investment in improved seed. 2) Government regulations, formal and informal, must give minimal hindrance to honest and prudent business operations. These two requirements have particular significance in many developing countries.

Discussion

To satisfy the primary criteria for success, seed companies must integrate variables such as: 1) the pollinating system of the crop, 2) options for manipulation of the pollinating system, 3) supply and cost of labor for emasculation or other preparations for hybridization, 4) the yield of the crop, 5) the commercial value of the crop per unit of land, 6) the seeding rate of the crop, 7) the seed yield in the seed production field, 8) the extra yield to be expected from heterosis, 9) the implications of hybrid uniformity, 10) the most important traits to improve in the crop, and ease of manipulating them, 11) ease of demonstrating improvements in new hybrids, 12) availability of inbred parents in public or private domains. Three examples illustrate the consequences of integrating these variables.

Hybrid maize. The first hybrids yielded only about 15% more than the better open pollinated varieties. They yielded three or four times as much as inbred lines, but farmers did not grow inbred lines. The pollination system – natural outcrossing and with complete separation of male and female flowering organs – ensured ease of emasculation (detasseling) and plentiful supplies of pollen for hybridization. In addition, cytoplasmic male sterility eventually was developed as an option for avoiding the labor needed for hand emasculation. Despite failure of one cytoplasmic system due to disease susceptibility, other systems are available and in use. The commercial value of the maize crop per unit of land was not particularly high, compared to high value crops such as tomato, but seeding rates were low for a field crop (one seed gives about 300 in return), and seed yields in the hybridization field (to make double cross hybrids) were relatively high. Therefore farmers could afford to buy hybrid seed at a price that was high enough to give a profit to the seed companies. Yield and standability were both susceptible to improvement by use of the inbred/hybrid method and improvements could be demonstrated easily to farmers. Uniformity of hybrid varieties helped farmers to distinguish hybrids from open pollinated varieties and increased ease of making critical comparisons. Uniformity of hybrids improved ease in developing cultivars for specific product needs or ecological niches, but also increased the dangers of uniform susceptibility to unforeseen disease or insect problems. In the critical early years of hybrid commercialization, inbreds were supplied by public breeding institutions at the universities and in the USDA; in later years private firms produced their own proprietary lines for use in-house or for lease to seed companies that specialized in production and sale of hybrid seed. Hybrid maize in the USA was commercialized successfully as a joint public/private enterprise. It has since been commercially successful in Canada and Europe and, increasingly, in many developing countries.

Hybrid wheat. Wheat hybrids could yield up to 30% more than their parents, but hybrids have to be made within a class of wheat to maintain milling and baking quality, and such crosses typically yield only about 5-15% more than their parents. Wheat is a self-pollinated inbred crop, has perfect florets, limited supplies of pollen, and a relatively brief period of stigma receptivity. Hand emasculation is impractical for commercial seed production, but cytoplasmic male sterility allows production of hybrid seed on a field scale. Value of the crop per unit of land is similar to that for maize (both crops are commodities), but seed yield in the crossing field is low and seeding rates for commercial production are high relative to maize (one wheat seed will produce 30 to 50 grains). Therefore if the seed company prices the hybrid seed safely above cost of production, the seed cost from the farmer's point of view will be very high. Yield and standability are important, but milling and baking qualities of the grain must also be rigorously maintained. Thus, wheat breeders must manipulate more traits than maize breeders to increase hybrid yield by incorporation of diverse germplasm. Hybrids are not more uniform than standard inbred cultivars, thus there is no advantage or disadvantage in this respect. In the early years of development of hybrid wheat, public wheat varieties were readily available as female parents, since they nearly always lacked fertility restoration genes, but because of this same factor, companies had to develop their own male inbred lines, usually by introgressing restorer genes from widely divergent germplasm. Unlike the early years of development of hybrid maize, public breeders gave very little input to hybrid wheat breeding; this led to under-investment in the development of germplasm and breeding methods (particularly for restorer males) in the important start-up period. Linkage drag slowed progress in developing males that contributed high yield and other performance traits (such as new disease resistance) to their hybrids, and the concurrent rapid increase in yield and performance of standard inbred cultivars meant that hybrids could not compete with standard cultivars. The problem was aggravated by the higher price and requirement for annual purchase of the hybrid seed. In the USA several attempts at commercializing hybrid wheat were abandoned after companies became convinced that commercial production of hybrid wheat could not generate profits for farmers and seed companies simultaneously. Interest in hybrid wheat is still present, particularly in regions where wheat yields and commercial value are relatively high, but successful commercialization is still conjecture.

Hybrid tomato. Tomatoes are a self-pollinating inbred crop, flowers are perfect. Although genetic sterility is available, hand emasculation and pollination are preferred for making hybrids. Crossing is performed in countries where labor costs are low. Tomatoes are a high value crop, grown for either fresh market or processing, and seeding rates are low compared to the value of the commercial crop. Although hybrids exhibit heterosis for yield, their unique attraction is that the hybrid method facilitates use of complementary genes for disease resistance as well as for traits affecting product quality such as shelf life. Hybrids also exhibit greater yield stability. In the USA 100% of fresh market and 80% of processing tomatoes are F_1 hybrids.

Conclusions

Demonstration of heterosis for yield and other traits in many crops (and the example of the commercial success of hybrid maize) has prompted efforts to commercialize hybridization of cross pollinated field crops, self pollinated field crops, and numerous vegetable and bedding floral crops. As a general rule, hybridization of cross pollinated field crops has been commercially successful for farmers and seed companies, relatively unsuccessful with self pollinated field crops (with the exception of sorghum and rice), and successful with high value vegetable and bedding crops. Cytoplasmic male sterility has been the method of choice for hybridizing field crops (maize also can be detasseled). Vegetable and ornamental crops are hybridized in a variety of ways including cytoplasmic male sterility, hand emasculation, genetic male sterility, self incompatibility, and production of gynoeious or highly pistillate monoecious plants. For all crops research is in progress on use of chemical male sterilants and/or genetic engineering to produce new systems for hybridization.

Heterosis for the Development and Promotion of the Seed Industry

R.B. Hunter

Novartis Seeds Inc., RR # 1 Plattsville, Ontario, N0J 1S0, Canada

The commercial exploitation of heterosis has been one of the driving forces in the rapid and extensive development of privately funded crop breeding research efforts around the world. Nowhere is this more evident than in the development of privately funded maize breeding in the USA. Hybrid maize was the first major food crop to be developed utilizing extensive private funding. In the 1930s, the hybrid seed corn industry was in its infancy. At that time there were very few privately funded maize breeding programs. Those that existed relied very heavily on materials from publicly funded programs. During this time, most maize growing states had one or more publicly funded maize breeding programs.

Today, in the USA, almost all commercially directed breeding efforts aimed at the development of maize hybrids have shifted from public to privately funded research. Frey (1996) reported that, in 1994, there were 509.7 private industry science person years (SY) devoted to dent maize breeding research and product development in the USA -- 94% of the total breeding effort in dent maize. Of the 27.1 state budgeted SYs working on field maize, only 3.1 SYs were devoted to cultivar development. There was no federally funded field maize research directed at cultivar development. In addition to the privately funded field maize breeding effort, private industry investment in sweet corn and popcorn hybrid maize breeding accounted for an additional 46.4 SYs. The total publicly funded effort for sweet corn plus popcorn was reported to be 7.2 SYs.

A key conclusion of the Frey study was that privately funded research in the USA has concentrated on species for which the cultivars grown are entirely hybrid or a mixture of hybrids and pure lines. Private industry devoted 654 SYs to major crops with entirely hybrid cultivars -- field maize, sorghum, sunflower, sweet corn, sugar beet, and muskmelon. Three crops -- tomato, pepper, and onions -- with both hybrid and pure line cultivars accounted for an additional 119 breeding SYs in private industry. In contrast to the situation with hybrid crops, the public sector has focused more on species dominated by pure line cultivars.

The decision of private industry to invest in plant breeding for a given species has not been based solely on the presence of and degree of heterosis. Other major factors include the market value, the competitive structure, and the presence of intellectual property protection systems. The right mix and balance of the above factors has been the stimulus behind the rapid development of privately funded breeding research in many areas of the world. Examples include hybrid canola in Canada, hybrid maize in Thailand, and hybrid sugar beets in Europe and the USA.

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Logistics of Seed Production and Commercialization

A.B. Maunder

DEKALB Genetics Corporation, Retired

Introduction

An obvious need of developing country agriculture is technology transfer, such as with planting improved seed, from national or international research improvement programs to the producer, both subsistence as well as the large operator. For any crop the existence of dependable markets, relatively large areas of cultivation, and a desire on the farmers' part to increase yields through hybridization indicate that farmers might benefit from the presence of commercial seed firms. Advantages and likely reasons for success would be: 1) dependable supply, 2) acceptable quality/purity, and 3) an improved level of performance (Maunder et al. 1994). To develop a seed industry means providing a reasonable return on investment without undue government restrictions, since capital risk will be required.

Discussion

Over the past 70 years since the hybridization of maize, numerous field crops and vegetables have benefited from the phenomenon coined by Shull in 1917 as "heterosis" (Crabb 1947). Examples include plants, characterized by both perfect and imperfect flowers, with genetic and cytoplasmic-genetic sterility, protogyny, incompatibility, and genetic markers allowing for wind, insect, or hand pollination (Table 1). Location of seed production will be determined by region of crop adaptation, which will determine parental line performance in relation to frost free days, temperature means and extremes, relative humidity, adequate moisture, often by irrigation, well drained soils, and minimal abiotic and biotic stresses. Certainly freedom from weedy species of the specific crop will be essential. Also, the availability of temporary labor for field activity such as roguing, de-tasseling, harvesting and proximity of the hybrid seed produced to its intended market must be considered to reduce costs. Equipment required beyond conventional farming machinery may include a pesticide applicator and stationary or mobile harvester/combine. Seed conditioning equipment would be the principal investment, along with a reasonably useable building for this equipment and seed storage. Costs of such equipment based on US prices for such crops as corn, sorghum, and sunflower may approach US\$75,000 (Table 2). Bags, holding bins, and scale have not been included.

Parental lines may be obtained from international agricultural research centers, non-government organizations, national agricultural research programs, or USAID. Ready availability of such parental seed stocks will determine the need for foundation maintenance as will certification/purity restrictions imposed by government seed laws. Successful hybrid production depends on high quality parental seed planted in the correct sequence to assure pollination nicking and in the correct ratio of male to female for adequate volume of pollen; examples being sorghum 3:1, corn 2:1 to 4:1, sunflower from 2:1 to 7:1 and wheat from 1:1 to 3:1 (Wright 1980). Vegetable crop ratios also range from 1:1 or 4:1 (D. Holmes, pers. comm.). Roguing before, during, and following pollination is essential to maximize purity and to meet inspection requirements. Harvest procedures include removal of male ahead of female; possible need for desiccation to avoid seed damage or dryer expense; careful separation by lots; and properly cleaned harvest and conditioning equipment within and between pedigrees. Seed moisture at harvest and temperature in storage or during drying will significantly affect germination and dormancy.

To commercialize a seed crop requires marketing and distribution. If the customer base is within the immediate trading area of the seed production, distribution is greatly simplified.

Seed may be obtained by 1) direct sale, 2) from a store dealer or, 3) from farmer dealers – the latter approach most often used in the development of the US seed industry, with larger distributors providing more services and becoming dominant in some markets. This trend has developed to better provide financing and service after the sale; large seed companies are greatly increasing their efforts to provide agronomic services which include product information and likely causes of abiotic and biotic stress and potential control. At the time of purchase the grower may additionally receive information on germination, seed size, and specific seed lots.

Conclusions

Success as a seedsman, once an infrastructure is in place, will relate to many variables among which will be the capacity to adequately meet demand. Seed purity and germination will greatly influence customer satisfaction. Adequate storage facilities to handle carry-over surplus production must be available. Minimizing carry-over not only supports higher quality but is financially significant. This leads to pricing of product, which must reflect the grower contract, commercial grain price, and inflation rates. Collection of revenues from seed sales may be an issue, especially when agricultural income is unstable. Finally, depending on the quantity and quality of competition, the product must develop a customer base large enough to support the available seed industry. Success at this entry level can then lead in future years to a form of in-house research activity to provide a proprietary and improved product.

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Table 1. Specific field and vegetable crops currently hybridized and the method of pollination.

Field Crops				Vegetables			
Maize	w	Cotton	i h	Onions	i	Squash	i
Sorghum	w	Alfalfa	i	Broccoli	i	Beets	w
Wheat	w	Oil palm	h	Cauliflower	i	Cantaloupe	h
Canola	w i	Millet	w	Cabbage	i	Cucumber	i h
Sunflower	i	Castor	w	Tomatoes	h	Eggplant	h
Rice	w h	Sugarbeet	w	Watermelon	h	Pepper	h
				Carrots	i	Spinach	w
w by wind		i insect transmission		h hand pollination			

Table 2. Equipment to condition 1,000 t of maize, sorghum or sunflower based on US cost estimates.

Component for Conditioning	Estimated cost U.S. export*
Seed Cleaners and sizer	\$32,000
Ideal length grades	4,500
Pre-mix tank	2,700
Seed treater	3,300
Elevator	8,000
Conveyors (2)	8,000
Total	58,500

*FOB prices plus packing

Exploitation of Heterosis: Uniformity and Stability Considerations

J. Janick

Department of Horticulture, Purdue University, West Lafayette, Indiana 47907-1165, USA

Introduction

Production of hybrids of seed-propagated crops is a successful breeding techniques because it exploits heterosis, promotes homogeneity in allogamous (cross pollinating) species, and is a way for commercial breeders to control their product. Uniformity is one of the principal benefits of hybrids for three reasons: product uniformity is essential in marketing, particularly in horticultural species; uniformity in maturity permits crop scheduling; and uniformity in plant structure and maturation permits efficient mechanical harvest. With the increasing importance of urban markets, product uniformity is an essential feature of crop quality. There are two dimensions to crop uniformity of hybrids: (1) *genetic homogeneity* and (2) *genetic stability*.

Genetic Homogeneity

Genetic homogeneity refers to uniform populations as a result of identical genotypes. This can be achieved by vegetative (clonal) propagation which includes apomixis, by inbreeding to create inbred or pure lines, or by intercrossing inbred lines to create heterozygous F₁ hybrids. In seed propagated, allogamous species where open pollinated populations consist of a mixture of genotypes, genetic homogeneity can be achieved by inbreeding to create inbred or pure lines but the decline in vigor associated with inbreeding makes the production of such homogenous lines unacceptable as a breeding method. Genetic homogeneity with high vigor can be achieved by intercrossing divergent inbred genotypes with high homozygosity while selecting within and between inbred lines for adaptability, vigor, combining ability, and stability (see below). Genetic homogeneity in single crosses is a function of the degree of homozygosity of the parents, thus genetic homogeneity in hybrids can be increased by increasing the homozygosity of the inbred parents through inbreeding. In autogamous (self pollinating) species, genetic homogeneity of parental populations and hybrids are equivalent because each population consists of identical genotypes, one homozygous and the other heterozygous.

Genetic Stability

Genetic stability (homeostasis) refers to reduced genotype x environment interaction, particularly under stress. Open pollinated populations of allogamous populations have genetic stability by the virtue of their genetic heterogeneity, which creates population buffering. Population buffering is absent in homogeneous single crosses, but single crosses with high genetic stability can be selected. Genetic stability is an inherited feature that can be incorporated into heterotic combinations and can be increased by using three-way and double-cross hybrids, because of the presence of population buffering. However, yields of double or three-way crosses can always be surpassed by appropriate single crosses. The selection of adapted single crosses with high yield and high stability has been responsible for the consistent increase in maize yields in the United States since their introduction in the early 1960s.

Uniformity vs. Stability in Subsistence Agriculture

Hybrids have been considered an unwise choice for subsistence farmers for two reasons. The first is the requirement for cash outlay for seed, but this argument is specious if the value of the hybrid will provide a yield return that will more than compensate for the extra seed costs. The second is the fear of higher risk that uniformity imposes in response to severe biotic stress, such as insect predation and disease, a risk that would be catastrophic for those existing on the margins. This risk is real if the available hybrids are unadapted but the risk is negligible with adapted hybrids. Furthermore, risk can be alleviated by planting a range of hybrids to avoid the yield penalty of open pollinated populations.

The unavailability or inability to use superior germplasm by subsistence farmers must be considered another factor that traps subsistence farmers in a downward cycle of poverty. Solutions to this dilemma could be economic (the better availability of credit) or technical (the creation of apomictic hybrids permitting farmers to save their own seed).

Apomixis and Heterosis

W. Hanna¹, P. Ozias-Akins² and D. Roche¹

¹US Department of Agriculture-Agricultural Research Service, and ²Department of Horticulture, University of Georgia Coastal Plain Experiment Station, PO Box 748, Tifton, Georgia 31793

Introduction

Interest in apomixis to produce true-breeding hybrids propagated by seeds has steadily increased during the past 35 years as more information is available on the genetics and manipulation of this asexual reproductive mechanism. The discovery of sexual plants in apomictic species to produce apomictic hybrids (Bashaw and Hussey 1992), new information on the genetics of apomixis (Nogler 1984; Asker and Jerling 1992), progress in transferring apomixis from wild to cultivated species (Asker and Jerling 1992), progress made in molecular mapping of the genes controlling apomixis (Hanna et al. 1996) and the rapid advances being made in molecular techniques have all contributed to renewed interests and efforts to use apomixis to produce superior hybrids.

Factors favoring use in plant breeding

Apomixis has been reported in over 300 species in at least 35 different plant families (Hanna and Bashaw 1987). Various mechanisms for apomixis are present in plants. However, in cultivated plants apomixis is mainly found in the tertiary gene pools. A number of studies indicate that apomixis is genetically controlled by simple inheritance which favors genetic manipulation in plant breeding (Asker and Jerling 1992). The manipulation of apomixis within a species to produce apomictic cultivars as well as the expression and manipulation of apomixis in interspecific sexual \times apomictic crosses have both demonstrated that genes controlling apomixis could be used to produce true-breeding hybrids (Hanna et al. 1993). Molecular markers are also being linked to apomixis (Hanna et al. 1996; Ozias-Akins et al. 1993) which will facilitate marker-assisted selection.

Challenges

In traditional backcrossing, problems in both male fertility (to allow transfer of genes controlling apomixis through the pollen) and female fertility (to allow economic levels of seed production) need to be overcome. The lack of F_2 data and the inability to use apomicts as female parent in crosses limits to some degree the genetic data that can be obtained. Molecular markers linked to apomixis are being identified but recombination between these markers and the genes controlling apomixis (needed to further map the locus) have been limited.

Using apomixis to improve production

Apomixis is in the early stages of making a contribution to crop improvement. Bashaw and Hussey (1992) reported on the use of apomixis to produce apomictic forage hybrids in *Cenchrus* by traditional crossing methods. Hanna et al (1993) reported on the progress being made in transferring apomixis from *Pennisetum squamulatum* to cultivated pearl millet. Significant progress is being made in identifying molecular markers associated with apomixis (Ozias-Akins et al. 1993; Leblanc et al. 1995).

Apomixis would have the most immediate potential for improving production in crops such as wheat, rice, and soybean where efficient methods for producing hybrids are not readily available. In crops such as maize, sorghum and pearl millet where effective cytoplasmic-nuclear male sterility systems are present, apomixis would not only simplify hybrid production but also allow breeders to produce and use unique gene combinations to maximize yield.

'Uniformity' and 'high-yield' are two traits that come to mind when the term 'hybrid' is used. Although high yields may be universally desirable, uniformity may not be necessary for most food crops grown around the world. In fact, some genetic variation in farmers' fields allows for adaptation to diverse environmental and stress conditions, resulting in more reliable production. Although uniformity of a hybrid is always a possibility with apomictic hybrids, genetic diversity is also a possibility by blending one or more superior apomictic hybrids or by introducing the gene controlling apomixis into landraces and local ecotypes to random mate within the population. Blended hybrids could be genetically diverse but uniform for such selected characteristics as height, maturity or seed size. Introduction of the gene controlling apomixis into a landrace or local ecotype would allow for production and perpetuation of unique, high-yielding genotypes which would have a competitive advantage and slowly increase production.

Apomixis has the potential for major impact by increasing food, forage and fiber production around the world. For some crops the genes controlling apomixis can be transferred by traditional methods from wild to cultivated species. However, it appears that molecular and transgenic methods will be needed to transfer apomixis in most crops (genera without apomixis).

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B19 - Hybrid Wheat Development in Australia and a Proposal for Hybrid Wheat Blends for Developing Countries

P. Wilson

Hybrid Wheat Australia, P.O. Box 662, Tamworth, NSW 2340 Australia

Introduction

Hybrid wheat breeding began in Australia in the mid-1960s with the introduction of seed of male sterile *Marquis*. Commercial hybrids were released in the 1980s, but it was not until the release of *Hybrid Mercury* and *Hybrid Apollo* in 1994 that hybrids have been perceived by wheat growers as offering a viable alternative to self-pollinated farmer saved variety seed, due to the high cost of hybrid seed and the moderate level its yield advantage (approximately five times the cost of farmer saved variety seed and 10-15% over the best varieties). To change this means either increasing the hybrid yield advantage or reducing relative seed cost by improving seed production procedures, reducing seeding rates or reducing hybrid planting seed size. This paper deals with a proposal to reduce seed costs by producing 'blend' hybrids; that is, a physical mixture of (male) parent and hybrid seed.

Methods

The conventional procedure used to produce hybrid wheat seed -- planting alternating strips of male and female parents, where the male, by wind or mechanical means, pollinates the female -- is inefficient, resulting in a seed set on the female of only 50-80%, and costly, because it requires careful and separate planting and harvesting of the two parents and use of unproductive separator strips. Moreover, seed production is normally performed in areas where conditions favor high productivity, implying additional handling, storage and transport costs to deliver it to farmers. A key factor causing incomplete seed set is the difficulty in effectively moving wheat pollen from the male to the female over distances, in Australia, of up to 12 m (Vries 1971). The distance for pollen travel is significantly reduced when a mixture of the two parents is sown in a single block. In an experiment planted in 1996, the yield of seed from parental blends was compared to the yield of hybrid seed produced in conventional strips. The treatments were sown into 8m x 2m plots in a split plot design, with 3 replications. The ratios of male to female for both the blends and the strips is given in Table 1.

Results

Seed production was more efficient using the blend procedure with no difference between blend ratios (Table 1). The seed set was not estimated by counting grains in individual ears but the yield levels relative to the lower yielding male suggest seed set was on the order of 90% for the blends and 80% in the strips. The fact that all treatments outyielded the male is indicative of the known lower yielding ability of this particular line, whereas the female is a very high yielding variety. It is significant that seed yield of the blend with a male:female ratio as low as 20:80 was as high as the blends with a higher proportion of male, and better than the strip production.

Discussion

The yield performance of the blend and pure F₁ hybrids is still to be evaluated in replicated yield trials. Theoretically one could expect the hybrid yield advantage to be decreased by approximately the proportion of male in the blend, presuming the male has a yield potential similar to normal high yielding varieties. In reality, competitive effects particularly related to the early vigour of hybrids may alter the theoretical yield reduction. The low yield potential of the male used in these blends may also be significant. It could be expected that between 15 and 30% of the hybrid yield advantage would be lost in a 20:80 male:female blend where the seed set on the female was 90% or better. The proportion of male seed could be modified by judicious seed sizing where male parents with small seed size are used. More sophisticated techniques to reduce the proportion of male plants in the blend-hybrid could be envisaged. For example the introduction of herbicide dominant resistance into the female but not the

male would enable hybrid growers to eliminate most male plants from the hybrid crop using normal weed control procedures. The main advantage of blend hybrids is the potential for farmers in favourable seed production areas to produce their own blend-hybrid seed. The additional cost of blend-hybrid seed compared with normal variety seed would be determined by the cost of the blend-hybrid parent seed plus any production-associated royalty charges.

The estimated additional cost of farmer produced blend-hybrid seed over farmer saved variety seed would be between A\$100 and A\$200 per ton, depending on the pricing of the blend-hybrid parent seed and royalties (Table 2). Farmers could produce blend-hybrid seed for A\$300 to A\$400/ton compared to variety seed at A\$200/ton and the purchase price of pure F₁ hybrid seed of A\$900/ton. The blend hybrid would have a theoretical yield advantage of between 7 and 8.5% compared to the 10% yield advantage for the pure F₁ hybrid. As well as being a more cost effective means of increasing grain yield, blend-hybrids would also reduce the financial outlay for the purchase of hybrid seed and utilise the existing infrastructure for farmer saved seed.

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Table 1. Seed yields from a conventional and blend-hybrid production experiment in a well watered site in N.S.W. Australia

Entry	Male:female	Yield (kg/ha)
Conventional seed production		
Female	50:50	4475
Male		3717
Blend seed production		
Blend 1	50:50	5013
Blend 2	35:65	5009
Blend 3	20:80	5006
LSD (P <0.05)		425

Table 2. The additional cost of producing blend-hybrid seed compared to the cost of farmer-saved variety seed.

Seed type	Planting seed cost (A\$/t)	Seed rate (t/ha)	Seed yield (t/ha)	Additional production cost of blend-hybrid (A\$/t)	Royalty (A\$/t)	Total additional cost of blend-hybrid (A\$/t)
Normal variety	\$250	0.04	3.000			
Blend-hybrid	3000	0.04	2.700	\$44	\$100	\$144
	4000	0.04	2.700	\$59	\$100	\$159
	5000	0.04	2.700	\$70	\$100	\$170

B20 - Two-Line Hybrid Breeding in Maize

Zhao Zengyun, Chen Zong-Long

Maize Program, Yunnan Academy of Agric. Sciences, Kunming 650205, Yunnan Province, People's Republic of China

Introduction

Cytoplasmic male sterility (CMS) has been used in hybrid maize seed production for more than 30 years, but the area of CMS hybrid maize has increased quite slowly in China. One major risk with CMS is the susceptibility of specific cytoplasm to *H. maydis* pathogens. Genetic male sterility (GMS) appears to offer a way to avoid this hazard, but the double heterozygous maintainer for lines is still a difficult problem. L.P. Yuang (1990) summarized research on photo-sensitive and thermo-sensitive genic male sterility in rice and proposed that two-line hybrid breeding could be a practical way to apply GMS. In 1992, Z.Y. He found a GMS maize line, Qun-6-ms, which was sterile under high temperatures and fertile at lower temperatures. To exploit this germplasm further, its sterility-fertility converting characters must be studied under a range of environments.

Methods

Experiments were conducted at 5 sites at 500, 1,000, 1,500, 2,000, and 2,500 masl near 25°N latitude in Yunnan plateau, People's Republic of China, 1996. The GMS material used in the experiments was Qun-6-ms from Hainan Academy of Agricultural Sciences. Three planting times were used at each location. A local, normal line was used as check. Plants were arranged in 2-row plots, 5 m rows. Temperature and light interception from planting date to tasselling at each location were recorded. Percent sterile plants with indehiscent glume was estimated and abortive pollen was inspected under the microscope using 1% I-KI dyeing.

Results

1. Qun-6-ms belongs to a TGMS group for which the critical point of sterility-fertility conversion is around 24.8°C daily mean temperature, the percentage of sterile plants under higher temperature conditions ranged from 67 to 100%. This was modified by sunshine hours from planting to tasselling (the longer the sunshine duration the higher in the percentage of sterile plants -- Table 1.)
2. The sterility of Qun-6-ms appeared to be regulated by glume indehiscence. Some anthers contained a few vital pollen grains.
3. Pollen abortion and floret degeneration at high temperatures (Table 2.)

Conclusion

Theoretical and practical problems exist with TGMS breeding systems. The sterility expression of Qun-6-ms was influenced by several climate factors, principally daily temperature during male inflorescence development, modified by sunshine hours and accumulated temperature in situ. Thus seed production of hybrids using this system is limited by locations and seasons. Although Qun-6-ms is popular for its good combining ability and restoration, it must be improved for a lower sterility-fertility converting temperature and a reduced sensitivity to sunshine duration and other climate factors, especially for the subtropical low latitude plateau.

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Table 1. Climate factors and sterility of Qun-6-ms.

Site alt. (masl)	Time	Temperature 1 wk prior to tasselling			Hrs. sunshine, planting to tasselling	Plants with indehiscent glumes (%)	Sterile plant (%)
		Mean	Min.	Max.			
500	1	20.2	17.4	24.7	956.5	100	0
	2	20.2	17.7	24.8	1024.0	100	0
	3	20.1	17.8	24.9	973.3	100	0
1000	1	24.6	21.4	28.9	1097.2	100	66.7
	2	25.7	21.2	33.0	1120.8	100	93.3
	3	24.8	19.8	31.6	1173.8	100*	100.0
1500	1	21.8	16.5	26.3	1197.0	100	0
	2	20.9	18.1	25.4	1197.0	100	0
	3	21.9	19.1	26.2	1174.3	100	0
2000	1	21.6	17.7	25.6	1232.8	100	12.5
	2	21.3	17.1	25.4	1276.9	100	42.9
	3	21.3	17.3	25.3	1232.4	100	27.0
2500	1	21.2	18.1	24.6	1532.4	100	0
	2	20.5	16.4	25.0	1510.3	100	0
	3	19.6	15.9	24.4	1303.2	100	0

Table 2. Abortion of pollen from Qun-6-ms.

Site alt. (masl)	Time	Irregular pollen	Round, sterile pollen	Slight-dyed pollen	Normal pollen
500	1	2.0	3.3	5.4	10.8
	2	3.3	4.7	6.8	11.2
	3	3.8	4.4	4.8	7.5
1000	1	2.4	1.6	23.1	4.6
	2	1.2	1.6	47.0	0.4
	3				
1500	1	0.2	6.1	9.5	7.5
	2	0.2	1.4	9.6	6.5
	3	0	2.3	23.8	11.9
2000	1	7.4	29.4	23.5	4.7
	2	9.6	34.5	21.6	3.9
	3	6.8	27.4	17.1	5.6

Unit: The average pollen number of 25 microscope fields.

B21 - Utilization of Maize Hybrids in Cuba

C.M. Torres, E. Benitez, and E. Rodríguez

Programa de Mejoramiento de Maíz I.I. H. "Liliana Dimitrova", Ministerio de la Agricultura, La Habana, Cuba

Introduction

This study was conducted to show superiority of hybrids over open pollinated varieties in 1992 in Cuba.

Results

In a trial conducted during 1992 involving seven hybrids and eight open pollinated varieties, the hybrids averaged 1.43 t/ha (Table 1). This superiority was due to greater grain weight per ear (120 vs 97 g/ear), ears per area (4.42 vs 4.00 ears/m²) and ears/plant (1.03 vs 0.97). Thus, use of hybrids could result in 14,000 tons of maize grain and 42,000 tons of grain ears for each 10,000 hectares cultivated in Cuba each year.

Table 1. Yield and other agronomic traits of the hybrids of open pollinated varieties evaluated during 1992.

Entry	Yield (t/ha)	Days to silk	Plant Ht. (cm)	Ear Ht. (cm)	Plants/ (m ²)	Ears/ (m ²)	Ears/ (m ²)
<i>Hybrids</i>							
Cuba T5	5.91	52	276	151	4.33	4.44	1.03
Cuba T3	5.90	52	279	164	4.33	4.33	1.00
Cuba T6	5.50	50	279	143	4.33	4.44	1.3
HSV t59	5.15	50	275	143	4.33	4.33	1.00
HDT66	5.05	59	277	140	4.22	4.33	1.03
Cuba T9	4.94	48	286	149	4.33	4.56	1.05
HSV T73	4.80	51	284	158	4.44	4.33	0.99
Average	5.32	52	279	150	4.33	4.42	1.03
<i>Open pollinated varieties</i>							
Pichilingue 7928	4.51	56	271	140	4.22	4.22	1.00
Guarare 8328	4.51	56	263	116	4.11	4.00	0.97
VS T6	4.48	56	284	135	4.22	4.11	0.97
Francisco	4.03	52	290	186	4.00	3.89	1.00
Gibara	3.76	54	283	165	4.00	3.89	0.97
Tuson	3.61	58	278	139	4.11	3.78	0.90
QPM S093	3.59	52	263	130	4.11	4.11	1.00
Across 8126	2.62	45	243	118	4.33	4.00	0.92
Average	3.89	54	272	141	4.11	4.00	0.97
<i>Hybrids vs OPVs</i>	1.43	-2	7	9	0.22	0.42	0.06

B22 - Advances in the Development of QPM Maize Hybrids in Ghana

S. Twumasi-Afryie and P.Y.K. Sallah

Crops Research Institute, P.O. Box 3785, Kumasi, Ghana

Introduction

Maize is an important source of protein and energy in infant nutrition in Ghana. However, normal maize protein has low levels of the essential amino acids, lysine and tryptophan. Research at CIMMYT (Mexico) and elsewhere has produced maize germplasm which possess elevated levels of lysine and tryptophan (Vasal et al., 1993). The focus of breeding work in Ghana, using quality protein maize germplasm, is the development of streak-virus-resistant, open pollinated and hybrid varieties which perform equal to or better than normal maize under production (Twumasi-Afryie et al. 1994, 1997). This programme led to the release of an open-pollinated variety "Obatanpa" which has been widely adopted in Ghana (Twumasi-Afryie et al. 1994, 1997) The release of Obatanpa generated wide interest in QPM which led to requests for the variety from several countries in Africa and elsewhere. Current efforts are aimed at releasing QPM hybrids.

Methods

In 1990, several early generation QPM inbred lines were collected from the CIMMYT Maize Program for further inbreeding and selection in Ghana. Also, inbred lines were developed locally using CIMMYT Populations 62 and 63. Based on topcross data, nine QPM inbred lines were evaluated in diallel crosses at four locations in Ghana. Several 3-way cross hybrids were generated from inbred lines with high GCA effects. The 3-way hybrids were evaluated in the major agro-ecological zones in Ghana. QPM hybrids that showed good performance were simultaneously tested in Ghana and in an international trial offered by the Crops Research Institute (CRI) Maize Programme in 1995 and 1996. The 10-entry trial consisted of six QPM 3-way hybrids, Obatanpa (QPM OPV), and Abeleehi (normal maize OPV), plus two checks nominated by cooperating scientists. In all, 40 sets of the trial were sent to 20 countries in Africa, Central America, South America and Asia. Data from 14 countries have been obtained and analyzed.

Results

Five inbred lines showed high and positive GCA effects for grain yield (Table 1). These lines were from CIMMYT Populations 62 and 63. The results from the international QPM trials showed that the QPM hybrids were more productive than the normal maize and the QPM composites developed in Ghana. The hybrids also maintained their superior performance in almost all the countries where they were tested. The most outstanding QPM hybrids were GH132-28, GH110-5 and GH2328-88. The three hybrids have been proposed for release in Ghana.

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Table 1. Estimates of general combining ability effects for grain yield, plant height, and days to 50% silking of nine QPM inbred lines crossed in diallel and tested at four locations in Ghana.

Parent		Origin	Grain yield (kg/ha)	Plant height (cm)	50% silking (days)
ENT70	CIMMYT	Pop.62	111.32	-0.24	1.02
ENT 5	CIMMYT	Pop.62	170.32	-5.81	-0.84
P23	CIMMYT	Pop.62	50.32	-9.24	-0.84
ENT24	CIMMYT	Pop.62	328.46	4.62	0.30
ENT28	CIMMYT	Pop.63	498.32	5.05	0.73
ENT27	CIMMYT	Pop.63	208.46	12.33	1.16
ENT6	CIMMYT	Pop.62	-656.40	-17.38	-1.98
ENT88	CIMMYT	Pop.63	-252.68	2.48	-0.41
ENT 89	CIMMYT	Pop.62	-258.11	8.19	0.87
S.E.(gi-gi)			171.7	4.0	0.40

B23 - Genetic Contributions to National Maize Yield Increases in Hungary, 1871-1995

L.C. Marton, T. Szundy, B. Györfly and Z. Berzsenyi

Agricultural Research Institute of the Hungarian Academy of Sciences, Martonvásár, Brunszvik út 2., Hungary 2462

Introduction

Maize has played an important role in Hungarian crop production since the end of the last century. For several decades its growing area has exceeded 1 million hectares. The joint examination of maize yield averages and changes in variety over the last 100 years provides a good illustration of the role of breeding in improving yield averages. The contribution of genetic gain to yield improvements in Hungary was estimated to be 26% (Györfly 1976) or 30% (Berzsenyi - Györfly 1995), and in the USA 63-79% (Russell 1974), 57-60% (Duvick 1977) or 71-89% (Duvick 1983). This study describes changes in the Hungarian national yield average in light of variety changes.

Methods

The contribution of genetic gain was expressed as kg/ha/year or as a percentage of the national yield average increment. Annual changes in the national yield average increment were determined using regression analysis (Sváb 1981). The period examined (1871-1995) was divided into three phases: I) 1871-1950, traditional cultivation, with no significant change in technology; II) 1951-1985, all major production factors underwent substantial changes, fertiliser rates increased from 15 kg/ha to 350 kg/ha total active agents, the use of herbicides and machinery became general, and the planting density increased from 30,000 to 70,000 per hectare; III) 1986-1995, fertiliser application dropped to a quarter of the previous quantity.

Results

The national average rose from 1 t/ha to 1.5 t/ha at the beginning of the century, when Italian varieties were replaced by American ones (Fig. 1). Hungarian varieties developed in the 1930s raised the average 2 t/ha, still without any change in the technology. The increase in average yield over 80 years (1871-1950) was thus 1 t/ha; 12.5 kg/ha/year. In phase II the yield average rose from 2 t/ha to 6 t/ha over 35 years, representing an increase of 114 kg/ha/year. This increase gradually accelerated from 20 kg/ha/year in the fifties to 245 kg/ha/year by 1985. In phase III the use of fertiliser drastically declined: the present rate is less than 100 kg/ha, leading to a 30% reduction in yields over the last 10 years.

Conclusions

Between 1871 and 1950 improvements in the genetic capacity of the varieties led to a national yield increase of 12.5 kg/ha/year without any change in the technology. The introduction of hybrids and up-to-date technology led to an acceleration in this increase, which was over 100 kg/ha/year over the next 30 years, and even exceeded 200 kg/ha/year for a short time. In earlier examinations (Berzsenyi - Györfly 1995) the effect of major production factors in increasing yield averages was evaluated over this same period, and the role of variety was estimated to be 30%. The role of variety in the increase in the national yield average from 1950 onwards was over 30 kg/ha/year, and more than 75 kg/ha/year in the early eighties. This value is similar to the genetic gain measured in North America for the increase in yield averages. Despite the use of the most up-to-date hybrids, however, over the last ten years the reduction in fertiliser rates has meant that the yield increase has not only slowed, but has become negative (in 1986-1995 the increase was -283 kg/ha/year).

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Yield (t/ha)

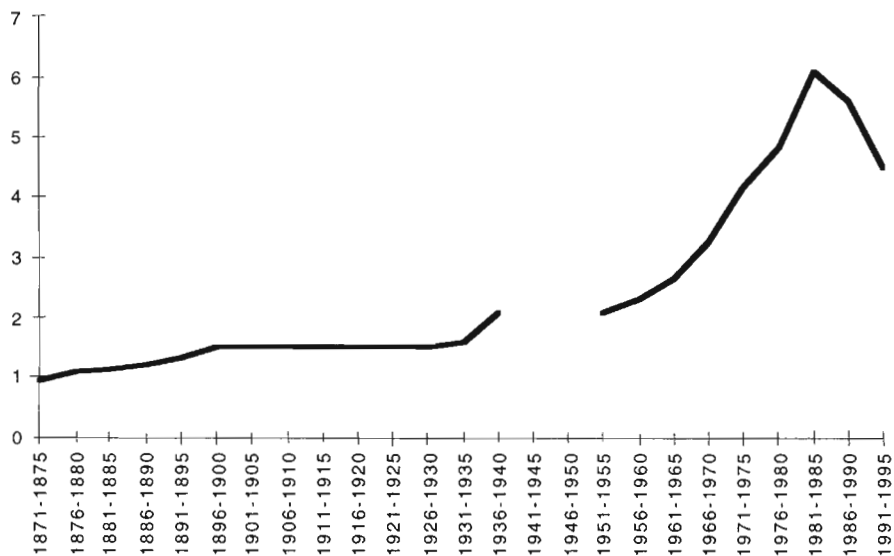


Figure 1. Maize yields (5-year averages) in Hungary, 1871-1995.

B24 - Performance and Potential of Hybrid Rice in Tropical Asia: Lessons from Indian Experience

P.L. Pingali and A. Janaiah

Rigorous efforts of the last 6-7 years resulted in the development and release of few rice hybrids in India, Philippines and Vietnam during the 1994 crop season. These hybrids are higher yielding but lower priced compared to conventional inbred varieties. Yield gains of hybrid rice over the inbred varieties are 16-18% in Philippines, 20-25% in Vietnam and 12-15% in India. Hybrid rice production has a nearly 12-15% higher production cost per hectare. Moreover, output prices for hybrid rice grain are lower than the inbred varieties primarily due to low grain quality. Therefore, the yield gains of hybrid rice could not significantly surpass additional production costs and lower output price. However, the Indian experience shows that the hybrid rice outyields conventional high yielding varieties (HYVs) by 30-40% (1.8-2.1 t/ha) at locations where crop management is above 60%. But hybrid rice is also more susceptible to pests and diseases.

Hybrid rice seed (F_1) production is labour intensive; it requires about 240 man-days of additional labour per hectare. Hybrid seed production is 1.8 times profitable than conventional HYV cultivation. Hybrid seed production in the cooperative sector is twice as profitable as growing seed for private companies.

Hybrid rice would find more demand in countries where much rice area is under irrigation, land-to-person ratios are high, and the literacy rate is high. Countries with these features are Vietnam, Philippines and Indonesia, where hybrid rice would be more profitable and acceptable. In India, rice farmers' low levels of crop management, low grain quality, and the high proportion of illiteracy among the workforce would hamper the widespread adoption of hybrid rice in the short run. However, these constraints can be remedied through strong research and development efforts in the long run.

