Journal of the Iowa Academy of Science: JIAS

Volume 98 | Number Article 6

1991

Genetic Variation Among and Within S1 Progenies of Maize

R. J. Getschman
Iowa State University

A. R. Hallauer
Iowa State Universtiy, hallauer@iastate.edu

Jour. Iowa Acad. Sci. 98(3):127-133, 1991

Genetic Variation Among and Within S_1 Progenies of Maize[1]

R.J. GETSCHMAN[2] and A.R. HALLAUER[3]

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

Inbred line development consumes a great portion of the breeder's time and resources in maize (*Zea mays* L.) breeding programs. Source populations for line developmenr often are developed by selfing F_2 populations developed from elite line crosses. Visual selection is practiced among and within selfed progenies during the selection process for one or two generations before evaluated in testcrosses for combining ability. Effective discrimination among and within inbred and testcross progenies depends on the amount of genetic variation present. The objective of this study was to determine the effectiveness of selection among and within S_1 progenies developed from crosses of related and unrelated lines. Estimates of among-progeny variance were significant and, in all instances, larger than the estimate of within-progeny variance. Additive genetic variance accounted for the genetic variation among progenies of related and unrelated line crosses. Estimates of variability among and within S_1 progeny testcrosses were not different from each other and were less than among and within S_1 progenies themselves. In this study, it seems that the choice of testers was not appropriate to distinguish combining ability among progenies for both types of crosses, within the precision of this experiment. On the average, 70.7% greater genetic gains would be realized with among S_1 progeny selection vs. within S_1 progeny selection.
INDEX DESCRIPTORS: *Zea mays* L., corn, selection, testcrosses, breeding methods

Development of inbred lines for use in hybrids is the primary breeding objective in applied maize (*Zea mays* L.) breeding programs. Source germplasm available to maize breeders includes genetically narrow-based F_2 populations and broad-based open-pollinated varieties, synthetics, and composites. Crosses between elite inbred lines to form segregating F_2 populations are used extensively because of the greater probability of obtaining useful inbred lines. The goal is to obtain transgressive segregates superior to either parent from the elite line crosses. Efficient use of resources in the more promising germplasm sources for the extraction and development of inbred lines is, therefore, a critical aspect of maize breeding programs.

The inbreeding system used most frequently in developing inbred lines of maize is self-pollination within the chosen population, followed by growing the selfed progeny on an ear-to-row basis (Russell and Hallauer, 1980). This type of pedigree selection permits selection among and within progenies at all levels of inbreeding, and effectiveness of selection depends on the genetic variation present. Expected genetic variation among and within inbred progenies has been derived, and selection should be more effective among progenies than within progenies at all levels of inbreeding (Hallauer and Miranda, 1988).

Evaluation of lines in hybrids is the more important aspect of applied maize breeding because the ultimate value of inbred lines is their use in hybrids. The generation for the evaluation of lines in hybrids varies among maize breeders and germplasm sources because of the relative importance given to visual selection for plant and ear traits during inbreeding. Proponents of early testing desire a measure of relative general combining ability of progenies in the S_1 or S_2 (one and two generations of selfing in the F_2 population) generation, and progenies inferior for general combining ability are eliminated during the early generation of inbreeding (Sprague, 1946). Effective discrimination among the progeny crosses (testcrosses), however, depends on the magnitude of genetic variation among and within progeny testcrosses, including the level of inbreeding, level of dominance, and the type of tester used (Rawlings and Thompson, 1962).

Objectives of our study were to estimate genetic components of variance among and within S_1 progenies developed from related (B73 and B84) and unrelated (B73 and Mo17) line F_2 populations, to estimate genetic components of variance among and within S_1 progeny testcrosses, and to compare variance component estimates obtained of the S_1 progenies themselves with those of the progeny testcrosses.

