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Predicted and realized grain yield responses to full-sib family selection in CIMMYT maize (*Zea mays* L.) populations*

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Summary. The maize (*Zea mays* L.) improvement program of the International Maize and Wheat Improvement Center (CIMMYT) develops broad-based maize populations and, until recently, improved all of them through full-sib family selection with international testing. The purpose of this study was to estimate the genetic and genetic × environment variance components for ten of those populations and to measure expected yield improvement from full-sib selection. Mean yield ranged from 3.35–6.81 t ha^{-1}. For five populations the average yield in the last cycle was higher than in the initial cycles. Several populations showed no improvement or yielded less in the final cycle of selection, either because selection intensity was low or because strong selection pressure was applied simultaneously for several traits. Variation resulting from differences among family means within cycles and from interaction between families and locations within cycles were significant in all populations and cycles. Results indicate that variability among full-sib families was maintained throughout the cycles for all populations. The large σ^2_{ge}/σ^2_g ratio shown by most populations suggests that yield response per cycle could be maximized if the environments in which progenies are tested were subdivided and classified into similar subsets. The proportion of the predicted response realized in improved yield varied for each population.

Key words: Multilocational progeny trials – Full-sib selection – Variance components – Selection response

Introduction

In the maize improvement program of the International Maize and Wheat Improvement Center (CIMMYT), broad-based, widely-adapted maize populations that vary in climatic adaptation (lowland tropical, subtropical, and highland) and maturity (early, intermediate, and late) are developed and improved. An integral step in improving the populations has been evaluation of full-sib families grown in international trials. Families selected on the basis of multilocational trials are used in improving the population and in forming experimental varieties for distribution to national maize research programs (Paliwal and Sprague 1982; Vasal et al. 1982).

Several intrapopulation selection methods have been developed to improve populations, as summarized by Sprague and Eberhart (1977), Gardner (1978), Hallauer and Miranda (1981) and Hallauer (1985). Yield improvement through the full-sib family selection method has been reported to range from 2%–4% per cycle. Pandey et al. 1986 and 1987) have reported on the use of this method with CIMMYT maize populations. Their data showed that in eight late-maturing tropical populations improved for several traits, progress per cycle in yield ranged from −3.12% to 4.06%. In four intermediate-maturity populations, the rate of progress was 0.48%–3.16% per cycle, with an average of 2.11%. Several cycles of full-sib selection have been completed in most of CIMMYT's tropical and subtropical maize populations.

The objectives of this study were: (1) to summarize data on grain yield from cycles of full-sib selection in ten of those maize populations; (2) to estimate genetic and genetic × environment interaction variance components and determine how these components have been changed

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by selection; and (3) to predict genetic gains from full-sib family selection in the ten populations.

Material and methods

Each population handled by the CIMMYT maize improvement program is evaluated every other year in an International Progeny Testing Trial (IPTT) that is sent to cooperators at up to six locations worldwide. In those trials, 250 full-sib families, along with 6 local checks, are evaluated in a 16 × 16 simple lattice design with 2 replications. Each plot consists of one 5 m row of 22 plants, giving a final density of 53,333 plants ha^{-1}. The trait considered in this study was grain yield ($t\ ha^{-1}$), adjusted to 15% moisture and calculated at 80% shelling.

Eight full season lowland tropical populations with maturity between 115 and 120 days (Tuxpeño-1, Mezcla Tropical Blanca, Antigua Veracruz 181, Amarillo Cristalino-1, Amarillo Dentado, Tuxpeño Caribe, Cogollero, and La Posta), one full-season subtropical population with maturity of 115 days (ETO Blanco), and one intermediate-season lowland tropical population with maturity of 110 days (Antigua-Republica Dominicana) were studied. The germplasm components of these populations are listed in various CIMMYT publications (CIMMYT 1982 and 1984).

In the first two cycles, the full-sib selection scheme used (starting in 1974) required two seasons (1 year) per cycle of selection (System 1), and 40% of the full-sib families were selected. Beginning in the third cycle, the system was modified such that four seasons (2 years) were needed to complete a cycle (System 2). Selection intensity remained the same as in System 1, but within-family selection (Pandey et al. 1986) was added. System 1 was employed during the first two cycles of selection in Tuxpeño-1, Mezcla Tropical Blanca, Antigua Veracruz 181, Amarillo Cristalino-1, Amarillo Dentado Tuxpeño Caribe, Cogollero, and La Posta but in only the first cycle with ETO Blanco and Antigua-Republica Dominicana.