B25 - Indian Initiative for the Development of Hybrid Wheat

V. Mahajan and S. Nagarajan

Directorate of Wheat Research, P O Box 158, Karnal - 132 001, Haryana, India

Wheat production in frontline districts (viz. Ludhiana, Karnal, Bulandahahr etc) of the northwestern plain (the wheat bowl of India) has stabilized to yield gains of only one per cent per year. Innovative approaches like exploitation of heterosis hold promise to attain another jump in wheat productivity.

Even though efforts on hybrid wheat were initiated in the early 1950s, the commercial success of hybrids produced using the chemical hybridizing agent (CHA) approach was evident by the late 1980s. The advantage of CHA is that there is no need for special development of sterile and restorer parents, enough seed can be produced and an extensive testing can be done, losses from poor cross pollination are avoided, and the time needed to transfer male sterility to agronomically useful varieties through backcrossing using conventional CMS system is saved.

The Directorate will study problems of hybrid wheat on five fronts: 1) identifying parental lines exhibiting superior heterosis over the best check; 2) identifying chemical(s) that cause male sterility without affecting female fertility, and related issues; 3) manipulating floral structure to favor outcrossing; 4) identifying and controlling floral diseases that affect hybrid seed production; and 5) developing reliable CMS and restorer systems. Other major challenges facing the hybrid wheat network are high seed rate, chasmogamy florets, allopolyploidy, susceptibility to floral diseases, high seed production costs, and lack of free flow of information between public and private organizations.

Parental lines should exhibit good specific combining ability primarily for characters such as higher tillering, high grain weight, more spikelets, responsiveness to inputs, resistance to lodging and major diseases like rusts and blight. The wheat hybrid should exhibit at least 20% higher yield than the best check at an economically lower seed rate.

In addition to appropriate selection of parental lines, effective seed production depends on synchronization of parental lines and identification of appropriate dose and time of application of an environmentally safe CHA that selectively causes male sterility without affecting female fertility or the economic feasibility of seed production technology.

The Directorate of Wheat Research has initiated its program on hybrid wheat in 1995 primarily using the CHA approach for irrigated, normal sown, northwestern plain conditions. Several CHAs were tested out of which CH 9701 exhibited near complete male sterility and 50% female sterility when sprayed at a spike length of 8 mm and dose of 700 ppm. This CHA produced similar effects on a wide range of genetically diverse genotypes of comparable maturity groups in environments such as Karnal and Ludhiana. Outcross (F_1) seed was shrivelled, however, and had 90% germination at harvest. By further focusing research efforts on CH 9701 wheat hybrids can be developed.

Results from 1995-96 indicate receptiveness of the plant to CHA at a growth stage of 8 mm or less and better performance under late sowing, as the minimum temperature was 5°C higher than in the early sowing period.

B26 - Exploitation of Heterosis to Enhance Sorghum Productivity in India

B.S. Rana and S. Kaul

All India Coordinated Sorghum Improvement Project, National Research Centre for Sorghum, Rajendra Nagar, Hyderabad 500 030, India

Introduction

The production of approximately 24,000 t per annum of certified seed of public sorghum hybrids and their rapid adoption over 60% of the 12 million ha of sorghum area, in addition to use of private sector hybrids, is testimony to the role hybrids have played in doubling rainy season (kharif) sorghum productivity in India and maintaining production (6.3 million t/yr) from a much reduced (54%) area, sparing land for high demand crops such as oilseed, pulses and cotton.

Material and Methods

Three sets of data were examined to document hybrids' superiority. The popularly grown kharif hybrids CSH1, CSH 5, CSH 6, and CSH 9 and recently evolved hybrids CSH 13 (K&R), CSH 14, and CSH 16 and their parental lines were evaluated extensively in coordinated trials. Hybrid performance over three years (1994-1996) has been summarized here. We also examined the relative productivity of varieties and hybrids (10 each) over 29 locations. Data on hybrids and their B and R lines from 5-6 locations each between 1992-1996 were examined to estimate heterosis, based on large plot size (21.6 sq.m). The correlations among F_1 hybrids and their corresponding B and R parents were computed.

Results

The average productivity of hybrids released in 90 rainfed locations over three years ranged 3.08 to 3.89 t/ha (Table 1). The genetic gain over CSH 1 was 7-16% in early hybrids and 9-26% in medium maturing hybrids. The experimental hybrid SPH 660 exhibited 29% improvement over CSH 1. Heterosis over mid-parent of F_1 , B and R lines over nine locations was 53.4% in CSH 5, 52.6% in CSH 9, 35% in CSH 13 and 39% in CSH 14. The comparative performance of 10 varieties and 10 hybrids over 29 locations (1994-95) is given in Table 2. Hybrids on an average were 18.6% superior to varieties for grain yield, while varieties produced an average 18.6% more fodder. However, the best hybrid CSH 16 maintained a similar heterozygote advantage over the best variety (SPV 1025) for grain yield. The best three varieties and a hybrid in these experiments had $b = 0.96$ in stability analysis, while b values of next best hybrids were 1.06 and 1.22, indicating their response to better environments. The overall yield of hybrids in the 104 experiments selected was 4.1 t/ha, vs 3.02 and 3.09 t/ha for B and R lines; an average heterosis of 48% over B lines and 43% over R lines (Table 3). The mean grain yield of B and R lines were positively correlated with F_1 yield. The correlation between heterosis over B and over R was also significant ($r=0.38^{**}$).

Conclusions

The accelerated growth in the productivity of hybrids CSH 1 to CSH 16 over 30 years is due to an optimum plant type, accumulating desirable genes for productivity, incorporating resistance in parental lines, and exploiting better heterotic combinations. Parental line improvement has allowed a 29% gain in the productivity of latest hybrids over CSH 1, besides resistance to leaf diseases and grain molds. Some 13,000 t of CSH 9 are sold every year; this and other hybrids have replaced local varieties on a large scale. Further diversification in maturity and height led to the development of the dual purpose hybrid, CSH 13 (K&R), adapted to both rainy and post-rainy seasons, and the early maturing CSH 14, which yields nearly as much in 102 days as CSH 9 in 110 days. CSH 14 6.75% more productive per day (35 kg/ha/day) than CSH 9, but CSH 13 (K&R) produces 4.4% more grain, 45% more fodder, and has shown wide adaptability in national and international trials. Parental line improvement will enable further gains in per day productivity, since F_1 yields are predictable as $Y = 1969 + 0.71^{**} X_1$ and $Y_2 = 1808 + 0.748^{**} X_2$, where X_1 and X_2 are yields of B and R lines. If F_1 hybrids of 5.0 t/ha productivity in

rainfed conditions are to be developed, B and R lines of 4 t/ha grain yield need to be bred. Use of heterotic loci may permit the same high yield levels in F_1 , even with parental lines of slightly lower potential. Though recent varieties are 10% superior to popular hybrids CSH 5 and CSH 6 released two decades back, the latest hybrid is 18.6% superior to those varieties. Thus the 3.5 t/ha yield level achieved in the mid-1970s through hybrids could be achieved through varieties in the mid-1990s, and the investment in hybrid breeding has been always more profitable.

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Table 1. Average sorghum grain yield under rainfed conditions, India, 1994-1996 (Loc. 90).

Hybrid (Early)	Grain yield (t/ha)	Per cent CSH 1	Hybrid (Midlate)	Grain yield (t/ha)	Per cent CSH 1
CSH 1	3.08	100	CSH 5	3.35	109
CSH 6	3.31	107	CSH 9	3.61	117
CSH 14	3.58	116	CSH 13	3.77	122
SPH 660	3.96	129	CSH 16	3.89	126

Table 2. Sorghum varieties and hybrids under rainfed situations, India (Loc. 29).

Genotype	Grain yield (t/ha)	Fodder yield (t/ha)	Days to maturity	Plant height (cm)	Grain mold (1R - 5S)
Varieties(10)	3.00	10.0	113	207	2.3
Hybrids(10)	3.56	8.2	108	174	2.5
Hyb/var(%)	118.6	81.4	90.7	84.0	109

Table 3. Correlations and heterosis between yields of sorghum hybrids and B and R lines, India. (N = 104, ** Significant at $p < 0.01$)

Genotype	Correlation B-line	Correlation R-line	Mean (t/ha)	Heterosis % over
Hybrids	0.607**	0.670**	4.12	-
B-lines		0.658**	3.02	48.0
R-lines		-	3.09	43.4

B27 - Evaluation of Single- and Three-Way-Cross Hybrids and the Economics of Seed Production in Sunflower

K. Virupakshappa and B.H. Halaswamy

Project Coordinating Unit (Sunflower) U.A.S., GKVK, Bangalore 560065, India

Introduction

The hybrids under commercial cultivation in India have been single-cross hybrids, where uniformity is a distinct advantage. However, the yield of a single-cross hybrid is low in seed production plots (5 Q/ha), resulting in higher seed costs. Production of three-way cross hybrids is one way to increase seed production yield. Three-way crosses exceeded single-cross hybrids by 120 kg/ha in seed yield in a study by Vilichku (1987) and are not significantly different in commercial seed and oil yields (Galeev and Vilichku 1986; Dedio 1992). Three-way hybrids are stable across a wide range of environments (Fick and Zimmer 1976; Vilichku 1987).

Methods

Fourteen three-way cross (TWC) hybrids and ten single-cross (SC) hybrids were produced using five A, B, and two restorer lines. The hybrids were evaluated along with commercial grown single cross checks in a RCBD with three replications during summer 1996. In a separate experiment, seed production of one TWC and two respective SC hybrids was carried out in large replicated plots to compare the quantity of hybrid seed realized in each case during rainy season 1995-96.

Results

Performance of some of the superior TWC hybrids are presented (Table 1). Two TWC hybrids were significantly better than the check hybrid KBSH-1. All three TWC hybrids were significantly superior to their respective single crosses for seed yield, head diameter, 100-seed weight and percent seed set (Table 1). The increase in yield of the TWC hybrid over the check hybrid was 15%. The TWC hybrid seed production yield was 1421 kg/ha, compared to single-cross seed yields of 602 and 516 kg/ha (Table 2). The increased yield for the TWCs was due to increased head diameter, stem girth, number of filled seeds, and 100-seed weight.

Conclusions

TWC hybrids have higher seed production and reduced seed costs over SC hybrids, in addition to their better performance in commercial grain and oil yields. The third parent involved in the synthesis of TWC hybrids helps buffer against environmental fluctuations (Bounnit et al. 1985).

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Table 1. Mean performance of yield and other component characters in sunflower.

Sel no.	Hybrid	Seed yield (kg/ha)	% increase over KBSH-1	Head diameter (cm)	100 seed wt. (g)	Seed set (%)	Oil content (%)
1.	(234A×851B)×6D-1	1858	14.8	13.3	4.83	89.5	47.7
2.	(234A×207B)×6D-1	1846	14.1	12.6	5.12	92.2	46.4
3.	(851A×207B)×6D-1	1523	-5.8	13.2	5.49	93.0	47.7
4.	234A × 6D-1	1099	-	11.3	4.40	88.6	46.4
5.	851A × 6D-1	1175	-	12.7	4.63	91.5	51.3
6.	207A × 6D-1	717	-	11.1	4.58	88.1	47.3
7.	KBSH-1(C)	1618	-	13.1	4.81	88.7	47.9
	SE ± Kg/ha	163.86	-	0.68	0.33	3.14	0.92
	CD at 5%	454.20	-	1.90	0.90	8.69	2.54
	CV %	23.84	-	9.46	11.66	6.24	3.47

Table 2: Comparison of TWC hybrids with their respective SC hybrids for yield and other characters in seed production plots.

Hybrid	Seed yield (kg/ha)	Head diameter (cm)	Stem girth (cm)	No.of filled seeds	Seed set %	100 seed wt.(g)
(234A×207B)×6D-1	1421	14.1	2.93	878	91.8	3.59
234A × 6D-1	602	11.8	1.91	566	85.5	2.64
207A × 6D-1	516	11.7	2.10	338	78.5	2.84

B28 - Strategies for Utilizing Heterosis in Wheat, Rice and Oilseed Brassica in India

B.E. Zehr, V.P. Ratnalikar, L.M.M. Reddy and L.V. Pandey

Maharashtra Hybrid Seeds Co. Ltd. (MAHYCO), Research and Development Centre, Dawalvadi - Jalna, Maharashtra 431 203, India.

Introduction

Private seed companies play an increasingly important role in agricultural development through crop improvement. Maharashtra Hybrid Seeds Company (MAHYCO), one of India's oldest and largest, was established in 1963 and currently markets over 300 hybrids. MAHYCO has been investing in research and development of hybrid crops for over 30 years, and current hybrid development efforts involve research on 35 crop species. Work on hybrid wheat, rice and oilseed Brassica is relatively recent. Hybrid vigor and production results are encouraging enough to warrant marketing of F_1 hybrids.

Results and Status of Hybrid Wheat

Research on hybrid wheat has been based on cytoplasmic male sterility (CMS) and restoration factors derived from *Triticum timopheevi* (Lucken 1973), incorporated into Indian wheat germplasm (*T. aestivum*). Advanced and experimental data from on-farm strip trials gave average yield gains as high as 41% over common wheat varieties (identical seeding rates), with a maximum yield of 6,690 kg/ha (Table 1). F_1 hybrids are produced using wind pollination, with female:male row planting ratios of 3:1. Female seed set averages 75 to 80% with seed yields of 1,200 to 1,500 kg/ha. Male sterility and fertility restoration appear stable. MAHYCO will soon test market its wheat hybrids.

Results and Status of Hybrid Rice

We are studying the development of rice hybrids based on the WA ("wild abortive") CMS source, obtained through IRRRI and originating from *Oryza sativa f. spontanea* in China (Lin and Yuan 1980). Advanced and experimental hybrid data indicate an average yield gain as high as 36% over two common varieties (identical seeding rates), with a maximum yield of 9,390 kg/ha (Table 1). Pollination during hybrid production is enhanced by clipping flag leaves 1 to 2 days before heading, spraying of GA-3 @ 60 ppm at 20% and 50% flowering of panicles, and supplementary rope pulling or shaking to promote pollen dispersion. Female:male row planting ratios for hybrid production are either 4:2, 6:2, or 8:2, depending on genotypes. Female seed set averages 50 to 60% with seed yields of 1,500 to 2,000 kg/ha. Male sterility appears stable, with fertility restoration of 90 to 95%. Seven MAHYCO rice hybrids are scheduled for marketing in 1997.

Results and Status of Hybrid Oilseed Brassica

Brassica juncea represents 80% of all oilseed *Brassica* acreage in India. Two systems of male sterility are being used in *B. juncea* research: CMS and functional male sterility (FMS). CMS sources are from related and wild species; *B. oxyrrhina* (Prakash and Chopra 1990), *B. tournefortii* (Rawat and Anand 1979), *Diploaxis siifolia* (Rao et al. 1994). FMS was derived from a spontaneous mutation in *B. juncea*; sterility is achieved through early and elongated extension of stigma, which are receptive to pollination for a longer period when corresponding anthers are extruded from spikelets. Advanced and experimental hybrid data based on designed trials indicated a 65% increase in average oil yield over three common varieties (hybrid seeding rates half that of varieties), with a maximum oil yield of 1,648 kg/ha, 42% of kernel weight (Table 1). The FMS based hybrids appear to be more productive than those based on CMS, which can be attributed to complete fertility restoration in the FMS system. F_1 hybrid production is carried out through wind and insect pollination, with female:male row planting ratios of 4:1 for *oxyrrhina* CMS and 2:1 for the other sterility sources. Female seed set averages 75 to 90% for *oxyrrhina* CMS (seed yields of 800 to 1,200 kg/ha) and 30 to 50% for the other sterility sources (seed yields of 300 to 500 kg/ha). Both CMS- and FMS-based sterility are observed to be stable; however fertility restoration of maximum 90% has been observed in CMS, while 100% fertility restoration is common for

the FMS system. The FMS system behaves as genetic male sterility (GMS) in hybrid production, and thus female rows require rouging of fertile plants (one-half of those present). Three MAHYCO *Brassica juncea* hybrids are under marketing in 1997, with additional hybrids to be marketed in the near future.

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Table 1. Performance data from selected advanced and experimental hybrid trials.

Hybrid/ varietal check	Sterility system	Grain or oil yield (kg/ha; % oil content)	% increase over highest variety check	Number of locations	Seeding rate (kg/ha)
Advanced and Experimental Wheat Hybrids					
MWH-5	CMS	4697	40%	20	50
MWH-3	CMS	4657	39%	20	50
MWH-6	CMS	4619	38%	20	50
HD-2329	Variety	3355	–	20	50
EWH-499	CMS	6690	41%	2	50
EWH-331	CMS	6217	31%	2	50
EWH-500	CMS	6168	30%	2	50
HD-2329	Variety	4729	–	2	50
UP-2338	Variety	4445	–	2	50
Advanced and Experimental Rice Hybrids					
MPH-518	CMS	8350	36%	10	20
MPH-519	CMS	8098	32%	2	20
MPH-516	CMS	7707	26%	4	20
JAYA	Variety	6136	–	38	20
RASI	Variety	4931	–	27	20
EPH-3	CMS	9390	32%	2	20
EPH-4	CMS	8789	24%	2	20
EPH-1	CMS	8268	17%	2	20
JAYA	Variety	6343	–	2	20
RASI	Variety	7085	–	2	20
Advanced and Experimental <i>Brassica juncea</i> Hybrids					
MRH-5	CMS	1064 [42]	21%	45	2.5
MRH-7	CMS	1022 [41]	16%	45	2.5
MRH-1	CMS	973 [41]	11%	45	2.5
PUSA BOLD	Variety	878 [41]	–	45	5.0
KRANTI	Variety	866 [40]	–	45	5.0
ERH-5	FMS	1648 [42]	65%	4	2.5
ERH-6	FMS	1608 [42]	61%	4	2.5
ERH-7	FMS	1479 [41]	48%	4	2.5
PUSA BOLD	Variety	997 [41]	–	4	5.0
KRANTI	Variety	972 [41]	–	4	5.0

B29 - Yield and Seed Quality of Maize Hybrids Derived from INIFAP and CIMMYT Germplasm Combinations

A. Espinosa-Calderón¹, J. Ortiz C.², N.O. Gómez M.¹, and A. Ramírez F¹.

¹ Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP), Mexico

² Colegio de Postgraduados, Mexico

Introduction

The selection of basic germplasm in a breeding program is one of the fundamental decisions, and an important and decisive factor, for the success of breeding programs (Hallauer 1993; Córdova and Mickelson 1995). Researchers from Mexico's Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP), using as source germplasm some populations and lines at an early stage of inbreeding from CIMMYT, have developed outstanding inbred lines, some of which form part of commercial hybrids already released by INIFAP. The objectives of this study were to: 1) determine the productive capacity of three-way cross and single-cross hybrids obtained from the combination of INIFAP and CIMMYT germplasm, relative to corresponding commercial checks; and 2) evaluate the yield and seed quality of the different maize hybrids according to their conformation as three-way or single crosses.

Materials and Methods

Fifteen single-cross (INIFAP X CIMMYT) hybrids and 27 three-way cross (INIFAP X CIMMYT) hybrids were evaluated against four single-cross hybrids (CML247 x CML254, HI-1, H-513, and H-430) and three three-way cross hybrids (H-515, P-3288, and C-385). The single-cross and three-way cross hybrids were obtained from the inbred lines and single crosses presented in Table 1. The 49 materials were evaluated in a 7X7 Triple Lattice Design, using a five-meter row as the effective plot, at the INIFAP experiment station field in Iguala, State of Guerrero, Mexico, during the 1995 spring-summer season, and under rainfed conditions. The experimental variables were grain yield, days to male flowering, plant and ear height, percent of large and medium sized seed, and weight of 50 seeds.

Results

There was no advantage in using the triple lattice design to do the analysis, and a randomized complete blocks design was used instead. The coefficient of variation (CV) for yield was 20.5% and the overall mean yield was 5,930 kg/ha. The comparison across means (Tukey) defined three ranges of significance. The highest yields were for the three-way cross hybrids H-430 X CML268 with 8,198 kg/ha and H-513 X CML56 with 7,894 kg/ha; whereas the lowest yield corresponded to the INIFAP single-cross H-430 with 3,777 kg/ha (Table 2). Within the 16 highest yields there were 12 three-way cross hybrids and only four single crosses. In five of these 12 three-way crosses the hybrid H-430 was the female parent, and in the other seven the hybrid H-513 was the female parent. Of the three INIFAP lines, two (D-471 and TTC-C2) formed part of two high yielding hybrids each, whereas the line Across 7522-S6 was a parent in the low-yielding hybrids (Table 2). The best yielding check hybrid was the three-way cross H-515 with 6,290 kg/ha, which is 30.3% lower than the highest yielding hybrid (H-430 X CML268). However, this latter hybrid was seven days later than H-515, which would be a disadvantage. In the lower yield range we found the hybrids with H-513 as the female parent and the lines CML273 and CML277. The CIMMYT single-cross CML247 X CML254 yielded 5,160 kg/ha. and 87% large seed (H-513 yielded 90% large seed). The INIFAP single-cross (H-430) had the lowest yields and only 58% large seed.

Conclusions

In addition to high yield potential as a commercial hybrid, H-513 X CML56 seed could be produced using a single cross which shows high yield potential, good seed quality, and a cycle of male and female flowering similar to that of the commercially recommended H-514. Using H-513 as the female

parent, several three-way crosses could be formed that present better yield and other traits than H-515 or P-3288. The best combinations from this study should be evaluated at other locations.

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Table 1. Maize genetic material (inbred lines and single crosses) from INIFAP and CIMMYT used for combination and evaluation of resulting hybrids.

CIMMYT Lines	Origin	CIMMYT Lines	Origin	INIFAP Lines	Origin	Single crosses	Origin
CML17	Pop. 22	CML266	Pop. 22	D-471	B-670	247X254	CIMMYT
CML55	Pool 24	CML267	Pop. 22	TTC-C2	Pop. 29	H-430	INIFAP
CML56	Pool 24	CML268	Pop. 23	Across7522	Pop. 22	H-513	INIFAP
CML247	Pool 24	CML269	Pop. 25	<i>Checks</i>			
CML248	Pool 24	CML270	Pop. 29	P-3288	Pioneer		
CML250	Pop. 21	CML271	Pop. 29	H-515	INIFAP		
CML254	Pop. 21	CML273	Pop. 43	C-385	Cargill		
CML255	Pop. 21	CML277	Pop. 43	HI-1	INIFAP		

Table 2. Comparison of mean yield and other variables (Tukey at 0.05 probability) for INIFAP x CIMMYT hybrids.

Ent	Hybrid	Yield (kg/ha)	Male Flowr. (days)	Plant height (cm)	Ear height (cm)	% of large seeds	% medium seeds	50 seed weight (g)
18	H-430 X CML268	8198 a	66	255	112	83	15	14.4
40	H-513 X CML56	7894 a	58	243	110	81	16	14.3
14	CML255 X D-471	7664 a	60	255	105	94	5	16.2
29	H-430 X CML255	7613 abc	61	240	112	85	14	12.9
33	H-513 X CML269	7375 abc	59	245	98	72	26	14.7
41	H-513 X CML270	7334 abc	58	243	97	91	8	16.2
42	H-513 X CML271	7321 abc	60	247	83	80	17	16.7
26	H-430 X CML270	7058 abc	58	248	100	93	6	17.4
27	H-430 X CML271	6944 abc	60	248	110	42	48	12.9
39	H-513 X CML55	6831 abc	63	225	95	87	11	14.5
23	H-430 X CML17	6828 abc	63	243	100	71	25	14.2
15	CML255 X TTC-C2	6792 abc	62	238	102	91	7	14.2
12	CML254 X D-471	6589 abc	63	248	108	98	2	15.1
3	CML273 X TTC-C2	6550 abc	63	230	85	93	5	16.9
37	H-513 X CML267	6517 abc	62	243	105	82	16	13.0
36	H-513 X CML277	6310 abc	60	240	100	92	6	13.8
45	H-515	6290 abc	59	237	97	94	5	14.8
20	CML247 X CML254	5160 abc	66	227	92	87	11	14.7
46	H-513	5118 abc	65	238	83	90	8	14.0
47	P-3288	4771 abc	61	247	108	70	24	11.9
48	H-430	3777 c	65	235	100	58	37	12.1
	H.S.D. (0.05)	4099	9	39	34	29	24	3.9

B30 - Economics of Hybrid Maize Adoption

P.W. Heisey,¹ M.L. Morris,¹ D. Byerlee,² M.A. López-Pereira³

¹Economics Program, International Maize and Wheat Improvement Center (CIMMYT)

²The World Bank

³President, Ecohon, Honduras, and Affiliate Economist, Economics Program, CIMMYT

Introduction

The area planted to hybrids is greater for maize than for any other crop. In 1992, 99% of the maize area in industrialized countries and 44% of the maize area in developing countries was planted to hybrids (CIMMYT 1994). During the 1960s and later, maize breeders in many developing countries emphasized open-pollinated varieties (OPVs), believing them to be more suitable for small farmers. More recently, interest in hybrid maize in developing countries has revived. Understanding the technical and economic factors influencing the profitability of hybrids at the farm level, as well as the technical, economic, and institutional factors affecting the profitability of hybrids to the seed industry, provides insight into the prospects for further diffusion of hybrid maize in developing countries. More fundamentally, these basic factors can help to explain prospects for diffusion of hybrids of any crop.

Methods

Hybrid seed adoption patterns are explained by demand and supply factors. Three non-price factors affect farm level profitability of hybrid seed: (1) the yield advantage of hybrids, (2) the seed rate, and (3) the cost of capital, learning costs, and the perceived riskiness of the technology. Figure 1 shows the yield advantages hybrids must have over farmers' current cultivars to repay the additional cost of hybrid seed and generate a 100% marginal rate of return, at different yield levels for current cultivars and different seed:grain price ratios. Seed rates are held constant. Factors influencing the market entry decision by seed companies include (see Griliches 1957): (1) seed production costs, which are related both to technical factors such as the seed yields of inbred lines and economic factors such as the prices of land, labor, and capital; (2) market structural conditions such as the total size of the market and average maize area per farm, (3) organization of the seed industry, (4) the cost of research innovation, and (5) the economic and political importance of maize. These demand and supply factors interact to determine seed price. Seed price is clearly an important factor in the initial adoption and diffusion of hybrid maize, and less important in mature seed industries. A two limit tobit model was estimated to explain observed proportions of total maize area planted to hybrids in 32 developing countries in 1992. Explanatory variables represented prices, market structural conditions, the cost of innovation, the importance of maize, and regional dummy variables.

Results

Across developing countries, greater use of hybrids is associated with larger farm size (LANDPCAP), higher per capita income (LNGNP), better road infrastructure (LNINFRA), and greater breeding investment (LNBRDENS). Reduced use of hybrids is associated with higher seed prices (RATIO), higher proportion of maize area in lowland tropical environments (LLTROP), and greater proportion of maize used for direct human consumption (HUMCONS) (Table 1). The breeding investment variable was significant only in equations with regional dummies (Table 1), suggesting that greater investment in maize breeding may lead to greater hybrid use, but this effect is obscured by significant regional differences in the level of this investment.

Conclusions

A growing number of "success stories" indicate that hybrid maize can be widely adopted in developing countries, even by small-scale producers, but the performance of the germplasm and seed prices are crucial. The use of hybrid maize is likely to be greater in the presence of conditions that provide profit opportunities for suppliers of the technology. Institutional innovation in seed industry organization and

greater efficiency in research should be the focal points for policies designed to increase the use of hybrid technology.

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Table 1. Effects of variables affecting technology demand and supply on area planted to hybrid maize, 32 developing countries, 1992. Two-limit tobit model with dependent variable proportion of total maize area planted to hybrids. +++, ++, ***, **, ns: p<0.01, two-tailed, p<0.05, two-tailed, p<0.01, one-tailed, p<0.05, one-tailed, not significant. All tests asymptotic t-tests.

Variable	Model 1	Model 2
CONSTANT	74.6+++	-77.7++
RATIO	-3.18***	-3.16***
LANDPCAP	17.3**	
HUMCONS	-0.418++	
LNGNP		20.1***
LNINFRA	10.9***	7.98***
LLTROP	-0.381***	-0.409***
LNBRDENS	5.72**	5.74**
SSA	17.4 ns	31.6+++
ASIA	-4.48 ns	14.4 ns
WANA	-43.0+++	-39.5+++
σ	17.5+++	16.9+++
log likelihood	-133.92	-132.66
p-value ^a	0.00	0.00

^atest of joint significance of regional dummy variables.

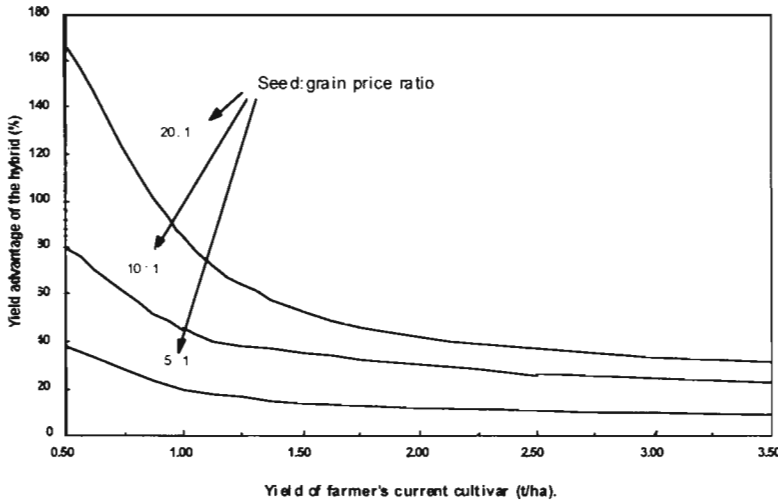


Figure 1. Yield advantage over farmer's current cultivar required to repay additional cost of hybrid seed and generate 100% marginal rate of return.

B31 - Three-way Crosses as an Alternative for Producing Maize in Veracruz, México

F. Rodríguez, M. Sierra, O. Cano, and G. Castañón.

Programa de Maíz del Campo Experimental Cotaxtla. INIFAP. Apdo. postal 429. Veracruz, Ver. C.P. 91700.

Introduction

In Veracruz state about 400,000 ha can be planted to improved seed of maize. Three-way-cross hybrids offer a viable alternative for maize production because of their advantages in yield, seed production, and line maintenance. The main objective of this research was to determine the yield and agronomic characteristics of three-way crosses in tropical maize.

Methods

We evaluated 64 three-way crosses on a tropical experiment station at Ignacio de la Llave, Veracruz, during Spring-Summer 1996. We used a CRBD design and three replications with plots of 1 row 5m long and 80 cm wide and about 62,500 plants per ha. We measured plant height, ear height, days to tassel, days to silk, plant aspect, root and stalk lodging, ear aspect, ear rot, and husk cover .

Results

The analysis of variance indicated significant differences for treatments. The coefficient of variation was 14.4%. Table 1 shows the yield and agronomic characteristics of the best three-way crosses. Ten genotypes were statistically different in yield from the rest. The best three-way crosses were (LRB-14 x D-539) x CML258, CML264, CML254, or CML267. CML247 x CML254 had the best response when crossed with LT-168, H-513, LT-163, and LT-181. These three-way crosses were resistant to stalk lodging and registered less ear rot than the check, VS-536. (LRB-14 x D-539) x CML258 yielded 8.9 t/ha -- 42% more than the check. The hybrid also did not lodge and had an excellent husk cover.

Conclusions

Some three-way crosses with good yield and agronomic characteristics were identified for use in tropical environments. LRB-14 x D-539, generated by INIFAP, showed good heterosis when crossed with CMLs and CML247 x CML254.

Table 1. Yield and agronomic characteristics of three-way-cross maize hybrids, Veracruz, Mexico, 1996.

Genealogy	Yield (t/ha)	% over check	Days to tassel	Days to silk	Stalk lodg.	Ear rot	Husk cover
1. (LRB-14X D539)XCML258	8944*	142	57	60	0	7	0
2. (CML247XCML254)CML15	8374*	135	55	57	1	4	8
3. (CML247XCML254)XLT168	7939*	126	56	58	0	7	4
4. (LRB.14XD-539)XCML 264	7920*	126	55	57	0	14	21
5. LT-167X LT-155	7684*	122	53	55	0	14	6
6. (CML247XCML254)X CML5	7538*	120	54	56	1	4	3
7. (CML247XCML254)XH-513	7496**	119	55	57	1	2	1
8. (LRB-14XD-539)XCML254	7493**	119	57	60	2	4	7
9. (CML 247XCML254)XLT-163	7455**	119	56	58	2	10	18
10.(CML247XCML254)XLT-181	7197**	115	53	55	2	10	10
11.(LRB-14XD-539)XCML267	7040	112	57	60	1	14	22
12.(CML247XCML254)XCML8	7015	112	55	57	0	8	21
13.(CML247XCML254)XLT-159	7014	112	54	56	2	2	7
14. LT-164 X LT-155	6997	111	54	56	5	17	19
15. LT- 165 X LT-155	6877	109	54	56	5	5	12
16. (CML247XCML254)XLT-172	6851	109	55	57	1	11	4
17.(CML247XCML254)XCML4	6829	109	57	59	0	6	14
18. LT-166 X LT-155	6811	108	56	58	6	11	6
19 (LRB-14XD-539)CML247	6804	108	57	60	0	2	1
20. (CML247XCML254)CML3	6670	106	57	59	5	10	6
21. VS-536	6283	100	57	59	10	28	13
22. C-343	6063	96	57	59	2	12	9
MEAN	6258						
C.V. %	14.17						

* Significant differences 0.05 probability.

** Significant differences 0.01 probability.

B32 - Use of CIMMYT Germplasm to Develop Maize Hybrids at the UNAM

M. Tadeo-Robledo, A. Espinosa-Calderón, R. Martínez M., A.M. Solano, A. Piña D.V.

Facultad de Estudios Superiores Cuautitlan - UNAM, Instituto Nacional de Investigaciones Forestales y Agropecuarias.

Introduction

The highland transition zones of the *El Bajío* region -- located between 1800-2200 masl in the states of Hidalgo, Puebla, Michoacan, México, Jalisco, Oaxaca, San Luis Potosi, Zacatecas, Aguascalientes, and Querétaro -- are sown to approximately 500,000 hectares of maize and have high yield potential. Particularly in areas of irregular rainfall, hybrid H135 has been very successful, resulting in an increase in use of certified seed from 18 to 67% in the state of Hidalgo in a very short time (Espinosa 1993). As a result of the production and sale of seed of this hybrid, seed companies started breeding programs to develop additional hybrids. The Facultad de Estudios Superiores Cuautitlán of the National Autonomous University of Mexico (Universidad Nacional Autónoma de México, UNAM) selected superior lines from CIMMYT and developed its own lines from commercial hybrids (Tadeo et al. 1994). Crosses between CIMMYT and UNAM lines resulted in hybrids Puma 1157 and Puma 1159, and improved hybrids are now available from advanced cycles of the same germplasm. This work reports on the performance of these hybrids.

Methods

From the commercial lines, hybrids and other materials were developed with tolerance to lodging, disease resistance, low tillering, and low ear height (Espinosa and Carballo 1987). CIMMYT lines were used as testers on maize developed by UNAM during 1992. Hybrids P-1157 and P-1159 were identified as superior. Newer hybrids involve more lines from UNAM and CIMMYT.

Results

During 1992-1995 across eight locations Puma 1159 averaged 10.3 t/ha compared with 8.8 t/ha for H-135 (Table 1). The Puma hybrid is earlier, has a better shelling percentage, and is tolerant to rust but susceptible to head smut caused by *Ustilago maydis*. The hybrid Puma 1157 yielded 11.7 t/ha, 24% higher than H-135 during the same period. During 1995-1996 200 new hybrids were evaluated with P-1157, P1159 as checks; hybrid UHT96E410 yielded 12.4 t/ha, compared to 6.9 t/ha for H-135, and has shorter plants and higher ears with earlier maturity (Table 3). These may be grown in the Valle del Mezquital after wheat harvest.

Table 1. Yielding of Puma 1159 and other hybrids in highland transition zones of El Bajío, Mexico.

Location	Year	Puma 1159	H-135	%	A-791	%
Cuautitlan, Méx.	1992	12700	12000	106	—	—
Tezontepec, Hgo.	1993	15123	15115	100	12650	119
Tula, Hgo.	1993	12461	10500	119	10125	123
Cuautitlan, Méx.	1993	13907	10400	134	—	—
Iturbe, Hgo. (1)	1994	3931	1906	206	1384	284
Tula, Hgo. (1)	1994	3329	1694	196	1298	256
Tula, Hgo. (1)	1994	4684	1848	253	—	—
Tezontepec, Hgo.	1995	14700	14327	103	10871	135
Tlaxcoapan, Hgo.	1995	13582	11916	114	10204	133
Cuautitlan, Méx.	1995	8353	8032	104	6966	120
		10277	8773	117	7643	134

Table 2. Yield of Puma 1157 and other hybrids in highland transition zones of El Bajío, Mexico.

Location	Year	Puma 1157	H-135	%	A-791	%	Criollo
Cuautitlan, Méx.	1992	14403	—	—	—	—	5344
Texcoco, Méx.	1993	10748	10250	105	—	—	—
Tula, Hgo.	1993	13907	10500	132	10125	137	10129
Tlaxcoapan, Hgo.	1994	14365	13435	107	13326	108	—
Tlaxcoapan, Hgo.	1994	14131	12840	110	12789	110	—
Iturbe, Hgo. (1)	1994	2797	1694	165	1298	216	1442
Tula, Hgo. (1)	1994	5780	1848	313	—	—	—
Tezontepec, Hgo.	1995	16885	14327	118	10871	155	—
Tlaxcoapan, Hgo.	1995	14808	11916	124	10204	145	—
Cuautitlan, Méx.	1995	9001	8032	112	6966*	129	—
		11682	9427	124	9368	125	—

Table 3. Grain yield and agronomic traits of new hybrids compared to commercial checks. Cuautitlan, México, 1996.

Hybrids	Yield (kg/ha)	Days to silk	Plant ht. (cm)	Ear ht. (cm)
UHT96E410	12,421	77.0	209	114
UHT96E415	11,638	84.7	235	145
UHT96E416	11,333	88.7	229	149
UHT96E418	10,588	80.3	227	150
UHT96E417	9,845	83.7	232	157
UHT96E408	9,824	79.0	208	120
UHT96E409	9,587	77.3	207	116
UHT96E412	9,048	80.7	216	132
UHT96E407	8,749	79.3	216	134
A-791	8,649	93.7	244	151
P-1157	8,019	84.7	231	155
H-137	7,984	82.7	248	172
H-135	6,903	89.3	247	164

B33 - Maize Single Crosses Evaluation and Hybrids Prediction for Mexican Lowland Tropics

J.G. Rodriguez V., Ma. C. Vega S., J. Espinoza V., E. Navarro G., A. Castro G.

Mexican Maize Institute, Universidad Autonoma Agraria Antonio Narrro (IMM-UAAAN), 25315 Buenavista, Saltillo, Coahuila, Mexico.

Introduction

To increase corn yield in humid lowland Mexican tropical regions (rainfall average over 900 mm), better varieties of maize besides the different versions of the Tuxpeño race used are needed. The new options may have lower plant-ear height (around 2.1 m and 1.1 m) and resistance to root-stalk lodging. The IMM-UAAAN programs have been selecting inbred lines at four contrasting tropical locations: two in the coast of the states of Veracruz and Jalisco (Groups 1 and 4), one in the *El Bajío* region (G2), and one in Rio Bravo, Tamaulipas (G3), to identify elite lines for use in hybrids and synthetic varieties.

Materials and Methods

Griffing's (1956) diallel Method 4, Model I was used to generate 136 single crosses from 17 selected inbred lines (5 from G1; 6 from G2; 4 from G3, and 2 from G4) during 1985 A (dry season). The single crosses plus eight commercial hybrid as checks were evaluated during 1985 B (rainy season) at six different sites located from 18°20' to 19°40' N and 95°14' to 103°30' W. Four locations are under 150 m above sea level; another is at 1,560 m, and the highest is at 1700 m altitude. The experimental design was a 12 x 12 lattice, two replicates at each sites; plot size 5 m single row, 21 plants each. Statistical analysis was performed for ear yield (15.5% humidity), time to tassel, and plant and main ear height. A combined analysis for ear yield was performed through a complete block design. Combining ability (CA) analysis of variance was done for the same traits as above (Martinez 1988) and the GCA and SCA effects were calculated for ear yield by locations and combined analysis. The three-way and double-cross hybrid prediction was done through the "B" method of Jenkins (1934).

Results

Genotypes differed ($P < .01$) for the traits at all six locations except for grain yield in Cd. Guzman, Jalisco and Nopalapan, Veracruz (Table 1). Group 1 lines crossed to Group 2 lines generally provided the best hybrids at all sites. Lines of Group 1 had been selected specifically for humid, tropical conditions and those of Group 2 were from a Tuxpeño population. Analysis showed GCA effect differences ($P < .01$) for all traits everywhere and SCA effects on time to tassel and plant-ear heights. The highest GCA effects were for 7 out of 17 lines (3 from G1, 2 from G2, and 1 each for the other groups). High and positive SCA effects were observed mainly for crosses among lines with high GCA. Thirty promising three-way crosses and 59 double-crosses were predicted. Table 2 shows the yield, GCA and SCA for the outstanding seven lines.

Conclusions

The direct single crosses of the 17 selected inbred lines showed great variability for all traits. GCA effects (highly significant for all traits) were larger than SCA effects. The predicted three-way and double-cross hybrids are promising combinations (over 6 t ha⁻¹ ear yield) in both hybrid formation or synthetic varieties for Mexican tropical regions.

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Table 1. Means and statistical significance¹ for traits (crosses) measured across six locations.