MATERIALS AND METHODS

Two single crosses (B73 × Mo17 and B73 × B84) were self-pollinated to obtain the F_2 population for each single cross. Within each F_2 population, 140 S_1 (F_3) progenies were obtained by self-pollination of the S_0 (F_2) plants. No intentional selection was practiced among the S_0 plants at the time of self-pollination. Each S_1 progeny was planted ear-to-row, and five self-pollinations were made within each S_1 progeny row to produce S_2 (F_4) progeny seed. Two S_2 progenies per S_1 progeny were chosen from 100 S_1 progenies of each F_2 population. S_2 progenies were considered random selections, with the only constraint being that adequate seed per S_2 progeny was available for evaluation in replicated trials and inclusion in a crossing block to produce testcross seed. The 400 S_2 progenies were the materials available to estimate genetic variability among and within S_1 progenies themselves and in testcrosses.

The choice of lines included in the crosses was based on their origin and relation to the 'Reid Yellow Dent' and 'Lancaster Sure Crop' heterotic pattern used in the U.S. Corn Belt. B73 and B84 were derived from Iowa Stiff Stalk Synthetic after five [BSSS(HT)C5] and seven [BSSS(HT)C7] cycles of half-sib selection with Ia13 [(L317 × BL349) (BL345 × MC401)] as tester (Russell, 1972, 1979). B73 and B84 are classified as Reid Yellow Dent type lines, and the cross will be referred to as a related line cross. Mo17 was derived by pedigree selection from the cross of the two inbred lines CI187-2 and C103 (Zuber, 1973). CI187-2 was derived from 'Krug' open-pollinated variety, a strain of Reid Yellow Dent, whereas C103 was derived from Lancaster Sure Crop. Although some germplasm of Mo17 traces to Reid Yellow Dent, Mo17 performs and has an appearance similar to Lancaster Sure Crop lines. B73 × M017, therefore, is a cross of lines that represents the heterotic pattern of Reid Yellow Dent × Lancaster Sure Crop and will be referred to as an unrelated line cross.

The 200 S_2 progenies of each of the two F_2 populations were planted in separate isolation fields to produce testcrosses in 1985. Single-cross testers were used to provide vigorous pollen sources. The tester for S_2 lines derived from the unrelated F_2 population (B73 × Mo17) was H99 × A619. H99 and A619 are classified as Oh43 types, which are intermediate to the Reid Yellow Dent (B73) and Lancaster Sure Crop (Mo17) lines included in the unrelated line cross. The tester for the related line cross (B73 × B84) S_2 progenies

[1]Journal Paper No. J-14192 of the Iowa Agric. and Home Econ. Exp. Stn., Ames, IA 50011. Project No. 2778. Part of a dissertation submitted by the senior author in partial fulfillment of the requirements for a Ph.D. degree.
[2]Station Manager, DEKALB Plant Genetics Research Station, Dayton, IA 50530.
[3]Professor of Agronomy, Iowa State Univ., Ames, IA 50011.

was Mo17 × MBS2040. Mo17 and MBS2040 are Lancaster Sure Crop type lines, making the tester a logical choice for lines with Reid Yellow Dent germplasm. The S_2 progenies were detasseled, and seed from about 15 plants of each line was bulked within lines to provide testcross seed. The testcrosses were genetically equivalent to S_1 plant × tester testcrosses because seed of each S_2 progeny was bulked. The 400 testcrosses were used to estimate the genetic variability among and within testcrosses of the related and unrelated line crosses.

The 400 S_2 progenies were evaluated at two locations in 1985. To provide additional data for the S_2 progenies themselves, two locations were planted in 1986. Because remnant seed supplies were not adequate for all progenies, only 86 of the original 100 S_1 progenies (172 S_2 progenies) from the unrelated line cross and 80 of the original 100 S_1 progenies (160 S_2 progenies) from the related line cross were common for the 1985 and 1986 progeny evaluation trials. Additional S_2 progenies were substituted for those that had inadequate seed for testing in 1986. The 400 testcrosses were evaluated at three locations in 1986 and 1987,

All trials used a two-row plot 5.49 m long with 76.2 cm between rows. Plots were overplanted and thinned at the 6- to 8-leaf stage to the desired plant density of 62,140 plants ha^{-1}. Cultural practices recommended for good corn production were used at all locations.