For various reasons (lack of a replication, numerous missing plot values, extremely high coefficients of variation, and no moisture percentage reported), not all of the locations within cycles in which full-sib progenies were tested have been included in the combined analyses. Progeny trials were conducted at only one site in most countries except Mexico, where two sites were used in some years. The number of sites included in the analyses for each cycle of each population ranged from two to six and is given in Table 1.

Statistical analysis

Lattice analysis was done for each trial site in a given year. The adjusted treatment means computed for each site were used in combined analysed of variance, with sites and entries as main effects, according to the procedure described by Cochran and Cox (1957, Chapt. 14). The error term in the combined analysis was the average effective error for each analysis pooled over sites. Families and environments were considered random effects. The components of variance in each of the combined analyses were calculated by setting mean squares equal to their expectations and solving the equations for the parameters contributing to the expectations. Predicted re-

Table 1. Grain yield means ($t\ ha^{-1}$) of ten populations of maize for various cycles of full-sib recurrent selection, their standard errors (in parenthesis) and number of testing sites (below) included in the combined analysis

Populations	Cycle means						
	C0	C1	C2	C3	C4	C5	C6
Tuxpeño-1	5.20 (0.27) 5	4.85 (0.21) 3	5.34 (0.17) 5	5.55 (0.61) 2	4.83 (0.10) 6	–	–
Mezcla Trop. Blanca	–	5.44 (0.19) 5	4.74 (0.08) 5	5.35 (0.18) 4	6.24 (0.26) 5	5.42 (0.22) 5	6.55 (0.27) 2
Antigua Veracruz 181	5.81 (0.15) 3	5.02 (0.18) 4	4.43 (0.12) 4	4.35 (0.11) 5	4.98 (0.20) 3	4.98 (0.08) 6	5.84 (0.25) 2
Amarillo-Cristalino-1	5.05 (0.13) 4	4.50 (0.10) 5	3.88 (0.12) 5	4.43 (0.09) 5	5.64 (0.16) 5	3.67 (0.07) 4	5.98 (0.17) 2
Amarillo Dentado	4.57 (0.23) 3	4.89 (0.10) 6	4.50 (0.17) 5	4.54 (0.09) 5	4.85 (0.11) 5	4.98 (0.15) 4	–
Tuxpeño Caribe	6.10 (0.47) 5	6.58 (0.35) 4	3.81 (0.10) 4	4.87 (0.27) 4	6.02 (0.25) 3	6.81 (0.34) 4	–
ETO Blanco	4.88 (0.18) 5	3.35 (0.08) 4	–	4.41 (0.12) 4	4.05 (0.23) 3	–	–
Antigua-Rep. Dominicana	4.80 (0.08) 5	4.92 (0.09) 4	4.87 (0.07) 6	5.66 (0.25) 3	4.85 (0.06) 6	–	–
Cogollero	4.85 (0.17) 3	4.65 (0.18) 4	5.23 (0.13) 5	4.18 (0.31) 3	5.34 (0.29) 2	5.96 (0.11) 3	–
La Posta	–	5.33 (0.19) 4	5.46 (0.20) 3	6.13 (0.10) 6	4.58 (0.28) 3	–	–

sponse per cycle of full-sib progeny selection was calculated using the variance components estimates derived from the combined analyses of variance.

Results and discussion

As expected, there was great variation among environments within cycles for most of the populations. Variation resulting from differences among full-sib family means within cycles and variation caused by interaction between families and locations within cycles were significant in all of the populations and cycles (data not presented).

The yield of each population in each cycle averaged over environments is given in Table 1. Mean yield ranged from 3.35 t ha^{-1} (ETO Blanco in Cl) to 6.81 t ha^{-1} (Tuxpeño Caribe in C5). Grain yield varied among cycles because of differences in environmental conditions from one cycle (year) to another. But even though cycle means were confounded with the year effects, average grain yields of Mezcla Tropical Blanca, Amarillo Cristalino-1, Amarillo Dentado, Tuxpeño Caribe, and Cogollero were higher in the last cycle than in the early ones. Antigua Veracruz 181 and Antigua-Republica Dominicana, on the other hand, gave similar yields in the earliest and latest cycles of selection, while Tuxpeño-1, ETO-Blanco, and La Posta yielded less in the last cycle of selection than in early ones. The apparent lack of improvement in yield can be explained by the low selection intensity applied among families (40%), the large genotype × environment interaction, and the strong selection pressure applied for several traits simultaneously (disease resistance and reduction in plant and ear height). Significant progress has been achieved for traits other than grain yield (Pandey et al. 1986, 1987).