Location	Days to tassel	Height (cm)		Ear yield Mg ha ⁻¹
		Ear	Plant	
1. CBTa 17	57	238	134	7.74
2. ITA 18	55	246	139	9.33
3. Tepalcingo, Mor.	67	201	102	8.20
4. Cd. Guzman, Jal.	85	188 ns	97 ns	3.33 ns
5. Tehuantepec, Oax.	53	200	84	5.19
6. Nopalapan, Ver.	60	148	65	4.69
Combined analysis	-	-	-	6.41

¹ All significant at $P \leq .01$, otherwise indicated. The CV was far less than 20%, exception to ear yield at location 6.

‡ Locations 1 and 2 are both at Ursulo Galvan, Veracruz.

Table 2. General combining ability for ear yield for individual sites and combined analysis of variance for seven selected lines.

ID	Locations						Combined
	1	2	3	4	5	6	
ANH-43-68	.950	1.056	.238	.193	.049	-.213	.376
ANH-61	.204	.756	.606	-.277	.237	.366	.315
ANH-43-46	.805	.674	-.019	.575	-.164	.038	.313
V524-212	.073	.204	-.175	.706	.714	-.195	.220
V524-223	.430	.609	.365	-.167	.155	-.544	.146
ANS-10	-.137	.132	.162	-.048	-.051	-.051	.005
AN-348-111	-.420	-.3111	.057	.309	.461	.034	.186

B34 - Male Sterility as an Efficient Method of Exploiting Heterosis in Maize

E. Partas

Maize and Sorghum Research Institute, Pascani, Criuleni, Republic of Moldova

Introduction

In order to use heterosis efficiently, eliminate detasseling, and avoid unification of cytoplasm, a program of investigation and application of CMS is conducted. This program includes genetic identification of CMS sources; studying lines for reaction on CMS; breeding CMS and Rf analogues for elite lines; studying the degree of influence of sterile cytoplasm on morphological and agronomic traits of hybrids, to identify the best nuclear-cytoplasmic combinations and transfer of hybrid seed production. To determine the degree of influence of C, M, T, and N cytoplasm on heterosis, the isogenic variants of 733 hybrids on a sterile and fertile base were developed and tested during 1982-1995.

Results

The results show that hybrids with M and C analogues are as productive as normals. During 1991-1995 different lots of hybrids (min. 5, max. 32) with 16 sources of cytoplasm (CA, EK, J, K, L, M, ML, R, S, W; BB, C, ES, PR, RB, and N) were tested. As a rule CMS sources do not affect heterosis significantly for important characters, but in some hybrids differences between CMS variants were significant. Statistical analysis of the degree of influence of sources and types of cytoplasm, genotypes, and their interaction on variability of traits have shown that the CMS sources and types exert a non-significant influence on agronomic traits of hybrids (grain yield, humidity of grain, period to silking and to maturity, susceptibility to *Ustilago maydis*), but cause significant variability of some tassel traits (tassel length - max. 10.8%; length of tassel penduncle - max. 34.5%; number of tassel branch - 3.6%; kernels number - max 51.7%). Nevertheless, the effects of nuclear-cytoplasmic interaction are considerable (Table 1), and suggest the need to breed CMS variants for hybrids and select the best one.

Based on our results, seed of all Moldavian commercial hybrids is produced using M and C types of CMS with full fertility restoration. In the future 2-3 other sources of CMS will be included in seed production to increase cytoplasmic diversity. All prospective hybrids are tested on 2-3 types of CMS. Taking into account the results of hybrid testing, the stability of sterility of parental lines, and the stability and completeness of restoring fertility in hybrids, the best type of CMS for each hybrid is used in seed production. For the female parent of the most our hybrids the degree of male sterility rate is 99-99.5%, that is enough for obtaining 98-96% of cross-pollinated seed. In 1985-1995 more than 1.2 million tons of seed of 16 Moldavian hybrids was produced, 55% on M (S) and 45% on C types of CMS (Table 2).

Conclusions

CMS-Rf remains an efficient method of exploiting of heterosis and producing hybrid of maize. C and M (S) types of CMS exert a non-significant influence on important agronomic and biological traits of hybrids and are best for seed production. To avoid genetic vulnerability and increase cytoplasmic diversity new sources and types of CMS should be used.

Table 1. The degree of influence (%) of genotypes, cytoplasm and their interaction on maize hybrid characters (1996, 159 hybrids, 16 cytoplasm, 15 characters).

Characters	Genotypes			Cytoplasm			Interaction		
	Mean	Min.	Max.	Mean	Min.	Max.	Mean	Min.	Max.
Plants height	59.7	47.2	75.9	6.3	0.0	18.2	13.0	4.4	27.7
Height to ear	77.3	38.2	87.4	1.3	0.0	6.1	8.3	3.2	18.1
Length of tassel peduncle	65.3	37.7	97.6	16.5	0.1	34.5	11.8	0.2	27.8
Length of tassel	40.8	23.1	86.9	4.0	0.6	10.8	14.3	3.7	19.9
Tassel branches number	90.8	84.0	95.9	1.2	0.0	3.6	3.2	1.2	6.2
Length of ear	63.3	20.7	79.9	1.1	0.0	7.6	8.3	0.3	27.5
Kernels row number	81.2	44.0	94.4	1.0	0.0	6.6	7.3	0.8	14.6
Kernels number	33.3	5.2	54.9	8.0	0.0	51.7	24.4	11.6	38.7
Period to maturity	92.6	78.3	27.1	0.6	0.0	5.8	3.2	0.3	11.1
Period to silking	97.3	95.1	98.4	0.1	0.0	0.4	0.5	0.3	0.9
Lodging	67.5	57.2	81.9	1.1	0.0	5.9	6.4	2.6	11.5
Suscep. to <i>U. maydis</i>	26.6	0.0	44.6	2.2	0.0	7.5	14.0	0.0	27.1
Grain moisture	96.2	95.3	97.5	0.3	0.0	2.0	1.0	0.2	2.2
Grain yield	38.7	14.0	64.2	1.2	0.0	3.5	13.3	0.8	29.8
Selection index	50.1	34.0	73.7	1.0	0.0	2.0	12.2	0.8	29.1

Table 2. Use of CMS in corn seed production of Moldavian hybrids.

Years	Number of hybrids on CMS			Seed production, tons		
	M	C	Total	M	C	Total
1985-1990	8	5	13	288,176	199,037	487,213
1991	7	5	12	96,905	92,975	189,880
1992	6	5	11	64,996	62,563	127,559
1993	5	4	9	83,175	72,375	155,548
1994	6	4	10	75,534	63,292	138,826
1995	10	4	14	57,041	74,847	131,888
Total				665,827	565,087	1,230,914
%				54.1	45.9	100

B35 - Grain Yield of Maize Hybrids and Open-Pollinated Varieties Under Different Input Levels in Mozambique

M. Denic

SEMOC, C.P. 2402, Maputo, Mozambique

Introduction

Grain yield of maize grown on small-scale farms in Mozambique has been about 0.6 t/ha for the last 10 years (FAO, 1995), whereas in the last season it ranged from 0.2 to 1.2 t/ha (DINA, 1995). Under such conditions one can question the benefits of growing hybrid maize, especially given the economic situation and poor infrastructure (lack of money, access to the seed each year, higher price of hybrid seed, etc.) of the country. Data of Jones and Wendt (1994) demonstrated that grain yields obtained in Malawi with hybrids were superior to those obtained with open-pollinated varieties (OPVs) both under low and higher fertilizer levels. On the other hand, data of World Vision Int. (1992) showed no benefits of growing hybrid maize under smallholder conditions in Mozambique. The aim of this work was to compare the grain yields of hybrids and OPVs obtained on SEMOC's farms under low, medium and high inputs.

Materials and Methods

Commercial and advanced experimental hybrids and OPVs from several countries of the SADC region and from CIMMYT and IITA were used in these trials. Most trials used complete randomized block designs, with two-row plots, 5 m row length, 0.8 x 0.5 m row/plant distance with 2 plants per hill. Low and high input trials (16 total) were run two years (1988/89 and 1989/90 hot season; Table 1). Medium and high input trials lasted six years (1990/91-1995/96; Table 2). Details are presented in SEMOC's Annual Reports (1989-1996) for each period. Trials under low input levels were without application of fertilizers, herbicides and insecticides. Trials under medium inputs received 69 kg of nitrogen per hectare (two top dressings of urea), and treatments with herbicides and insecticides. Trials with high inputs received the same as for medium inputs, plus basic N-P-K fertilizer (12:24:12) at rates of 250 kg in Umbeluzi and Lionde, and 350 kg in Chimoio and Namialo.

Results

Hybrids averaged 16 and 20% higher yields than OPVs at three locations under high and low inputs, respectively (Table 1). At Lionde, OPVs performed better than hybrids both under low and high inputs. A remarkable yield difference (57%) between hybrids and OPVs was found under low inputs. Hybrids performed 13 and 6% better than OPVs in sets of trials under medium and high inputs, respectively.

Conclusions

Higher yields were obtained with hybrids than with OPVs in all locations except Lionde. Under extremely poor growing conditions OPVs performed better than hybrids. The fact that at Lionde, hybrids performed worse than OPVs even under high inputs-higher yield (about 4 t/ha), can be ascribed to poor adaptability of hybrids to higher temperatures at this location.

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Table 1. Grain yield of hybrids and OPVs under low and high input levels at four locations in Mozambique during 1989 and 1990.

Type of variety		Umbeluzi		Lionde		Namialo		Chimoio		Mean w/o Lio	
		Low	High	Low	High	Low	High	Low	High	Low	High
Hybrid	Mean	2.98	4.20	1.07	3.95	3.19	4.96	7.08	8.30	4.42	5.82
	S.e.	0.49	1.22	1.07	2.70	1.47	2.26	1.71	1.56	1.33	1.26
OPV	Mean	2.73	3.45	1.68	4.23	2.37	4.00	5.50	7.28	3.53	4.91
	S.e.	0.68	0.86	0.46	1.80	1.08	1.51	1.03	0.94	0.99	1.20
OPV : Hybrid		0.92	0.82	1.57	1.07	0.74	0.81	0.78	0.88	0.80	0.84

Table 2. Grain yield of hybrids and OPVs under medium and high input levels in Mozambique from 1991 to 1996.

	Hybrids			OPVs			OPVs:hybrids		No. of entries	No. of trials
	Med	High	Med:high	Med	High	Med:high	Med	High		
Mean	4.35	6.26	0.69	3.80	5.87	0.65	0.87	0.94	1946	90
S.E.	0.22	0.28	-	0.22	0.37	-	-	-	-	-

B36 - Impact of Hybrids on Maize Productivity and Production in Nigeria

M.A.B. Fakorede¹, S.K. Kim², J.M. Fajemisin³, J.G. Kling⁴, S.O. Ajala⁴, and A. Menkir⁴

¹Department of Plant Science, Obafemi Awolowo University, Ile-Ife, Nigeria

²Formerly Maize Improvement Program, IITA, PMB 5320, Ibadan, Nigeria

³IITA Savanna Station, c/o WARDA, Bourke, Cote d'Ivoire

⁴Maize Improvement Program, IITA, PMB 5320, Ibadan, Nigeria

Introduction

Maize breeding in Nigeria has gone through several phases since 1950 when an epiphytotic of American rust (*Puccinia polysora*) nearly wiped out the crop in West Africa. In the early stages open-pollinated varieties (OPVs), specifically composites and synthetics, were developed. Use of hybrid varieties was not possible primarily because companies were not available to produce hybrid seed in commercial quantities. Interest in research on use of hybrids re-surfaced in the early 1970s and hybrid maize research programs were initiated at the National Cereals Research Institute, Ibadan (now at Badeggi), and the University of Ife (now Obafemi Awolowo University, OAU), Ile-Ife. In 1979, hybrid development became an integral part of the Maize Improvement Program at IITA. In 1982, the federal government of Nigeria provided a special grant to IITA to develop within 3 years hybrid maize varieties for Nigeria. Thus, IITA took on the leading role and coordinated national agricultural research and extension systems (NARES) to develop hybrid maize. Nigeria's dream became a reality in 1984 when experimental hybrids were tested both on experiment stations and in farmers' fields. That year, 150 ha of farmers' fields was planted to hybrid maize. On average, hybrids were 25 and 43% higher yielding than the best OPVs in the forest and savanna zones, respectively, with yields in those areas as high as 9.4 and 11.8 t/ha. Hybrids were released in 1984 for farmers' use and, by 1985, about 6,000 ha was sown to hybrids, representing a new era in Nigerian agriculture.

This paper brief describes three areas of Nigerian agriculture in which hybrids have made a significant impact: 1) the yield potential of maize; 2) maize production and area; and 3) the establishment of seed companies and use of improved seeds.

Productivity

At the initial stages of the hybrid program, the OAU Program extracted inbred lines from improved, popularly grown OPVs such as TZSR-W, TZPB, TZB, and Western Yellow. IITA, on the other hand, exploited heterosis from diverse sources of germplasm. Productive hybrids were identified from Tuxpeño dent x Caribbean flint, tropical x temperate, lowland x midaltitude, and white x yellow crosses. Average grain yield of the best white and yellow hybrids (with commercial names Oba Supa 1 and Oba supa 2, respectively) were 29 and 15% higher than the best OPVs. Because of the dependence of the hybrid program on good OPVs and vice-versa, several populations have been improved that now perform equally well or better than the initial hybrids. New hybrids extracted from these improved populations are 20-46% higher yielding than the best commercial hybrid presently available.

One important impact of hybrid maize is the dramatic shift in production from the rainforest and forest-savanna transition zones (that used to be the "maize belt of Nigeria") to the Northern Guinea Savanna (NGS) and Midaltitude Savanna (MAS) zones. The NGS ecology has the greatest potential for maize cultivation in Nigeria. Within a decade, hybrid maize has displaced sorghum (the traditional crop) in much of this zone.

Productivity in the farmers' fields has been well monitored by Sasakawa Global 2000 (SG 2000) in three savanna states: Kaduna, Kastina and Funtua. Hybrids on average yield 78% more than OPVs and cost-benefit analyses show that net income of farmers growing hybrids is more than double that of farmers

growing OPVs. The net income of hybrid maize farmers in the SG 2000 villages ranged from US\$325 to 500 per hectare.

Total area under maize and total production

Land area under maize increased from about 0.65 million ha in 1984 to about 5.4 million ha in 1994. Corresponding figures for total grain production went from 1 to 7 million tons, respectively. The increases were especially dramatic as of 1987, two years after hybrid maize was released to the farmers. Growth rates for land area under maize and total grain production were 0.55 million ha and 0.62 million tons per annum for the 1984-94 period.

Establishment of seed companies and use of improved seed

Established in 1975, the National Seed Service (NSS) was the custodian of all publicly-bred varieties. NSS also produced foundation and certified seeds. When hybrids became available, the federal government facilitated the establishment of seed companies with significant assistance from IITA. The seed companies currently operating in Nigeria are Premier Seeds, Zaria (established in 1985, the first commercial seed company in West and Central Africa); UTSeeds, Jos (1989) and UAC Seeds, Zaria (1993). Operations of these companies are primarily based on hybrid maize (for example, 76-94% of the gross income of Premier Seeds for 1986-95 decade was from hybrid maize).

The high demand for improved maize seed in Nigeria has led to the rationalization of seed production, making it possible for entities such as semi-governmental and non-governmental (voluntary) organizations to be involved in seed production and distribution. Under this arrangement, inbred-line maintenance is now the responsibility of the institution that developed the material. NSS produces foundation seed and is still the custodian of all OPVs. The World Bank-financed Agricultural Development Project (ADP) in each state makes direct contact with farmers and now produces certified OPV seed using foundation seed from NSS. Hybrid seed production is restricted to registered commercial companies only. The National Seed Certification Program is responsible for seed certification.

Conclusion

Introduction of hybrid maize has triggered a Green Revolution in Nigeria. For more than a decade the Nigerian government has banned the importation of maize and Nigerian farmers have produced maize to feed the people as well as provide raw material for the brewing industry, flour mills, feed mills, and food processing factories. Research into other industrial uses such as corn oil production is in progress.

B37 - The Role of Hybrids in Combating Diseases, *Striga*, and Low Nitrogen Stress in Maize in Tropical Africa

J.G. Kling¹, A. Menkir¹, S.O. Ajala¹, J.M. Fajemisin¹, and S.K. Kim²

¹International Institute of Tropical Agriculture (IITA), PMB 5320, Oyo Rd., Ibadan, Nigeria

²International Agricultural Research Institute, Kyungpook National University, Taegu, 702-701 Korea

Introduction

Maize is the major cereal crop in sub-Saharan Africa, primarily for human consumption. Average yields are only about 1 t ha⁻¹, due to disease and insect pressures, weeds and parasitic plants, and abiotic stresses including drought and low nitrogen fertility. High-yielding cultivars grown with appropriate management practices can yield more than 10 t ha⁻¹ in favorable environments such as the moist savanna region of West and Central Africa. A maize hybrid development program was begun by the International Institute of Tropical Agriculture (IITA) in Nigeria in 1979 to exploit this potential. With the development of adapted hybrids, three private seed companies were established in Nigeria, providing efficient distribution of high quality seed to farmers. This paper presents evidence that hybrids can also offer greater yield stability in less favorable environments subject to biotic and abiotic stresses.

Methods

Maize streak virus (MSV) resistant maize populations from IITA were crossed to IITA and CIMMYT populations and to US public inbred lines to generate a series of tropically adapted inbred lines with good combining ability (Kim et al. 1987). These inbreds were included in the Maize Inbred Resistance (MIR) project, University of Hawaii, and screened for disease and insect resistance throughout the world (Brewbaker et al. 1989). Additionally, diallel crosses among IITA inbred lines have been evaluated for resistance to foliar diseases, downy mildew (*Peronosclerospora sorghi*), *Striga hermonthica* (Kim 1994), and tolerance to low N stress (Kim 1997; Kling et al. 1997).

Results and Conclusions

Hybrids with resistance or tolerance to *Striga* were evaluated at four sites in 1996 (Table 1). The best hybrid produced 2.3 t ha⁻¹ more grain than the susceptible hybrid under artificial infestation with *S. hermonthica*, whereas yield differences under noninfested conditions were not significant. Experiments have shown that hybrids with N stress tolerance exhibit the greatest advantage over open-pollinated varieties under moderate N fertility (60 kg N ha⁻¹). Hybrid 8644-27 has been identified as N-stress tolerant, and inbreds KU1414-SR and Tzi 25 have good combining ability for grain yield under N stress. Tropical inbred lines with downy mildew resistance were introduced from Thailand and the Philippines, and converted for resistance to MSV at IITA. In genetic studies conducted over three years, crosses between Tzi 18 (susceptible) and KU1414 (resistant) had only a 22% incidence of downy mildew, whereas 88% of the plants of the most susceptible hybrid were infected with downy mildew. Combining abilities of elite tropical inbred lines for important diseases, *Striga* reaction, and low N tolerance are summarized in Table 2. Experience over the past fifteen years has shown that maize hybrids with high, uniform levels of disease and pest resistance and tolerance to abiotic stresses provide greater yield stability in less favorable environments in tropical Africa.

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Table 1. Performance of maize hybrids under *Striga hermonthica* infestation across four sites[†] in 1996.

Cultivar	Pedigree	Maize damage rating [‡]	Maize emergence [§] 5 m row	Grain yield (Mg ha ⁻¹)	
				infested	noninfested [¶]
9143-20	Tzi3STR97 x Tzi12STR	4.4	21.8	3.3	5.4
9022-13 STR	Tzi3STR x Tzi12STR	5.2	42.4	3.2	6.8
9150-4	Tzi3STR77 x Tzi12STR	4.9	29.5	2.9	5.9
8425-8	Tzi25STR x Tzi18	4.9	20.3	2.9	6.3
9044-27 STR	Tzi35STR x Tzi18STR	4.7	25.9	2.8	6.6
9145-11	Tzi3STR31 x Tzi15STR	4.8	30.0	2.7	6.0
8535-23	TZMi101 x TZMi407	5.1	24.0	2.4	5.7
Acr 93 TZL Comp. 1-W	Open-pollinated variety	4.9	18.3	2.3	5.2
9021-18 STR	Tzi3STR x Tzi15	5.5	27.7	2.3	6.6
9044-31 SR/SR STR	Tzi25STR x Tzi35	5.7	22.2	2.2	6.1
9141-6	Tzi3STR21 x Tzi15STR	5.3	16.0	2.1	5.4
8338-1 (susceptible)	Tzi9 x Tzi10	7.0	45.1	1.0	5.5
Mean		5.2	25.8	2.5	6.0
se		0.33	-	0.42	0.43
P>F cultivars		0.0011	0.0397	0.0089	0.2792
P>F sites x cultivars		0.0001	0.0118	0.0001	0.2533

[†] Mokwa and Abuja, Nigeria; Ferkessedougou, Côte d'Ivoire; and Garoua, Cameroon.

[‡] 1-9, where 1=no damage symptoms and 9=severe damage symptoms.

[§] Data were log transformed for analysis. Means presented are backtransformed.

[¶] Data from Mokwa and Abuja, Nigeria, only.

Table 2. Tropical inbred lines that possess resistance (R) or tolerance (T) to biotic and abiotic stresses as indicated by estimates of GCA in various genetic studies.

Inbred line	<i>Puccinia polysora</i>	<i>Bipolaris maydis</i>	<i>Curoualaria</i> spp.	Stalk rots [†]	Ear rots [‡]	Downy mildew	<i>Striga hermonthica</i>	low N stress
Lowland IITA								
TZi 3	R	R		R	R		T	
TZi 4	R	R	R		R			
TZi 8	R		R					
TZi 11				R			R/T	
TZi 12			R				T	
TZi 17				R				
TZi 18	R							
TZi 24		R	R					
TZi 25			R				R/T	T
TZi 30							R	T
Introduced lowland								
KU1414	R	R	R			R		T
KU1409	R	R	R			R		
MIT-11 S3						R		
Midaltitude IITA								
TZMi 102			R		R			
TZMi 103							T	
TZMi 302					R			
TZMi 407			R		R		T	

[†] Stalk rots evaluated include *Botryodiplodia theobromae* and *Fusarium moniliforme*

[‡] Ear rots evaluated include *Botryodiplodia theobromae*, *Fusarium moniliforme*, and *Macrophomina phaseoli*

B39 - Exploitation of Heterosis in Maize at Kasetsart University, Thailand

C. Aekatanawan, S. Jampatong, C. Aekatanawan, N. Chuichoho, C. Balla, C. Chutkaew

National Corn and Sorghum Research Center, Kasetsart University, Pakchong, Nakhon Ratchasima 30320, Thailand, Lop Buo Rural Agriculture Development Project, Kasetsart University, Chatuchak, Bangkok 10900, Thailand, Dep. of Agronomy, Kasetsart University, Bangkok 10900, Thailand

Introduction

In Thailand, maize hybrids, especially single crosses, have played the most important role in this decade for increasing average yield per hectare and total product for national consumption and export. Hybrid seed use in this country has been increasing very rapidly from 40 t in 1981 to 12,500 t in 1996 (75% of total seed use). The Kasetsart University (KU) hybrid maize breeding program was initiated in 1978. Our objectives were 1) to develop superior inbred lines for commercial use in producing superior, stable, and high-yielding hybrids, and 2) to develop heterotic groups by introgression of exotic germplasm as diverse sources.

Materials and Methods

Heterotic patterns were investigated by using a 10-population diallel (Gardner and Eberhart 1966, Analysis 111) at the National Corn and Sorghum Research Center (Suwan Farm). In the past, advanced populations (Suwan 1, Suwan 2, Suwan 3, Suwan 5, etc.) under S₁ recurrent selection, were the only source of lines for further inbreeding. More recently, line improvement was done using recycling of elite lines which had some weaknesses by using pedigree and backcross methods. Partially inbred lines (S₃-S₅) were evaluated by crossing with inbred testers, and line x tester analysis was used. Their testcrosses were evaluated in two different environments (early and late rainy seasons at Suwan Farm). Elite hybrids were tested over three to five years in various environments on research stations and farmer's fields. Only outstanding hybrids which gave yields over the commercial hybrid check were released to farmers.

Results

From the population diallel analysis, the Suwan I-KS 6 pattern was the most useful. The cross of Suwan 1 (S)C1 x KS 6(S)C2 gave heterosis of 18.5%. Released Kasetsart hybrids and inbred lines during 1982-97 are shown in Tables 1 and 2, respectively. Most Kasetsart inbred lines from Suwan 1, Suwan 3, and KS 6 varieties combined better with K_j 21 and K_j 45 than other diverse inbreds. K_j 21 was developed from Pacific 9 hybrid, which had Mo17 derivatives, and K_j 45 was the second-cycle recovered line of K121.

Conclusions

Most KU inbred lines were developed as "spin-offs" from the S₁ recurrent selection program. This approach, conducted in concert with an applied breeding program, enhanced the systematic genetic advance of populations per se, lines per se, and their combining ability, especially for the advanced cycles. The heterotic patterns currently used in the KU hybrid maize breeding program are (Suwan 1, Suwan 3, Suwan 5, KS 6)-Mo 17 derivative patterns. Consequently, inbred lines with introgression of temperate germplasm are available for use in tropical breeding programs.

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Table 1. Kasetsart hybrids released during 1982-97.

Hybrid	Type	Check	No. of trials	Year of release	Pedigree	Average yield (t/ha)	% over check
Suwan 2301	SC	Suwanl(S)C8	37	1982	K _j 3 x K _j 11	5.6	10.5
Suwan 2602	TC	Suwan 2301	37	1986	(K _j 3 x K _j 11) x K _j 20	6.2	11.4
Suwan 3101	TC	Suwan 2602	95	1991	(K _j 27 x K _j 28) x K _j 21	6.6	16.0
Suwan 3501	SC	Suwan 3101	109	1993	K _j 32 x K _j 21	7.7	8.7
Suwan 3502	SC	Suwan 3101	48	1993	K _j 36 x K _j 21	7.8	8.5
Suwan 3503	SC	Suwan 3101	63	1993	K _j 43 x K _j 21	7.7	10.3
Suwan 3504	SC	Suwan 3101	125	1993	K _j 44 x K _j 21	7.7	10.2
Suwan 3601	SC	Suwan 3504	101	1995	K _j 44 x K _j 4-5	6.7	4.5
Suwan 3851	SC	Suwan 3504	57	1997	Kei 9405& x K _j 4-5	7.5	11.1

SC = Single cross, TC = Three-way cross. & Kei 9405 = Suwanl(S)C10(HLT)CI-F,-S,-159-I-I-I-I.

B40 - Evaluation of Yield and Agronomic Traits of Maize Hybrid in Thailand

Y. Chanatachume, P. Grudloyma, S. Noradachanon, S. Tongchaey, D. Kongtien

Nakhon Sawan Field Crops Research Center, Takfa, Nakhon Sawan, Thailand 60190

Introduction

Maize (*Zea mays*) is one of the most important cereal crops in Thailand both as an export product and as an animal feedstuff. However, the amount of export of maize grain rapidly decreased from 3.73 million tons in 1985 to 0.14 million tons in 1994 (Agricultural Statistics of Thailand Crop Year 1985/86-1994/95). This was because of the booming of the livestock and feed industries started since the late of 1980s. If the present trend continues, maize utilization in Thailand will increase to 4.58 million tons in 1999. However, domestic maize area declined from 1.98 million hectares in 1985 to 1.41 million hectares in 1994, meaning that production growth over 1985-1996 was mainly due to the use of high yielding varieties and hybrids; more than 60% of the planting area in 1996 was covered by hybrid maize. But greater emphasis on hybrid maize research and development is required, both by government organizations and private companies.

Methods

Experimental yield trials of maize hybrids were conducted for 6 years from 1991 to 1996 with 16-42 hybrids per experiment and 5-7 locations per year. The hybrids tested were pre-commercial hybrids developed from both government and private sectors. An open pollinated variety (OPV) "NS 1" released by the Department of Agriculture (DOA) in 1989 was included in these experiment as a check. The experimental design used was RCB with 4 replications. Seeds of those hybrids and the OPV were sown in 4 rows of 5 m per plot with the spacing of 75 x 25 cm and harvested only from the two central rows. Average yield and performance of some important agronomic traits were compared across location for each year between those hybrids and the OPV.

Results

The mean yield of all hybrids across locations and years was higher than those of NS 1 (Table 1), with a superiority ranging from 114 to 137%. However, there was no increase in the mean yield of hybrids or NS 1 during the six years of testing, probably the effect of genotype x environment interaction. The average mean yield across locations and years of all hybrid was 22% higher than that of NS 1 indicating an increase in hybrid yield of 3.7% per year (Table 1).

Conclusions

The average yield across locations and years of all hybrids was higher than that of NS 1, however there was not much difference between those hybrids and NS 1 for plant and ear height, number of days from emergence to 50% silking, seed moisture content and shelling percentage (data not shown). The average number of ears per plant of hybrids was observed to be higher than that of NS 1 while there was less root and stalk lodging in hybrids than NS 1 (data not shown). The advantages of these traits should have given higher yield to the tested hybrids in comparison to NS 1.

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Table 1. Mean grain yield (t/ha) across locations of hybrids and NS 1 tested in 1991-1996.

Year	Hybrids	NS 1	Experimental mean	Relative yield (%)
1991 (16) ¹ (6) ²	6.25	5.15	6.18	121
1992 (27) (5)	7.81	6.70	7.77	116
1993 (27) (7)	6.70	5.84	6.67	114
1994 (28) (6)	6.03	5.11	5.99	118
1995 (28) (7)	6.04	4.77	5.99	127
1996 (42) (6)	5.52	4.22	5.49	137
Mean	6.39	5.30	6.35	122

¹ Number of tested hybrids, ² Number of locations

B41 - Past, Present, and Future Prospects of Maize Hybrids in Uganda

J.B. Imanywoha and D. Kyetere

Cereals Program, Namulonge Research Institute, P.O. Box 7084, Kampala, Uganda

Introduction

Although hybrid maize has been grown in Uganda for some time (Rubaihayo et al. 1989), hybrids have not been adopted for commercial production except in Eastern Uganda highlands. This is due to a number of factors including lack of any yield advantage over local open pollinated varieties (OPV) under farmer management, the susceptibility of hybrids to maize streak virus (MSV), the high price of imported hybrid seed, the lack of commercial farmers, and the absence of seed companies to market hybrid maize. Early attempts to introduce hybrids seed occurred in the 1950s, when hybrids resistant to *Puccinia polysora* were introduced from Kenya, but these did not adapt well to Ugandan conditions (Jameson 1970). In the 1960-70s, locally developed OPVs outyielded Kenyan hybrids, and in the mid-1980s hybrids from IITA were introduced, tested and found to be superior to locally developed varieties (Rubaihayo et al. 1989), but never released. There is now a renewed interest in maize hybrids caused by the newly emerging group of commercial farmers, high local and regional demand for maize, demand for quality maize seed, the willingness of the national seed project to switch from OPVs to hybrids, and a concerted government policy to increase maize production more than 100% over 1992 production (Uganda Environment Report 1994). In 1994, as a result of directives from the Ministry of Agriculture, the Ugandan maize research program started a hybrid development program under short, medium and long term strategies.

Methods

Under the short-term strategy, a number of available commercial hybrids were to be tested. This included 92 hybrids from CIMMYT-Zimbabwe, 15 from IITA-Ibadan, 9 from Cargill-Zimbabwe, 3 from Pioneer-Zimbabwe, 5 from the Kenya Seed Company, 20 from Sensako-S. Africa, 19 from Seed Company-Zimbabwe, and 27 from Pannar-S. Africa that have been tested for adaptability. Superior hybrids were included in advanced and multilocational trials. The medium-term strategy involves use of available inbred lines from international agriculture research centers. Under this plan 217 advance inbred lines from CIMMYT-Zimbabwe were tested for adaptability and selected ones used in test crosses and diallel crosses. The long-term strategy involves extraction of inbreds.

Results

From the short-term tests, three hybrids from CIMMYT-Zimbabwe have performed well. They are resistant to MSV and northern leaf blight (NLB) caused by *Exserohilum turcicum* and tolerant to gray leaf spot (GLS) caused by *Cercospora zea maydis* (Table 1). Two of them are candidates for release this year and are undergoing on-farm evaluation and demonstrations. Each of the two hybrids outyields the commercial variety by more than 2 t/ha. All maize hybrids from International Seed Companies succumbed to at least one and sometimes several major diseases. From medium-term strategy, 10 hybrids have been selected for future evaluation and 8 inbred lines have been selected for use in synthetic variety production for resource constrained farmers. Extraction of inbreds from the local populations is at S₃ stage.

Conclusions

The first release of two hybrids tolerant to GLS will occur this year. The National Seed Company will be privatized and, to remain viable, will have to market hybrids. On the other hand, breeders are finding it increasingly difficult to breed and maintain OPVs that are resistant to all the three major diseases. It is therefore possible to conclude that the future of Uganda maize industry will rest on hybrids and synthetic varieties.

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Table 1. Yield and disease reaction of some selected hybrids.

Genotype	Yield Kg/Ha	Disease reactions		
		NLB	GLS	MSV
CIMMYT-1	5626	1.5	2.5 (1.26*)	2.0 (1.5*)
CIMMYT-2	7627	2	2 (2.75*)	1.5 (2.2*)
CIMMYT - 3	7283	1.5	3.01 (1.75*)	1.5 (2.2*)
INTERN. 1	7756	1.5	1	NA
INTERN. 2	5667	4	3	NA
INTERN. 3	6819	3	3.5	NA
INTERN. 4	5397	5	3	NA
INTERN. 5	6960	4.5	3.5	NA
INTERN. 6	5879	2.5	3	NA
LONGE 1	4070	3	2.5	3
(Check)				

B42 - Heterosis and Prospects for Marketing Sorghum Hybrids in Niger

I. Kapran, M. Adamou, M. Abdou, S. Souley, N. Kondo, INRAN B.P. 429 Niamey, Niger
J.D. Axtell, G. Ejeta, T. Tyler, Purdue University, W. Lafayette IN 47907, USA

Introduction

Sorghum, the second most important food crop in Niger, is grown under rainfed conditions in regions that receive 400-800 mm of precipitation yearly. Sorghum area in Niger increased from less than 0.5 to 2.0 million ha during 1961-96, but average yields over the same period declined from 0.6 to 0.2 t/ha (FAO/SMIAR 1997), mainly due to the crop's moving into more marginal lands and use of low-yielding, local cultivars. Sorghum improvement research in Niger started in the 1950s with the French research institute for tropical agriculture (IRAT) and emphasized open-pollinated varieties until the establishment of the National Institute for Agricultural Research (INRAN) (Chantereau and Adamou 1977). In the 1980s, INRAN and the International Sorghum and Millet Program (INTSORMIL) began joint evaluations of sorghum hybrids under the marginal conditions common to Niger.

Materials and Methods

Experimental hybrids were synthesized from adapted germplasm provided by the Purdue Sorghum Research Program and tested at several INRAN field research stations. Selected hybrids gradually moved from observation nurseries or preliminary trials to advanced yield trials at several locations for two to three years. The experimental design included at least one open-pollinated local variety as a check. Elite hybrids resulting from these national tests were also evaluated in the West African Sorghum Hybrid Adaptation Trial (WASHAT). Data collected include estimates of maturity, plant height, plant stand, grain yield and grain quality, and reactions to biotic and abiotic stresses. An elite hybrid, TX623A x MR732, later named NAD-1, was successfully tested in demonstration trials in farmers' fields and, since 1989, has been used in seed production experiments to evaluate the feasibility of commercial hybrid seed production.

Results and Discussion

Agronomic evaluation. In annual data from INRAN sorghum breeders, experimental hybrid yields averaged 2 t/ha; the best hybrids yielded as much as 6.5 t/ha, whereas best variety checks never exceeded 3.8 t/ha (Table 1). These results confirm the findings of two graduate thesis projects conducted at Purdue University and initiated the emphasis on sorghum hybrid research in Niger. Kapran (1988) reported heterosis values of 45% under irrigation and 66% in rainfed conditions. In the same tests, hybrids also outyielded local checks by 61% with irrigation and 49% under rainfed conditions. Tyler (1988) found that hybrids with parents grouped as exotic, intermediate, or local were higher yielding than their respective parents by respective averages of 127%, 83%, and 66%. Through these early thesis projects and subsequent INRAN/INTSORMIL collaborative tests, the value of heterosis for Niger's agriculture was demonstrated.

NAD-1, a medium-maturing, white-seeded hybrid with good tolerance of mid-season drought (common in Niger), was the most attractive cultivar to breeders and farmers alike. In national trials, its yield average was 3.1 t/ha between 1986 and 1992. Also in the 1989 WASHAT trial, it ranked third of 20 entries for grain yield at nine locations across West and Central Africa (ICRISAT/WASIP 1989). Estimates of NAD-1 yield potential under farmer management were obtained starting in 1993 (Table 2). Averages vary from 1.7 to 3.3 t/ha. Despite severe drought conditions, the hybrid was superior to Mota Maradi (MM), an early-maturing and widely adapted local variety. In on-farm trials of the regional sorghum network, NAD-1 yielded 80% more than the average of farmer checks.

Experimental seed production. NAD-1 seed production by INRAN grew from a 200 m² plot in 1989 to several hectares today. Under good management, the equivalent of 1.5 t/ha of hybrid seed has been obtained, repeatedly demonstrating that hybrid seed production is possible in Niger.

Seed business activity. Having a hybrid that appeals to farmers and can be produced are key elements for seed marketing. For the first time in Niger, hybrid seed was sold in 1996 at eight times the price of sorghum grain. However, INRAN, as a public research organization, has no mandate for commercial seed activity. We are actively approaching extension, farmer co-ops, and individuals that potentially could turn into commercial seed producers. It is concluded that heterosis can be used to improve agricultural productivity in Niger and similar Sahelian countries. Sorghum hybrid NAD-1 also demonstrates the value of heterosis in other important crops like millet. The momentum created by this hybrid is today being used by INRAN, INTSORMIL and the Sahelian Center of ICRISAT to educate policy makers and private producers on the need for and advantages of launching a seed industry in Niger.

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Table 1. Yields of sorghum hybrids at research stations in Niger, 1984-92.

Year	Hybrids tested (number)	Grain yield		
		Trial mean	Best hybrid (t/ha)	Local variety
1984	22	2.3	5.6	--
1985	17	—	4.0	—
1986	149	2.5	2.7	1.1
1987	147	2.6	5.5	3.2
1988	81	1.9	4.9	2.7
1989	67	2.8	6.5	3.8
1990	49	2.4	5.0	3.0
1991	78	1.8	2.0	1.0
1992	88	1.9	4.6	--

Table 2: Yield of elite sorghum hybrid, NAD-1, under farmer conditions in Niger, 1993-96.

Year/ Activity	Local variety	NAD-1 over local	
		(t/ha)	(%)
1993 demonstrations	--	2.4	---
1994 demonstrations	--	3.3	---
1995 NAD-1 vs. MM trial	1.0	1.6	60
1996 NAD-1 vs. MM trial	0.7	1.7	143
Regional network trial	1.0	1.8	80

B43 - Use of Heterosis for Testcross Evaluation and Enhancement of Soybean Germplasm

K.S. Lewers and R.G. Palmer

Agronomy Department, Iowa State University, Ames, Iowa 50011, U.S.A. and USDA ARS Iowa State University, Ames, Iowa 50011 USA

Introduction

Soybean [*Glycine max* (L.) Merr.] is an important oilseed legume and is an autogamous plant species. Hybrid seed production is usually done by manual cross-pollination. The use of genetic male-sterile, female-fertile soybean plants with insect-mediated cross-pollination to produce hybrid seed is feasible. The *ms1*, *ms2*, *ms3*, *ms4*, *ms5*, and *ms6* mutants (Palmer et al. 1992) and a new mutant (Jin et al. 1997) are available. The pollen fertility locus, *Ms6*, is linked to the flower color locus, *W1*, and recombination values in the coupling phase for *Ms6* - *W1* were between 2.48 ± 0.1 and 3.18 ± 0.1 (Skorupska and Palmer 1989). *W1* plants have purple hypocotyls and purple flowers and *w1 w1* plants have green hypocotyls and white flowers. Lewers et al. (1996) determined that, in lines segregating for the *ms6* and *w1* alleles in coupling phase, more than 92% of the green-hypocotyl seedlings are expected to be male sterile, and approximately 97% of the purple-hypocotyl seedlings will be fertile. Use of the closely-linked marker system for the production of hybrid seed for research purposes was termed the Cosegregation Method (Lewers et al. 1996).

Methods

Five soybean lines were developed by backcrossing the *ms6-w1* alleles into germplasm that included a plant introduction from Japan (PI 416.941), a plant introduction from the former USSR (PI 384.474) and three commercial lines with greater than 25% exotic germplasm in their pedigrees (Glenn from ProfiSeed, Inc., CX155 from DeKalb Genetics Corp., AG020 from Asgrow Seed Co.). The sixth line used was the donor source of the *ms6-w1* alleles. Two testers were used to evaluate the six lines cosegregating at the *Ms6* and *W1* loci in coupling phase. The testers were three near-isogenic lines each of cv Clark (Clark *e2*, Clark *e2 Dt2*, and Clark *e2 S* and cv Harosoy (Harosoy, Harosoy *Dt2*, and Harosoy *S*). The *Dt2* allele conditions semideterminancy, the *S* allele conditions short internodes, and the *e2* allele conditions earlier maturity such that all the Clark *e2* near-isogenic lines are Maturity Group II. A randomized complete-block design compared the testcross lines with the testers and the lines to be evaluated. Agronomic evaluations were made on replicated three-row plots at three locations for two years. The data were sorted by environment (year-location) and treatment. An analysis of variance was conducted to obtain genotypic means and error mean-square values for each agronomic trait. These means were used to calculate F_1 midparent heterosis values (F_1 -midparent), high-parent heterosis values (F_1 -high parent), and T_i values (St. Martin et al. 1996). A second analysis of variance was conducted using the F_1 midparent values for each agronomic trait to determine the value in testcross evaluation of the *Dt2* or *S* alleles and of the choice of tester.