Data were obtained for all trials for stand, grain yield, and grain moisture. Stand was recorded as number of plants per plot before flowering and converted to plants ha^{-1}. Grain yield was recorded as total amount of shelled grain harvested per plot, adjusted to 155 g kg^{-1} grain moisture, and expressed as Mg ha^{-1}. Grain moisture percentage of the shelled grain was recorded at the time of harvest and expressed as g kg^{-1}. Percentages of root and stalk lodging and dropped ears were determined in all environments for the S_2 progeny trials and in four of six environments for the testcrosses. Number of root lodged (plants leaning more than 30° from the vertical), stalk lodged (plants broken at or below the ear node) plants, and dropped ears (ears detached from the plant) was recorded immediately before harvest. Percentages of root and stalk lodging and dropped ears were determined by dividing the recorded number of lodged plants and dropped ears by the previously recorded stand for each plot. The percentages for each of the three traits were used in the analyses of variance. The number of days from planting to 50% of the plants shedding pollen was recorded for all plots in two environments for the S_2 progeny trials and in one environment for the testcross trials. Ear height (cm) was measured from the ground to the top ear-bearing node on 10 competitive plants per plot in one environment for each of the S_2 progeny and testcross trials. Average ear height for each plot was used in the analyses of variance.

The experimental design used in all trials was an entries-within-sets arranged in incomplete blocks with two replications per set. Each experiment at each location was partitioned into five sets, with each set including 80 of the 400 entries. The 80 entries within each set of the S_2 progeny trials included 40 S_2 progenies representing 20 S_1 progenies from the related (B73 × B84) and unrelated (B73 × Mo17) line crosses. The testcrosses of the same 80 entries for each set of the S_2 progeny trials included the entries for the testcross trials. The 80 entries were randomized within each replication of each set for each trial.

Analyses of variance were conducted for each trait for each set, pooled for sets for each environment, and combined over environments (three for S_2 progeny trials and six for testcross trials). The sums of squares and degrees of freedom for entries were partitioned into sources due to among (S_1) and within (S_2/S_1) S_1 progenies. The among and within sources of variation were further partioned for the related and unrelated line crosses and related vs. unrelated contrast. The entry × environment source of variation was partitioned in the same manner as for the entry source of variation. Environments and entries were assumed to be random effects in the linear model for the analyses of variance. Direct F-tests were available for all sources of variation in the analyses of variance pooled over sets for each environment and all except entries sums of squares in the analyses combined over environments. Only those entries that were common to the 1985 and 1986 S_2 progeny trials (172 unrelated line cross and 160 related line cross S_2 progenies) were included in the analyses of S_2 progenies and testcrosses.

Estimates of components of variance for among and within genotypes and their corresponding interactions with environments were calculated by equating observed mean squares to the expected mean squares. Similar estimates of components of variance for the partitions (unrelated, related, and unrelated vs. related) among and within S_1 progenies were calculated from the appropriate mean squares. Standard errors of the estimates of components of variance were calculated by the methods of Anderson and Bancroft (1952).

Estimates of heritability (h^2) were calculated from the estimated components of variance among and within S_1 progenies for both crosses and for each cross separately for all traits for S_2 progenies themselves and their testcrosses. Heritabilities were calculated on a progeny mean basis by use of the formulae:

$$h^2\text{Among} = \sigma^2_{S1}/(\sigma^2/re + \sigma^2_{ES1}/e + \sigma^2_{S1}; \text{ and}$$

$$h^2\text{Within} = \sigma^2_{S2/S1}/(\sigma^2/re + \sigma^2_{ES2/S1}/e + \sigma^2_{S2/S1}), \text{ where}$$

σ^2_{S1} is the estimated component among S1 progenies, σ^2_{ES1} is the estimated component for environment × S1 progenies, $\sigma^2_{S2/S1}$ is the estimated component within S1 progenies, $\sigma^2_{ES2/S1}$ is the estimated component for environment × S2/S1 progenies, σ^2 is the experimental error, e is the number of environments (3 for S2 progenies themselves and 6 for their testcrosses), and r is the number of replications (2 for all trials). Standard errors of the heritability (SEh^2) estimates were calculated by the method suggested by Dickerson (1969).