Estimates of genetic variance (σ_g^2) for each cycle of selection were significantly different from zero (greater than twice their standard error in all populations (Table 2). Estimates of genetic × environment inteaction variance (σ_{ge}^2) exceeded twice their standard error in most populations except for Tuxpeño-1 in C3, Cogollero in C4 and La Posta in C2. In general, the magnitude of the estimates of the genetic component was similar to that reported by Hallauer and Miranda (1981) for maize populations of the U.S. Corn Belt.

Low estimates of genetic variance components were found for C1 of Tuxpeño-1 (0.07), C2 of Amarillo Dentado (0.07), and C2 of Tuxpeño Caribe (0.08). The increased genetic variability in Tuxpeño-1 from C2 (0.15) to C3 (0.25), in Mezcla Tropical Blanca from C5 (0.10) to C6 (0.30), and in Amarillo Cristalino-1 from C5 (0.10) to C6 (032) may have been the result of incorporating superior germplasm from CIMMYT gene pools into the populations (Pandey et al. 1986).

Increases in the estimates of genetic variances may be associated with higher average yield performance. Tuxpeño-1 yielded 5.55 t ha^{-1} in cycle C3, Mezcla Tropical Blanca yielded 6.55 t ha^{-1} in cycle C6, and Amarillo Cristalino-1 produced 5.98 t ha^{-1} in cycle C6. From information about the type of yield trial environment required to foster maximum response from selection, Allen et al. (1978) determined that estimates of genotypic variance increased in high-yielding environments. Estimates of genetic variance components and genetic × environment components obtained from combined analyses involving limited number of environments will have large sampling errors. Comstock and Moll (1963) noted that, when the reference group of environments is subdivided into subsets that have similar environments within subsets, genetic variance among genotypes within subsets is increased relative to genetic × environment interaction variance. What was previously genetic × environment interaction effects are incorporated into genetic effects. Increasing the range or diversity of environments will always increase the genetic × environment interaction, which is why it is very difficult to select for very broad adaptability in maize. The more diverse the environments, the less likely it is that one will make progress from selection. Conversely, selection for specific adaptability to a limited set of similar environments will result in maximum progress.

In general, the results indicate that variability among full-sib progenies was not reduced throughout selection cycles in all populations. Thus, further improvement through selection should be possible.

In most populations there was considerable variation among cycles in the estimates of the genetic × environment interaction component. Tuxpeño Caribe showed high estimates of σ_{ge}^2 in C1, C2, and C5 (1.74, 0.82, and 1.10, respectively). Tuxpeño-1 had a high interaction component in C0 and C2 (0.68 and 0.54, respectively), as did Mezcla Tropical Blanca in C4 (0.93). The average proportion of the genetic × environment component of variance relative to the genetic variance component is given in the last column of Table 2. The average ratio is high for most of the populations. Tuxpeño-1, Mezcla Tropical Blanca, and Tuxpeño Caribe had estimates of σ_{ge}^2that are on the average, 2.78, 2.16, and 6.17 times as great as those of σ_g^2. The mean ratios of σ_{ge}^2/σ_g^2 for Amarillo Dentado, ETO Blanco, Antigua-Republica Dominicana, Cogollero, and La Posta were 1.92, 1.34, 1.04, 1.13, and 1.16, respectively.

In a review of recurrent selection programs, Hallauer and Miranda (1981) report the estimate of σ_{ge}^2 to be about half that of σ_g^2 (0.52). In summarizing yield components of variance for seven cycles of reciprocal full-sib selection in two maize populations, Hallauer (1984) reports that the maximum value for the σ_{ge}^2/σ_g^2 ratio was 0.94 in C1. Crossa and Gardner (1987) estimated genotype and

Table 2. Components of variance, their standard errors (in parenthesis) and mean ratio σ^2_{ge}/σ^2_g for grain yield in various cycles of full-sib recurrent selection in ten populations of maize