Results

Significant levels of F_1 midparent heterosis were found for every trait measured. The number of testcrosses for which significant positive or negative midparent or high parent heterosis was found is given for each trait measured (Table 1). Grain yield of pod-parent lines was generally higher than that of the testers; only PI 384.474 yielded less than the testers. Midparent heterosis was significant and positive for PI 384.474, AG020, and CX155, and heterosis levels among these lines were not significantly different from one another. T_i values for all lines, except PI 384.474, were significantly positive. Only AG020 and CX155 had significant heterosis and T_i values. Significant interaction effects on heterosis by pod parent and tester were observed for all agronomic traits (Table 2). The choice of tester is important and should represent the material in the breeding program the breeder wishes to improve. The *Dt2* and *S* alleles did not facilitate germplasm evaluation.

Conclusions

The Cosegregation Method produced enough hybrid seed for the experiment. Significant F_1 and F_2 midparent heterosis were observed for nearly all traits including grain yield. The choice of tester was important in determining parental value of germplasm. Germplasm rankings using *per se*, and T_i values were in agreement with each other more than with F_1 midparent heterosis values ranking. T_i value ranking exerted greater selection pressure than did F_1 heterosis ranking. Choice of ranking should be used in conjunction with *per se* values and will depend on breeding goals.

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Table 1. Number of soybean testcrosses (N=36) for which significant ($P=0.05$) F_1 midparent heterosis was found.

Trait	Positive heterosis	No heterosis	Negative heterosis
Maturity date	14 † ‡	21	1
Lodging	2 §	34	0
Plant height	18 ¶	17	1
Grain yield	7	29	0
Harvest index	13	20	3
100-seed weight	3	31	2
% Seed protein	0	34	2
% Seed oil	5	29	2 #

† Positive heterosis indicates later maturation, and negative heterosis indicates earlier maturation.

‡ Five lines showed high-parent heterosis.

§ Positive heterosis for lodging indicates increased lodging.

¶ Two lines showed high-parent heterosis.

One line showed high-parent heterosis.

Table 2. Significance ($P=0.05$) of tester, stem type, pod-parent line, and interaction effects for expression of agronomic-trait heterosis among 36 soybean testcross lines.

	Maturity	Lodging	Plant height	Grain yield	Harvest index	100-seed weight	Seed protein	Seed oil
Testers	NS †	NS	*	*	*	*	NS	*
Stem types	*	NS	*	NS	NS	NS	NS	*
Stem types x testers	*	NS	*	NS	*	*	NS	*
Pod-parent lines	*	*	*	*	*	*	*	*
Pod-parent lines x testers	NS	NS	NS	*	*	*	*	NS
Pod-parent lines x stem types	NS	*	NS	Ns	Ns	Ns	*	NS

† * Significant at $P = 0.05$; NS = not significant at $P = 0.05$.

B44 - Maize Production Situation and Use of Heterosis to Increase Maize Yields in Vietnam

Tran Hong Uy

Director, National Maize Research Institute, Dan Phuong, Ha Tay, Vietnam

Food production in Vietnam has increased from 19 million tons in 1989 to 29 million tons in 1996. Formerly a food importer, Vietnam now exports 2-3 million tons of food each year. These are the results of new agricultural policies and new technologies, such as use of improved varieties and, especially, exploitation of heterosis in rice and potato. Our scientists have quickly developed hybrid maize and rice varieties and released them to farmers in recent years.

In 1990, only 5 ha of hybrid maize was grown in all of Vietnam. By 1996, 36% of the maize area was planted to hybrids. In 1997, hybrid maize area could reach 50%-55%, about 300,000 ha. By the year 2000 the hybrid maize area will be 1 million ha., accounting for 70% of the area with average yields as high as 5 t/ha, and an output of 3 million tons.

In the last few years a series of new maize hybrids have been released. The yield potential of the non-conventional ones (LS-3, LS-4, LS-5, LS-6, LS-8) is 3-7 t/ha; that of conventional hybrids (LVN-1, LVN-2, LVN-4, LVN-5, LVN-10, LVN-11, LVN-12, LVN-16, LVN-20) is 4-13 t/ha.

Due to use of maize hybrids, Vietnamese maize production has doubled during the last five years.

B45 - Evolution of the Maize Hybrid Programme in Zambia

C. Mungoma

Maize Research Programme, Golden Valley Research Centre, P. O. Box 54, Fringilla, Zambia

Introduction

Maize is the most important cereal crop in Zambia. Per capita consumption is about 160 kg per annum. Hybrid maize has been cultivated since the early 1960s but it was not until 1970 that the first Zambian bred hybrid was released. It is estimated that 65% of the maize area is planted to hybrids, 5% to open pollinated varieties, and 30% to recycled seed (CIMMYT 1994). Up until 1964 the country depended on hybrids from Zimbabwe, which has a long history of maize breeding (Eicher 1995). These hybrids required about 160 days to reach maturity, and there was a need for earlier maturing varieties that were also disease and insect resistant.

Methods

A breeding programme was begun to develop single-cross hybrids, three-way-cross hybrids, double-cross hybrids, top crosses, synthetics, and open pollinated varieties of varying maturities that would also possess insect and disease resistance, soil acid tolerance, drought tolerance, and desirable plant and kernel type. Germplasm collected from Eastern and Southern Africa, CIMMYT, Europe (especially Yugoslavia) and the USA underwent recurrent selection to develop open-pollinated varieties and inbred lines for hybrid development. Pedigree and backcross breeding was the main source of inbred lines.

Results

By 1970 the programme had released two open pollinated varieties and a hybrid, ZH1, which was not widely adopted. Excellent progress began in 1978. The first achievement was the improvement of the popular Zimbabwean hybrid, SR52, released in 1983 under the name of MM 752. Since then several types of hybrids have been released with different attributes to suit all agroecological zones and all categories of farmers (Table 1). To reduce the cost of seed, the breeding programme produces single-cross hybrids based on sister crosses instead of pure inbred lines. Released hybrids have great yield potential (Table 2) and national maize averages of 2.7 Mg/ha have been reported in some years (CSO/MAFF 1984-1995). Yields are still low due to other management problems, but are among the highest in the region. We have started a stress breeding programme for drought and low N tolerance.

Conclusions

The Zambian Maize Breeding Programme is among the successful programmes in southern Africa. Hybrids developed have contributed to the increase in the national average yield of maize. The programme has shown that, with a viable seed industry, farmers in the developing countries can benefit from hybrids.

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Table 1. Characteristics of Zambian maize hybrids.

Name and year of release	Days to maturity	Yield potential (Mg/ha)	Characteristics
GV 412 (1995)	100-120	4.0	Top cross, white semi-flint
MM 441 (1992)	110-120	5.0	Double cross, white dent
MM 501 (1984)	120-130	6.0	Single cross, white semi-dent
MM 502 (1984)	135-145	7.5	Single cross, white semi-dent
MM 504 (1984)	125-135	6.5	Three-way cross, white dent
GV 512 (1995)	135-145	6.5	Single cross, white semi-dent
MM 601 (1984)	135-145	7.5	Single cross, white semi-dent
MM 603 (1984)	135-145	7.0	Three-way cross, white dent
MM 604 (1984)	145-155	7.0	Three-way cross, white dent
MM 612 (1988)	145-155	7.0	Double cross, white dent
MM 62 (1992)	145-155	7.0	Single cross, yellow dent
GV 61 (1995)	130-140	7.0	Single cross, yellow dent
MM 752 (1983)	155-165	8.0	Single cross, white dent
GV 702 (1995)	145-155	9.0	Single cross, white dent
GV 703 (1995)	150-160	9.0	Three way cross, white dent
GV 704 (1995)	150-160	10.0	Single cross, white dent

Table 2. Mean yields (kg/ha) of Zambian hybrids in multilocal yield trial, 1995/96.

Variety	Golden Valley	Zamseed Farm	Msekera	Mansa	Senga Hill	Mazabuka	Mean
GV 412	6540	7134	6800	3421	6950	9473	6703
MM 441	8901	8250	7919	4539	6489	10940	8040
GV 512	8439	9306	9160	5849	8211	10720	8614
MM 501	9468	6792	6432	4262	9301	11420	7946
MM 601	9474	11170	6362	6580	13070	11760	9736
MM 604	7836	8624	7357	5689	9996	12350	8642
GV 702	8533	10680	7696	6094	12680	12200	9647
GV 703	10467	10350	8696	6067	10940	13380	9983
GV 704	10422	12380	9072	8444	12682	12390	10898

Source: 1995/96 Maize Research Programme Annual Report.

B46 - Benefits from the Use of Hybrid Maize Technology in Zimbabwe

L. Machida

Department of Research and Specialist Services, Crop Breeding Institute, P.O. Box CY 550, Causeway Harare, Tel 263 4 704531, Fax 263 4 728317

Introduction

Zimbabwe established a hybrid maize breeding programme under the leadership of Mr H.C. Arnold in 1932 (Rattray 1988). The first double cross hybrid in Zimbabwe, SR1, was released in 1948 and yielded 18% more than Hickory King (the most popular open pollinated variety at that time). The single-cross hybrid, SR52, released in 1960 outyielded Hickory King by 60% (Rattray 1988). The success of SR52 made Zimbabwe the first country to grow single cross hybrids commercially (Rattray 1988). The contributions of hybrid maize technology to yield improvement in commercial farming has been estimated as 45% (Tattersfield 1982) and in communal farming 30% (Mashingaidze 1994). It is not easy to measure the impacts of hybrid maize technology in Zimbabwe, but yield trends in the commercial farming sector since the inception of the hybrid maize breeding programme provide some idea of the effects of hybrid maize in Zimbabwe.

Materials and Methods

We used annual statistics of maize production, area, and percent area planted to hybrids dating as far back as 1913/14 (courtesy of the Ministry of Agriculture). Annual average yield levels in metric tonnes per hectare in the farmers fields were calculated by dividing total maize production per year by total maize area per year.

Results

Before the hybrid phase, average maize yields fluctuated between 0.8 and 1.8 t/ha (Figure 1). However, after the introduction of double cross hybrids, yields started rising beyond 2.0 t/ha. With the introduction of SR52 in 1960, yields rose to an average 5.0 t/ha. The period of the rising trend in the hybrid adoption coincides with the period of rising yield levels. Yields leveled off when hybrid adoption reached 100%.

Conclusions

The adoption and use of hybrid maize in Zimbabwe clearly increased maize yields. In addition, it led to the establishment of a highly developed seed industry which has benefitted farmers through improved services. Hybrid technology has also facilitated the release of new hybrids through use of inbred lines in hybrid combinations and backcross programmes. The use of hybrid maize technology also means that Zimbabwe is in a better position to utilize biotechnology in maize improvement. However it should be acknowledged that other disciplines -- including soil productivity, agronomy, extension, crop protection, and seed services -- also contributed to yield improvements by providing an environment favourable for hybrids to express their potential, and these disciplinary contributions are difficult to separate from those of hybrid technology.

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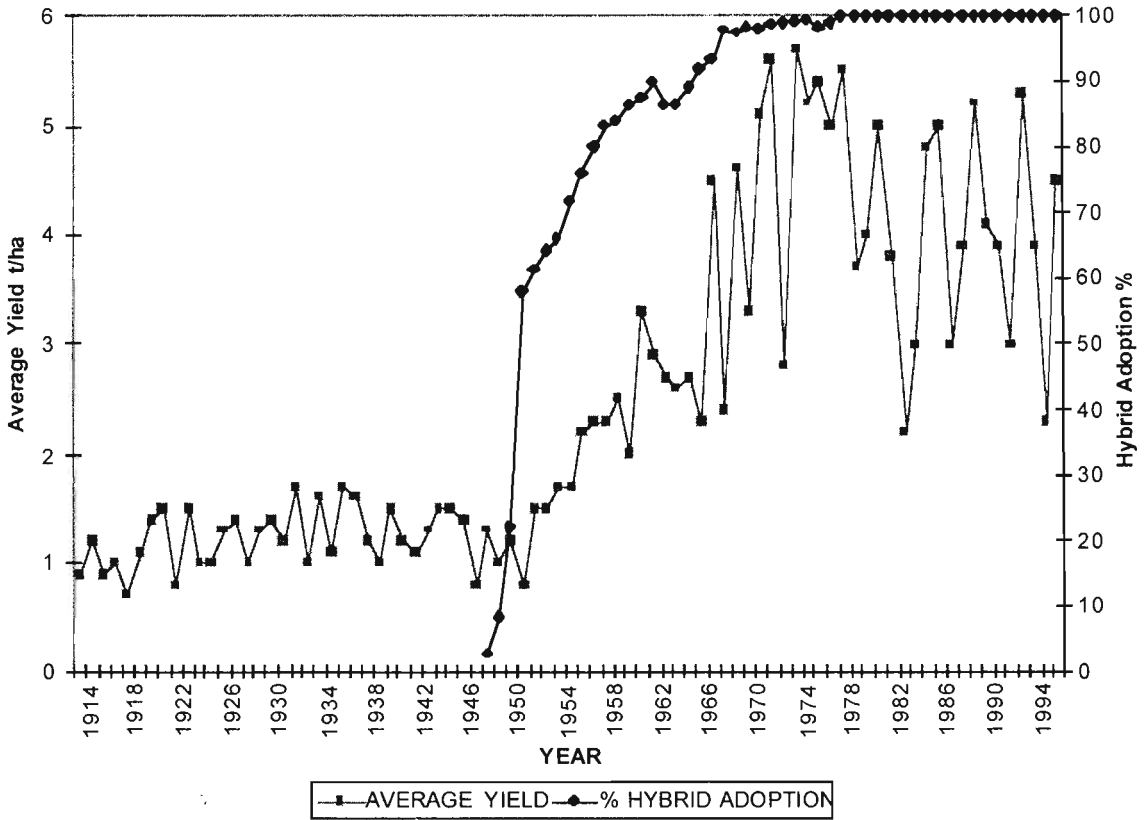


Figure 1. Annual average maize yields (1914-1996) and hybrid adoption (1948-1996), Zimbabwe. (Source: Ministry of Agriculture, Zimbabwe).

Temperate Maize and Heterosis

A.R. Hallauer

Department of Agronomy, Iowa State University, Ames, IA 50011-1010, USA

Introduction

The expression of heterosis in maize for temperate areas was first reported by Beal (1880) with crosses between open-pollinated cultivars. Interest in the potential of cultivar crosses was continued, but the more or less random crossing of pairs of cultivars did not provide consistent evidence that cultivar crosses were distinctly superior to the open-pollinated cultivars themselves (Richey 1922). Possible reasons why cultivar crosses were not more widely accepted and used include the choice of cultivars to produce cultivar crosses, experimental techniques to measure differences between cultivars themselves and their crosses, and the phenotypic similarity of the cultivars themselves and their crosses. Methods to exploit the expression of heterosis in temperate maize were suggested by of Shull (1909) and Jones (1918); i.e., development of pure lines (inbred lines) and their evaluation in crosses. During the 1920s, extensive research efforts were initiated by the state agriculture experiment stations and the U.S. Department of Agriculture to test the concepts of Shull (1909) and Jones (1918). Double-cross hybrids were made available to the growers in the 1930s. By 1950, nearly 100% of the U.S. Corn Belt maize area was planted with double-cross hybrids.

Development of Breeding Methods

The breeding procedures suggested by Shull (1909) and Jones (1918) were used, but it became evident that it was easier to develop inbred lines than to determine their relative merits in crosses. Studies were conducted to determine if relations between yields of inbred lines and their crosses, between plant and ear traits of inbred lines and their crosses, and between inbred line plant and ear traits and yield of their crosses. Generally, the relations were small and inconsistent. Methods were developed to evaluate combining ability of inbred lines in testcrosses (Jenkins and Brunson 1932), to predict double-cross hybrid performance (Jenkins 1934), and at what stage of inbreeding to evaluate lines for combining ability (Sprague 1946). Eventual value of the inbred lines, therefore, was determined by their performance in crosses. Breeding methods developed during this period have become standard methods to evaluate the potential of inbred lines in crosses. The major change was the replacement of double-cross hybrids with single-cross hybrids.

Heterotic Groups

The concept of heterotic groups in temperate areas gradually evolved from empirical evidence of crosses among inbred lines. It was determined that hybrids produced from inbred lines having different origins (i.e., developed from different open-pollinated cultivars) tended to have greater, consistent yield levels than hybrids of inbred lines originating from the same source population. Level of relatedness, or diversity, suggested that hybrids should include inbred lines that have different origins. In its simplest form, Falconer (1981) demonstrated that heterosis can be expressed as $\Sigma y^2 d$, where d is the level of dominance and y^2 is the difference in allele frequency of the parents. Dominance is expressed for most traits of maize. The relative magnitude of heterosis expressed in crosses, therefore, depends on differences in allele frequencies. Empirical data and theory suggest the importance of heterotic groups, and they are considered in breeding programs for developing superior hybrids. But the distinctiveness of the heterotic groups is not always clear because of earlier intermatings of lines between groups.

Conclusion

The expression of heterosis in hybrids has been exploited to the fullest extent in temperate areas. Breeding methods have evolved to identify superior genotypes that are recycled to enhance the distinctiveness of heterotic groups. Genetic progress has been realized in developing improved inbred lines and hybrids since the introduction of the double-cross hybrids during the 1930s. Refinements in breeding methods, recycling of superior genotypes, and persistence of adequate genetic variation suggest that genetic improvements in hybrids can continue.

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Tropical Maize and Heterosis

S.K. Vasal¹, H. Cordova², S. Pandey², and G. Srinivasan²

¹ CIMMYT, Asian Regional Maize Program, P.O. Box 9-188, Bangkok 10900, Thailand

² Maize Program, CIMMYT, Apdo. Postal 6-641, 06600 Mexico D. F., Mexico.

The use of hybrid technology in tropical maize dates back to the early 1950's. The past hybrid research in tropical maize has witnessed successes, failures and slow evolution, due mainly to shifting emphasis on population vs hybrid research, lack of seed production infrastructure, difficulties in producing parental and hybrid seed, insufficient hybrid superiority, and, more recently, reduced research funding for public institutions. Developing countries that have made significant advances in the use of hybrid technology include Brazil, China, Thailand, Kenya, Vietnam, Venezuela, Egypt, Turkey, El Salvador, and Zimbabwe. Current hybrid options being exploited in developing countries range from non-conventional to conventional (multiparent to two-parent hybrids).

Tropical maize germplasm available for hybrid development is voluminous but generally does not tolerate inbreeding well. Thus, good tropical maize lines have been difficult to develop. The need to develop hybrid-oriented source germplasm has been emphasized and several appropriate strategies for achieving this suggested (Vasal 1993; Vasal et al. 1995). Useful tropical maize germplasm and associated heterotic patterns have been documented (Wellhausen 1978; Goodman and Brown 1988). Such information on recently developed and improved germplasm at CIMMYT and elsewhere has also been published (Vasal et al. 1986; Pandey and Gardner 1992), but the available information on superior tropical maize inbreds, their heterotic patterns, and testers is not extensive.

New methodologies and efforts that promise to have large impacts on the exploitation of hybrid technologies in developing countries include a rapid shift from intra- to interpopulation selection, better integration of population improvement and hybrid research, availability of newer and better germplasm sources for extraction of inbred lines, more efficient methods for inbred development and enhancement (including use of inbred evaluation nurseries and of molecular technology), and opening of global markets enhancing the opportunities for the private sector to invest in production and marketing of hybrid seed. Hybrids are now being tested in regional and international trials (Cordova et al. 1996) and the availability of superior hybrids in recent years has greatly increased (Table 1). CIMMYT has made 366 inbred lines (designated CIMMYT maize lines, or CMLs) with adaptation to varying climatic conditions available to its research partners, increasing the availability of superior inbreds as well (Table 2). Germplasm with tolerance to drought, low N, acid-soils, and to other diseases and pests is now available to develop inbred lines (Edmeades et al. 1995). Exotic (especially temperate) germplasm is being used to develop lines and hybrids for the tropics. The spread of two-parent hybrid maize technology in recent years in some countries has been dramatic and encouraging.

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Table 1. High-yielding hybrids in the International trials for white (CHTTW) and yellow (CHTTY) grain maize hybrids, 1994.

Trial No.	Number of locations	Hybrid code	Yield (Mg ha ⁻¹)	Best check (%)
CHTTW	26	CML 247 x CML 254	6.97	112
		CML 247 x CML 274	6.94	111
		CML 264 x CML 273	6.87	110
		CML 264 x CML 258	6.74	108
CHTTY	32	CML 287 x CL-00331	5.67	103
		CML 287 x CML 298	5.41	98
		CML 287 x CL-02808	5.34	97
		T4A* x CML 297	5.35	97

* T4A = Pop. 24 C5HG219 x Pop. 36 C5HC279.

Table 2. Means for grain yield and other characters of yellow inbred lines developed from different source populations.

Material	No. of lines	Grain yield (Mg ha ⁻¹)	Days to 50% silking	Plant ht. (cm)	Moisture (%)
Population 24	12	3.30	60	157	23.0
Population 27	5	3.80	62	171	23.8
Population 36	5	4.05	59	175	21.6
Population 79	1	3.56	62	168	25.0
Population 28 TSR	8	3.05	63	158	22.3
Pool 22	3	2.81	60	145	21.7
Sint. Amar. TSR	30	3.37	61	162	24

Heterosis in Important US Vegetable Crops

T.C. Wehner

Department of Horticultural Science, Box 7609, North Carolina State University, Raleigh, NC 27695-7609, USA

Introduction

Some of the earliest research on heterosis was in the vegetable crops. Hayes and Jones reported hybrid vigor for fruit size and number in cucumber in 1916. In 1936, Jones and Emsweller discovered cytoplasmic male sterility in onion, making hybrid production economical. Growers adopted hybrid cultivars rapidly when they were made available by the seed industry. However, hybrid cultivars have not been exploited commercially as much in self-pollinated vegetable crops as in cross-pollinated ones. Major self-pollinated vegetable crops in the USA include the legumes (bean, *Phaseolus vulgaris*; pea, *Pisum sativum*), Solanaceae (eggplant, *Solanum melongena*; pepper, *Capsicum annuum*; tomato, *Lycopersicon esculentum*), and lettuce (*Lactuca sativa*). Cross-pollinated vegetable crops include the cucurbits (cucumber, *Cucumis sativus*; melon, *Cucumis melo*; squash, *Cucurbita* spp.; watermelon, *Citrullus lanatus*), the Cole crops (broccoli, cabbage, cauliflower; *Brassica oleracea*), root and bulb crops (carrot, *Daucus carota*; onion, *Allium cepa*), asparagus (*Asparagus officinalis*), and spinach (*Spinacia oleracea*). Advantages of hybrid cultivars in the vegetable crops include expression of heterosis for yield and other traits, protection of proprietary parental lines, combined expression of dominant alleles from the parents, and production of unique traits from the parents. For this discussion, the vegetable crops will be grouped according to their use of heterosis: self-pollinated with few seeds per cross, self-pollinated with many seeds per cross, cross-pollinated with little outcrossing, or cross-pollinated with much outcrossing.

Self-pollinated, few seeds per cross

In some of the self-pollinated vegetable crops, such as bean, pea, and lettuce, there has been no use of heterosis or hybrid cultivars. In those crops, self-pollination occurs naturally, cultivars are inbred lines, there is no inbreeding depression, cross-pollination is difficult (other than controlled crosses in a breeding program), little heterosis is expressed for yield, and no economical mechanism exists for mass production of hybrid seeds. In **bean** and **pea**, the cultivars are inbred lines. Generally, there is no heterosis or inbreeding depression for yield. Hybrids are difficult to produce because of perfect flowers that enclose the stamens and style. In bean, efforts have been unsuccessful to incorporate the extrorse stigma (stigma facing away from pollen) trait from the (naturally outcrossing) scarlet runner bean (*Phaseolus coccineus*). Extrorse stigma might provide a way to make hybrids economically to protect proprietary inbred lines developed by seed companies. Opportunities for hybrid production are even worse in **lettuce**, where only 10 to 20 seeds are produced per pollination, and 250,000 seeds/ha are required to plant the crop. The pollen is sticky, and is not carried by insects or wind. Also, some of the important traits (lettuce mosaic and corky root rot) are controlled by recessive genes, making it necessary to incorporate them into both parents of the hybrid.

Self-pollinated, many seeds per cross

In the Solanaceae, important crops such as **eggplant**, **pepper**, and **tomato** have been easily adapted to hybrid production. In those crops, hand pollination is easy, many seeds are produced from each cross, and significant heterosis is expressed for important traits like yield (estimates average 60% for eggplant and tomato and 35% for pepper). In those crops, hybrid cultivars are being produced widely.

Cross-pollinated, little outcrossing

In the Cucurbitaceae, crops such as cucumber, melon, squash, and watermelon have been adapted to hybrid production. In those, cross-pollination is easily enforced, often there are methods for mass production of hybrid seeds, many seeds are produced from each cross, and heterosis is usually expressed for important traits like yield. In cucumber, there is no inbreeding depression and little heterosis. However, hybrids are used to provide gynoecious sex expression and for protection of proprietary inbreds. Hybrids are made by crossing gynoecious with monoecious inbreds in isolation using bees as pollinators. A major advantage of this system is that the hybrid is gynoecious, producing more pistillate nodes than normal cultivars. The extra pistillate nodes give gynoecious cultivars an advantage in early yield, and are useful for once-over harvest production systems. Gynoecious hybrids have been produced in melon, but inheritance of sex expression is different than in cucumber. It has been difficult to stabilize sex expression in melon for reliable production of hybrids. Also, pistillate flowers produce oval fruits, and the market demands the round fruits produced by perfect flowers. Since there is only 8% heterosis, and no inbreeding depression, and because of the difficulties with hybrid production, most cultivars are andromonoecious inbreds. Summer squash (*Cucurbita pepo*) hybrids are produced using two monoecious inbreds. One is converted to gynoecious sex expression by spraying it with ethrel at the 2 and 4 leaf stages. That system does not work well for winter squash (*C. maxima* and *C. moschata*), so most cultivars are open-pollinated. Watermelon hybrids are made by hand pollination, although male sterility is being researched for possible reduction in labor requirement. Hybrids provide greater uniformity in crop production than open-pollinated cultivars, and protect proprietary parental inbreds. However, much of the industry is now using hybrids between tetraploid and diploid inbreds as a method for producing seedless (triploid) cultivars.

Cross-pollinated, much outcrossing

The Cole crops (broccoli, cabbage, and cauliflower), root and bulb crops (carrot, onion), and other crops (asparagus, spinach) in this group have been adapted to hybrid production using diverse methods. In these crops, pollination control is difficult, but methods have been developed for mass production of hybrid seeds. However, hybrids are often earlier and more uniform than open-pollinated cultivars, and heterosis is expressed for important traits like yield. Heterosis of 12 to 15% occurs in broccoli, cabbage, and cauliflower, and they express some inbreeding depression. Those crops have sporophytic self-incompatibility to enforce outcrossing, but bud pollination can be used to self-pollinate plants. Hybrids are produced by planting two self-incompatible inbreds in isolation. Seeds harvested from the two lines are mostly hybrid. Hybrids were adopted widely by growers because of increased uniformity and earliness, permitting fewer harvests of the crop. Unfortunately, self-incompatibility does not always prevent self-pollination, so the parent plants can be found in production fields. Because of that, breeders have begun using cytoplasmic male sterility for hybrid production. Beet and carrot express much inbreeding depression, so lines usually are not advanced beyond S₅. When cytoplasmic male sterility was discovered, hybrids began to replace open-pollinated cultivars. Hybrids are produced using bees in isolation to move pollen from normal to male sterile inbred lines. Onion was one of the first crops to make use of cytoplasmic male sterility for hybrid production. Onion hybrids are 14 to 67% better than open-pollinated cultivars, and are widely used in the USA (less in Europe). Asparagus has a single gene for control of sex expression, with male (Mm) plants producing higher yield than female (mm) plants, which use some of their energy reserves each year to produce seeds. Since male plants occasionally have perfect flowers, it is possible to self-pollinate males to do progeny testing to develop super males (MM). Hybrids produced by crossing a female line with a super male line will be all male. Males yield 25 to 38% more than females. Also, hybrids can yield 64 to 149% more than open pollinated cultivars. Spinach is 60% outcrossed, and is wind pollinated. Hybrids can be produced using genetic control of sex expression, crossing gynoecious with androecious inbreds. Hybrids show 16 to 20% heterosis over standard cultivars.

Oilseeds and Heterosis

J.F. Miller

USDA-ARS, Oilseeds Research Unit, Northern Crop Science Laboratory, PO Box 5677, Fargo, North Dakota 58105 USA

Introduction

Heterosis, here synonymous with hybrid vigor, is extremely important in producing sunflower hybrids, increasing in importance in rapeseed, and has potential for utilization in producing hybrid soybean. Soybean, rapeseed, and sunflower are the three largest oilseed crops in the world, accounting for approximately 78% of world vegetable oil production. Estimation of heterosis and its role in yield improvement have been made in all three crops. In addition, heterotic patterns and estimates of genetic diversity are equally important in breeding strategies of these oilseed crops.

Discussion

Sunflower. Hybrid sunflower first became a reality in the early 1970s with the discovery of cytoplasmic male sterility and an effective genetic male fertility restoration system. Of the approximately 16.5 million hectares of sunflower grown in the major producing countries, 11.5 million are now planted to hybrids. When hybrid technology becomes available, the switch from varieties to hybrids is usually swift and complete. Heterosis is the number one factor contributing to the switch. As few varieties are now being developed in those countries producing hybrids, heterosis estimations are more difficult. In the USA, hybrid performance compared to the open-pollinated variety Peredovik 92 showed that hybrids averaged 34% heterosis in yield. In several countries sunflower hybrids have a distinct advantage over open-pollinated cultivars in addition to yield. Dominant genes controlling disease resistance need to be present in only one parent of single-cross hybrids. Hybrids have more uniform plant height, flowering date, and seed quality, with uniform height and maturity important for mechanical harvesting and uniform flowering important for chemical control of insects. Hybrids can also have superior self-fertility, increasing yields in areas lacking pollinator populations. Major heterotic groups have been determined, among which the Russian, Argentinean, restorer (wild species derived), and Romanian derived germplasm appear to be the most important (Vear and Miller 1993).

Rapeseed. F₁ hybrids produced by crossing inbred lines have shown heterosis in yield of 30 to 60% over midparents in both spring and winter forms of *Brassica napus* and spring forms of *B. rapa* (Semyk and Stefansson 1983; Grant and Beversdorf 1985). This level of heterosis has resulted in considerable effort to develop commercial hybrids in Canada, Australia, Western Europe, and the USA. Use of hybrids, taking advantage of the degree of heterosis in yield, will be even more important as cytoplasmic male sterility systems, restoration, and efficient seed production become further refined and in place (Downy and Rakow 1987). Using RFLP analysis, 38 of 43 clones tested were polymorphic among cultivars and inbreds of rapeseed (Diers et al. 1996). The 38 clones revealed 90 polymorphic fragments which were used to calculate genetic distance. Seven major clusters were identified and appeared to be grouped together by geographic origin. This clustering was consistent with heterotic responses observed in crosses between these groups.

Soybean. High-parent heterotic responses of 3 to 26% for yield in hybrid soybeans have been reported, with an average of 13% (Burton 1987; Nelson and Bernard 1984). In one study, a hybrid exceeded the yield of the best pure-line cultivar over two years and two locations (Nelson and Bernard 1984). These results provide evidence that hybrid soybean can provide significant heterosis for yield and that future research could be devoted to feasibility aspects. The primary barrier to commercial use of hybrid soybean is the lack of an economical method of seed production, limited pollen transfer by insects, and the sheer amount of hybrid seed needed to plant one hectare, making the cost of seed too high when taking into account the degree of heterosis (Fehr 1987). Genetic diversity patterns of North American

soybean cultivars document the widely held view that Northern and Southern cultivars trace to contrasting genetic bases (Gizlice et al. 1994). However, analyzing coefficient of parentage data with multivariate and regression procedures, the North-South distinction accounted for only 21% of the variability found in soybean pedigrees (Gizlice et al. 1996). Heterotic groups tracing to introduced cultivars from China, Japan, and Korea (Hymowitz and Bernard 1984), could be utilized in choosing parents in breeding programs to increase diversity in soybean cultivar development.

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Wheat and Heterosis

J.P. Jordaan, S.A. Engelbrecht, J.H. Malan, H.A. Knobel

Hybrid Wheat Program, SENSAKO Co-op Ltd., P.O. Box 556, Bethlehem 9700, South Africa

Introduction

The possibility to produce hybrids in wheat has, as in all other crops, met with enthusiasm. Notwithstanding the successes which were dramatic in other crops, wheat hybrids over a period of 30 years have not been successfully commercialized. This unfortunate situation was mostly caused by highly competitive and successful research in the public sector achieving genetic improvement of wheat at a constant rate by using conventional techniques and procedures; apathy from wheat breeders to adopt to procedures fundamental to success in hybrid development, and also the erosion of genetic diversity caused by the introgression of genetic unrelated germplasm in a background with acceptable adaptation, milling and baking characteristics.

Hybrid Technology

Many breeders and institutions have withdrawn from research on wheat hybrids. Those who have persisted are experiencing positive results achieved by adaptation of improved technology to exploit genetic diversity and effective selection procedures for heterosis. Different characteristics in parent pools were combined in hybrids to be complementary, resulting in overall higher yields and better disease expression. In some cases the production techniques and technology have been devised to exploit heterotic expression at lower seeding rates, and raise yield potential to be responsive to environmental changes.

Genetic Engineering Options

Intervention by genetic engineering is necessary to address major problems encountered in the hybrid approach: the use of molecular markers to effectively identify distinct gene pools; identification and transfer of effective CMS restorer genes from the R to the A, B or D genomes; as well as nuclear-encoded male sterility.

Heterosis in Present-day Hybrids

The definition of heterosis and the explanation of its genetic bases are important for heterosis theory. In practice, however, hybrids must outperform conventional varieties to be commercialized. Costs to produce hybrid seed, whatever mechanisms used, must be compared with the net profits from growing hybrids as compared to conventional varieties. These may be improved by selection of hybrids with higher yield potential, by implementing more effective seed production procedures, or adapting cropping systems which feature lower seeding rates. It has been shown lately that wheat hybrids yield significantly more and are more consistent than conventional cultivars, with an increased responsiveness to higher yield potential conditions (Bruns and Peterson 1997; Peterson et al. 1997 and Jordaan 1996). In the SENSAKO program for intermediate wheats, which comprises genotypes showing only a response to photoperiod, hybrids were compared to the two most lately released conventional cultivars. The best hybrid in the trial outyielded the conventional varieties by 28% on average. The linear regression of mean yields was calculated for the hybrid on an environmental index which was regarded to be the mean of the pure lines at each location. A 95% confidence interval was calculated for the hybrids' regression. Adjusting the data base to yield (US\$ ha⁻¹) and correcting relative input costs due to more expensive hybrid seed (1.78 US\$ vs. 0.53 US\$) at a constant seeding rate of 25 kg ha⁻¹ or providing for different seeding rates at different yield potentials (5 kg per ha⁻¹ seed at 750 kg ha⁻¹ yield to 25 kg ha⁻¹ seed at 5000 kg ha⁻¹ yield) did not alter the superiority profile of the hybrid. This confirms that present-day heterosis in wheat can be commercialized.

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Exploitation of Heterosis for Shifting the Yield Frontier in Rice

S.S. Virmani

Plant Breeder cum Deputy Head, International Rice Research Institute, P.O. Box 933, Manila, Philippines

Although heterosis in rice has been known since 1926, the effectiveness of its commercial exploitation to increase varietal yields in this crop has been demonstrated only during past two decades. Currently, heterotic rice hybrids are cultivated on about 55% of the rice area in China and account for 66% of that country's rice production (which is 20% of the world total). During the past four years, India and Vietnam have also started commercializing this technology and plan to cover about 2.5 million ha by 2000 AD.

On an average, about 15% standard heterosis for yield has been observed in rice, resulting in about 1 t/ha extra yield. Heterosis is higher in indica/japonica hybrids than indica/indica or japonica/japonica hybrids. Hybrids can be developed for a range of growth cycles. The yield advantage of hybrids over inbred checks is higher in high yielding environments than in low yielding ones, although percent heterosis may diminish due to the higher mean yields of the check varieties at higher yielding environments. Increased yield in heterotic rice hybrids is due to their increased dry matter (resulting from higher leaf area index (LAI) and higher crop growth rate) and increased harvest index (resulting from their increased spikelet number and grain weight). The increased growth rate of hybrids has been attribute to faster cell division as compared with parents.

The per se performance, genetic diversity and combining ability of parental lines are the criteria used to breed rice hybrids. The genetic diversity of parental lines can now be better determined by using molecular marker technologies. Molecular markers also help in tagging heterotic gene blocks and accumulating these in parental lines to improve their combining ability.

As in other crops, the genetic basis of heterosis in rice has not been understood clearly. It is conceded, however, that dominance, apparent overdominance due to non-allelic interaction, linkage disequilibrium and cytoplasmic-nuclear interactions all contribute. Japanese researchers have reported heterosis for cell division rate in rice caused by dominance and additive gene effects; the mean degree of dominance was higher than unity, indicating expression of overdominance. In recent studies in China, some rice hybrids showed profound alteration of gene expression compared to parental lines as revealed by messenger RNA-amplification. Regulation of gene expression in the hybrid environment includes enhancement, selective transcription, silencing and co-suppression; besides activity of specific genes was found silenced in parental lines.

Cytoplasmic-genetic male sterility is the most effective and widely used genetic tool to commercially exploit yield heterosis in rice. Photo- (PGMS) and thermo-sensitive genic male sterility (TGMS) systems appear to hold promise for the future. Wide compatibility genes are also available to develop inter-varietal group (viz., indica/japonica) rice hybrids with enhanced heterosis. Research on apomixis in rice has to develop true breeding rice hybrids usable by even resource poor farmers.

Rice hybrids with the required level of disease/insect resistance and acceptable grain quality can be developed by choosing appropriate parental lines. Basmati rice hybrids are also being developed in India, Pakistan and IRRI. Low temperature tolerance of hybrids at the vegetative stage makes them adaptable to certain stress environments, including *boro* season (in India, Bangladesh, North Vietnam, and Myanmar). Heterosis observed for early seedling and vegetative vigor and root traits should be helpful for their adaptation to salinity prone irrigated areas and certain drought and/or submergence prone rainfed lowland rice ecosystems.

Rice hybrids are more responsive to basal and mid-tillering N applications than inbred lines. Application of N at flowering increases leaf N concentration, Rubisco content, and photosynthetic rate of flag leaves. Grain filling percentage and yield of tropical hybrid rice is improved significantly by late-season N application. Rectangular planting and increased hill density improved the grain yield of hybrid (but not inbred) rice by enhancing sink size. To attain full expression of yield potential of rice hybrids, specific crop management strategies should be developed.

Economically viable hybrid rice seed production systems are available that yield 1-3 t/ha of hybrid seed in large-scale plots. There appear to be opportunities for further increases in seed yields – yields above 6 t/ha have been reported from China. Being labor intensive, hybrid rice seed production technology can generate rural employment opportunities in developing countries; in high wage and labor scarce countries (viz., USA, Brazil, Japan) prospects of its mechanization are being explored.

Commercial exploitation of heterosis in rice has already made tremendous impact on rice production in China. During the next 5-10 years, it should also make economic impact in those countries with high labor-land ratios and large irrigated areas (viz., India, Vietnam, Philippines, Bangladesh, Indonesia and Sri Lanka). IRRI, FAO and selected national programs have established an international task force on hybrid rice to expedite the process and more fully realize the potential of this technology for helping meet global rice demand in the 21st century.

Hybrid Rye and Heterosis

H.H. Geiger¹ and T. Miedaner²

University of Hohenheim, ¹Institute of Plant Breeding, Seed Science, and Population Genetics, ²State Plant Breeding Institute, D-70593 Stuttgart, Germany

Introduction

Rye (*Secale cereale*) is a major cereal crop throughout many regions of Central and North Europe. The largest areas are in Russia (3.5 mill. ha), Poland (2.4 mill. ha), Belorussia (1.0 mill. ha), and Germany (0.86 mill. ha) (Madej 1996). The world production of rye grain is 29.5 million tons per year and goes mainly for feed and breadmaking. In contrast to most other small grains, rye is a strictly cross-pollinated species. The first experimental data documenting heterosis in rye were published early this century (Fruwirth 1913), but hybrid breeding became possible only after Geiger and Schnell (1970) and Geiger (1972) had detected a source of cytoplasmic genic male sterility (CMS) and dominant fertility restorers, respectively. The University of Hohenheim subsequently began a comprehensive breeding program which led to the release of the first hybrids in 1985. Breeding companies supported this early work and soon set up programs of their own. As a result, the performance of hybrid rye has increased dramatically over the past 15 years (Fig. 1). The most recent hybrids are outyielding the best open-pollinated variety by about 20%. In the late-1970s, early-1980s, hybrid rye breeding was also started in Poland, the former USSR and DDR, Sweden, and Hungary (EUCARPIA 1996). In Germany, about 60% of the rye acreage is presently grown to hybrids.

Heterosis

Rye strongly reacts to changes in the level of heterozygosity. Inbred lines suffer from severe depressions in vigour, and crosses between unrelated inbreds display impressive amounts of heterosis for all developmental and yielding characteristics. Interestingly, the performance/heterozygosity relationship changed greatly since the onset of hybrid breeding 25 years ago. The grain yields of the inbred lines *per se* increased faster than those of their crosses, leading to a decrease not only in the absolute but also in the relative heterosis for grain yield, kernels per spike, and 1000-kernel weight (Table 1). Rye is mainly grown on light, sandy soils and under low input conditions. Relative heterosis for grain yield was significantly higher under low compared to high nitrogen supply (Hartmann 1997) and on sandy compared to loamy soils (Wilde *et al.* unpubl.). When hybrid rye breeding was started in Germany, there were two largely unrelated adapted gene pools, Petkus and Carsten, leading to a 15 - 20% heterotic increase for grain yield in population crosses (Hepting 1978). These pools were used for the development of seed-parent and pollinator lines, respectively. Other populations, particularly from Northeast Europe, were later on integrated into one or the other of these pools according to genetic distance as measured by the heterotic pattern of testcrosses. Average heterosis for quantitative resistance to fungal diseases such as powdery mildew, foot rot, and head blight was found to be small or negligible (Miedaner *et al.* 1995). Resistance breeding, therefore, is necessary in both the seed and pollinator parent pool. Low to medium heterosis was observed for resistance to sprouting (Wehmann *et al.* 1991).

Hybrid seed production

All present commercial hybrids are based on the "Pampa" CMS system. Male-sterile plants produce strongly degenerated, non-dehiscing anthers without any viable pollen. Fertility restoration is still a matter of concern since none of the released hybrids is fully restored and the degree of restoration is significantly affected by the environment (Geiger *et al.* 1995). New exotic sources of restoration are presently being tested for their effectiveness and genetically analyzed by molecular markers. To reduce costs of seed production, a CMS single cross (AxB) is used as seed parent and a restorer synthetic (C) as pollinator parent in commercial hybrid seed production. Absolutely strict pollen isolation is required to multiply the parental inbred lines, to maintain the CMS version of parent A, and to produce the CMS single cross AxB. This is only possible in areas where no rye is grown otherwise. The final (certified) seed

is produced in a mixed stand of about 95% seed parent and 5% pollinator synthetic. The male component cannot be separated from the certified seed .

Conclusions

As a cross-pollinated crop, rye displays high amounts of heterosis for most economically important traits. Hybrids, therefore, soon turned out to be more attractive to farmers than open-pollinated varieties. Continued progress in hybrid breeding steadily increased this superiority and most of the European rye area will likely to be sown to hybrids for the foreseeable future. Further research is needed to improve fertility restoration, disease resistance and feeding quality, and new germplasm sources must be identified and integrated. Modern biotechnological methods, especially DNA marker techniques, offer great promise. Biometrical and population genetic research is required to develop optimum breeding plans that exploit traditional and emerging tools.

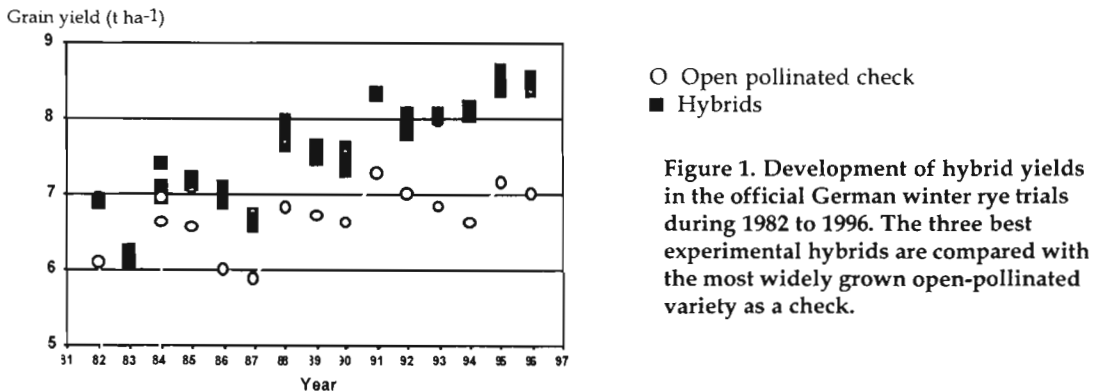
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Table 1. Mean midparent and hybrid values and relative heterosis (midparent value = 100) for grain yield, kernel number per spike and 1000-kernel weight of eight early and fifteen advanced single-cross hybrids (tested across 5 environments in 1974-1975 and across 4 locations in 1997, respectively)

Character	Early hybrids 1974-1975 ¹			Advanced hybrids 1997 ²		
	Mid-parent value	Hybrid value	Relative heterosis (%)	Mid-parent value	Hybrid value	Relative heterosis (%)
Grain yield (t ha ⁻¹)	2.13	6.53	207	4.27	8.14	81
Kernel no. per spike	23.1	56.5	145	35.3	46.7	32
1000-kernel wt. (g)	19.4	29.8	54	28.3	37.2	31

¹ Data from Geiger and Wahle (1978). ² Data from Wilde *et al.* (unpubl.).



Cotton and Heterosis

W.R. Meredith, Jr.

Research Geneticist, USDA-ARS, Box 345, Stoneville MS 38776, USA

Cotton, *Gossypium* species, is a major world field crop and in 1997 is expected to be grown on 33.7 million hectares. Probably 96% of the plantings will be *G. hirsutum* L., and 4% will be *G. barbadense* L. These two species are allotetraploids and are native to the New World. Two Old World species, *G. arboreum* L. and *G. herbaceum* L., are grown mainly in India and Pakistan. In its native habitat, cotton was a perennial, but is grown as an annual in at least 44 countries (Townsend 1997).

Numerous studies have shown that cotton expresses almost the same levels of heterosis as modern corn. Meredith (1984) summarized the yield results from 18 studies and reported an average of 18% heterosis over midparent and a range of 3 to 33%. The yield components that most influenced yield were number of bolls per unit area and boll weight, with an average heterosis of 13.5 and 8.3%, respectively. Heterosis for fiber properties has generally not been significant; heterosis for length, strength, and fineness averaged 2.0, 0.1, and 0.0%, respectively (Meredith 1984). Davis' (1978) review showed that interspecific hybrids of *G. hirsutum* X *G. barbadense* produced high yielding F₁s with superior fiber properties. Interspecific hybrids' length frequently showed dominance, or overdominance, fineness was improved, and fiber strength was greater than in the upland cultivar. The major fiber quality property that showed negative results was the increase in neps (fiber entanglements) of the F₁s over either parent.

The most dependable male sterility system has been the cytoplasmic and restorer factor system from *G. harknessii* Brandg (Meyer 1975). Several applied breeding organizations have attempted to use male steriles to produce hybrids, but none have become commercially successful. Also, attempts in the USA to use male gametocides and commercialize F₂ populations have been unsuccessful. F₂s have the potential to produce populations with yield and fiber quality combinations superior to the best commercial cultivars (Meredith 1990). The possibility that F₂s have a wider range of adaptation has not been adequately studied. Reid (1995) in Australia, reported that F₂s yield over that of their parents' was only greater in lower yielding environments.

In general, the use of heterosis in cotton has not been commercially successful. The exception has been in India. Basu (1995) summarized hybrid research results showing that 42% of India's cotton was produced from F₁ hybrids. He states that the key to its success was "the utilization of the vast labor force, particularly women and children, available in rural India." It is interesting that one of the parents of the first successful hybrid, 'Hybrid 4', was a Stoneville, USA, nectarless strain. The other parent was India G67. In countries where a large labor force is available, the production of F₁s and F₂s seems a viable approach to utilizing heterosis.

Genetic engineering offers at least two methods of utilizing heterosis. The first approach is historical: producing new male steriles and appropriate restorer factors. The second is to make use of the large number of new transgenic, herbicide resistant cottons. It would require having natural crossing nurseries in which transgenic cottons would be used as male parents. The herbicide would be used to remove all non-hybrid plants resulting from the open pollination that occurred on female lines.

There are several reasons for the lack of success in utilizing heterosis commercially. These are lack of dependable male steriles and restorer systems, of good combiners, and of efficient seed production practices. While the first two challenges have been met with some success, the major limiting factor is an economical method of producing F_1 or F_2 seed. The use of heterosis in cotton has not yet reached the level of success envisioned 50 years ago, but it still offers potential for significantly improving the yield, fiber quality, and pest resistance of future cotton cultivars.

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Trees and Heterosis

J.L. Brewbaker and W.G. Sun

Dept. Horticulture, University of Hawaii, 3190 Maile Way, Honolulu, HI 96822; Hawaii Agricultural Research Center, Aiea, HI 96701

Scope of Review

This review grandly assumes its embrace of all species of trees (defined as woody perennials, largely single-stemmed, exceeding 3 m in height). It thus ranges from forest trees to industrial crops, shade trees, fruit trees and trees like *leucaena* that are harvested bimonthly for fodder.

Manifestation of Hybrid Superiority

A useful term applied to the vigor of hybrid trees is "hybrid superiority" (Dieters et al. 1995), that recognizes the enhanced economic value of hybrids (vs. midpoint of parents) as having two major aspects: 1) complementarity, the complementary recombination of parental traits; and 2) true hybrid vigor or heterosis, *sensu strictu*. This review considers both aspects of hybrid superiority, since they are often inseparable. Hybrid superiority appears to characterize one or another trait in all tree species that have been studied, making this review a formidable task. Even more daunting is the fact that yield (e.g., wood, total biomass, fodder) of trees has many components that are virtually unknown (e.g., root biomass), and that can change with time during growth. Given these provisos, hybrid superiority is a commercial fact in most tree genera and notable in eucalypts, poplars, pines, casuarinas, oil palms and *leucaenas*. It is primarily evident from interspecific crosses, which occur with considerable ease in woody genera. Typically more than 50% of interspecific tree crosses produce hybrids (Sorensson and Brewbaker 1994). Seed set and sterility of hybrids is rarely of concern in forest species. Hybrid superiority is common among inter-provenance crosses where genetic distances are relatively large, but generally is reduced as such distances diminish (Wang et al. 1996).

Complementarity in Hybrid Superiority

Complementarity is perhaps a major component of hybrid vigor in most trees, since they are customarily grown for long duration in polymorphic ecosystems with very limited environmental control (Wang et al. 1996). The homeostatic properties of hybrid systems thus become of great importance. An example from species of *Larix*, the larch, where 33-year old European hybrids have three times the biomass of the parent species:

<i>Larix</i> species	<i>L. decidua</i>	<i>L. leptolepis</i>	Hybrids
Needle size	Small	Large	Large
Needle Number	High	Low	High

A second example from the tropical genus, *Leucaena*, where hybrids exceed the parents in range of adaptability:

<i>Leucaena</i> species	<i>L. pallida</i>	<i>L. leucocephala</i>	Hybrids
Cold tolerance	High	Low	High
Heat tolerance	Low	High	High
Psyllid resistance	High	Low	High

Heterosis in Hybrid Superiority

Heterosis in tree growth is evident in many hybrids and perhaps best illuminated in studies of *Populus*, the genus of poplars and aspens. New analytical methods to estimate the number of quantitative trait loci (QTLs) affecting traits in trees and their additive and dominance effects are being developed (Li and Wu 1996). Increasing importance is being attributed to the role of a few major QTLs in heterosis that

have a higher probability of dominance and epistatic effects (Bradshaw and Stettler 1995). It is clear that many minor QTLs affect traits involved in the wood yield increases of hybrids. Multiple allelism is recognized increasingly as a fact for most QTLs in highly-outcrossed tree species, in alleles that differ greatly between species. There is continuing debate about overdominance among major QTLs, and suspicion that pseudo-overdominance (POD) is in fact the cause. POD involves interactions in hybrids between beneficial dominant alleles and deleterious recessives at closely-linked loci, an automatic feature for example of chromosomes bearing the S locus in self-incompatible species (common among woody perennials). Additive effects characterize most hybrid vigor, but the role and importance of dominance varies greatly. There is much evidence that multiplicative gene interactions affect composite traits such as wood yield (Li and Hu 1996). Standardization or transformation can minimize such scale effects (Dieters et al. 1995), but can also obscure the true nature of gene interactions both within and between loci (epistasis). Thus, the nature of gene action underlying heterosis in trees is not well or easily understood (Namkoong and Kang 1990).

Utilization of Hybrid Superiority

The ability to market cloned hybrids is essential to commercialization of many trees, and breeding for clonability becomes a requisite exercise. The use of vegetatively propagated F_1 hybrids is extensive in *Eucalyptus*, *Populus* and *Pinus* spp. In many instances seedlessness is associated with hybrid superiority of ornamental or fruit trees; e.g., sterility of 3N hybrids in bananas or in leguminous ornamentals (e.g., *Cassia*, *Plumeria*). Seedless triploid interspecific hybrids show superior wood production in *Leucaena*, where the legume pods represent a major carbon sink (Sorensson and Brewbaker 1994). The use of F_2 populations can be economic; e.g., interim use of non-inbred hybrids of *Pinus elliotii* x *P. caribaea* (Nikles 1993). Advanced generation populations of hybrids, analogous to synthetics (or composites) in maize, are being marketed from inbred-derived F_2 s of the polyploid *Leucaena leucocephala*, where heterosis is only slightly less than F_1 hybrids and a broad-germplasm base is required.

Breeding Strategies for Hybrid Superiority

Tree improvement goes through phases familiar to all breeders, but hybrid development normally lacks an extended phase of inbreeding due to high genetic loads (Wang et al. 1996). Maize breeders are familiar with similar loads in native racial materials, and must resynthesize from inbreds to create "inbreeding-tolerant" populations. However, selfed families can be a good index of hybrid performance. Sublining has been practiced within tree populations to minimize inbreeding (Namkoong and Kang 1990). The question of the value of reciprocal recurrent selection in tree improvement is open to debate, since contributions of dominance seem generally to be small. Added to the concepts of general combining ability (GCA), foresters speak of general hybridizing ability (GHA) in relation to interspecific hybrids. GCA within species is not always a good predictor of GHA for stem form and yield in trees. Breeding schemes that combine recurrent selection for GCA with cycles of GHA evaluation, if they can be performed economically, perhaps best optimize genetic gains (Dieters et al. 1995).

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B48 - Heterosis and Combining Ability among White Maize Elite Inbred Lines

J.G. du Plessis

ARC-GCI, Private Bag X1251, POTCHEFSTROOM 2520, Republic of South Africa

Introduction

Much of heterosis is fixable in cross-fertilized plants (Gallais 1988). To exploit different sources of variability, it is necessary to improve *per se* values of lines and their combining abilities. Crosses of unrelated inbred lines of maize show greater heterosis than crosses of related lines (Moll et al. 1962). This study was to obtain information on the combining ability for quality characteristics in white elite maize lines (du Plessis 1993), using yield and kernel density data.

Methods

The parental material consisted of seven white maize elite inbred lines, three of which had one parent in common, two had a further common parent, whereas the other two were genetically unrelated to any other line. These lines represented the K-, M- and F-heterotic groups of the Agricultural Research Council, Grain Crops Institute (ARC-GCI). The K-heterotic group has the open pollinated variety, Pride of Saline, as an ancestor; M- was developed from a white conversion of the Australian line 21A; and F- has white conversions developed from the open pollinated variety, Teko Yellow. All possible crosses were produced by hand pollination. Two dryland trials were conducted during the 1988/1989 season, at the climatically different localities Ukulinga (29° 44'S, 30° 24'E) and Potchefstroom (25° 03'S, 31° 07'E). At Potchefstroom plots consisted of four 15-hill rows, equivalent to a stand of 2.3 plants/m². Only the two centre rows of each plot were harvested. At Ukulinga plots consisted of three 30-hill rows, equivalent to a stand of 4 plants/m². The centre row of each plot was harvested. The trials were hand harvested. Grain yield was calculated from ear mass assessments, using the calculated shelling percentage and adjusted to 12.5% moisture. Kernel density determinations were made using a modified cage method (du Plessis 1994) developed by Wessel-Beaver, Beck and Lambert (1984). Griffing's Model I (F₁, reciprocal crosses and parents), was used to estimate genetic effects.

Results

Analysis of variance computed for both traits showed significant differences over localities, and among hybrids. The combining ability analysis suggested the presence of significant variation due to general combining ability (GCA) for kernel density (Table 1). Only K64R-22 and M162W had a GCA effect significantly greater than zero for grain yield. Estimations for specific combining ability (SCA) for yield indicated that the majority of crosses showed significant variation (Table 2). Variation for kernel density was much lower (Table 3). All crosses were highly heterotic for yield, as they performed significantly better than the best parent; little heterosis for kernel density was detected (data not shown).

Conclusions

Inbreeding resulted in the accumulation of non-additive genes for yield, which can be utilised in specific crosses. The low heterosis for kernel density may be the result of the high standards for grain quality set by breeders in the RSA.

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Table 1. Estimates of general combining ability (GCA) effects (g) among seven white maize elite inbred lines evaluated for yield and kernel density at Potchefstroom and Ukulinga.

	Potchefstroom		Ukulinga	
	Yield (kg ha ⁻¹)	Kernel density (g ml ⁻¹)	Yield (kg ha ⁻¹)	Kernel density (g ml ⁻¹)
Parents				
K64R-22	-1.0181**	-0.0046**	-0.7236*	-0.0024
M37W	0.2603	0.0157**	0.4264	0.0200**
M162W	1.0665**	-0.0043**	0.4290	-0.0105**
P3	0.5029	0.0150**	-0.1115	0.0102**
P157	-0.0764	-0.0191**	0.1509	-0.0186**
P213-7	-0.2785	-0.0060**	0.1919	-0.0050*
P217-8	-0.4566	0.0033	-0.3631	0.0064**
* and ** indicate significance of difference at P = 0.05 and P = 0.01 respectively.				
	μ	SE _(parents)	LSD _(0.05)	LSD _(0.01)
Yield(P)	5.7883	0.2624	0.5143	0.6717
Yield(U)	5.2055	0.3178	0.6228	0.8135
Kernel density(P)	1.233	0.002	0.0036	0.0048
Kernel density(U)	1.214	0.002	0.0040	0.0053

Table 2. Estimates of specific combining ability (SCA) effects among seven white maize elite inbred lines evaluated for yield, combined over the locations Potchefstroom (above diagonal) and Ukulinga (below diagonal).

Parent	K64R-22	M37W	M162W	P3	P157	P213-7	P217-8
K64R-22	-	0.853**	-0.495	0.069	1.069**	0.447	-0.194
M37W	1.663**	-	1.757**	-1.733**	0.499	1.252**	0.891**
M162W	-0.588	0.791*	-	1.217**	0.462	0.849**	0.682**
P3	0.360	-1.502**	1.634**	-	1.215**	1.834**	0.565*
P157	0.462	1.066**	0.755**	1.278**	-	-0.553*	0.453
P213-7	1.336**	0.998**	1.589**	-0.244	0.315	-	0.280
P217-8	-0.322	0.970**	-0.696*	1.107**	0.705*	0.779*	-

* and ** indicate significance of difference at P = 0.05 and P = 0.01 respectively.

Potchefstroom: LSD P_{0.05} = 0.514, LSD P_{0.01} = 0.672.

Ukulinga: LSD P_{0.05} = 0.623, LSD P_{0.01} = 0.814.

Table 3. Estimates of specific combining ability (SCA) effects among seven white maize elite inbred lines evaluated for kernel density, combined over the localities Potchefstroom (above diagonal) and Ukulinga (below diagonal).

Parent	K64R-22	M37W	M162W	P3	P157	P213-7	P217-8
K64R-22	-	0.0203**	-0.0031	0.0093	0.0100	0.0103	0.0043
M37W	0.0267**	-	-0.0050	-0.0126*	0.0002	-0.0083	0.0074
M162W	0.0055	0.0048	-	0.0024	0.0065	-0.0133*	0.0007
P3	0.0031	-0.0109	0.0162*	-	0.0005	-0.0043	0.0115
P157	0.0169*	-0.0138*	0.0084	-0.0040	-	-0.0002	0.0155**
P213-7	0.0184**	-0.0123	0.0031	-0.0076	0.0112	-	0.0174**
P217-8	-0.0047	0.0162*	-0.0116	0.0210**	0.0048	0.0279**	-

* and ** indicate significance of difference at P = 0.05 and P = 0.01 respectively.

Potchefstroom: LSD P_{0.05} = 0.015, LSD P_{0.01} = 0.019.

Ukulinga: LSD P_{0.05} = 0.016, LSD P_{0.01} = 0.022.

B49 - Heterosis and Combining Ability of Elite Highland Maize Lines Under Nitrogen-Stress vs. Non-Stress Conditions

G. Srinivasan¹, J.L. Torres¹, and M. Bänziger²

¹CIMMYT, Mexico, ²CIMMYT, Harare, Zimbabwe

Introduction

Maize is grown in approximately 6.5 m. hectares in tropical highlands in developing countries (CIMMYT 1988). Because of the various risks involved in highland environments, the farmers usually plant these maize under resource-poor conditions. Drought and low soil nitrogen are two of the most important yield limiting factors faced by farmers in the highlands (Eagles and Lothrop 1994). The high cost of inorganic fertilizer and lack of adequate credit facilities coupled with remoteness of the highland maize growing areas makes it extremely difficult for highland farmers to provide the soil nutrients needed. An economically viable and environmentally friendly alternative is to improve maize germplasm for nitrogen-use efficiency. CIMMYT has made significant progress in identifying lowland tropical source germplasm which shows a high level of tolerance under low-N conditions (Lafitte and Edmeades 1994 a,b) and, through recurrent selection, has made significant improvements for this trait in selected germplasm. Encouraged by these results, a concerted effort was started in 1996 to screen diverse elite germplasm for tolerance to low-N under highland environments.

Materials and Methods

Soil nitrogen from the experimental block G-10 at El Batán, Mexico was systematically depleted by growing a maize crop during the main season (April-Nov) in 1995 followed by a winter crops of oats without any added nitrogen. The crop residues were removed from the field to avoid any nitrogen from the stover. During the 1996 main season, the first experimental plots of maize were grown under low-N conditions. An adjacent field was designated as control where nitrogen was applied using the normal recommendations. To increase the stress, an adjacent crop of wheat was drilled on the side of the ridge next to the maize crop. Results from three 10 x 10 diallel studies are presented here. The 30 parents used for the study were advanced generation inbred lines with early maturity and white semi-dent grain type and developed for the highland environments of Mexico. The diallel crosses were made during 1995 cycle and the reciprocal crosses (eg. P1 x P2 and P2 x P1) were mixed. Each of the three diallels had 45 crosses, and 4 checks were planted in a 7 x 7 square lattice design with three reps. The plot size was 5 m rows planted 0.75 m apart with a plant to plant spacing of 20 cm; a plant density of 66,000 plants per hectare. Each of the three diallels was planted in four environments: low-N, and high N at the CIMMYT experimental station at El Batán, Mexico (2,150 masl); Metepec, Toluca (2,650 masl); and Aguascalientes (1,800 masl). Data on grain yield (t/ha.), anthesis-silking interval (ASI), plant and ear height are reported. General combining ability (GCA) and specific combining ability (SCA) effects were calculated for these four traits using Griffing's Model IV analysis (Griffing 1959).

Results

The mean grain yield of hybrids in the three diallels across all four environments was 7.5, 8.2, and 8.8 t/ha for diallels 1, 2 and 3. The best hybrids yielded as high as 12.4 t/ha. Yield comparisons between low-N and high-N environments showed a yield reduction of 45% in diallel 1, 50% in diallel 2 and only 30% in diallel 3. Among the 135 single-cross hybrids tested, there was a wide range of variability both for yield potential and yield reduction under low-N conditions, used as a simple and practical measure of tolerance to the N stress. Other secondary traits measured such as senescence score, leaf chlorophyll content, ASI, ear number were all correlated with this yield response. Both the GCA and SCA effects for yield were highly significant for all trials. However the ratio of GCA/SCA - a measure of additive vs. dominance effects -- revealed that under stress conditions in all the three diallels there was a higher additive effect relative to dominance gene effects (Table 1). However, in all the other three environments under normal conditions, in most cases there was a much higher dominance effect as shown by a higher SCA sum of squares relative to the GCA sum of squares. Similar results have been

observed for other abiotic stresses such as drought. The performance of the lines under four environments showed that GCA for grain yield was quite variable in most inbreds. However, one line, CML 349, stood out as a consistent high combiner for yield across environments. This line was made available by the CIMMYT Maize Program to its research partners in May 1997, and is being used extensively as a male parent in several of the elite single- and three-way cross hybrids under on-farm testing in farmers' fields.

Conclusion

These three diallel trials have helped us in identifying a few elite inbred lines which show a high level of tolerance to low-N stress. Promising hybrids for such environments have been also identified and, with the diverse germplasm that is available to CIMMYT, the likelihood of identifying good sources of tolerance to abiotic stresses such as low-N is good. With the private and public sector maize researchers starting to use some of these elite lines, we are optimistic that the high level of heterosis shown in some of these CIMMYT lines could be used as potential parents for crossing with national program germplasm.

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Table 1. GCA and SCA sums of squares for grain yield (t/ha) for diallels 1, 2 and 3 under four environments, 1995.

Trial	Source and D.F.	Low N (El Batán)	High N (El Batán)	Aguascalientes	Toluca
Diallel 1	GCA - 9	116.3	127.2	77.1	46.9
	SCA - 35	86.6	221.7	108.6	78.4
Diallel 2	GCA - 9	146.4	131.7	45.9	77.1
	SCA - 35	76.0	109.2	78.5	108.6
Diallel 3	GCA - 9	255.6	307.2	237.9	222.6
	SCA - 35	168.9	348.8	211.9	138.9

Table 2. GCA for grain yield (t/ha) of inbred lines showing significant positive GCA from three diallel trials in four environments, 1995.

Trial	Pedigree	Low N (El Batán)	High N (El Batán)	Aguas-calientes	Toluca
Diallel 1	Pob.85 C3 HC36-3-2-1-1-3-b	0.5	0.7	-0.3	0.5
	HTBA89 43-1-1-2-1-3-b	0.6	1.5	0.4	-0.5
	Pob.800C5 HC37-3-4TL-1-1-1TL-b-b	1.2	0.5	-0.7	0.3
	CML 246	0.2	-0.8	1.1	0.3
Diallel 2	Pob.85 C3 HC36-3-2-2-2-b	1.1	0.5	-0.3	0.9
	HTBA89 48-1-1-2-1-1-b	-0.1	0.9	0.3	-0.1
	CML 242	0.0	-0.2	1.4	-0.2
Diallel 3	CML 349	2.7	2.2	1.0	1.7
	CML 244	0.2	0.2	1.5	0.2

B50 - Heterosis in Acid Soil-Tolerant Maize Germplasm

L. Narro, S. Pandey, C. De León, J.C. Pérez, F. Salazar, and M.P. Arias

South American Regional Maize Program, Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT), Apdo. Aéreo 6713, Cali, Colombia

Introduction

Maize is planted on 8 to 20 million ha of acidic soils (Pandey et al. 1994; Salazar et al. 1997), characterized by subsistence farming and yields of less than 400 kg/ha. Acidic soils have poor agricultural quality due mostly to their low pH, their Al and Mn toxicities, and their deficiencies of Ca, Mg, and P. Soil acidity can be corrected through the application of alkaline compounds such as lime; but acid tolerant maize cultivars provide an efficient, ecologically clean, less costly remedy, and complement liming, where available. The yield potential of acid tolerant, open pollinated varieties on acid soils is about 3 t/ha; that of acid tolerant hybrids is over 5 t/ha. We report here on the heterotic patterns of our acid tolerant germplasm and the use of heterosis to develop tolerant hybrids.

Materials and Methods

Up through 1995, three yellow (SA3, SA4, and SA5) and three white (SA6, and SA7, and SA8) tropical maize populations were improved for grain yield and tolerance to soil acidity, using S_1 recurrent selection with alternate cycles of full sib (FS) recombination. Some 250-300 S_1 lines from each population were evaluated in replicated trials and 5 m row plots under acid conditions (pH 4.2) at 4 locations in Colombia, where Al saturation was adjusted to both 50 and 60% by liming. Major traits considered were seedling vigor, symptoms of Al toxicity and deficiencies in P and other minor elements, plant vigor during growth, and grain yield, with 10% selection pressure at both the S_1 and FS. To define heterotic patterns of the six populations, diallel crosses were made. F_1 s were evaluated in five acid soil environments in replicated trials. Tuxpeño and Eto, one of the most widely used heterotic patterns in the tropics, were also crossed to each population. Populations were considered as fixed and environments as random variables. Gardner and Eberhart's analyses II and III were used for the diallel. For hybrid development and selection of testers, 63 S_6 lines derived from the white and yellow populations were crossed to acid soil tolerant and susceptible varieties, hybrids, and lines. F_1 crosses were tested in replicated trials in both acid and non-acidic soils in South America. Analysis of variance and general and specific combining abilities were determined. In addition, 55 acid soil tolerant yellow lines from each of two known heterotic patterns and a few lines from CIMMYT, Mexico, were crossed in a Design II mating of sets of 5 x 5. The resulting single crosses were evaluated in replicated trials in acid and nonacid soil environments. Variance and general and specific combining abilities were analyzed.

Results and Discussion

The diallel study revealed that yellow populations SA3 and SA5 were heterotic with SA4 and white populations SA7 and SA8 were heterotic with SA6 (Pandey et al. 1994; Salazar et al. 1997) (Table 1). As a result, SA5 with SA3 were merged to develop SA3. Similarly, SA8 was merged with SA7 to develop SA7. The new populations are heterotic to SA4 and SA6, respectively. Crosses of tolerant x tolerant, tolerant x susceptible, and susceptible x susceptible varieties developed in 1990 showed high-parent heteroses of 19.9, 10.4, and 24.7%, respectively. High-parent heteroses among crosses of selections from the same populations made in 1992 were 12.3, 8.1, and 17.2%, respectively. The crosses of these four populations with Tuxpeño and Eto revealed that SA3 and SA7 belonged to Eto heterotic pattern and SA4 and SA6 to Tuxpeño heterotic pattern. Evaluation of hybrids developed for the tester studies and the Design II study revealed that some of the superior hybrids under acid soil conditions also gave superior performance under nonacid soil conditions (Table 2). Some superior hybrids under acid and nonacid soil conditions involved lines with and without acid tolerance. Inbred lines CML 16 and CML 304 and the single-cross CML 247 x CML 254 were developed under nonacid soil conditions. Our data suggest that germplasm selected under both acid and non-acid conditions can be crossed to develop superior hybrids for both soil types.

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Table 1. Average grain yield and high-parent heterosis for crosses between varieties of maize of different genetic backgrounds evaluated under acid soil conditions.

Pedigree	Yield (Mg ha ⁻¹)	High-parent heterosis (%)	Pedigree	Yield (Mg ha ⁻¹)	High-parent heterosis (%)
90 SA3 x 90 SA4	3.10	16.6*	92 SA3 x 92 SA4	4.07	16.3*
90 SA3 x SA5	2.72	2.4	92 SA3 x SA5	3.78	8.0
90 SA3 x SA6 ¹	2.83	6.4	92 SA3 x SA6	4.02	14.9*
90 SA4 x 90 SA5	2.65	13.4	92 SA4 x 92 SA5	3.56	11.2
90 SA6 x 90 SA7	2.40	18.8*	92 SA6 x 92 SA7	3.47	10.5

* Significant at P < 0.05.

¹ Genetic background of population SA3 is similar to that of SA8.

Table 2. Grain yield and rank of the best hybrids (pedigree in bold) evaluated under acid and nonacid soils during 1996.

Trial and pedigree	Number of entries evaluated	Acid soils			Non-acid soils		
		Number of environments	Rank	Yield (t/ha)	Number of environments	Rank	Yield (t/ha)
Yellow testers							
SA3-C4HC (19 x 25)-2-6-4-5 x (LASP2 x LASP3)	172	8	1	4.61	3	1	7.4
White testers							
SA8-C1HC(27x3)-1-1-4-8- x CML 16	100	4	1	5.68	2	10	7.15
SA8-C1HC(27x3)-1-1-2-7 x CML 16			2	5.14		61	5.66
SA8-C1HC(27x26)-1-1-4-3 B x (CML 247 x CML 254)			3	5		5	7.5
SA8-C1HC(27x3)-1-3-1-11 x (CML 247 x CML 254)			33	4.20		1	8.01
SA7-C2HC (13 x7)-1-1-1-5 x CML 16			77	3.50		2	7.82
Yellow Design II							
SA3-C4HC (19x25)-2-6-4-5B x SA4 HC7-1-5-1-3-4-7-B	275	7	1	5.36	3	197	5.44
SA3-C4HC (16x25)-2-4-8-7B x SA4 C2HC(7x15)2-3-5-1B			2	5.36		54	6.43
SA3-C4HC (16x25)-2-4-8-5B x SA4 C2HC(7x15)2-2-2-3B			3	5.26		85	6.12
SA3-C4HC (19x25)-2-6-5-6B x SA4 HC7-1-5-1-3-1-6B			4	5.08		1	7.57
SA5-C2HC(2x20)-2-7-3-8B x CML 304			115	3.86		1	7.57

B51 - Performance of Tropical Maize Lines Derived from Different Germplasm Sources, in Crosses with Related and Unrelated Testers

S.K. Ramanujam, S.K. Vasal, M. Barandiaran, F. San Vicente, A. Ramirez, G. Avila, J. Crossa, and S. Pandey

International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico

Introduction

Lines derived from improved germplasm are expected to be superior to those derived from unimproved materials (Hallauer and Miranda 1988). Broad- and narrow-base germplasm is routinely used by breeders to derive superior inbred lines and use of narrow-base germplasm (F_2 populations, etc.) is receiving greater emphasis (Bauman 1981). Although use of testers with a relatively lower frequency of desirable alleles from unrelated populations is supported by theory, an elite inbred line from a heterotic population is more desirable as a tester for practical maize breeding programs (A.R. Hallauer 1996, personal communication). The present study was conducted to guide selection of appropriate germplasm and testers to develop superior inbred lines in a tropical maize breeding program.

Materials and Methods

The study involved 15 lines: 3 from the population Tuxpeño-1 (P1); 3 from Tuxpeño-1 improved for inbreeding tolerance (P2); 3 from crosses involving two S_2 lines from Tuxpeño-1 (P3); 3 from crosses between S_2 lines from Tuxpeño-1 and a heterotic pool, Tropical Late White Flint or Tuxpeño Caribe (P4); and 3 from crosses between S_2 lines from Tuxpeño-1 selected for inbreeding tolerance (P5). The materials were crossed to a line from Mezcla Tropical Blanca (T1: a population with a similar heterotic pattern), a line derived from Blanco Cristalino-3 (T2: heterotic with Tuxpeño-1), and a line from ETO Blanco (T3: heterotic with Tuxpeño-1). The resulting 45 testcrosses were evaluated in replicated 7 x 7 simple lattice trials at Poza Rica, Cotaxtla, and Tlaltizapan, Mexico; at Cali, Colombia; and in Côte d'Ivoire, during 1996. Grain yield adjusted to 15.5% moisture and 85% shelling is presented. Standard analysis of variance and AMMI (Additive Main Effect and Multiplicative Interaction; Gauch 1988) were used to assess the main effects (general combining ability; GCA) of lines and testers and line x tester interactions (specific combining ability; SCA).

Results and Discussion

The lines from P1 yielded the highest (7.84 Mg ha⁻¹) across environments and testers, followed by lines from P4 (7.67 Mg ha⁻¹) (Table 1). All P1 and two P4 lines also had high and positive GCA for yield. The germplasm giving rise to lines in P1 and P4 is expected to have greater genetic variability than that of P2 (7.22 Mg ha⁻¹), P3 (7.18 Mg ha⁻¹), or P5 (7.25 Mg ha⁻¹), as the latter groups either involve parental populations developed by recombining a few inbred lines (P2 and P5) or those based on S_2 lines of Tuxpeño-1 (P3). Tester T3 yielded 7.53 Mg ha⁻¹, the highest in crosses with all lines, and also had a high GCA (0.091 Mg ha⁻¹). The second unrelated heterotic tester (T2) yielded the lowest (7.35 Mg ha⁻¹) and also had the lowest GCA (-0.084 Mg ha⁻¹) effect. The related tester (T1) was intermediate in yield (7.43 Mg ha⁻¹) and had a GCA effect of -0.01.

Conclusions

The results indicate that lines derived from genetically more variable germplasm yield more in hybrid combinations than those derived from narrow-based germplasm. The two unrelated testers provided conflicting results. Our data suggest that the choice of testers should be based on the experiences of each breeding program.

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Table 1. Grain yield ($Mg\ ha^{-1}$), GCA, and SCA effects of 15 white inbred maize lines derived from different source germplasm, crossed to three testers.

Source		T1		T2		T3		Mean	GCA	Mean
Germplasm	Lines	T1	SCA	T2	SCA	T3	SCA			
P1	1	7.83	0.08	7.20	-0.47	8.24	0.40	7.76	0.32	
P1	2	7.56	-0.47	8.26	0.31	8.30	0.17	8.04	0.60 *	
P1	3	7.97	0.24	8.03	0.38	7.21	-0.62	7.74	0.30	7.84
P2	1	7.52	0.09	7.22	-0.14	7.58	0.05	7.44	0.00	
P2	2	6.92	0.22	6.34	-0.29	6.87	0.07	6.71	-0.72 *	
P2	3	7.56	0.06	7.70	0.28	7.25	-0.34	7.50	0.07	7.22
P3	1	6.82	-0.01	6.86	0.10	6.84	-0.09	6.84	-0.59	
P3	2	7.81	0.56	6.71	-0.46	7.25	-0.10	7.25	-0.18	
P3	3	7.03	-0.41	7.61	0.24	7.72	0.17	7.45	0.02	7.18
P4	1	7.41	-0.44	7.83	0.05	8.34	0.39	7.86	0.43	
P4	2	7.83	-0.11	7.74	-0.12	8.27	0.23	7.95	0.52	
P4	3	8.11	0.92 *	6.36	-0.76 *	7.13	-0.16	7.20	-0.23	7.67
P5	1	7.41	-0.31	7.64	-0.01	8.14	0.32	7.73	0.30	
P5	2	6.49	-0.25	7.39	0.73 *	6.35	-0.48	6.75	-0.69 *	
P5	3	7.13	-0.16	7.36	0.15	7.39	0.00	7.29	-0.14	7.25
Mean		7.43		7.35		7.53				
GCA		-0.01		-0.08		0.09				

* significant at 0.05 level.

B52 - Heterosis and Combining Ability of CIMMYT Subtropical Maize Inbred Lines and their Performance in Hybrid Combinations

S. Castellanos, H. Córdova, A. Ortéga, E. Preciado, S. Gonzáles, A. Terrón, R. Gaytán, and R. López.

Maize Program, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 México D.F., México.

Introduction

Keeping well defined heterotic patterns in a maize hybrid development program is of utmost importance to exploit heterosis efficiently and increase the probabilities of success. Adoption of improved maize cultivars in developing countries could be interpreted as slow, because as of 1993 no more than 50% of the maize area was planted to improved cultivars (Vasal and Srinivasan 1993). The private sector and public national programs have shown great interest in hybrids as a way to speed the release of new, high yielding cultivars. CIMMYT germplasm has been used by national programs to develop 842 open pollinated and hybrids cultivars between 1966-1990, which are cultivated on about 13.5 million ha in developing countries (López-Pereira and Morris 1994). Studies on the heterosis and combining ability of CIMMYT germplasm have been conducted by many breeders at CIMMYT (Beck, et al. 1991; Vasal, et al. 1992; Cordova and Mickelson 1995). The CIMMYT subtropical intermediate maturity white (SIW) heterotic pattern involves Populations 501 and 502, which showed 28.3% high parent heterosis in their C_0 cross evaluated at three locations (Bjarnason 1993). The main objectives of this study are to estimate the combining ability of two sets of elite lines from the CIMMYT SIW heterotic groups "A" & "B", and identify high performance crosses as potential cultivars and elite lines for further research.

Methods

Twelve elite S_3 lines from heterotic group "A" and 11 from group "B" derived from C_1 of reciprocal recurrent selection of the CIMMYT SIW heterotic pattern were crossed in a North Carolina Mating Design II. The 132 crosses plus 3 checks were evaluated at six locations in Mexican subtropical environments: Celaya, Guanajuato; Tlajumulco, Jalisco; Aguascalientes, Aguascalientes; Ciudad Obregón, Sonora; Tlaltizapán, Morelos; and Ameca, Jalisco. Entries were arranged in an alpha lattice (0,1) experimental design with two reps and one-row plots. Trial management (cultural practices, fertilization, and pest control) followed local recommendations and needs. Traits recorded included yield ($Mg\ ha^{-1}$), days to 50% anthesis and silking, plant and ear height, root and stalk lodging, rotten ear, plant and ear aspect, and main diseases. Analysis of variance and estimates for general and specific combining ability (GCA and SCA) by location and across locations were obtained for yield ($Mg\ ha^{-1}$) and *Fusarium* stalk rot (%).

Results

Table 1 shows the best ten single crosses across locations, which outyielded the best seed industry check, A-7545, by more than $1.0\ Mg\ ha^{-1}$. The average of the best ten single crosses was $11.1\ Mg\ ha^{-1}$, vs. $9.89\ Mg\ ha^{-1}$ for the best check. The best crosses had less than 5% rotten ears -- low for some locations. The experimental check, CML-78 x CML-321, whose second parent is derived from Population 502, yielded $10.1\ Mg\ ha^{-1}$. GCA estimates for the two sets of lines and SCA for the crosses were highly significant, as well as the interactions of these with locations. Sister lines L-22 and L-23 from Population 502 were associated with the highest GCA estimates (1.23 and $1.07\ Mg\ ha^{-1}$ respectively) and were involved in seven of the best ten crosses. Lines L-10, L-5 and L-12 from Population 501 gave the highest GCAs (0.87 , 0.69 and $0.67\ Mg\ ha^{-1}$ respectively). Figures 1 and 2 show the performance of the best GCA lines from each heterotic group across the set of lines from the opposite heterotic group. Lines with high GCA for yield also showed low GCA for *Fusarium* stalk rot. The best crosses were L-1 x L-15 and L-9 x L17, with SCA estimates of 1.35 and $1.26\ Mg\ ha^{-1}$, respectively.

Conclusions

The performance of the best crosses within these two sets of lines suggests that enough heterosis is being exploited in this CIMMYT heterotic pattern. The highest GCA lines from Population 502 also showed agronomic characteristics which could be used for screening germplasm in future research in CIMMYT's Subtropical Maize Subprogram. Many new and superior experimental crosses were identified for extensive evaluation by national programs and the private sector.