Populations	Cycle components of variance														Mean ratio
	C0		C1		C2		C3		C4		C5		C6		
	σ^{2*}_g	σ^{2**}_{ge}	σ^2_g	σ^2_{ge}	σ^2_g	σ^2_{ge}	σ^2_g	σ^2_{ge}	σ^2_g	σ^2_{ge}	σ^2_g	σ^2_{ge}	σ^2_g	σ^2_{ge}	σ^2_{ge}/σ^2_g
Tuxpeño-1	0.13 (0.04)	0.68 (0.07)	0.07 (0.03)	0.20 (0.05)	0.15 (0.03)	0.54 (0.04)	0.25 (0.10)	0.21 (0.13)	0.22 (0.03)	0.30 (0.03)	–	–	–	–	2.78
Mezcla Trop. Blanca	–	–	0.18 (0.03)	0.32 (0.05)	0.12 (0.02)	0.08 (0.02)	0.12 (0.03)	0.19 (0.05)	0.24 (0.05)	0.93 (0.06)	0.10 (0.03)	0.41 (0.06)	0.30 (0.06)	0.29 (0.05)	2.16
Antigua Veracruz 181	0.35 (0.04)	0.08 (0.04)	0.23 (0.04)	0.25 (0.04)	0.10 (0.02)	0.17 (0.03)	0.26 (0.03)	0.21 (0.03)	0.24 (0.04)	0.07 (0.05)	0.22 (0.03)	0.21 (0.02)	0.24 (0.05)	0.10 (0.05)	0.78
Amarillo Cristalino-1	0.21 (0.03)	0.08 (0.03)	0.18 (0.03)	0.20 (0.03)	0.12 (0.02)	0.14 (0.03)	0.15 (0.02)	0.10 (0.02)	0.26 (0.04)	0.34 (0.04)	0.18 (0.02)	0.10 (0.02)	0.32 (0.05)	0.08 (0.04)	0.78
Amarillo Dentado	0.24 (0.04)	0.26 (0.05)	0.14 (0.02)	0.14 (0.03)	0.07 (0.02)	0.32 (0.04)	0.24 (0.03)	0.18 (0.02)	0.21 (0.03)	0.21 (0.04)	0.09 (0.02)	0.28 (0.04)	–	–	1.92
Tuxpeño Caribe	0.11 (0.05)	1.74 (0.11)	0.10 (0.04)	0.82 (0.07)	0.08 (0.02)	0.16 (0.02)	0.13 (0.04)	0.38 (0.07)	0.19 (0.03)	0.16 (0.04)	0.14 (0.05)	1.01 (0.07)	–	–	6.17
ETO Blanco	0.27 (0.04)	0.43 (0.04)	0.14 (0.02)	0.09 (0.02)	–	–	0.20 (0.03)	0.15 (0.03)	0.11 (0.03)	0.26 (0.05)	–	–	–	–	1.34
Antigua-Rep. Dominicana	0.14 (0.02)	0.12 (0.02)	0.09 (0.02)	0.08 (0.02)	0.23 (0.03)	0.08 (0.02)	0.16 (0.04)	0.32 (0.05)	0.12 (0.02)	0.13 (0.02)	–	–	–	–	1.04
Cogollero	0.18 (0.03)	0.12 (0.04)	0.13 (0.03)	0.26 (0.04)	0.16 (0.03)	0.21 (0.03)	0.09 (0.04)	0.17 (0.07)	0.17 (0.05)	0.01 (0.06)	0.14 (0.02)	0.12 (0.02)	–	–	1.13
La Posta	–	–	0.20 (0.04)	0.12 (0.05)	0.26 (0.04)	0.06 (0.05)	0.18 (0.03)	0.21 (0.03)	0.11 (0.04)	0.29 (0.06)	–	–	–	–	1.16

* σ^2_g = Genetic variance among full-sib families

** σ^2_{ge} = Genetic × environment interaction variance genotype × environment variances among S_1 lines derived from three populations containing different amounts of exotic germplasm. The interaction component of variance of one population was not significantly different from zero, and the average σ^2_{ge}/σ^2_g ratio over the three populations was 0.11. Reeder et al. (1987) evaluated the effects of six cycles of reciprocal full-sib selection in two maize populations. The average ratios between additive × environment variance and additive genetic variance of populations BS10 and BS11 were 0.10 and 0.07.