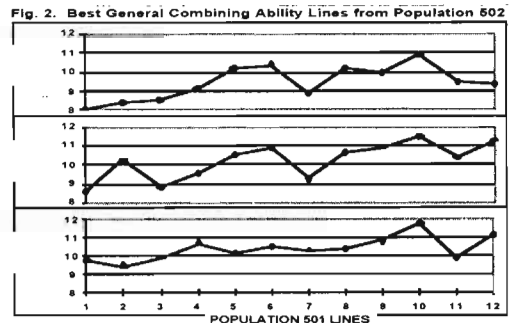
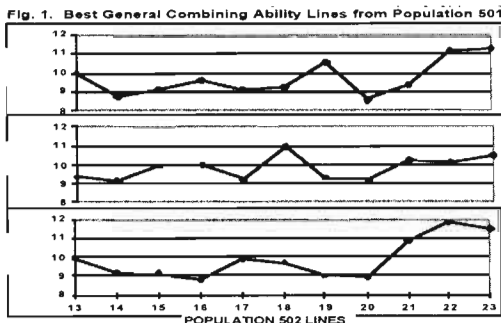
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Table 1. Best 10 single crosses among elite lines from SIW Hete. Groups "A & B"(Pops. 501 & 502) SSCW964 ; Across Locations 1, 2, 3, 4, 6, 7; México, 1996B.

Ent. no	PEDIGREE (CIMMYT)	Yield1 T/Ha	Yield2 T/Ha	Erott (%)	Silk date	Plt ht (cm)	Ear ht Plt ht	Fus (%)	Plt asp	Ear asp	Rlodg (%)	Slodg (%)	Bhcov (%)
109	P501c1#-401-3-1-2-B x P502c1#-771-2-2-1-1	11.78	12.22	3.6	81	216	0.55	3.1	3.3	2.5	5.8	0.8	2.4
110	P501c1#-401-3-1-2-B x P502c1#-771-2-2-1-3	11.44	11.95	4.3	82	219	0.56	2.9	3.0	2.4	3.9	0.0	2.0
132	P501c1#-886-3-1-1-B x P502c1#-771-2-2-1-3	11.27	11.79	4.4	78	214	0.56	6.4	3.2	2.3	1.0	1.9	2.5
131	P501c1#-886-3-1-1-B x P502c1#-771-2-2-1-1	11.13	11.64	4.4	79	213	0.57	16.3	3.6	2.5	2.2	4.9	1.8
90	P501c1#-140-3-1-1-B x P502c1#-488-2-2-1-B	10.93	11.39	4.0	76	225	0.54	9.9	3.5	2.9	2.3	3.6	1.9
99	P501c1#-303-1-1-2-2 x P502c1#-771-2-2-1-3	10.93	11.26	2.9	81	229	0.54	2.8	3.2	2.4	1.3	0.9	0.9
108	P501c1#-401-3-1-2-B x P502c1#-771-1-1-1-B	10.87	11.34	4.1	80	222	0.55	4.3	3.2	2.4	1.9	1.0	2.4
66	P501c1#-284-1-1-3-B x P502c1#-771-2-2-1-3	10.87	11.57	6.1	81	215	0.54	4.0	2.9	2.6	2.7	1.8	2.2
93	P501c1#-303-1-1-2-2 x P502c1#-480-3-4-1-1	10.84	11.39	4.8	81	224	0.52	11.0	3.4	2.4	2.6	4.3	12.6
98	P501c1#-303-1-1-2-2 x P502c1#-771-2-2-1-1	10.84	11.18	3.0	83	226	0.52	3.4	3.4	2.4	3.5	0.5	2.0
*128 CML-78 x CML-321		10.09	10.59	4.7	78	226	0.48	25.9	3.2	2.4	3.8	6.3	8.1
133 A-7545 (ASGROW)		9.89	11.18	11.6	77	222	0.51	27.7	3.5	2.8	5.0	1.9	14.0
MEAN		9.06	9.66	6.3	79.2	208.3	0.5	12.1	3.3	2.9	3.4	3.4	7.4
LSD 0.05			2.42	8.6	4.9	19.7	0.1	20.8	1.0	0.7	11.3	12.1	15.8
CV (%)			12.78	8.3	3.2	4.8	6.1	13.0	15.5	13.0	10.2	11.4	11.5

Notes: Yield1= Yield in which has been taken out the percentage of ears rotten; and Yield2= Yield without any change about ears rotten.



B53 - Combining Ability of CIMMYT Subtropical and Tropical Elite White Maize Lines: Potential for Hybrid Development Across Mega-environments

H. Córdova, H. Mickelson, S. Castellanos, E. Preciado, A. Terrón and R. López

Maize Program, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico, D.F., Mexico

Introduction

Developing more competitive cultivars for farmers involves developing more efficient research strategies. The adaptation and stability of elite germplasm across locations is the main criterion in developing broadly adapted cultivars (Córdova et al. 1996). Joint efforts to exploit the final products of individual breeding programs would allow new cultivars to be developed more quickly and inexpensively and provide information for future breeding strategies. The subtropical and lowland tropical maize subprograms at CIMMYT have individually developed many elite lines for use in hybrids to be tested in their specific environments of adaptation. The aim of this study was to gain new knowledge about how the lines combine between groups and thus improve the stability of our products across mega-environments.

Methods

Eight subtropical intermediate white lines (four classified as heterotic group "A" and four as heterotic group "B") and four elite tropical late white lines classified as heterotic group "A" were selected to form a 12x12 diallel. The 66 single crosses plus four checks were evaluated under an alpha lattice design 10x7 and grown in Poza Rica, Ver. (40 m), Tlaltizapán, Mor. (960 m), San Pedro Lagunillas, Nay. (1,200 m), Celaya, Gto. (1,750 m), Gómez Farias, Jal (1,600 m) and Cd. Guzmán, Jal. (1,500 m), six locations which represent tropical and subtropical environments in Mexico. The experimental plot was two five-meter rows, spaced 75 cm apart; final plant density ranged from 53,000 to 82,000 plants ha⁻¹. Traits evaluated were days to 50% silk, plant and ear height and ear and stalk rots, grain yield adjusted to 145 g kg⁻¹ moisture. Analysis of variance was performed for all variables at individual sites and across sites. The Griffing IV (1956) method (only on F₁ crosses) was used to estimate general and specific combining ability (GCA and SCA) effects (Sughrue and Hallauer 1997). Environments were considered as random and crosses as fixed effects for the analysis of variance.

Results

Mean yield across environments was 7.5 Mg ha⁻¹, with a range from 4.6 Mg ha⁻¹ for La Lagunilla to 12.2 Mg ha⁻¹ for Celaya. The environments used were very contrasting and resulted in highly significant GxE interactions for yield in the combined analysis of variance. GCA (additive genetic effects) explained 60% of the variance for crosses, while SCA (non additive effects) explained the remaining 40% (data not shown). Four single cross hybrids showed excellent yield performance and ear rot resistance in comparison with the best checks. P₃xP₈ yielded 9.0 Mg ha⁻¹ and mean yield for the best check was 7.9 Mg ha⁻¹. P₁xP₇ and P₃xP₇ showed high yield potential, resistance to fusarium ear rot and cercospora disease, and good husk cover. The superior crosses showed only 1% ear rot, whereas the checks suffered a mean damage of 19%. Crosses involving CIMMYT maize lines (CMLs) 311 and 247 showed resistance to cercospora gray leaf spot. The best six subtropical x tropical single crosses consistently outyielded tropical x tropical and subtropical x subtropical crosses at each location and across locations. Mean yield of the best six crosses was 9.0, 10.3 and 11.1 Mg ha⁻¹ for tropical x tropical, subtropical x subtropical and subtropical x tropical, respectively (Fig. 1). The highest positive estimates for SCA for yield were observed in crosses P₃xP₈=1.0, and P₅xP₁₁=0.9. Significant, negative SCA values were found in P₁₀xP₈= -1.0 and P₁₁xP₁₂= -1.1. The highest positive values for GCA corresponded to P₇=0.9 and P₈=0.55, with cross-performance mean of 8.4 and 8.1 Mg ha⁻¹, respectively (Table 1).

Conclusions

At all locations, the best single cross expressed higher yield and better agronomic characteristics than the common check, ASGROW 7520. The best cross for each location and across locations was consistently a subtropical x tropical cross, and yielded higher than the best tropical x subtropical or subtropical x subtropical heterotic crosses. The highest GCA and SCA for yield were associated with line P₇ and hybrid P₃xP₈, respectively; and the lowest GCA and SCA for ear rot corresponded to line P₁ and hybrid P₂xP₄, respectively. These results suggest new options for using tropical and subtropical germplasm to develop broadly adapted products.

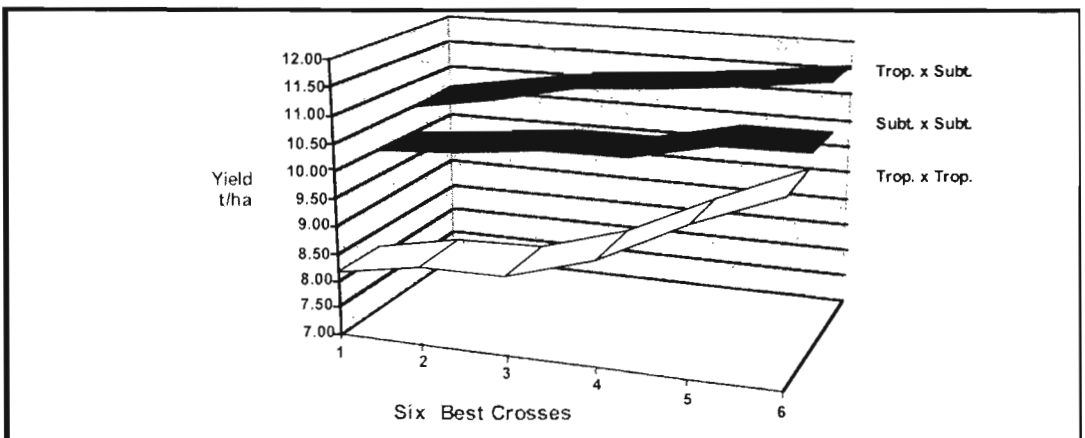
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Table 1. GCA and SCA estimates (Mg ha⁻¹) of eight subtropical and four tropical intermediate white lines, evaluated in six environments in 1995.

Parent	no.	SCA										GCA	Line mean	
[CML 264]..	1	-										0.24	7.79	
[CML 273]..	2	-1.24	-									0.10	7.65	
[CML 247]..	3	0.26	0.17	-								-0.13	7.42	
[CML 254]..	4	-0.41	-0.44	0.18	-							-0.87	6.68	
CML 320	5	0.61	0.42	-0.60	0.05	-						0.01	7.55	
CML 78	6	-0.42	-0.07	0.11	-0.08	-0.39	-					0.01	7.56	
89[L/LMBR]..	7	0.39	-0.14	-0.18	-0.06	-0.42	0.56	-				0.85	8.40	
CML 311	8	-0.03	-0.34	1.03	0.58	-0.50	-0.19	0.02	-			0.55	8.10	
CML 321	9	0.37	-0.09	-0.20	0.07	0.29	-0.52	-0.61	0.25	-		0.11	7.66	
P34c9F115...10	10	0.02	0.48	0.13	0.68	-0.53	0.25	0.05	-1.00	0.42	-	-0.20	7.35	
G.H."B" F21..11	11	0.22	0.77	-1.06	-0.79	0.90	0.49	0.55	0.06	-0.17	0.09	-	-0.51	7.04
G.H."B" F34..12	12	0.22	0.47	0.15	0.21	0.17	0.26	-0.17	0.11	0.21	-0.58	-1.1	-0.16	7.38
		1	2	3	4	5	6	7	8	9	10	11		
† Calculated using adjusted means												Location mean =	7.55	
												Std error of GCA est. =	0.35	
												Std error of SCA est. =	0.42	

Figure 1. Yield (Mg ha⁻¹) of the best six crosses within each type of germplasm across six contrasting locations.



B54 -General and Specific Combining Abilities of Tropical Maize Lines

N. Espinosa Paz and A. Ramírez Fonseca

Campo Experimental Centro de Chiapas (CECECH), Mexican National Institute of Forestry, Agriculture, and Livestock Research (INIFAP), México

Introduction

The selection of maize inbred lines for use in developing hybrids can be based on general combining ability (GCA) and specific combining ability (SCA) (Sprague and Tatum, 1942). The objective of this research was to determine the SCA of tropical maize lines to develop hybrids and synthetics for the hot humid regions of Mexico.

Materials and Methods

Forty-two lines from INIFAP, state of Chiapas, were classified in three groups based on the maturity. The first group comprised 12 early-maturing lines, the second 13 lines of intermediate maturity, and the third 17 late maturing lines. Within groups, 6x6, 8x5, 10x7 crosses were made (Ramírez Fonseca 1994) during 1995. These single crosses were evaluated at Iguala, state of Guerrero, and Ocozocoautla, state of Chiapas, in a simple lattice design during 1996.

Results

In the first group, lines 990, 994, 996 and 999 had high GCA and crosses 990 x 1003, 993 x 999, 994 x 1001 and 995 x 1002 had high SCA (Table 1). In the second group, lines 1007, 1008 and 1013 had high GCA and crosses 1006 x 1016, 1008 x 1012, 1008 x 1013, and 1011 x 1015 had high SCA (Table 2), in the third group, lines 1018, 1023, 1026, 1030, and 1031 had high GCA and crosses 1017 x 1013 and 1020 x 1028 had high SCA (Table 3).

Conclusions

The study identified 26 maize lines showing high GCA and SCA to develop hybrids and synthetics for the hot humid zones of Mexico.

Table 1. General combining ability (GCA) and specific combining ability (SCA) for early inbred lines evaluated during 1996.

H\M	998	999	1000	1001	1002	1003	ACGh
990	-1214	-1159	580	381	372	1125	460
993	773	876	-777	-375	-230	-268	-182
994	135	-495	-41	1370	-1059	-674	549
995	596	-563	4	-628	910	-322	-756
996	443	102	-112	-235	239	-437	486
997	-730	242	345	94	-152	-192	-557
GCAm	80	580	-873	-51	42	220	

H = female, M = Male.

Table 2. General combining ability (GCA) and specific combining ability (SCA) for intermediate inbred lines evaluated during 1996.

H/M	1012	1013	1014	1015	1016	GCAh
1004	443	-1195	392	110	270	232
1005	359	105	-239	545	-748	-217
1006	-1630	73	119	582	858	-656
1007	-388	420	246	-242	-34	759
1008	939	743	-62	-1655	36	1063
1009	17	521	138	-631	-43	-277
1010	438	-1042	449	568	-411	-18
1011	-178	381	-1044	729	112	-888
GCAm	289	529	-362	107	-565	

H = female, M = Male.

Table 3. General combining ability (GCA) and specific combining ability (SCA) for late inbred lines evaluated during 1996.

H/M	1027	1028	1029	1030	1031	1032	1033	GCAh
1017	-577	-36	-23	1352	-609	299	281	-55
1018	-298	15	-745	133	-4	-125	344	402
1019	-150	408	-570	-362	340	75	315	-346
1020	229	897	73	-318	-133	-701	-43	-78
1021	211	-257	264	-143	109	-281	14	-161
1022	155	63	524	-198	-246	-40	-257	-214
1023	-44	-692	3	440	541	-164	-83	320
1024	17	-97	-92	-400	362	460	-251	242
1025	440	598	-4	-57	-215	74	-831	-438
1026	21	-892	-70	163	-136	403	511	326
GCAm	-1050	-527	-108	576	799	-61	373	

H = female, M = Male.

B55 - Heterosis in Backcrosses of 10 Mexican Maize Landraces

F. Márquez-Sánchez, L. Sahagún-Castellanos, J.A. Carrera-Valtierra, and E. Barrera Gutiérrez

Universidad Autónoma Chapingo, Centro Regional Universitario de Occidente, Manuel M. Dieguez 113, Sector Hidalgo, Guadalajara, Jalisco, México 44680

Introduction

There are 50 maize landraces reported in Mexico. Of these only four are used intensively in breeding: Chalqueño for the high plateau; Cónico for the same area with limited rainfall; Celaya for the *El Bajío* region; and Tuxpeño for the rainy coast of the Gulf of México. Other landraces are not used mainly because of their poor plant type and adaptability. However, some have outstanding traits in their area of origin, such as the long ears of the Jala and Comiteco landraces, and Crossa et al. (1990) showed an average heterosis among landraces of some 30% -- a potential resource that has not been used in maize hybridization.

Methods

Ten landraces of the North Pacific coast and Southeastern México (Harinoso de 8, Jala, Tabloncillo, Vandeño, Tepecintle, Tehua, Tuxpeño, Olotillo, Olotón and Comiteco) were crossed each to a number of improved populations of maize. These donor populations have short plant height, high yield and were adapted to the North Pacific coast. The BC_0-F_1 was recombined through hand pollination to obtain BC_0-F_2 plants. Desirable segregants of this generation based on ear size and plant height were used to produce BC_1-F_1 backcrosses. Approximately two hundred plants of the BC_1-F_1 generation were planted, and some 20-30 desirable segregants were intercrossed. From the BC_1-F_2 generation on, using always some four hundred plants as abase population, generations were advanced by intercrossing phenotypes of short plant height and good ear size. No special attention was given to the ear traits of the landrace from which the backcrosses were obtained. The 10 original landraces and the first backcrosses in F_3 (BC_1-F_3) were evaluated at temperate and tropical sites in Mexico (Table 1).

Conclusions

Higher average yields in BC_1 were due both to heterosis still present in the backcross and to the effect of selection. It was observed that those races whose area of origin was not the general area of Cotaxtla showed a negative improvement in this environment.

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Table 1. Yield of 10 Mexican maize landraces and their backcrosses to the landraces in F₅ at two sites in Mexico.

Population	Tlajomulco, Jalisco (temperate)			Cotaxtla, Veracruz (tropical)		
	kg/plot	%	dif.	kg/plot	%	dif.
Olotillo	4.800	72.0		3.584	84.3	
Olotillo BC ₁	6.639		1.839	4.250		0.660
Tepecintle	6.749	78.4		3.740	81.0	
Tepecintle BC ₁	8.603		1.854	4.615		0.875
Comiteco	8.102	106.3		4.634	80.2	
Comiteco BC ₁	7.622		-0.480	5.775		1.141
Olotón	6.102	72.2		2.202	55.9	
Olotón BC ₁	8.447		2.345	3.937		1.735
Vandeño	8.165	98.1		4.745	106.6	
Vandeño BC ₁	8.319		0.154	4.452		-0.293
Harinoso 8	7.004	105.0		5.528	113.5	
Harinoso 8 BC ₁	6.668		-0.336	4.870		-0.658
Tuxpeño	8.938	96.0		5.983	122.2	
Tuxpeño BC ₁	9.311		0.373	4.896		-1.087
Tehua	6.906	79.0		4.039	77.2	
Tehua BC ₁	8.737		1.831	5.231		1.192
Jala	6.950	75.1		5.055	106.5	
Jala BC ₁	9.252		2.302	4.745		-0.310
Tabloncillo	7.725	90.4		4.132	95.6	
Tabloncillo BC ₁	8.542		0.817	4.320		0.188
X Originals	7.144	87.0		4.364	92.7	
X BC ₁	8.214		1.070	4.709		0.345

B56 - Yield and Stability of Single- and Three-way Tropical Maize Hybrids Across 36 Environments

S.K. Vasal, S.K. Ramanujam, M. Barandiaran, F. San Vicente, A. Ramirez, G. Avila, J. Crossa, and S. Pandey

International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico

Introduction

Genotype \times environment interaction (GE) influences the stability of performance of genotypes and is of major concern to plant breeders. Cultivars with greater genetic uniformity have been reported to be more sensitive to environmental fluctuations. Sprague and Federer (1951) obtained a larger GE in maize for single crosses than for double crosses. However, Eberhart and Russell (1969) reported that several single crosses were as stable across environments as more heterogeneous hybrids and Borrero et al. (1992) observed no differences in yield and stability of $S_1 \times S_1$, $S_2 \times S_2$, $S_3 \times S_3$, and $S_4 \times S_4$ line hybrids. Use of maize hybrids is increasing in the tropics where environmental variations are larger than in the temperate areas but few studies have been conducted there relating the level of heterogeneity of germplasm with its stability of performance. The objective of this study was to compare performance and stability of genetically more uniform single-cross hybrids with relatively more heterogeneous three-way cross hybrids across several tropical lowland environments.

Material and Methods

Eleven single-cross (CMS) and seven three-way cross hybrids (CMT) were developed using tropical yellow maize lines derived from CIMMYT populations Antigua-Veracruz-181, Amarillo Cristalino-1, Cogollero, Sint. Am. TSR, and Populations 78 and 79. The hybrids were formed during 1994 at Poza Rica and Tlaltizapan in Mexico and evaluated in 36 locations around the world in 1995. A randomized complete block design with four replications was used. A plot consisted of two rows 5 m long and planting arrangement provided a density of approximately 53,000 plants/ha at all sites. Grain yield (mg ha^{-1}) adjusted to 15.5% moisture and 85% shelling is reported here, although several other agronomic traits were also recorded. Eight environments were classified as high (HY)-, 19 as intermediate (IY)-, 9 as low (LY)- yielding, using the Additive Main effect and Multiplicative Interaction (AMMI) method (Gauch 1988), which was also used to assess the stability.

Results

The hybrids yielded 8.22 Mg ha^{-1} in HY, 5.42 Mg ha^{-1} in IY, and 2.89 Mg ha^{-1} in the LY environments. On the average, single-crosses yielded similar to three-way crosses across all environments (5.36 vs. 5.49 Mg ha^{-1}), HY (8.15 vs. 8.32 Mg ha^{-1}), and LY (2.92 vs. 2.85 Mg ha^{-1}) (Table 1). In IY, three-way crosses yielded higher (5.55 vs. 5.33 ; $P < 0.05$) than single-crosses, on the average, but the highest-yielding hybrid in IY was a single-cross, CMS 933080 (S11; 5.89 Mg ha^{-1}), which also yielded highest in LY (3.52 Mg ha^{-1}), and across all environments (5.95 Mg ha^{-1}). S11 was also highly stable in those environments. In IY, two 3-way crosses, CMT 933180 (T2) and CMT 933156 (T7), were 2nd and 3rd in yield and had good stability. The examination of variance components and the AMMI analysis (data not shown), revealed no differences in the stability of single vs. 3-way crosses, except in the case of IY where the latter were more stable (Figure for IY not shown). In LY, only CMT933030 (T1) ranked third in yield and was surpassed by two single-crosses, S11 and CMS 933984 (S9) in yield and stability (Figure not shown)

Conclusions

Yield and stability of single- and three-way crosses were generally similar but the highest yielding and most stable hybrid across all environments was a single-cross. The slight but nonsignificant superiority of three-way crosses over single-crosses across all environments, HY, and IY may suggest a role for genetic heterogeneity. However, the highest-yielding and most stable hybrid in the study was a single-cross. This suggests that breeders should base selection of superior cultivars on their performance.

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Table 1. Grain yield (Mg ha⁻¹) of 11 single- and 8 three-way maize hybrids across eight high-yielding (HY), 19 intermediate-yielding (IY), and 9 low-yielding (LY) lowland tropical environments, during 1995.

Hybrids+	All sites	HY	IY	LY	Hybrids+	All sites	HY	IY	LY
CMS 933072 (S1)	5.68	8.82	5.58	3.10	CMS 933094 (S10)	5.48	7.98	5.63	2.93
CMS 933064 (S2)	4.89	7.67	4.74	2.73	CMS 933080 (S11)	5.95	8.81	5.89	3.52
CMS 943018 (S3)	5.29	8.40	5.29	2.51	CMT 933030 (T1)	5.71	8.85	5.61	3.15
CMS 943022 (S4)	4.79	7.11	4.97	2.35	CMT 933180 (T2)	5.52	8.30	5.78	2.48
CMS 943008 (S5)	5.11	7.77	5.21	2.54	CMT 933194 (T3)	5.18	7.51	5.29	2.86
CMS 943012 (S6)	5.18	8.20	4.95	2.98	CMT 933204 (T4)	5.38	8.11	5.42	2.87
CMS 943002 (S7)	5.31	8.01	5.38	2.78	CMT 933152 (T5)	5.46	8.18	5.57	2.81
CMS 943010 (S8)	5.58	8.22	5.62	3.14	CMT 933188 (T6)	5.51	8.62	5.42	2.95
CMS 933084 (S9)	5.68	8.68	5.45	3.51	CMT 933156 (T7)	5.66	8.67	5.77	2.77
General mean	5.41	8.22	5.42	2.89					
LSD0.05	0.18	0.43	0.24	0.33					
Mean (single cross)	5.36	8.15	5.33	2.92					
Mean (3-way cross)	5.49	8.32	5.55	2.85					
LSD0.05	0.15	0.58	0.18	0.15					

+ The code CMS indicates a single-cross and CMT a three-way cross hybrid.

B57a - Heterosis and Combining Ability Among Improved Tropical White Maize Populations

F.M. San Vicente¹, A. Bejarano¹, C. Marin¹, and J. Crossa²

¹FONAIAP, Centro Nacional de Investigaciones Agropecuarias (CENIAP), Apdo. Postal 4653, Maracay 2101, Venezuela

²International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico

Introduction

Maize production in Venezuela is based largely on hybrid seed (CIMMYT 1994). The widely known heterotic pattern, Tuxpeño × ETO, has been exploited successfully by maize breeders. However, in recent years there has been some concern about limited genetic gains in new hybrids. In the past, selection schemes emphasized intrapopulation recurrent selection and proved effective in improving populations (García et al. 1996). Reciprocal recurrent selection methods allow for better integration between population and hybrid improvement. In studies on the combining ability of CIMMYT's tropical white maize germplasm, results from the tropical early and intermediate white germplasm indicated low heterosis for yield in most crosses (Beck et al. 1990). Among tropical late white germplasm, Population 32 crossed well with Populations 22 and 29 (Vasal et al. 1992). Exploring new heterotic patterns among improved Venezuelan maize populations is vital in order to maximize their use for hybrid research and development. Our objectives were to determine the combining ability and heterotic patterns among Venezuelan adapted white maize populations, and to identify suitable germplasm for use in applied breeding programs.

Materials and Methods

Genetic materials included four populations improved by Venezuela's national maize program, three populations improved at CIMMYT, and two populations improved by national maize programs of Nicaragua and El Salvador. A 9-population diallel cross was developed at Maracay, Venezuela, during the 1993 winter cycle. The parents, their crosses, and four checks were evaluated at five locations (Maracay, Santa Cruz, Yaritagua, Valle La Pascua, Maturin) in Venezuela. The experimental design was a simple lattice with two replications per location. The experimental unit consisted of two 5 m rows spaced 80 cm apart. Final plant density was approximately 52,000 plants/ha. Data were recorded for days to silk, plant height (cm), shelled grain yield, and percent grain moisture at harvest. Grain yield (t/ha) was adjusted to 15.5% moisture for all plots. Combined analysis of variance was conducted for all traits. Analysis III of Gardner and Eberhart (1966) was used to obtain estimates of general (GCA) and specific combining ability (SCA) for parents and their crosses.

Results

Combined analysis of variance revealed highly significant differences for parents, crosses, GCA, and SCA for days to silk, plant height, and grain yield. For grain yield, 62% of the total sums of squares among crosses could be explained by SCA, whereas 38% was explained by GCA. Yields of the parents ranged from 2.98 for CD77 to 4.38 t/ha for MC. Yields of the crosses ranged from 3.72 (CD77 × P32) to 5.28 t/ha (P49 × NB12). Six crosses showed high parent heterosis values in excess of 20%, including the highest yielding cross. Highly significant favorable GCA effects were observed for AB and NB12 for grain yield, and TS and CD91 for plant height (Table 1). CD77 × CD91 (0.49 t/ha) and P49 × NB12 (0.54 t/ha) recorded the highest SCA effects for grain yield (Table 2).

Conclusions

Both additive and nonadditive effects were involved in the expression of grain yield, but nonadditive effects were relatively more important. Significant gains are expected from both intra and interpopulation recurrent selection schemes. High-parent heterosis values greater than 20% in six crosses

suggest their suitability for further improvement in hybrid development. On the average, similar yields were observed for dent x dent, flint x dent, and flint x flint crosses. NB12 (derived from Pop. 76 in Nicaragua) was not only the best general combiner for yield but also when crossed to P49 produced the highest yielding hybrid. Two crosses (CD77 x CD91 and CD77 x NB12) involving flint populations were among the top five performing entries, that could be used as new heterotic patterns to serve the special needs of Venezuela's maize flour industry for flint hybrids. These new heterotic patterns identified in our study should help accelerate hybrid development in Venezuela.

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Table 1. Estimates of general combining ability effects among nine Venezuelan adapted tropical white maize populations for yield, days to silk, and plant height combined across five environments during 1993.

Parents	Yield (t/ha)	Time to silk (days)	Plant height (cm)
SC3P73	-0.02	-0.19	-2.42
AB	0.25**	-0.36	-0.03
TS	-0.06	-1.03**	-17.13**
MC	-0.03	0.37	5.46**
CD77	-0.15	1.35**	12.12**
P49	-0.24**	0.56**	-3.11*
CD91	0.05	-0.89**	-6.72**
NB12	0.29**	-0.68**	1.77
P32	-0.07	0.88**	10.05**

*, ** Significantly different from zero at the 5% and 1% level of probability, respectively.

Table 2. Estimates of specific combining ability effects among crosses involving nine Venezuelan adapted tropical white maize improved populations for yield (t/ha) combined over five environments during 1993.

Parents	AB	TS	MC	CD77	P49	CD91	NB12	P32
SC3P73	0.04	0.38*	0.17	0.18	-0.20	-0.34	-0.28	0.05
AB		-0.16	0.13	0.01	-0.16	-0.07	-0.13	0.33
TS			0.07	0.26	-0.16	-0.22	0.00	-0.17
MC				-0.23	-0.35	0.06	-0.05	0.20
CD77					-0.34	0.49**	0.36*	-0.74**
P49						0.34	0.54**	0.33
CD91							-0.37*	0.10
NB12								-0.09

*, ** Significantly different from zero at the 5% and 1% level of probability, respectively.

B57b - Heterotic Patterns Among Tropical Late Yellow Maize Germplasm in Venezuela

F.M. San Vicente¹, A. Bejarano¹, J. Crossa², and C. Marin¹

¹FONAIAP, Centro Nacional de Investigaciones Agropecuarias (CENIAP), Apdo. Postal 4653, Maracay 2101, Venezuela

²International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico

Introduction

Hybrid maize technology has been completely adopted by Venezuelan farmers. Maize production in Venezuela has been mainly restricted to white maize for human consumption, whereas the animal feed industry has depended entirely on imported yellow maize. There is some concern about the complete dependence on foreign yellow maize, and breeders are trying to develop highly productive, stable and adapted yellow hybrids. Limited information about combining ability of tropically adapted yellow maize germplasm is available. Full-sib recurrent selection has been effective for population per se performance in some tropical late yellow maize germplasm (Pandey et al. 1986; Pandey et al. 1987; García et al. 1996). Crossa et al. (1990) summarized estimates of combining ability of CIMMYT's tropical late yellow maize germplasm. They concluded that crosses among lines extracted from Populations 24, 36 and Suwan-1 should maximize heterosis and are promising germplasm to be used in a hybrid breeding program. This study was conducted to determine germplasm most appropriate for Venezuela's national hybrid program, and to identify counterpart heterotic populations to be used as testers in initial stages of hybrid development and in future interpopulation recurrent selection schemes.

Materials and Methods

Genetic materials included eight populations developed by Venezuela's national maize program and one population developed at CIMMYT. The nine materials were crossed in a diallel fashion in Maracay, Venezuela in the 1993 winter cycle. The parents, their crosses, and four checks were evaluated in five environments in Venezuela: four locations (Maracay, Santa Cruz, Acarigua, and Valle La Pascua) during 1993, and one location (Maracay) during 1994. The experimental design was a simple lattice with two replications per location. The experimental unit consisted of two 5 m rows spaced 80 cm apart. Final plant density was approximately 52,000 plants/ha. Data were recorded for days to silk, plant height (cm), shelled grain yield, and percent grain moisture at harvest. Grain yield (t/ha) was adjusted to 15.5% moisture for all plots. Combined analysis of variance were conducted for all traits. Analysis III of Gardner and Eberhart (1966) was used to estimate general (GCA) and specific combining ability (SCA) effects for parents and their crosses.

Results

Significant ($P \leq 0.05$) or highly significant ($P \leq 0.01$) differences were observed for parents, crosses, and GCA for all traits. Average heterosis (parents vs. crosses) and SCA were only significant for days to silk and grain yield (data not shown). For grain yield, 76% of the total sums of squares among crosses could be explained by SCA, whereas 24% was explained by GCA (data not shown). Yields of the parents ranged from 4.63 for MF to 5.48 t/ha for C381. Yields of the crosses ranged from 4.77 (SG79 × CADMR) to 5.93 t/ha (SA11 × SPAM). Four crosses showed high parent heterosis values higher than 10%, including the highest yielding cross. Significant favorable GCA effects were observed for SPAM for grain yield, plant height and days to silk (Table 1). CDMR × CADMR (0.57 t/ha) and TCEC79 × CADMR (0.65 t/ha) recorded the highest SCA effects for grain yield (Table 2).

Conclusions

Both additive and nonadditive effects were involved in the expression of grain yield, but nonadditive effects were relatively more important. Significant gains should be expected from both intra and

interpopulation recurrent selection. High parent heterosis values greater than 10% in four crosses suggest their suitability for further improvement in hybrid development. CA3, C381 and SPAM had good performance per se and in crosses. On the average, materials derived from Thai Composite-1 (developed in Thailand) crossed well with CADMR (developed in Venezuela). Moreover, both germplasm sources are resistant to downy mildew. SPAM (derived from crossing Suwan-1 x La Posta) was not only the best general combiner for yield but also when crossed to SA11 produced the highest yielding hybrid (5.93 t/ha). SPAM and SA11, with semident grain texture, are among the promising germplasm that should be considered in formulating a hybrid program. This seems to be a potential heterotic pattern that could provide a preliminary basis for development of yellow maize hybrids in Venezuela.

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Table 1. Estimates of general combining ability effects among nine Venezuelan adapted tropical yellow maize populations for yield, days to silk, and plant height combined across five environments during 1993-94.

Parents	Yield (t/ha)	Time to silk (days)	Plant height (cm)
CA3	0.02	-0.19	-3.39
C381	0.03	-0.19	-2.30
CDMR	-0.03	0.01	-1.57
SG79	-0.15	-0.57**	-2.90
SA11	0.15	0.32	5.54**
TCEC79	0.01	0.36	0.85
SPAM	0.23*	-0.87**	-5.27**
CADMR	-0.25*	0.36	5.96**
MF	0.09	0.79**	3.08

*, ** Significantly different from zero at the 5% and 1% level of probability, respectively.

Table 2. Estimates of specific combining ability effects among crosses involving nine Venezuelan adapted tropical yellow maize improved populations for yield (t/ha) combined over five environments during 1993-94.

Parents	C381	CDMR	SG79	SA11	TCEC79	SPAM	CADMR	MF
CA3	-0.07	0.24	-0.06	0.33	-0.11	-0.54*	0.42	-0.21
C381		-0.08	0.21	0.05	0.17	-0.08	-0.22	0.02
CDMR			-0.18	-0.04	-0.40	-0.10	0.57*	0.01
SG79				0.19	-0.26	0.39	-0.50	0.21
SA11					-0.24	0.31	-0.32	-0.30
TCEC79						0.11	0.65**	0.08
SPAM							-0.44	0.35
CADMR								-0.15

*, ** Significantly different from zero at the 5% and 1% level of probability, respectively.

B58 - Heterosis in Maize Hybrids Developed from Subtropically Adapted Inbred Lines

M. Saleem¹, A. Aziz² and N. Hussain²

¹ Former Principal Maize Breeder, Cereal Crops Research Institute, NWFP; presently Associate Professor, Dept. of Plant Breeding and Genetics, Agric. University, Peshawar, Pakistan.

² Research Officers, Cereal Crops, Cereal Crops Research Institute, Nowshera, Pakistan.

Introduction

Maize yields in Pakistan are very low (1.2 t/ha). Although progress in the development of synthetic or open-pollinated maize varieties has been great, the impact of yield improvement is low primarily due to lack of a viable seed industry in the Northwest Frontier Province (NWFP; the major maize producing province) and the disinterest of national and multinational seed companies in producing open pollinated varieties.

We began deriving inbred lines from subtropically adapted elite maize populations in 1984 at the Cereal Crops Research Institute (CCRI), NWFP. Early maturing hybrids (85-90 days) from S₅ lines were developed and tested extensively for the subsistence farming systems (Saleem et al. 1993). Phenotypic selection of lines proved effective for early maturity, vigor, ear morphology and disease resistance (Inoue et al. 1982).

Methods

Four subtropical, locally adapted elite populations were selfed and selected through S₅ to develop early maturing (85-90 days) hybrids for subsistence farmers who use traditional management practices. Selected lines were further evaluated for GCA at the S_i level using well adapted local varieties as testers (Saleem 1989). Some lines were crossed in different combinations (although not always in a diallel cross) and a few inbreds were identified as specific combiners (Saleem 1990).

Selected hybrids were tested in replicated yield trials across locations and years (Tables 1, 2) under stressful conditions throughout the region using parental populations and commercial hybrids as checks.

Results

Two hybrids, a three-way and a double-cross, outyielded all others and were stable across environments (Table 1). The hybrids PSH 817 (Quaid) and PSH 107 (Shahbaz) yielded 11 to 35% higher than the parental populations, were 2 to 5 days earlier, and possessed improved disease resistance. Quaid and Shahbaz were officially approved for commercial cultivation. Hybrids developed from local lines were superior in yield to full season Pioneer Hybrids, particularly in the more stressful production environments of NWFP (Table 2).

Conclusions

Selection was effective in identifying high yielding, early maturing (90 days) hybrids for the high intensity cropping systems. Visual evaluation for early maturity, disease resistance, and ear and plant characters was effective. It was interesting to note the high degree of heterosis for yield between lines derived from the same population or from different populations. As a consequence, two hybrids were officially released during 1993 for commercial cultivation, one each for the Spring and Summer plantings.

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Table 1. Performance of early-maturing maize hybrids across sites, NWFP, Pakistan, 1992.

Variety	Pirsabak		Grain yield (Mg ha ⁻¹)					Days to 50% silk	% stalk rot
	1*	2	Swat	Mansehra	S.Naurang	D.I.Khan	Mean		
PSH-817 (Quaid)	9657	3494	9648	6667	4157	5733	6559	48	3
PSH-107 (Shagbaz)	9116	3763	9853	6133	4372	6667	6651	51	6
PSH-217	9390	2823	9290	4567	4305	6567	6157	50	5
PSH-157	9067	3457	9990	5433	3675	6000	6270	51	5
PSH-2912	8960	3653	9138	4267	4013	5033	5844	49	3
PSH-1229	8960	2843	8488	4933	4142	6300	5944	50	4
PSH-307	8850	3133	8105	5067	3817	6933	5984	50	5
PSH-1512	-	4400	7798	5600	3938	4867	5321	50	5
Sarhad Y (Check-1)	8187	2583	7103	3767	3738	5200	5096	49	10
Kissan (Check-2)	7710	3050	7093	5400	3863	4833	5325	47	6
LSD-0.05	934	-	1390	1456	-	1329			
CV%	7.90	16.00	11.00	19.20	22.30	15.70			

*Data from Spring 1992

Table 2. Grain yield (Mg ha⁻¹) of maize hybrids in different environments of NWFP, Pakistan, Kharif 1989.

Variety	Prisabak	Swat	Mansehra	S. Naurang	Mean
PSH-817 (Quaid)	5597	7550	5296	4036	5619
Pioneer-3747	3830	9460	5430	2121	5210
Pioneer-31827	3890	9333	5340	1923	5121
PSH-107 (Shahbaz)	3393	8110	4650	4100	5063
YEV-1081	4393	7503	4140	3466	4875
YEV-1085	4667	7313	4646	2676	4825
PSEV-4085	5017	7070	3596	2580	4565
Local Check	4070	6963	4193	2750	4501
Gauhar	3610	6607	3686	2756	4164
LSD-0.05	1276	1501	1322	680	
CV%	20.50	13.20	19.90	15.90	

B59 - Heterosis in Post-Rainy Season Sorghum Hybrids

S. Kaul and B.S. Rana

AICSIP, National Research Centre for Sorghum, Rajendernagar, Hyderabad 500 030 India

Introduction

Some 6 million ha of sorghum in India is grown the post-rainy, or *rabi* season (as opposed to the rainy or *khariif* season). Major yield constraints are lack of suitable hybrids, increasing moisture stress with crop growth, and susceptibility to shootfly, charcoal rot and low temperature.

Material and methods

To improve the adaptability of hybrids to post rainy season, a number of CMS and restorer lines have been developed recently. Utilizing four such CMS lines, 149 experimental hybrids were made and evaluated during 1994. Of these, the 14 most promising hybrids based on elite CMS line 116A were selected for further evaluation. These were tested in a replicated trial with one protected irrigation during 1995 post-rainy season. The recently released hybrid from this programme, CSH 15R, was used as a check. The restorer lines represented four genetic stocks (IS 1034, IS 2268, IS 2391, and IS 15717), four elite *rabi* lines (SPV 839, SPV 1258, SPV 1268, and RS 585) and six recently bred lines of diverse pedigrees. These parental line were grown along with F₁ hybrids. SPV 839 is a recently released variety while RS 585 is the R line of CSH 15R. Observations were taken on five random plants. Heterosis was calculated as increased vigour of F₁ over the better parent.

Results

The average grain yield of parents was 71 g as compared to 91 g in hybrids, representing 28.2% heterosis. The range of high-parent heterosis in F₁ hybrids for grain yield was -6.5 to 81.8%. In component characters, the range of heterosis was -16.7 to 16.7% for panicle length, -9.7 to 13.9% for panicle branches, -32.8 to 39.5% for grains per panicle branch, -26.3 to 8.5% for days to 50% flowering, and -8.2 to 55.4% for plant height. The panicle length ranged from 20 to 28 cm, whereas days to 50% flowering had a narrower range (74-77 days). In view of these variabilities, the per se performance as well as heterosis was studied in different groups of crosses. (Table 1).

Conclusions

The average heterosis of 28.2% for grain yield was more than for component characters, which ranged from -4.1% for number of grain per panicle branch to 12.7% for panicle branches. However, range of variation up to 81.8% in heterosis and 120 g/pl in grain yield per plant provided an opportunity to exploit heterosis. Hybrids involving genetic stock or *khariif* x *khariif* derivatives as R lines were high yielding in general and also showed significant heterosis (average 39.3 and 44.3% respectively). The grain yield in F₁s ranged from 83 to 120 g/pl and 85 to 104 g/pl, respectively, in these two types of crosses. This established a correspondence between per se performance and heterosis, where the high yielding group was also more heterotic. The B and R lines in these two groups are unrelated by descent and high heterosis can be attributed to genetic diversity between parental lines. Increased yield heterosis in crosses involving genetic stocks was also due to positive heterosis for grain per panicle branch. The average heterosis for grain yield involving R lines derived from *rabi* x *rabi* or *rabi* x *khariif* crosses was 17.8 and 12.3%, which is very low. The primary reason for this may be depletion of genetic diversity between parents due to involvement of a common variety M 35-1 in most of both CMS and R lines, for its other desirable attributes. There was a positive correlation ($r=0.814^{**}$) between grain yield and magnitude of heterosis in F₁s over the better parent. It is thus evident that high yielding hybrids also have high heterosis over better parents. Such promising hybrids are listed in Table 2. The highest yielding hybrid, 116A x IS 1034, was also most heterotic, followed by 116 A x SPV 1268 and 116 A x R 94 - 634. Other promising hybrids were 116 A x R 94- 752 and 116 A x R94-1336 (i.e., SPV 351 x SPV 221). R 94 - 634 and 752 have the common pedigree RS 29 x SPV 462. The R lines of these three hybrids

were derived from the kharif x kharif crosses which have high grain number per panicle but low levels of resistance to shootfly. These hybrids established 16-46% superiority over recently released hybrids. While heterosis for grain yield in the highest yielding F_1 s is associated with heterosis for grain per panicle branch, high yielding hybrids involving rabi x kharif derivatives also exhibited positive heterosis for plant height. The low heterosis in component characters was due to less genetic diversity among parental lines, primarily a result of selection for multiple traits where the weight given resistance for shootfly and charcoal rot was higher than for agronomic traits. F_1 yield ($Y=82.63 + 0.468**X$, where $X=\%$ heterosis) is predictable. Thus, breeding for a large degree of heterosis will enable the yield level of present day hybrids. However, difficulties in restoring full fertility due to low temperatures during flowering currently limit the expression heterosis in this season. Hence, further genetic enhancement of parental lines with high grain number per panicle, full fertility restoration under cold, and resistance to biotic stresses will play a crucial role in exploiting heterosis in the post-rainy season.

Table 1. Heterosis in post-rainy season sorghum hybrids according to type of cross.

R = rabi (post rainy); GS = genetic stock; R-K derivative from rabi X kharif (rainy) crosses; K-K = Cross derivative of kharif x kharif crosses; Het = heterosis.

Type of cross	Grain yield		Panicle branches		Grain/panicle branch		Plant height (cm)		
	Mean	Het %	Mean	Het %	Mean	Het %	Mean	Het %	
R x GS	Mean	94	39.3	73.8	9.8	47.3	21.5	202	8
	Range	83-120	15.3-81.8	67-82	(-)-6.9-13.9	38-60	(-)-9.1-40	190-218	3-12
R x R	Mean	90	17.8	65.2	-5.0	45.6	-18.9	204	21
	Range	72-109	(-)-6.5-28.6	51-74	(-)-9.7-2.8	37-57	-3.2.8-0.0	183-244	4-55
R xR-K	Mean	78	12.3	73.5	1.5	48.5	-12.5	186	9
	Range	76-80	11.1-13.4	71-76	(-)-4.1-7.5	40-57	(-)-5.0(-)20	180-192	6-13
R x K-K	Mean	95.8	44.3	73.5	0.3	49.5	-15.5	193	16
	Range	85-104	19.7-73.3	69-77	(-)-4.2-6.9	43-55	(-)-22.1-0.0	173-209	(-)-18-37

Table 2. Per se mean and heterosis(%) in selected hybrids.

Hybrid	Grain yield (g/pl)		Panicle branches		Grain/panicle branch		Plant height (cm)	
	Mean	Het%	Mean	Het%	Mean	Het%	Mean	Het%
116A x IS 1034	120	81.8	76	5.6	51	34.2	190	11.8
116A x IS 2268	90	32.4	70	-2.8	60	39.5	204	2.5
116A x SPV1268	109	55.7	65	-9.7	51	-10.6	183	19.6
CSH 15 R	82	17.1	66	-8.3	39	-32.8	198	10.0
116A x R94-634	104	73.3	69	-4.2	55	-9.8	178	19.6
116A x R94-752	99	52.3	77	6.9	53	0.0	209	16.1
116A x R94-1336	95	31.7	74	2.8	47	-14.5	207	37.1

B60 - Combining Ability and Heterosis in Eggplant

S. Ahmad

Horticulture Research Center, Bangladesh Agricultural Research Institute, Gazipur 1701, Bangladesh

Introduction

Eggplant (*Solanum melongena* L) is a major native vegetable widely cultivated and consumed in Bangladesh. The wide range of variability for different crop characters indicates their possible utility in a hybrid development program for eggplant. Heterosis for yield and yield components in eggplant has been demonstrated by many workers (Kakizaki 1931; Daskaloff 1937; Pal and Sing 1946, 1949; Kumar and Ram 1989). An attempt was made to develop F₁ hybrids of eggplant in Bangladesh, and the combining ability and heterotic performance for yield and yield components were studied in a five-parent cross.

Methods

The inbreds Uttara, Islampuri, Singhnath long, Khatkhatia long and Pusa Purple long (India) and their hybrids (excluding reciprocals) were used. The experiment was laid out in a complete randomized block design with three replications. Data were recorded on days to flowering, plant height, number of fruits/plant, fruit yield/plant, and fruit length and diameter. General and specific combining ability effects were estimated following the Method II approach of Griffing (1956).

Results

An analysis of variance for combining ability is presented in Table 1 showing that the general combining ability (GCA) and specific combining ability (SCA) were significant for all characters. Their estimates suggest the presence of additive and non-additive genetic variance in the population for the characters measured. Considerable variability existed among parents for GCA effects (Table 1). The GCA effects for late flowering was greatest for parent Islampuri and for early flowering the parents Uttara and Pusa Purple long were considered good general combiners (Table 2). Among parents, Islampuri was considered the best general combiner for late flowering and fruit diameter. The parents Pusa Purple long and Uttara showed the highest GCA effects for fruits/plant and were thus considered good combiners for increased number of fruits/plant. Both parents also had a high GCA effect for yield/plant. The best crosses with the highest estimates of SCA effects for fruit yield/plant were Pusa Purple long x Islampuri and Pusa Purple long x Uttara between poor x good and good x good combiners. The best cross for fruit yield was also good for fruits/plant.

Conclusion

High-parent heterosis was greatest for fruits/plant (60.09%), followed by yield/plant (48.27%) and plant height (16.02%) (data not shown). Three hybrids showed significant improvement in economic yield over the best parent selected from the aforesaid study. The improvement ranged from 2.23% to 58.34% over the mid parent and 2.19% to 48.27%, suggesting that hybrids "Pusa Purple long x Uttara", "Khatkhatia long x Islampuri" and "Pusa Purple long x Islampuri" could be released directly to farmers.

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Table 1. Mean of sum squares for combining ability for six characters in eggplant.

Source	df	Days to flowering	Plant height (cm)	Fruit/plant	Length of fruit (cm)	Diameter of fruit (cm)	Yield/plant (kg)
GCA	4	56.855**	187.92**	306.2725**	75.853**	8.315**	2.955**
SCA	9	4.434	13.922**	1,384.6400**	9.912**	1.1033**	-4.614**
Error	28	3.5746	0.4162	18.989	2.768	0.0823	0.125

** Significant at 1% level

* Significant at 5% level

Table 2. Estimate of GCA effect for six characters of five eggplant varieties.

Parent	Days to flowering	Plant height (cm)	Fruit/plant	Length of fruit (cm)	Diameter of fruit (cm)	Yield/plant (kg)
Pusa Purple long	-2.71**	0.3308	21.02**	1.1328	-0.533**	0.9194**
Khatkhatia long	1.86**	2.25**	-6.64**	-0.2	-0.3657**	-0.5681**
Shingnath long	1.00	5.3594**	-5.41**	4.942**	-0.6520**	-0.4664**
Uttara	-3.29**	-8.55**	20.26**	-3.342**	-2.728**	0.4428**
Islampur	3.142**	0.60**	29.22**	2.532**	1.87**	0.3271**
5%	1.3101	0.4469	3.0198	1.1529	0.1986	0.2449
1%	1.763	0.6016	4.0657	1.5522	0.2674	0.3298
S.E (g)	0.6391	0.2180	1.4731	0.5624	0.0969	0.1195

B61 - Exploitation of Heterosis in Oil Palm to Increase Oil Yield

N. Rajanaidu

Palm Oil Research Institute of Malaysia (PORIM), P.O. Box 10620, 50720 Kuala Lumpur, Malaysia

Introduction

The African oil palm (*Elaeis guineensis*) of commerce is a monoecious plant which is naturally cross-pollinated. Oil palm produces separate male and female inflorescences on the same palm and is pollinated mainly by the weevil *Elaeidobius kameruicus* from West Africa. Oil palm is the most productive oil bearing crop; a hectare of oil palm in good growing conditions produces on average 4.5 t palm oil ha⁻¹ yr⁻¹; 0.5 t kernel oil and 0.45 t palm kernel cake. This is almost three times the yield of coconut and about 10 times that of the soybean (Hartley 1988).

Seed production and use of heterosis in oil palm

There are three fruit forms in oil palm. Their classification is based on shell-thickness. *Dura* (P1) fruit form is thick shelled (Sh⁺ Sh⁺) and the *pisifera* (P2) is shell-less (Sh Sh⁻). The crosses between two homozygotes produce the thin shelled *tenera* (Sh⁺Sh⁻) (F₁), a heterozygote. The inheritance of shell in oil palm was discovered by Beirnaert and Venderweyen in 1941 in Belgian Congo. The characteristics of *dura* and *tenera* fruit forms are given in Table 1.

In oil palm hybrids (F₁), seeds are produced by control pollination of *dura* (P1) mother palms with shell-less *pisiferas* (P2) and the hybrid F₁ seeds are known as 'DxP' or *tenera* planting materials. Compared to *duras*, DxP oil palm planting materials, increase the oil yield by more than 30% [(24-18)/18 × 100]; thus resulting in higher oil yield per hectare. This can be considered as single locus heterosis where F₁ (Sh⁺Sh⁻) > P1 (Sh⁺Sh⁺). *Dura* (P1) improvement programme has given rise to outstanding *dura* palms with good fruit characteristics especially the oil to bunch (Lee Chong Hee 1997). It is also possible to select outstanding *dura* palms which have fruit characteristics similar to those of F₁ hybrid seeds. In this process, it is possible to simplify the oil palm breeding programme.

In oil palm, heterosis is also exploited at the population level. The reciprocal recurrent selection (RRS) scheme is adopted by a number of oil palm breeders. In this scheme, the *dura* and *pisifera* genotypes are kept as distinctly separate base populations. The *dura* populations are selected for high bunch weight and low bunch number. The Deli and Angola *duras* are placed in this category. The *pisiferas* were selected for high bunch number and low bunch weight. The Deli *duras* are very distinct populations derived from four *dura* palms planted at Bogor Botanical Gardens, Java, Indonesia in 1848. The crosses between Deli *duras* and African *pisiferas* were higher yielding than crosses between African *duras* with African *pisiferas*. Breeding schemes have been developed to exploit 'inter-origin' differences between Deli *duras* and African *teneras/pisiferas* (Gascon and de Berchoux 1964). The performance of the inter-origin crosses is attributed to the additive effect of a favourable combination of factors for bunch weight and bunch number from the parents. Even if only mid-values are obtained in the progeny, there may be an overall yield gain (Table 3).

Discussion and Conclusions

In oil palm the presence or absence of shell is determined by alleles at the 's' locus. The inheritance of shell-thickness and hybrid vigour in 'inter-origin' crosses is likely to be determined by dominance and epistatic effects.

Acknowledgment

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Table 1: Average bunch composition of *dura* and *tenera* fruit forms.

Traits	<i>Dura</i> (Sh* Sh') (P1)	<i>Tenera</i> (Sh*Sh') (F ₁)
Fruit to bunch (%)	60	60
Mesocarp to fruit (%)	60	80
Shell to fruit (%)	30	10
Kernel to fruit (%)	10	10
Oil to wet mesocarp (%)	50	50
Oil to bunch (%)	18	24

Note: *Pisifera* is female sterile but supplies pollen for seed production.

Table 2. Outstanding *dura* (P1) palms.

Palm No.	Oil to bunch (%)
1	26.6
2	25.9
3	25.6
4	27.0
5	26.8
6	25.8
7	27.1
8	28.4

Source: Lee Chong Hee 1977.

Table 3. Performance of 'inter-origin' crosses between Deli *duras* and African *teneras*.

Population	Bunch wt. (kg)	No. of bunches per annum	Product (kg)
Deli (P1)	15.0	6.0	90
African (P2)	10.0	9.0	90
Cross (mid-values) (F ₁)	12.5	7.5	93.75

B62 - Heterosis in Spring Triticale Hybrids

W.H. Pfeiffer, K.D. Sayre, M. Mergoum and J. van Beem

Wheat Program, International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico.

Introduction

The increasing demand for food in developing countries and the commercial success of various hybrid crops points to use of hybrid triticales (*X Triticosecale* Wittmack) as a strategy for sustainably enhancing production in underutilized and marginal environments. Triticale, a man-made synthetic crop developed from wheat and rye, possesses tolerance to several key stresses of developing country environments, including low moisture and acid soils, and displays the pollination control traits required for hybrid seed production. The research reported here evaluated heterosis for agronomic traits in CHA-produced triticale hybrids.

Methods

Thirty-one hybrids were produced by a chemical hybridizing agent (CHA) from 3 male and 15 female elite hexaploid spring triticales. All triticales used were complete R-genome types, except one 2D(2R) chromosome substituted type which was used as male parent. Male parents were selected based on performance under high production conditions. Female parents were selected on performance in different agro-ecological zones and for their contrasting yield component expression. Yield trials including hybrids and parents were conducted at Cd. Obregon, Sonora, Mexico, during the 1995-96 and 1996-97 growing cycles under high production conditions to evaluate grain yield and agronomic traits. A lattice experimental design with 2 replications was planted following normal farmer practices. Plots consisted of two beds, 3.5 m in length, sown at 300 viable seeds per m². Weeds and diseases were controlled.

Results

Combined analysis for 1995-96 and 1996-97 (Fig. 1) revealed on average 9.5% mid-parent and 5.2% high-parent heterosis for grain yield. Maximum heterosis values greater than 20% for grain yield for high-parent (22.9%), mid-parent (24.9%) and low parent (28.9%) comparisons were observed. Mid-parent heterosis for agronomic components were: biomass (9.1%), straw yield (9.0%), 1000-grain weight (11.4%), culm weight (12.0%), and spike weight (12.4%). Plant height (3.2%) and grain fill duration (2.5%) slightly increased in hybrids. Traits not effected by hybrid vigor were harvest index, number of grains/spike, days to flower and maturity, canopy temperature depression, leaf chlorophyll (SPAD) content, and test weight. Insignificant negative mid-parent heterosis was observed for spikes/m² (-2.6%) and grains/m² (-2.1%). Mid-parent heterosis for grain yield for substituted 2D(2R) x complete R genome hybrids (10.7%) was higher when compared with hybrids produced between complete R types (8.6%).

Conclusions

High heterosis for value-added traits suggests the feasibility of commercial triticale hybrids with substantial gains in genetic yield potential given the existing genetic variation. Hybrids can be successfully designed from inferior yielding parents which carry special attributes; for example, for disease resistance, involving less adapted alien sources to exploit potentials of marginal environments, or unique end-user quality traits. High heterosis in hybrids involving 2D(2R) substitution types suggests the presence of contrasting heterotic groups between the complete R and substituted 2D(2R) gene pools and/or heterotic effects from D genome chromosomes in hybrids. Future research is needed to identify spillover effects and target agro-ecologies for triticale hybrids, while feasibility studies involving socio-economic analysis of the use of hybrid technology by small farmers are essential to better address research partners' needs in developing countries.



Figure 1. Heterosis for grain yield in 31 spring triticale hybrids.

B63 - Heterosis and Inheritance of Productivity in Reduplicated Generations of Spring Wheat Hybrids

A.P. Golovochenko and V.V. Glukhovtsev

Povolzhsky Research Institute of Selection and Seed Production, 76 Shosseinaya St., Ust-Kinelsky, Kinel 446409, Russian Federation

Research was conducted on the inheritance of yield components of F_2 - F_3 spring soft wheat hybrids under conditions of the Central Volga Basin (Samara), Russia. Single-cross hybrids were obtained from crossing parental varieties. In a full 5×5 diallel study, including F_2 hybrids, overdominance and complementary epistasis were shown to be important in the inheritance of yield components. The dominance of genes had a positive direction. From F_2 to F_3 the number of crosses showing overdominance decreased from 33% to 10%. For grain weight per plant, heterosis was 33.3% in the F_2 crosses, 33.0% in the F_{3s} , 20.0% in the F_{4s} , and only 16.6% in the F_{5s} . F_{2s} showed a higher dehiscence per plant (22.7%) than F_{3s} (12.5%). Heterosis and dehiscence seem interrelated.

The sources of dominant genes that raised the hybrid productivity, 1000-grain weight, and grain weight of the main spike are the Saratovskaya 29, Eritrospermum 841, and Kutulukskaya (all from Russia); for grain yield per ear and per plant, sources are Nadadores (Mexico), and Kutulukskaya (Russia). The largest gains in hybrid productivity are realized if parents are selected for higher grain yield per plant and productivity per spike. Grain yield per spike and plant are also related to seed size. The authors suggest selecting for seed size and number on the main spike in F_2 - F_3 , but for seed size and grain yield per plant in F_4 . The presence of heterosis suggests that high yielding wheat hybrids can be developed.

B64 - Heterosis of Grain Sorghum Under Extremely Variable Growing Conditions in Semi-Arid Areas of Kenya

B.I.G. Haussmann^{1,2)}, A.T. Obilana³⁾ and H.H. Geiger^{1,4)}

¹ Institute of Plant Breeding, Seed Science, and Population Genetics, University of Hohenheim, D-70593 Stuttgart, Germany; ² ICRISAT, B.P. 320, Bamako, Mali; ³ ICRISAT, P.O. Box 776, Bulawayo, Zimbabwe; ⁴ Corresponding author

Introduction

Sorghum [*Sorghum bicolor* (L.) Moench] belongs to the major crops of the semi-arid tropics of Africa and Asia with mean grain yields of 780 and 1,140 kg ha⁻¹, respectively. Low soil fertility, poor stand establishment, and a highly unpredictable drought stress patterns are major production constraints. Grain production in extreme and variable stress environments may be improved by growing hybrids, gaining from heterosis for yield potential and stability. Two experiments were conducted to investigate hybrid vigour of grain sorghum under variable growing conditions in dryland regions of Kenya.

Materials and Methods

Genetic materials in Experiment I consisted of twelve unrelated single-cross hybrids and their 24 parent lines. Experiment II comprised three sets of factorial crosses between four female and four male lines each, and the respective 24 parent lines. All entries tested represented actual breeding materials from SADC/ICRISAT (Southern African Development Community/International Crops Research Institute for the Semi-Arid Tropics) Zimbabwe and ICRISAT India. The two experiments were each conducted in eight macro-environments (site/season combinations, differing in Experiment I and II) in the semi-arid to arid Makueni and Baringo District, during 1991-1993. Only grain yield data is reported here. Combined analyses of variance across environments, including stability analyses (Eberhart and Russell 1966) and estimates of ecovalence (Wricke 1962), were computed with logarithmically transformed data (Transformation: $Y' = \text{LN} [(\text{grain yield in g m}^{-2} / 10) + 1]$), since genetic and environmental effects were related in a multiplicative manner, indicated by Tukey's test for non-additivity (1949).

Results

Growing conditions during the experimental period were highly variable and included two non-stress and six stress environments (including preflowering, terminal, and extreme drought) in both experiments. Correspondingly, environmental means for grain yield ranged from 584 to 47, and from 595 to 167 g m⁻² in Experiment I and II, respectively. Hybrids significantly outyielded the homozygous parent lines under all environmental conditions, with a mean relative hybrid superiority of 54 and 47% in Experiment I and II, respectively (data not shown). The relative hybrid superiority ranged from 32 to 107% in the individual environments. In Experiment I, the highest hybrid superiorities were observed in the two lowest yielding environments; i.e., under extreme stress conditions. Contrastingly, there was no relationship between heterosis and stress intensity in Experiment II. Genotype x environment interaction (GxE) variances were larger than genotypic variances in both experiments. The average estimate of ecovalence was lower for hybrids than for lines, indicating that the hybrids contributed less than lines to the total GxE variance (Table 1). Stable entries were found among both lines and hybrids. On average, hybrids were slightly more stable than lines. Level and stability of grain yield were not associated.

Regression lines for the three highest yielding hybrids in Experiment I and their parent lines exemplify a variety of responses of entries to increasing environmental stress (data not shown). The differences in the regression lines among the parents resulted into rank changes at differing productivity levels. The slopes of the regression lines of two hybrids (SDSH 4 and SDSH 398) lay between those of their respective parent lines, while the slope of the third hybrid (SDSH 215) resembled that of the more stable parent (SPL 23B).

In Experiment II, variation among hybrids was determined by both, GCA and SCA effects. Lack of variation for GCA was noted among the tested female lines. The percentage ratio of SCA to the total genotypic variance was 27% for grain yield. The genetic correlation between line performance *per se* and GCA was tight for male ($r=0.93$, estimate exceeding its standard error twice) but non-significant for female parent lines. In Experiment I, midparent value and hybrid performance were genetically correlated with $r=0.74$ (estimate exceeding its standard error once). In both experiments, no association between midparent and hybrid performance was observed for the stability parameters.

Conclusions

Hybrid breeding holds promise for improving sorghum grain yield and stability in semi-arid areas of Kenya. To increase selection progress, the genetic variation in the gene pool of cytoplasmic-genic male sterile lines should be enhanced. If the prepositions for successful hybrid production and marketing are not fulfilled, synthetic or population varieties could be produced which capitalize on heterozygosity and can be regrown for a few seasons – an advantage for the small-scale farmers. Large G×E effects point to the necessity of evaluating breeding materials under a range of environmental conditions. In defining selection criteria, much weight should be given to specific adaptability to extreme drought stress, since achieving a reliable minimum grain yield is more important to the subsistence farmers than high yields in the rare favourable seasons.

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Table 1. Means and ranges (across genotypes) of lines and hybrids in Experiments I and II for performance level (\bar{Y}) and ecovalence (W) for grain yield [g m^{-2}], based on eight (two non-stress and six stress) environments.

Parameter	Experiment I		Experiment II	
	Lines	Hybrids	Lines	Hybrids
Mean	239	367	274	403
Range	165-316	340-411	196-380	161-488
$W^{1,2}$	Mean	73	43	28
	Range	11-226	4-109	5-103

¹ Logarithmic scale. ² Estimates multiplied by 1000.

B79 - Evaluation of Heterosis Among Short Season Populations of Maize

M.N. Aguerre, J. Lúquez, J.C. Suárez

Unidad Integrada Balcarce. CC 276, 7620, Balcarce, Argentina

Introduction

The performance of nine short-season maize (*Zea mays* L.) populations of different origins was evaluated to assess their usefulness as basic germplasm for the southeastern region of the Buenos Aires province, Argentina. The objective of the experiment was to evaluate the combining ability and "per se" performance of the populations.

Materials and Methods

Populations B73 and M17 were developed by combination of different versions of lines B 73 and Mo 17, respectively. Populations CCP and CSP were developed by INTA Pergamino, Argentina. Population CDB was developed at INTA Balcarce, crossing 13 commercial dent hybrids to combine genes from the Reid Yellow Dent and Lancaster Sure Crop heterotic groups. Populations Pool 29 (P29), Pool 40 (P40), Pool 41 (P41) and Compuesto Cristalino de Portugal are from CIMMYT (Origins TL86B6235, TL86B6230, TL86B6231 and Portugal 86, respectively). A series of diallel crosses were made among the populations, in the summer of 1992/93, at the Balcarce Experimental Station of INTA. There were 50 entries in the experiment, including the 36 crosses, the nine parents, and five commercial hybrids used as checks. The entries were evaluated in a randomized complete block design with three replications at three environments: Balcarce and Loberia in 1993/94, and Balcarce in 1994/95. Plots included two rows of 5 m long, planted at a density of 70,000 plants ha⁻¹. Analysis of variance for grain yield was adjusted, using number of plants as the covariant. A mixed model (Model III) was used, considering the effects of environments and replications as random, and treatment effects as fixed. Varietal (v_i), high-parent heterosis (h_{ij}), varietal heterosis (h_i), specific heterosis (s_{ij}), and average heterosis (h) effects were estimated following the Analysis II of Gardner and Eberhart (1966). The significance of the effects were determined with a L.S.D. test, with the variances estimated as proposed by Vencovsky (1971). General combining ability of each population (G_i) was estimated as $G_i = 1/2 v_i + h_i$, to obtain an estimate of the favorable additive effects (Gardner and Eberhart 1966). Cluster analysis was used to estimate relationships among populations, according to their h_{ij} . The Euclidean distance coefficient calculated from a standardized data matrix was used to make the groups, following the unweighted pair-group method using arithmetic averages (UPGMA) (Crisci and López Armengol 1983; Rohlf 1990).

Results and Discussion

Adjusted mean yield of all entries across environments was 6980 kg ha⁻¹, with a C.V. of 11.4%. Mean yield of the check hybrids was 9375 kg ha⁻¹, whereas the populations had an average yield of 5815 kg ha⁻¹, and the crosses among populations had an average yield of 6943 kg ha⁻¹. Average heterosis was 1128 kg ha⁻¹ (19%), a value similar to those estimated by Pérez Velázquez et al. (1995) and Hallauer and Miranda (1981). The h_{ij} estimates fluctuated between 2479 kg ha⁻¹ (47.9 %) for M17xP29 and -1763 kg ha⁻¹ for CSPxP40. Nineteen of the 36 crosses had significant estimates of h_{ij} . Only three estimates of h_{ij} were significant and negative (for the crosses CSPxP29, CSPxCCPORT and CSPxP40), all involving the population CSP, probably because of the high "per se" performance of CSP (7500 kg ha⁻¹). The results of the analysis II of Gardner and Eberhart for grain yield across environments showed significant differences for heterosis, specific heterosis, and for the interactions of environments with varietal effects, heterosis, average heterosis and varietal heterosis (Table 1). Average heterosis was not significant, due to its interaction with the environments. B73, CSP, CDB, and P41 had positive v_i values for the three environments. These populations had high yield per se, indicating the presence of favorable additive effects for each. The G_i values were positive and significant only for populations B73 and CDB, suggesting predominance of favorable additive effects. Populations B73, M17, and CDB showed positive h_i values in all environments. Populations CSP and P41, which had positive v_i values

in all environments, had negative h_j values. Population M17, which had positive h_j values, had a majority of negative v_i values. M17 could be used as male parent in crosses, to capitalize on those apparent favorable dominant effects. Values of s_{ij} varied between 817 kg ha⁻¹ and -856 kg ha⁻¹. Only 12 of the 36 crosses had significant s_{ij} values, with CDBxP29, CDBxCSP and M17xP29 having the highest positive estimates of s_{ij} . These results suggest the presence of dominant or epistatic favorable effects in the crosses of P29 with CDB and M17. The population CDB was formed to integrate genes from heterotic groups of Reid Yellow Dent and Lancaster Sure Crop. Because CDB had negative and significant estimates of s_{ij} in crosses with B73 and M17 suggests the existence of relatedness of genetic effects, as was expected. In spite of the s_{ij} estimates, CDBxB73 had high yield (8105 kg ha⁻¹), with significant h_{ij} effects. Among the evaluated populations, we selected CDB and B73 to derive female (or even male) lines, because of their G_j values. We selected the population M17 to derive male lines, because of its h_j values. P29 also was selected to derive male lines, because of its s_{ij} estimates in crosses with CDB and M17, as well as its h_{ij} estimates in crosses with CDB, B73, and M17. Three groups were formed with eight populations, with M17 isolated from the three groups. Group I was formed by B73 and CSP, joining other groups at lower levels of similarity. Group II was formed by CCP, CDB, CCPORT, and P40; and Group III by P29 and P41. Groups II and III were more related between them than with Group I. CDB, which is a population that shares genes with B73 and M17, was separated from both of them, in an intermediate group, as expected.

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Table 1. Analysis of variance of yield across environments.

Source of variation	df	S.S.	M.S	F	Pr > F
Varieties	8	245985005	30748126	2.27	> 0,0500
Heterosis	36	176129004	4892472	2.39	< 0,0050
Average heterosis	1	82511406	82511406	2.28	> 0,2500
Varietal heterosis	8	36504157	4563020	2.36	> 0,0500
Specific heterosis	27	57113441	2115313	2.58	< 0,0050
Var x Environments	16	216292440	13518278	18.16	< 0,0005
Heterosis x Environments	72	147172368	2044061	2.75	< 0,0005
Average het. x Environments	2	72144304	36072152	48.46	< 0,0005
Var heterosis x Environments	16	30830139	1926884	2.59	< 0,0010
Spec. heterosis x Environments	54	44197926	818480	1.10	> 0,2500
Combined Error	85	195033514	744403		

B65 - Combining Ability and Stability of Elite Maize Inbred Lines and their Single-Crosses

U.P. Klink¹, F. Ajudarte Neto¹, and J.R.Môro²

¹Zeneca Brasil Ltda - Cravinhos (SP) Brazil and ²Dep. de Biologia, UNESP, 14870-000. Jaboticabal (SP) Brazil

Introduction

Commercial single-crosses are increasing in importance in Brazil and efforts are being made by maize breeders to obtain genetic materials with high productivity and stability, as well as resistance to diseases and stalk and root lodging. In this paper the results of a partial diallel study are presented, including results on stability over environments and specific and general combining ability (SCA and GCA) of 9 elite inbred lines.

Methods

Nine elite inbred lines were crossed in a partial diallel system (4 x 5), and the parents and their F₁s were evaluated in Cravinhos (SP), Londrina (PR), Castro (PR), and Rio Verde (GO), during 1993-94. The trials were planted in the beginning of October, with plots of 4 rows with 5 m long. Data were analyzed for stability according the Eberhart and Russell (1966) model, and the diallel with the model proposed by Geraldi and Miranda F^o (1984). Group A was composed with 4 inbred lines derived from Suwan DMR (L1 - 4) and the group B by 5 inbred lines obtained from Maya (L 5 and L9) and from Tuxpeño (L 6 - 8). The single crosses were obtained from crosses between inbred lines from group A with those from the B group.

Results

Table 1 shows the partial diallel analysis of variance for grain yield (kg/ha) over locations. All effects were significant (p<0.01). Table 2 presents the average grain yield for inbred lines and their single-crosses, the GCA and SCA and the regression coefficient from the across-environments analysis. Two inbred lines were highly productive (3,804 and 4,403 kg/ha) and would allow the economic production of commercial single crosses, if used as the female. Most single produced more than 9,000 kg/ha and their b coefficients were similar.

Conclusions

In this sample of inbred lines there were at least four potential single crosses that could be commercially produced, with average grain yield above 10,000 kg/ha and with a reasonable level of stability across environments. The hybrids with lines 3 or 6 as parents would be preferred, because they had the best per se productivity.

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Table 1. Analyses of variance combined over four Brazilian locations for grain yield (kg/ha) of nine maize inbred lines and their 20 partial single crosses.

Source	df	Mean squares	F
Locations (L)	3	31159872.00	70.59**
Genotypes (G)	28	129246632.00	292.80**
Among Groups	1	36550164.00	82.80**
GCA-Group 1	3	3676196.00	8.32**
GCA-Group 2	4	5445318.00	12.33**
SCA-G1 x G2	20	568477112.00	128.78**
L x G	84	1891448.00	4.28**
L / G	87	2899738.50	6.56**
Error	224	441404.25	

Table 2. Mean yield (\bar{X}) and stability parameter estimates (b , s^2_d) for grain yield (kg/ha) of nine maize inbred lines and twenty single-crosses (SC) evaluated in four environments.

Genotype	X - kg/ha	b	s^2_d
LINE 01 - Suwan	2,375.5	0.32	2628491.0
LINE 02 - Suwan	2,904.2	0.81	234738.6
LINE 03 - Suwan	4,403.7	0.34	1229073.3
LINE 04 - Suwan	2,755.0	1.17	9439.2
LINE 05 - Maya	2,302.7	1.11	2643483.5
LINE 06 - Tuxpeño	3,804.0	-0.01	1686022.1
LINE 07 - Tuxpeño	1,935.7	1.30	1171233.6
LINE 08 - Tuxpeño	1,045.5	0.92	-6318.0
LINE 09 - Maya	1,542.2	0.35	61045.9
SC - 0105	10,192.5	1.00	-37577.0
SC - 0106	9,661.5	0.86	-44883.5
SC - 0107	10,033.2	1.12	4389.1
SC - 0108	9,846.0	1.46	57370.3
SC - 0109	9,217.7	0.76	123578.6
SC - 0205	9,140.2	0.92	-48755.2
SC - 0206	9,578.2	1.25	390128.5
SC - 0207	8,903.5	1.93	131271.2
SC - 0208	9,482.0	1.81	-73144.7
SC - 0209	7,995.0	0.13	-1555.6
SC - 0305	9,423.7	2.14	665866.4
SC - 0306	10,051.7	0.32	-12078.4
SC - 0307	9,765.2	1.78	117768.4
SC - 0308	10,103.2	0.87	-32120.3
SC - 0309	8,566.0	1.27	679073.1
SC - 0405	9,145.0	1.08	-32763.4
SC - 0406	9,369.0	0.75	3114797.2
SC - 0407	9,133.2	0.86	1289837.6
SC - 0408	9,101.0	0.82	579964.9
SC - 0409	8,265.5	1.43	1470086.3

B66 - Heterosis in Sorghum

Mehmet Ali TÜSÜZ

Mediterranean Agricultural Research Institute, P.O.Box.39, Antalya, Turkey

Introduction

Sorghum production in Turkey is becoming more important in the recent years. The production occurs mainly in the irrigated areas of southeast, with the double crop sorghum areas in Mediterranean and Aegean Region. Sorghum has been known under the name of "darylar" in Turkey. Heterosis is a common phenomenon in first generation hybrids of many species of plants. Heterotic manifestations which have been reported by many researchers in sorghum (*Sorghum bicolor* (L) moench) include earlier blooming, greater height, greater tillering, heavier seeds, and seeds that mature faster and greater production of grain. The study reported here was made to get a clearer picture of some of morphological differences between hybrids and their parent to compare the increases in grain production and other traits of hybrids.

Methods

A 10 x 10 partial diallel experiment was conducted in the summer of 1979 in Aegean Agricultural Research Institute field in Yzmyr. Randomized complete block design with four replications was employed. Heterosis and heterobeltiosis were calculated (Fonseca and Peterson 1968) and partial diallel analysis were used (Jones 1965). The rows each 5 meter long, were spaced 70 cm apart, the plants within a row being 7.8 cm apart, 4 rows for each sorghum variety were planted. Ten sorghum lines were NES 708, IS 166, NES 635, NES 688, NES 2005, IS 10952, NES 440, NES 1364, Local sorghum, NES 266. Plant height (cm), 50% flowering date, 1000-seed weight (gr), and year per plant (gr) were measured.

Results and Conclusions

Significant variation exist for all the agronomic characters studied in the F_1 combinations and their parents (Table 1). In comparisons among the parents, F_1 s showed almost 100% heterosis for the four characters studied. The highest midparent heterosis (20.58%) was found for the plant height. A local variety (from the Mula region) and NES 266 (Akdary) showed a markedly higher heterosis effect. Additive (a) and dominant (b) gene effects and specific combining ability (b_3) were significant for all traits.

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Table 1. Mean performance of parents, F₁s, mid-parent heterosis and heterobeltiosis in sorghum.

Characters	Mid parent mean	High parent mean	F ₁ mean	Heterosis (%)	Heterobeltiosis (%)
Plant height (cm)	114.25	132.22	143.86	20.8	8.80
50% Flowering date	86.08	83.65	80.54	-6.88	-3.71
1000 Seed weight (gr)	25.90	27.79	29.10	0.99	4.71
Yield per plant (gr)	277.75	295.19	333.98	16.83	13.14

B67 - Identification of Maintainer and Restorer Lines from Local and Improved Rice Germplasm in Assam, India

R.P. Borkakati, D.K. Baruah, S.K. Chetia and A.K. Pathak

Assam Agricultural University, Regional Agricultural Research Station, Titabar 785630, Assam, India

Introduction

In Assam rice is the principal crop occupying around 80% of the total cropped area in the state. Average rice productivity is quite low (1,289 kg/ha), but yields are fairly high (average 4,100 and as high as 7,000 kg/ha) in favorable areas, where farmers grow high yielding varieties. In these areas, further increases in productivity through use of inbred varieties seems limited, whereas hybrids offer good scope for yield gains. Many cytoplasmic genetic male sterile (CMS) systems have already been reported in rice (Virmani and Edwards 1983). In China mostly the CMS lines which were derived from the wild abortive (WA) source are being used in rice hybrid breeding program (Li and Yuan 1986). The genetic tools essential for producing F₁ hybrids mainly CMS, maintainer and restorer lines were developed in 1973 (Yuan et al. 1994). Apart from CMS lines as ideal starting material, identification of suitable maintainer and restorer lines is essential for a hybrid rice breeding program. The present investigation was undertaken to identify suitable maintainer and restorer lines for hybrid rice breeding.

Methods

Thirty-five rice varieties, both local and improved, were crossed during the wet season, 1995, with five WA CMS lines, PBCMS 2A, PBCMS 3A, and PBCMS 10A from Punjab and IR 58025A and IR 62829A from International Rice Research Institute (IRRI). The F₁ hybrids were grown during wet season, 1996. Five plants from each hybrid were labeled. Twenty to thirty florets from each plant were sampled at anthesis and fixed in 70% alcohol. Five to six anthers were taken at random from the collected florets and squashed on a slide in 1% iodine-potassium-iodide solution and examined under the microscope. All round and dark blue stained pollen grains were scored as normal fertile and irregular shaped, yellowish or brown colored ones were scored as sterile. About 200 to 300 pollen grain were scored from each slide and expressed in percentage. Two panicles per plant were bagged with glassine bags prior to anthesis to prevent cross pollination. Bags were harvested with panicles inside for seed counting to determine spikelet fertility and expressed in percentage. Based on pollen and spikelet fertility observations, the test varieties were classified as effective restorer (> 80% fertility), weak or partial restorer (20-80% fertility), weak maintainer (5-20% fertility) and maintainer (0-5% fertility).

Results

Potential maintainers identified were Guni, ARC 10372, Kapilee, Aditya, Krishna and Kushal for PBCMS 2A; Banglami, Guni, ARC 10372, Manoharsali, Kapilee, Chilarai, Annada, Krishna and Aghoni for PBCMS 3A; Heera, Mahsuri and Aghoni for IR 58025A and Satya for IR 62829A. Potential restorers identified were Luit and IR 50 for PBCMS 2A, Pankaj for PBCMS 3A and PBCMS 10A and Luit for IR 58025A (Table 1). The pollen parent behaved differently for different CMS lines, which indicates that the cytoplasm of the CMS lines interacted differently with the pollen parent.

Conclusion

The potential maintainers identified will be used in a back-crossing program for inducing cytoplasmic male sterility in local as well as improved rice varieties. Restorer lines will be used to develop suitable superior hybrids.

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Table 1. Restorer, maintainer reaction of some local and improved rice varieties in Assam , India with five CMS lines.

Variety	PBCMS 2A	PBCMS 3A	PBCMS 10A	IR 58025A	IR 62829A
Banglami	WM	M	PR	WM	PR
Heera	PR	PR	WM	M	WM
Rangadoria	WM	WM	PR	PR	PR
Guni	M	M	WM	PR	WM
ARC 10372	M	M	PR	WM	WM
Luit	R	PR	PR	R	PR
Lachit	PR	WM	PR	PR	PR
Manoharsali	PR	M	PR	WM	PR
Govind	PR	PR	PR	PR	PR
Madhab	WM	WM	PR	PR	WM
Kapilee	M	M	PR	PR	PR
Chilarai	WM	M	PR	PR	WM
Rasi	PR	PR	WM	PR	PR
N ₂₂	PR	PR	WM	PR	PR
Culture 1	PR	PR	PR	PR	PR
Annada	WM	M	WM	WM	WM
Aditya	M	PR	WM	PR	PR
IR 50	R	PR	PR	PR	PR
Krishna	M	M	WM	PR	PR
Jaya	PR	PR	PR	PR	PR
Mahsuri	PR	PR	PR	M	PR
Mansorobar	PR	PR	PR	PR	PR
Satya	WM	PR	PR	WM	M
Basundhara	PR	PR	PR	PR	PR
Lakhimi	PR	PR	PR	PR	PR
Aghoni	WM	M	WM	M	PR
Pankaj	PR	R	R	PR	PR
IET 8585	PR	PR	PR	PR	PR
IET 10016	WM	WM	PR	PR	WM
Moniram	WM	PR	PR	PR	PR
Pioli	PR	PR	PR	PR	PR
Ranjit	PR	PR	PR	PR	PR
Keteki	WM	WM	WM	WM	WM
Kushal	M	PR	PR	PR	PR
Bahadur	PR	PR	PR	PR	PR

R = Restorer, PR = Partial restorer, WM = Weak maintainer, M = Maintainer.

B68 - Two Line Hybrids in Cereals with Special Reference to Sorghum

U.R. Murty

National Research Centre for Sorghum, Rajendranagar, Hyderabad 500 030, India.