The high proportion of the genetic × environment component of variance relative to the genetic variance reported here indicates that the testing environments should be characterized and grouped according to physical factors such as altitude, latitude, soil type, weather patterns, etc. Classifying world testing environments and subdividing them into similar subsets would maximize expected progress from selection. The subset of environments for which a particular maize population should be improved could easily be identified. That step would reduce the observable magnitude of the genetic × environment interaction variance and allow the breeder to capitalize on specific interactions between genotypes and the subset of environments. Breeding for more specific adaptability or for more narrowly defined sets of environments should substantially increase progress.

Estimates of genetic and genetic × environment variance components and the total phenotypic variance among progeny means were used to predict genetic gains in yield performance expected from full-sib family selection in the ten populations included in this study. Predicted response based on full-sib progeny means is biased upward by dominance and epistasis.

Average predicted response per cycle for each system and yield improvement realized (Pandey et al. 1986, 1987) for each population and system are given in Table 3. For most of the populations, realized gains in System 2 are larger than those obtained in System 1. One possible reason for this difference is that genetic variance within full-sib families comprises 50% of the additive variance and 75% of the dominance variance, while genetic variance among full-sib families involves 50% of the additive variance and only 25% of the dominance variance. Thus, visual selection applied in System 2 exploits the greater genetic variance existing within full-sib families.

For System 1 the predicted gain is the average of the expected progress calculated for cycles C0, C1, and C2; for ETO Blanco and Antigua-Republica Dominicana, however, only the average predicted gain over C0 and C1 was considered. It was not possible to predict any additional response that might occur due to visual selection among S_1 families within full-sib families in System 2. The proportion of the predicted response realized in improved yield varied for each population and system. The expected and observed yield responses were similar for ETO Blanco in both systems and for Amarillo Cristalino-1, Amarillo Dentado, and La Posta in System 2. The agreement between expected and observed response in System 2 was due, in part, to the higher quality of the international trial data collected in later cycles of selection, compared with the early ones. Predicted gains were considerably larger than the realized responses for Tuxpeño-1, Antigua Veracruz 181, and Tuxpeño Caribe in both systems and Amarillo Cristalino-1, Amarillo Dentado, Antigua-Republica Dominicana, Cogollero, and La Posta in System 1. However, in Mezcla Tropical Blanca in System 1 and Antigua-Republica Dominicana and Cogollero in System 2, observed responses were greater than those predicted. In Cogollero the larger realized gain compared to predicted response may have been caused by the introgression of superior germplasm from gene pools.

Table 3. Average predicted gain and realized gain per cycle from full-sib selection for grain yield (t ha^{-1}) in ten populations of maize

Populations	Predicted gain*		Realized gain**	
	Sys 1	Sys 2	Sys 1	Sys 2
Tuxpeño-1	0.10	0.22	0.03	0.09
Mezcla Trop. Blanca	0.14	0.13	0.20	0.02
Antigua Veracruz 181	0.17	0.19	−0.18	0.14
Amarillo Crist.-1	0.15	0.17	0.00	0.16
Amarillo Dentado	0.12	0.19	0.00	0.18
Tuxpeño Caribe	0.08	0.12	−0.09	0.06
ETO Blanco	0.17	0.13	0.18	0.14
Antigua-Rep. Dominicana	0.12	0.13	−0.13	0.20
Cogollero	0.13	0.11	−0.06	0.22
La Posta	0.17	0.13	0.07	0.14

* 40% selection intensity in both systems

** Extracted from Pandey et al. 1986, 1987

Yield gains predicted for System 2 could have been underestimated because within-family improvement was not taken into consideration. Moll and Stuber (1971), in examining yield per cycle of a maize composite undergoing full-sib family selection, reported that all estimates of observed responses were considerably less than that predicted from variance component estimates. Moll and Smith (1981) found that the estimates of expected response compared favourable with the realized response for grain yield of four maize populations. The full-sib selection method employed by CIMMYT in conjunction with multilocational trials has been reported to be effective in improving grain yield (Paliwal and Sprague 1982; Pandey et al. 1986, 1987).

In general, the results of this study indicate that the genetic variability of the populations has been maintained throughout the cycles of selection. The international progeny trials play a major role in the improvement system. However, the high σ_{ge}^2/σ_g^2 ratio found for most of the populations suggests that the rate of improvment per cycle could be substantially increased if testing sites were chosen more systematically. For a given progeny trial, all sites should belong to the same environmental grouping but should still be diverse enough to represent the population of environments for which the breeding populations is intended. As national programs develop, maximum performance can be achieved by intense selection for adaptation to local environments. One of the goal of CIMMYT is to strengthen and provide guidance to the staff of national programs.

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