Introduction

Commercial cultivation of hybrid crop plants has led to quantum leaps in productivity. Starting with maize, heterosis has been exploited in sorghum, pearl millet, cotton, rice and a series of vegetables. A variety of mechanical, chemical and cytoplasmic genetic tools have been used to achieve hybrid seed production on a commercial scale. While these achievements were spectacular on a global basis, the commercial cultivation of F_1 hybrids has been highly skewed in favour of the developed countries and mostly the progressive farmers in developing countries. Attempts are therefore being made to reduce the cost of hybrid seed. The production of two-line hybrids in rice by making use of temperature and photoperiod-sensitive genetic male sterility (Yuan 1990) and similar attempts in sorghum using season-sensitive cytoplasmic genetic male sterility (Murty 1995) represent attempts in this direction. While production of uniline hybrids using apomixis should be the ultimate objective of plant breeders to achieve the goal of inexpensive hybrid seed, the two-line method represents an intermediate step in this direction and forms the subject matter of this report.

Methods

Uniline CMS lines. Presently commercial hybrids of sorghum are based on a single cytoplasm, the milo, or A1. The A2 cytoplasm released in 1977 (Schertz 1977) has been utilised in the present study. Through the use of paired backcrosses, 18 male steriles were developed. These lines are male sterile during the winter season but their male sterility broke down during the rainy and summer seasons, to varying extents. This partial male sterility resulted in seed set of varying extents. Seed harvested from such lines exhibited the same behaviour during different seasons; i.e., fully male sterile during the winter and partially fertile during the rainy and summer seasons. From this behaviour, it was possible to maintain a male sterile (A) line by selfing during the rainy or summer seasons without crossing to a maintainer (B) line, as is normally practised (Murty 1993). Eighteen such lines were tested for such behaviour during 3 seasons: winter, rainy and summer.

Two-line hybrids. The above lines were crossed to previously identified elite fertility restorers and the hybrids were tested for their fertility during the winter and rainy season.

Results

All 18 lines were male sterile and did not set any seed during the winter season. However, during summer, 11 lines exhibited male fertility of 10-90% and set seed ranging from 5-100% (Table 1). Pollen fertility as well as seed set varied not only among the different lines but also between individual plants of the same line. Out of several hybrids produced over several seasons, five hybrids during the rainy season and two hybrids during the winter season were found to be fully fertile (Table 2). One rainy season hybrid, designated as SSH-1, was found to have sweet stalks that make it suitable for alcohol and sugar production. It was tested in multilocation tests of the All India Co-ordinated Sorghum Improvement Project and ranked first for grain yield and sugar parameters (Table 3)

Conclusions

It was possible to develop male sterile parents that were stable for male sterility during the winter season characterised by short photoperiods (< 12 h) and low temperatures (<20°C). Breakdown of male sterility in these lines during summer with long photoperiods (>12 h) makes them amenable for use as uniline CMS lines, possibly to produce two-line hybrids that could help reduce commercial hybrid seed

costs 33%, as well as circumventing the problems of synchronisation of A and B lines and adequate pollen availability and dispersal.

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Table 1. Fertility status of 18 genotypes in A₂ cytoplasm during the winter and summer seasons.

Sterile during both winter and summer	S-3-742; S-6-815; IR-11-150; IR-12-160; IR-36-165; IR-37-162; IR-38-161; SR-48-18.
Sterile during winter and fertile during summer	MR-26-750; MR-28-840; SB-29-1085; CS-30-3541; S-30-918; S-34-980; IR-40-172; CSM-42-8; CSM-44-23; RS-49-29

. Fully fertile hybrids based on uniline CMS male steriles.

Rainy Season	Winter season
MR -26-750 x M 73	S-34-980 x M 35-1
MR -28-840 x M 2	IR -40-172 x M 35-1
MR -28-840 x M4	
MR-28-840 x M28	

Table 3. Comparative performance of SSH-1, a fully fertile sweet sorghum hybrid, in relation to a commercial sweet sorghum, SSV-84.

Character	SSV-84	SSH-1	CD (0.5%)
Grain yield (kg/ha)	1047.00	3324.00	697.00
Dry fodder yield (q/ha)	248.00	227.00	68.00
Total sugar yield (kg/ha)	1357.00	1402.00	37.00

B69 - Stability of Maize Double-Crosses Evaluated Under the "Safrinha" Conditions in São Paulo, Brazil

J.R. Môro, R.M. da Silva, and J.T. Ayala-Osuna

Dep. de Biologia, UNESP/FCAVJ - 14870-000 - Jaboticabal - SP - Brazil

Introduction

In recent years, farmers increasingly plant maize as a second crop in South and Central Brazil, generally after soybean harvest. This practice requires genotypes different from those used in the main season, in the beginning of the spring. During this second planting (safrinha) the water supply, temperature, and day length are reduced, and foliar disease incidence increases. Farmers do not use fertilizers in safrinha, so genotypes must efficiently exploit residual N in the soil. Finally, given changes in the climate and soil conditions over time, stability is a highly desirable trait.

Materials and Methods

Fourteen maize synthetics are being improved through recurrent selection in a pedigree scheme. Inbreds (F_4/F_5) of each synthetic are obtained by selfing and evaluated in crosses and per se. For each synthetic, from 8 to 15 elite inbred lines are selected and recombined, completing one cycle of selection. From 173 elite inbreds, selected per se and in single-cross combinations in the third cycle, 124 double-cross hybrids were obtained and in three environments during 1995-96: Jaboticabal (SP, two trials) and Barretos (SP). The hybrids were divided into 4 groups of 31, evaluated with 5 commercial checks in a triple 6x6 lattice design, with 2-row plots 5 m long. Data were analyzed for stability using the Eberhart and Russell (1966) model.

Results

Table 1 shows a summary of the ANOVA for grain production. The locations (L), hybrids (H), and the L x H effects were significant ($p < 0.01$), except for the L x H in group 3, that was significant at $p < 0.05$. In Table 2, the best double cross hybrids are shown, with their average productivity, the grain yield in each location, and the stability parameters. Only the hybrids better than the best check of the trial were listed. Average productivity in the first season at Jaboticabal (SP) was higher than in the other 2 trials. Later sowing involved drought risk at flowering, reducing average productivity in the latter two trials. Most of the double crosses were significantly more productive than the best checks, with good stability across environments. These materials were selected for disease resistance and for efficiency in water use under different soil and climate conditions.

Conclusions

Recurrent selection in a pedigree scheme, as used for improved maize synthetics in the Maize Program of the Department of Biology/UNESP, results in inbred lines with good heterosis and stability over environments with different levels of productivity. The double-crosses have these characteristics because the elite inbred lines used to make them were selected for disease tolerance and for efficiency in water and nutrient use.

Reference

Eberhart, S.A., and W.A. Russell. 1966. *Crop Sci.* 6:36-40.

Table 1. Anova for grain production (kg/ha) for 124 maize double-crosses evaluated in 4 groups of trials (31 DC+5 commercial checks) in 3 environments, Brazil, 1995-96.

SV	DF	Group 1	Group 2	Group 3	Group 4
Locations(L)	2	641571124.10	757390796.60	472716762.30	440430251.80
Replications\L	6	718030.20	5750747.10	3696175.70	10783866.70
Hybrids(H)	35	3376561.80	2404847.70	2247331.70	2119719.50
H x L	70	695564.70	794300.20	547566.30	1235632.30
Error	210	372699.18	498604.53	389989.05	568789.39
Average(Kg/ha)		5161.15	4721.38	4437.82	4263.64
CV%		11.83	14.96	14.07	17.69

Table 2. Grain productivity (kg/ha) and stability estimates (Eberhart and Russell 1966) for 124 maize double-crosses evaluated in 3 environments, Brazil, 1995/96.

Hybrid	JAB(20/12/ 95)	JAB(19/01/ 96)	BAR(20/12 /95)	MEAN	<i>b</i>	<i>s</i> ² _{<i>a</i>}
1A	8711	5441	3932	6028	0.99	166964
18A	8846	5463	3642	5984	1.07	71858
28A	9079	5796	2830	5902	1.28	-113497
8A	7846	5344	4063	5752	0.78	3326
30A	8908	5403	2705	5672	1.27	-114687
14A	9001	5234	2642	5626	1.31	-65649
22A	8273	5533	2831	5546	1.11	-88993
CHECK-1	7585	5869	3023	5493	0.92	273953
CHECK-2	8436	5005	2976	5472	1.13	11063
1B	9658	5395	3240	6098	1.23	91011
3B	9281	5500	2294	5692	1.32	-144564
10B	9243	5013	2174	5477	1.34	-133572
26B	7743	5241	2814	5267	0.93	-109369
8B	8256	4811	2142	5070	1.16	-165896
18B	7457	4916	2791	5055	0.88	-158951
9B	8341	4543	2430	5039	1.13	110730
22B	8414	4839	1851	5035	1.24	-152041
12B	7049	5526	2357	4978	0.87	691533
CHECK-2	7526	5176	2218	4974	0.99	122466
27C	7721	5428	2953	5368	1.14	-73713
25C	7601	4951	2579	5051	1.20	-124429
20C	7326	4891	2711	4976	1.10	-127105
26C	7325	4769	2726	4940	1.10	-127333
CHECK-2	7002	5175	2449	4876	1.08	142928
22D	8249	4837	2416	5168	1.40	938924
6D	6384	5991	2434	4937	1.04	492332
26D	7677	5011	1716	4802	1.47	-9548
14D	6604	5132	2483	4740	1.03	-189588
11D	5881	5396	2795	4691	0.80	62201
2D	6561	5233	2154	4650	1.12	-147701
15D	6501	4961	2465	4653	1.01	-184209
CHECK-1	6039	5470	2405	4639	0.94	161052

B72 - Pearl Millet Hybrids in India: Impact on Production and Productivity

O.P. Govila, K.V. Unnikrishnan, and B. Singh

Division of Genetics, Indian Agricultural Research Institute, New Delhi-110 012, India

Introduction

Pearl millet, *Pennisetum glaucum* (L) R.Br., is grown in the arid to semiarid tropics of the Indian subcontinent and Africa, primarily as a rainfed crop and for its stover and fodder. In India pearl millet is grown on about 10 million hectares where no other food crop can be grown due to low rainfall, marginal soils, and high temperatures. Genetic improvement for yield under these conditions is difficult. Single-cross hybrids of pearl millet have been in commercial use in India since 1965 with the utilization of cytoplasmic-nuclear male sterility (Athwal 1965; Burton 1958, 1965). During 1965-1984, hybrids and their seed parents have suffered from downy mildew, *Sclerospora graminicola* (Sacc) Schroet, causing occasional production losses (Govila et al. 1996). However, during the past ten years breeding efforts for downy mildew resistance (DMR), the development of hybrids for specific agroclimatic zones, and organized seed production and distribution in India have increased the production and productivity of pearl millet. During 1976-1981 production and productivity was 5.03 million tons per year and 463 kg/ha; this increased to 6.83 million tons per year and 683 kg/ha in 1991-1996.

Methods

After the collapse of popular hybrids due to downy mildew disease during 1983, IARI began a breeding programme to incorporate DMR into the seed parents. CMS lines 5141 B, Tift 23 B and restorer J 104, which are excellent general combiners but highly susceptible to downy mildew, were utilized as recurrent parents in a backcross breeding scheme. Agronomically desirable plants with DMR were simultaneously selected in the BC₂ generation and followed through the pedigree method. Finally, DMR CMS and restorer lines were developed (Tables 1, 2). After stabilizing the maintainer system, extensive crossing and testing was performed to develop high yielding DMR hybrids (Table 3).

Results

Pusa 23 is among the most widely cultivated hybrids, accounting for 47% of certified seed production in India during 1997; IARI hybrids in general comprised 55% of certified seed. We are now attempting to develop hybrids suitable for cultivation under low rainfall areas (less than 400 mm rainfall). So far, the hybrid technology has not been extended to such areas in India.

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Table 1. Performance of DMR CMS lines (A₁ cytoplasm) developed at IARI.

S. No.	Entry No.	Plant height (cm)	Days to 50% flowering	Effective tiller nos./ plant	Ear head girth (cm)	Ear head length (cm)	Yield/ plant (gm)	Downy mildew %
1.	393A	146	51	2.7	2.08	16.8	37.1	0.5
2.	579A	161	56	2.5	2.26	17.6	38.2	0.0
3.	585A	147	51	2.8	2.02	16.9	37.6	0.2
4.	96-366A	123	57	2.6	2.28	19.8	46.2	0.0
5.	189A	178	52	2.3	2.03	17.9	35.9	1.7
6.	490A	155	51	2.9	2.39	18.1	49.4	0.7
7.	1049A	173	55	2.7	2.23	16.3	39.8	0.2
8.	1089A	149	53	2.6	2.36	17.2	41.6	0.0
9.	841A (check)	152	50	2.5	1.98	16.1	38.3	2.2
10.	5141A (check)	156	55	2.9	1.81	18.8	34.8	27.8
*C.D. P = 0.05		5.5	4.2	0.6	0.13	1.6	4.6	

Table 2. Performance of inbreds developed at IARI through DMR breeding (all lines restore on A₁ cytoplasm).

S. No.	Entry	Plant height (cm)	Days to 50% flowering	Effective tillers/ plant	Ear length (cm)	Ear width (cm)	1000-grain weight (g)	Grain yield/ plot (kg)	Downy-mildew score
1.	PPMI 93	163	50	1.17	22.0	2.22	8.50	0.54	1.0
2.	PPMI 69	153	40	1.98	14.3	1.54	6.40	0.40	0.7
3.	PPMI 151	183	51	1.00	20.0	2.27	8.33	0.93	1.3
4.	PPMI 94	173	55	1.08	24.2	2.10	7.60	0.69	0.0
5.	PPMI 301	163	58	1.25	19.1	2.02	8.23	0.55	0.0
6.	PPMI 595	163	48	1.08	21.2	1.60	7.23	0.43	0.2
7.	PPMI 303	178	46	2.08	14.6	1.72	6.90	0.35	1.2
8.	PPMI 667	139	45	1.25	16.8	1.90	4.87	0.40	2.7
9.	J104 (check)	150	47	2.00	12.4	1.90	8.00	0.35	28.6
10.	D-23 (check)	166	54	2.00	18.1	2.21	9.48	0.52	2.5
C.D. P=0.05		4.3	4.8	0.7	1.3	0.08	0.16	0.04	

Table 3. Recent DMR hybrids of pearl millet released from IARI.

Hybrid	Parents	Average yield (kg/ha)	Days to 50% flowering	Days to maturity	Downy mildew (%)	Fodder yield (t/ha)
Pusa 23	841A x D 23	2312	48	77	1.7	5.3
Pusa 322	841A x PPMI 301	2463	51	81	1.8	5.6
Pusa 444	180A x PPMI 301	2260	47	77	4.9	3.9
Pusa 325*	490 x PPMI 303	2345	49	78	0.7	5.3
Pusa 605*	841A x PPMI 69	2247	49	78	0.8	5.1

* Identified for release and pre-release multiplication. Data from release proposals.

B74 - Expression of Heterosis for Yield and Yield Traits in Indian Wheat Crosses under Drill Sown Condition

S. Singh, R. Dhari and A.K. Joshi*

Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi, India

Introduction

In the wake of developing commercial hybrids, a number of workers have reported varying degrees of yield heterosis in wheat (Edwards et al. 1980, Shen et al. 1981, Perenzin and Borghi 1988, and Kratochvil and Sammons 1990) and have suggested the production of hybrids to exploit the non-additive type of gene action responsible for the expression of grain yield to break the existing yield plateau in this crop. Though cytoplasmic male sterility and fertility restorer systems are well known for wheat (Worland et al. 1987), precise information on the exploitable level of useful heterosis over the current varieties is often lacking, especially for drill sown conditions. We thus attempted to measure heterosis for yield and its attributes under such conditions for several crosses.

Methods

One hundred intervarietal crosses were developed during the 1994-95 and 1995-97 wheat crop seasons, utilizing diverse commercial wheat varieties of northern India. The parental varieties and their F_1 populations were sown in three replications in a randomized block design during two consecutive crop seasons (1995-96 and 1996-97). Sowing was done by hand using the drill sowing method. Each plot consisted of two rows of 3 m with a 30 cm row spacing. Check varieties HUW 206 and HUW 214 were also planted for comparison. The recommended package of practices was followed to raise a normal healthy crop. Whole plots were harvested separately to measure number of effective tillers per meter length, number of grains per spike, thousand grain weight (g), and grain yield (g). Heterosis expressed as percentage increase or decrease of F_1 over the better parent (heterobeltiosis) and check parent (standard heterosis) was calculated according to the methods suggested by Hays et al. (1955).

Results

Several crosses showed heterosis over checks for yield and associated yield components. For grain yield, the best hybrid was CPAN 3048 x HUW 206 followed by CPAN 4007 x HUW 206, BW 362 x HUW 234 and HUW 2005 x K 9107. However, only the first two crosses showed a heterosis for grain yield over the check parent HUW 243 of more than 20% -- the accepted minimum for commercial exploitation under the field conditions.

Conclusions

Standard heterosis below 20% is generally considered unacceptable to justify commercial use of a hybrid wheat. The highest cross combination obtained in this study showed only 24.48% heterosis for yield; marginally above the minimum. However, it does indicate some inherent expression of the extent of heterosis existing in these crosses for yield and its attributes. Since most are the commercial varieties, better expression of heterosis could be obtained by crossing more diverse genotypes with already established commercial cultivars suggested for cultivation in the irrigated areas of the northern and northeastern plain zones of India. The inclusion of more diverse genotypes could possibly be expected to give better heterosis under drill sown conditions and thus open avenues for use of rice hybrids in such areas of India.

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B75 -Heterosis for Yield and Other Characters in Upland Cotton

A. Unay, Cahit KONAK

Adnan Menderes University, Agricultural Faculty, Aydin-Turkey

Introduction

Heterosis for yield and quality characters in cotton has been reported by many researchers. It can be usually defined in two ways as F_1 /midparent, and F_1 /high parent (Silva et al. 1985), and useful heterosis (superiority to a check variety; Davis 1978). Meredith (1984) mentioned that heterosis was an indication of dominance, dominance x dominance epistasis, or both types of gene action. This research was carried out to evaluate F_1 hybrid vigor and useful heterosis in a line x tester analysis in cotton (*Gossypium hirsutum* L.).

Methods

The study was conducted at the Mediterranean Agricultural Research Institute's experiment Farm, Antalya, Turkey, 1991-1992. The population was established using the line x tester crossing method. Cotton cultivars Acala SJ 5 (6), Stonoville 825 N (7), GP 3774 (8), Lambright X 15-4 (9), Tamcot CAMD E (10), HYC 76-59 (11), and PD 4548 (12), were used as lines, and Cukurova 1518 (1; check variety), Nazilli 84 (2), Deltapine 50 (3), B 6396 (4) and C 4727 (5) as testers. The experiment was arranged in a randomized complete block design with four replicates. The experimental data were obtained from ten randomly selected plants in each plot. The observed characters were plant cotton yield (g), fiber length (mm), micronaire (mic.), fiber strength (pressley), and first picking percentage (%). Mid-parent, high-parent, and useful heterosis were estimated for each cross. Tests of significance were made by using a t-test.

Results

Heterosis for first picking percentage, seed cotton yield per plant, fiber length, micronaire and fiber strength ranged from -8.25 to 34.00%, from -22.22 to 35.36%, from -2.94 to 7.73%, from -8.12 to 23.86%, and from -3.61 to 4.99%, respectively (Table 1). Heterosis values were usually positive for all observed characters, especially first picking percentage, seed cotton yield per plant, and fiber length. Contrasts for heterobeltiosis in the characteristics except first picking percentage were negative.

Conclusions

The promising hybrids for heterosis, heterobeltiosis and useful heterosis were Stonoville 825 N x Cukurova 1518, Tamcot CAMD E x C4727, Tamcot CAMD E x Cukurova 1518, HYC 76-59 x B 6396, and PD 4548 X C4727 in the tests. Heterosis for fiber properties was generally smaller than that for yield and its components.

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Table 1. Percent mid-parent, high-parent, and useful heterosis in first picking percentage, seed cotton yield per plant, length, micronaire, and fiber strength.

	First picking percentage	Seed cotton yield per plant	Fiber length	Micronaire	Fiber strength
Heterosis (%)	-8.25-34.00	-22.22-35.36	-2.94-7.63	-8.12-23.86	-3.61-4.99
Heterobeltiosis (%)	-23.97-30.43	-26.76-30.45	-5.00-7.36	-19.40-23.51	-4.05-2.87
Useful heterosis (%)	0.00-52.08	-31.40-4.04	-2.36-7.36	-2.40-21.80	-2.17-5.50

B76 - Release of the Improved High Yielding Rice Variety "Nemat" with Good Cooking and Eating Characteristics

G.A. Nematzadeh, H.Arefi, R.Amani, and R. Mani

Rice Research Institute of Iran, P.O. Box 1658, Rasht, Iran

Introduction

Rice is a staple food in Iran and consumers prefer to use high quality rice. Local cultivars are mostly aromatic with high cooking and eating characteristics, but are potentially poor in yield. On the other hand, most improved varieties have high yields but lack suitable grain quality. Due to these reasons, most of the rice cultivation areas (>70%) are under local cultivars, and total rice production is insufficient, leading to sizable imports each year. To move toward self-sufficiency in rice, the Rice Research Institute of Iran (IR-RICE) improves high yielding aromatic rice with an acceptable eating quality for Iranian consumers; one example is the recently introduced hybrid, "Nemat".

Materials and Methods

Local aromatic high cooking and eating cultivars (Hassan Sarai and Sang Tarom), and improved high yield varieties and promising lines (Amol 3, RNR 1446 and PND 160 -2-1), were selected as parents of the hybridization breeding program. All possible crosses were done using the diallel mating system (Nematzadeh et al. 1985). Parents F_1 and F_1 were planted in an RCBD at Amol Rice Research Center. Nine important quantitative traits were recorded after 75% flowering, and physiological and chemical traits were analyzed after harvesting. Genetic analysis was done according to the Hayman (1954) and Griffing (1956) methods. Aside from this, the genetic interpretation of quantitative traits was conducted using the Juliano (1971), Cagampang et al. (1972), and Sood and Siddique (1978) methods. Finally, after 3 years of genetic studies on quantitative and qualitative traits and their breeding behavior, some crosses were selected and 6 superior pure lines resulted. Chemical treatments against pest and diseases were not done during the segregating generation. The quality of each selected single plant or lines were also analyzed. Yield trials were conducted.

Results

The results of the genetic studies of this long period (12 years) on the hybridization breeding program contain several tables and figures which are not be incorporated here. However, the significant result is that a new high yielding, improved variety (>8t/ha) with good cooking and eating characteristics was discovered and is called Nemat (Tables 1 and 2).

Conclusion

The improvement of high yield with an acceptable eating quality was the objective of IR-RICE. This aim was achieved through the hybridization breeding program and includes intensive genetic studies and high pressure selections (data not shown). Knowing the genetic behavior of important quantitative and qualitative traits and their relationship leads the breeder to fulfill his aims for the breeding program. Through this, the institute will be able to improve and introduce varieties with high yields and good qualities.

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Table 1. Important agronomic characteristics of the hybrid rice "Nemat" from the cross Sang Tarom x Amol3.

1-Tiller/plant	25	8-1000 weight	30 gr
2-Plant height	112 cm	9-Low grain length	9.99 mm
3-Panicle length	28 cm	10-Rice grain length	7.36 mm
4-Flag leaf	erect	11-Tolerant to	stem borer
5-Lodging	–	12-Resistant to	blast
6-Shattering	–	13-Yield	8t/ha
7-Maturity	relatively late		

Table 2. Important characteristics and response to stem borer and blast of the rice hybrid "Nemat" from the cross Sang Tarom x Amol3, in comparison with its parents.

Variety	AM	GC	GT	GE	AR	W.H	D.H	Bl	Ye
Nemat	26.4	M	L	4.8	S	11.5	13.1	2	>8
Amol3	29	H	L	2.3	N	59.9	72.8	6	
S. Tarom	23	S	M	2.5	H	17.2	21.8	8	

Am= Amylose Content

GC=Gel Consistency

GT=Gelatinization Temperature

GE=Grain Elongation

AR=Aroma

WH=white Head

DH=Dead heart

Bl = Blast

Ye = Yield

B77 - Evaluation of Heterosis among Iran's Rice Cultivars

H. Dorosti Hassan Kyadeh

Rice Research Institute of Iran P.O. B 1658 Rasht - Iran

Introduction

Rice area in Iran is almost 750,000 ha with an average yield of 3.8 t/ha. Rice is the second staple food grain after wheat. Iranian local varieties have high cooking quality. They have medium amylose content and are preferred on the market. Hybrid rice varieties are results of F_1 , therefore there is some unacceptable segregation for amylose gelatinization consistency and gelatinization temperature, hindering the hybrid rice breeding program in Iran.

Methods

A study was conducted to determine heterosis rate in local rice varieties. Four CMS lines from Iranian aromatic varieties -- Khazar A, Domsya A, Gharib A, and IR58025 A -- were used to make 15 hybrids. This experiment was carried out in a complete random block design with three replications. Thirty-day old seedlings were transplanted. Plot size was $2 \times 5 \text{ m}^2$ and spacing was $25 \times 25 \text{ cm}$ and fertilizer rate was $N=150$, $P=100 \text{ kg/h}$. Ten plants were selected randomly from each plot to measure the following characters: plant height, panicle length, number of spikelets per panicle, number of panicles/ m^2 , percent sterile spikelets, and growth period and yield at 14% moisture content.

Results

Mean of panicles/ m^2 ranged from 293 to 341, plant height from 110 to 141 cm. Panicle height was from 21.7 to 29.5 cm. Maximum spikelet sterility was observed in Gharib/Hassani. It was only in hybrids IR58025A/IR3441-97-1, IR58025A/IR4491-89-1 and IR58025 A/Ghil-3 that heterosis was observed to be superior to the check. However the male parent of these three hybrids are not local cultivars.

Conclusions

Selection of parents is important in developing hybrids. In this study we used local varieties as male sterile and other Iranian cultivars as male parents. So, it was observed that Iranian cultivars are not good restorers and did not exhibit heterosis, probably because they are genetically similar. Thus we should incorporate foreign cultivars, such as varieties from the International Rice Research Institute (IRRI) and Chinese varieties, into our breeding programs and search for restorer lines.

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Table 1. Morphological traits of Iranian rice hybrids.

Hybrid	Panicles/m ²	Plant height (cm)	Panicle length (cm)	Spikelet sterility (%)	Yield (t/ha)	Heterosis for yield
Khazar A/Taroum	285	125	28.5	17	3.68	-9.3
Khazar A/Molahi	293	126	29.5	16.5	3.6	-16.1
Khazar A/Salari	297	123	21.7	19.6	3.4	-20.9
Domsya A/Shahpacend	298	129	26	17.7	3.7	-13.9
Domsya A/Gil-3	299	139	26	18.1	3.8	-13
Domsya A/Gil-1	301	141	25.1	16.5	3.5	-18.6
Gharib A/Gil-1	309	140	23.4	21	3.3	-23.1
Gharib A/Hassani	307	131	26	23.1	3.6	-16.2
Gharib A/Hassan sarhi	293	130	25.5	21.5	3.81	-11.6
Gharib A/Sanghjo	315	127	24.5	21	3.9	-9.3
IR58025 A/Sapidroud	301	125	23	20.1	3.2	-13.9
IR58025 A/IR3441-97-1	320	126	23	24	4.7	9.3
IR58025 A/Gil-3	341	127	24.4	18	4.4	15.6
IR58025 A/IR4491-89-1	337	124	27.6	14.7	5.1	11.6
Sapidroud	397	110	25.2	13.4	4.3	

B78 - Identifying Heterotic Hybrid for Exploitation of Hybrid Vigor in Iranian Rice Varieties

M. Sattari

Hybrid Rice Project. Rice Research Institute of Iran, P.O. Box 145, Amol, Iran

Introduction

Rice is one of the most important food crops in Iran. It provides up to half the calories for more than 60 million people. In 1996, Iran's rice area was 600,000 ha with 3.5 t/ha average yield -- some 2.1 million tons/year. High population growth rates limit prospects for increasing rice land; farmers must produce more on less land with less labor and less water. There is, therefore, a pressing need for new technologies to increase rice production. Commercial exploitation of heterosis through use of hybrid rice is one strategy to meet this challenge.

Methods

Four CMS lines and six improved high-yielding and three local varieties were investigated for possible heterosis in their crosses (Table 1). The CMS lines were crossed with local and improved varieties (nine combinations) during summer 1995. The high-yielding variety 'Dash' was used as a check. Standard heterosis (%) was estimated over check. Hybrids and their parents were transplanted in rows with 20 plants per row and a row spacing of 20 cm. Ten plants of each genotype were randomly selected and evaluations done for plant height (cm), days to 50% flowering (day), panicles per plant and grain yield per plant (g).

Results

Results indicated that standard heterosis for all of combinations ranged from -39.3% to 25.5%. The highest heterosis was obtained for the crosses V20 A/IR9761-19-1R and PMS1 A/IR64. The lowest heterosis involved two crosses: V20A/Bejar and IR62829A/Amo12. Plant height ranged from 101 to 139.5 cm and panicles per plant from 13.8 to 21.5.

Conclusions

In practical breeding programmes, usually standard heterosis is considered, which is defined as the superiority of the F₁ hybrid over the highest yielding release check variety. According to this research, the high-yielding hybrids V20A/IR9761-19 1R and PMS1A/IR64 were identified as experimental hybrids to be multiplied for expanded testing.

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Table 1: performance of experimental hybrids at Rice Research Institute of Iran, Amol, Iran, 1995.

Cross and check	Days to 50% flowering	Plant height (cm)	Panicles per plant	Grain yield per plant (g)	Standard heterosis over check (%)
V20A/sephidrood	109	101	15.5	67.2	5.16
V20A/Bejar	105	105	16	38.7	-39.3
V20A/Domsiah	110	120.4	14.6	61.5	-3.6
V20A/IR9761-19-1R	98	113.5	15.6	80.2	25.5
IR62829A/Rashti	102	139.5	20.5	59.5	-6.8
IR62829A/Deilamani	86	136.3	21.5	74.2	16.2
IR62829A/Amol2	97	107	17.1	46.8	-26.8
Krishna/A/ch21	95	111	19.1	69.4	8.6
PMS1A/IR64	112	108	17.5	76.7	20.1
Dasht(check)	98	120.7	13.8	63.9	

V20A is from China, IR62829A from IRRI, Krishna A. and PMS1 A from India.

Heterosis: What Have We Learned, What Have We Done, and Where Are We Headed?

Arnel R. Hallauer

Department of Agronomy, Iowa State University, Ames, IA 50011-1010, USA

What Have We Learned?

The expression of hybrid vigor in plant crosses has been recognized for nearly 250 years (Zirkle 1952). Hybrid vigor in artificial plant hybrids was studied by Kolheuter in 1761 to 1766 for several plant species. Darwin and Mendel, reported hybrid vigor in plant crosses. Darwin stated that "... cross fertilization is generally beneficial and self-fertilization injurious", and Mendel reported hybrid vigor in his pea hybrids as having "... greater luxuriance which appears in all parts of the plants" Beal (1880), Sanborn (1890), McClure (1892), and others produced crosses between maize cultivars and reported that in most instances the crosses had yields greater than the parent cultivars. The hybrid seed was produced by planting the parent cultivars in alternate rows, detasseling the one parent, cross pollination of the detasseled parent by the other parent, and only harvest the seed from the detasseled parent for use by the producer. Although the genetic basis of hybrid vigor in the maize crosses was not understood by the early researchers of maize, significant conclusions were made from their studies: e.g., the cross must be made every year using new seed ... (Sanborn 1890); ... in cross breeding the parents usually have different imperfections, which often, more or less, compensate each other in the immediate decedents (Johnson 1891); and McClure (1892) described the effects of self-pollination, crossing, and growing of second-generation hybrid seed, and he stated that "corn cannot be improved by self-fertilization". The rediscovery of Mendel's paper in 1900 provided a genetic basis for interpreting the effects of self-fertilization and hybrid vigor in crosses.

What Have We Done?

After the rediscovery of Mendel's laws of inheritance, studies were conducted by East and Shull in maize that provided genetic interpretations of the effects of inbreeding and the expression of hybrid vigor in crosses between inbred lines (Shull 1952). Inbreeding occurred because of the fixation of less desirable alleles in the homozygous state, whereas hybrid vigor occurred with the restoration of heterozygosity in the crosses of pure lines. The level of heterozygosity seemed to be related to level of hybrid vigor expressed in crosses: hence, Shull suggested heterosis as a convenient term for hybrid vigor. Several theories were advanced to explain the expression of heterosis of crosses (Richey 1950; Sprague 1953), but none was acceptable to all. Although the exact genetic basis of heterosis has not been determined, breeding methods were empirically developed to capitalize on and exploit the heterosis expressed in crosses of maize (Sprague 1946; Richey 1946). Similar methods were developed for other crop species, based on the pure-line hybrid concept suggested by Shull (1909; 1910). Development, production, and distribution of genetically superior hybrids during the past 50 years have contributed significantly to the genetic advances made in crop species where hybrids can be economically produced and distributed.

Where Are We Headed?

Heterosis is one of the more widely recognized terms in plant breeding. Heterosis has made a dramatic impact on the development of breeding methods for many field crop, vegetable, ornamental, and tree species during the 20th Century. Heterosis generally suggests superiority over nonhybrids. Heterosis has been exploited commercially because the originators control the parents of the hybrids. Heterosis is exploited wherever possible, but the genetic basis of heterosis is not clearly understood. Heterosis will continue to have a significant role in the future of plant improvement: heterotic groups will become more distinct; selection methods developed to enhance expression heterosis between heterotic groups; molecular genetics may assist in the development and enhancement of heterotic groups; and techniques may be refined to predict potential crosses with the greatest expression of heterosis. The exact genetic basis of heterosis may never be known and understood because of interactions: interactions of alleles at

a locus, interactions of alleles at different loci, interactions of the nucleus and cytoplasm, and interactions of the genotypes and environment (Srivastava 1991). Because of the complexity of the interactions within genotypes and between genotypes and environments, only general explanations (e.g., accumulation of favorable alleles with partial to complete dominance) may be feasible. But heterosis will continue to have a major role in the future of plant improvement even though our knowledge of its genetic basis is limited.

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The Role of Heterosis in Meeting World Cereal Demand in the 21st Century

P.L. Pingali

International Maize and Wheat Improvement Center (CIMMYT), Apdo. Postal 6-641, 06600 Mexico D.F., Mexico

As we look ahead to 2020, the cereal supply situation in developing countries does not lend itself to complacency. Developing country demand for the basic cereals -- rice, wheat and maize -- is anticipated to grow at least 2% per annum. Unabated population growth combined with an unprecedented rise in per capita incomes is contributing to increasing per capita cereal demand. By 2020, developing countries will consume 90% of the world's rice, more than 60% of the world's wheat, and 55% of the world's maize.

The income-induced diversification of Asian diets is expected to reduce *per capita* rice consumption in that region, but overall demand for rice in Asia will continue rising because of the tremendous growth in population. The global demand for wheat should increase as a result of substitution out of rice and coarse grain cereals as incomes rise and populations become increasingly urban. While per capita demand for maize *as food* is expected to decline in all regions except sub-Saharan Africa, the use of maize *as feed* is expected to rise dramatically with the increased demand for livestock products. Given these projections, developing countries are expected to import some 200 million tons of cereals annually by the year 2020, even if cereal crop productivity growth continues at current levels of 1.5% per annum. In the absence of a significant increase in cereal crop productivity beyond current levels, the global availability of such import volumes at an affordable price is questionable.

The challenge of meeting future import demands and the consequences for food security appear even more daunting if one considers the reduced farm-level profitability of cereal production and the dramatic downturn in investments in agricultural research and research infrastructure. Virtually all future cereal production growth must come from increased yield per unit of land, since the opportunities for further area expansion are exhausted in Asia and extremely limited elsewhere. Yet the opportunities for further yield growth are also limited, at least in the case of rice and wheat, due to the narrowness of the economically exploitable gap between the technology frontier and farmer performance. Given current technology and relative price levels, it is not profitable for cereal crop farmers in either favorable or unfavorable environments to bridge this gap. New technologies designed to significantly reduce the cost per unit of output, either through increasing genetic yield potential or through an increase in input efficiencies, would substantially enhance farm level profitability for cereals. Exploiting heterosis could dramatically reduce production costs by increasing yield levels while enhancing input use efficiency.

The demand for hybrid technology is generally expected to be the greatest in the high potential production environments, especially in countries with large domestic demand for cereals. For wheat and rice, the irrigated environments were the primary beneficiaries of the Green Revolution, and sustaining productivity growth for these crops over the short-to-medium term in irrigated environments will depend largely on the successful exploitation of heterosis. Large countries such as India and China have made substantial progress in hybrid technologies for wheat and rice, but will need to intensify their efforts if they are to protect domestic consumers from the vagaries of the international market. Food exporting developing countries, such as Thailand for rice and Argentina for wheat, would only be interested in hybrids if their grain quality is comparable to varieties. In the case of maize, substantial inroads have already been made in the use of hybrids; further demand for hybrid technology would be associated with the rising demand for livestock feed, especially in Asia.

Although hybrids have been shown to outperform inbreds in low-potential environments, especially drought-prone areas, the demand for hybrids in these environments is likely to be low for the foreseeable future. The switch from a low yielding, low input traditional cereal crop production system to a commercial oriented, high input, hybrid production system is not likely to be profitable, especially in the absence of a good market infrastructure. The one significant exception is the movement of hybrid maize into traditional upland rice areas in Southeast Asia, the switch occurring because of the rapid rise in demand for feed maize in the region. The uplands of China are also witnessing the rapid spread of hybrid maize for feed.

From a research and seed industry perspective, the concentration of hybrid technology development on the high potential environments makes economic sense. The relative homogeneity of the high potential environments worldwide leads to high spillover benefits across borders and hence high returns to research investments. The costs of developing hybrid technology for low-potential areas will always be higher and the returns to research investments lower due to the relative heterogeneity of the production environment. Small yield gains in the high potential environments may make the adoption of hybrids profitable while large gains in the low potential environments may not. The research challenge in either case is to enhance the competitiveness of hybrids by increasing crop and seed yield per hectare, reducing seed prices, and improving grain quality.

In targeting the geopolitical and agroecological domains for the promotion of hybrids, it is important to identify and try to alleviate the infrastructural and institutional constraints to their adoption. The underdevelopment of the seed industry is often seen as a constraint to hybrid adoption. A more thorough assessment, however, might point to broader economic factors, including transport and market infrastructure, that have constrained adoption. In the absence of policy impediments, the seed industry has generally established itself in countries and regions where the underlying economic environment has been conducive to hybrid adoption. The lack of interest of the private sector in developing and disseminating hybrids for the marginal environments may be an exception to the above generalization. Growing concerns about intellectual property protection and plant patenting can be expected to constrain the movement of hybrids internationally and thereby reduce the spillover benefits of research and technology generation. Public-private linkages in the development and dissemination of hybrids are also affected by proprietary protection. Finally, contemporary policy reforms, especially the integration of world food markets, can have a significant impact on the comparative advantage of cereal production in individual countries and hence the profitability of adopting hybrids.

Research Needs in Heterosis

R.L. Phillips

Department of Agronomy and Plant Genetics and Plant Molecular Genetics Institute, University of Minnesota, St. Paul, MN 55108, USA

At the international symposium "The Genetics and Exploitation of Heterosis in Crops", many ideas will be presented regarding possible mechanisms to account for the important biological phenomenon of heterosis. Each hypothesized mechanism needs to be researched; this presentation will attempt to summarize the ideas that are researchable with today's tools and suggest research needs for the future.

Even though heterosis has been in the forefront of our thinking for many years, the phenomenon is not much better understood today than it was when Gowen's famous book on heterosis was published 45 years ago (Barabas 1992). Barabas (1992) said, "One of the greatest achievements in the 20th century was the utilization of the effect of heterosis....Obviously, a fantastic chain-reaction was widely expected: hybrids in all species of plants. However, the process came to an abrupt halt." A question which remains timely today is: Why does heterosis exist in some crops but not in others?

We may need to select a particular feature of heterosis and design our experiments around it. Will the participants of this conference agree, for example, that heterosis and inbreeding depression are flip sides of the same phenomenon? In Falconer's *Introduction to Quantitative Genetics*, he states that "Complementary to the phenomenon of inbreeding depression is its opposite 'hybrid vigor' or 'heterosis'.....That the phenomenon of heterosis is simply inbreeding depression in reverse can be seen by consideration of how the population mean depends on the coefficient of inbreeding". Will we accept, therefore, that any molecular explanation of heterosis also should explain inbreeding depression?

Is it possible that crops that are pure breeding have built-in heterosis? Are polyploid crops such as oat and wheat actually improved by maximizing heterosis among the genomes? Does barley have sufficient duplication among its DNA sequences to allow "pure breeding heterosis" due to heterozygosity between duplicate loci (AA, aa) as opposed to individual loci? How does it happen that corn and rice have different degrees of expression of heterosis yet at least two genomes of rice can be found among the chromosomes of corn?

We tend to think of heterosis as due to heterozygosity of many individual genes. Can the heterotic effect be of an even more global nature? Are there global changes to the genome (chromatin) that occur when different genotypes are brought together in a hybrid? Molecular biological technologies now allow the investigation of certain global considerations. DNA methylation, DNA content changes, silencing/co-suppression, paramutation, amplification, unequal crossing over, and other genetic phenomena can occur in the prezygotic, zygotic, or early developmental stages and alter the outcome based not strictly on the genotype of the parents. Elevated levels of epistasis might also be expected from such *de novo* changes (Rasmusson and Phillips 1997). We need to go beyond the thought of heterozygosity of a collection of individual genes to account for heterosis.

In this meeting, we will be searching for ideas where global gene expression changes occur when different genotypes are combined and especially for those that behave differently in the heterozygous versus homozygous states. We will be looking for a vision and a commitment to solve the molecular portion of the heterosis puzzle.

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