The genetic expectations of the S_2 progeny evaluation trials permitted the estimation of additive (σ^2_A) and dominance (σ^2_D) components of genetic variance. Homozygous inbred lines were used to produce the F_1, which was selfed to obtain the F_2 population. Only heterozygous loci will segregate in the F_2, and the average gene frequently at these segregating loci will be 0.5. Assuming gene frequencies of 0.5 and the other assumptions necessary for translating components of variance into their genetic expectations, estimates of σ^2_A and σ^2_D and their interactions with environments (σ^2_{AE} and σ^2_{DE}) can be determined from the among (σ^2_{S1}) and within ($\sigma^2_{S2/S1}$) S_1 progeny sources of variation (Mather and Jinks, 1971; Hallauer and Miranda, 1988). The genetic variation in the S_1 generation can be partitioned as the genetic variance among S_1 progenies (σ^2_{S1}) and the genetic variance within S_1 progenies ($\sigma^2_{S2/S1}$):

$$\sigma^2_{S1} = \sigma^2_A + (1/4)\sigma^2_D; \text{ and}$$

$$\sigma^2_{S2/S1} = (1/2)\sigma^2_A + (1/2)\sigma^2_D.$$

Estimates of σ^2_A were obtained by (2/3) $(2\sigma^2_{S1} - \sigma^2_{S2/S1})$. With substitution for the estimate of σ^2_A, estimates of σ^2_D were obtained as $4(\sigma^2_{S1} - \sigma^2_A)$. Estimates of environment × additive (σ^2_{AE}) and environment by dominant (σ^2_{DE}) components of variance were calculated similarly except that the estimates of the environment × genetic components of variance (σ^2_{ES1} and $\sigma^2_{ES2/S1}$) were used. Heritability estimates (h^2) in the narrow sense ($h^2 = \sigma^2_A/\sigma^2_P$) and predicted gains ($\Delta_G = (ck\sigma^2_A)/\sigma_P$) were calculated among and within S_1 progenies on the basis of the calculated estimates of components of genetic variance, where σ_P is square root of the phenotypic variance, c is parental control, and k is the selection differential.

Pearson product-moment correlations were calculated for traits between S_2 progenies and their respective testcrosses. The S_2 progeny and testcross trials were grown in different environments, which were considered as a random sample of possible year — location combinations of environments. Falconer (1981) and Casler (1982) have shown, if environments are a random sample and entries are randomized within each environment, the covariances between S_2

Table 1. Means and ranges for traits measured in S_2 progenies and their testcrosses for S_2 progenies obtained from related (B73 × B84) and unrelated (B73 × Mo17) line crosses.

Traits[a]	Lines			Testcrosses		
	B73 × Mo17	B73 × B84	LSD (0.05)[a]	B73 × Mo17	B73 × B84	LSD (0.05)[b]
Yield, Mg ha^{-1}						
Mean	4.57	4.96	0.24	7.22	8.31	0.18
Range	5.25	4.25		2.69	2.53	
Grain moisture, g kg^{-1}						
Mean	207	224	26.00	185	204	18.00
Range	69	79		42	47	
Stand, no. ha^{-1} (× 1000^{-1})						
Mean	54.0	52.3	0.34	59.0	59.4	0.14
Range	22.6	18.0		7.6	4.0	
Root lodging, %						
Mean	5.5	8.9	2.20	4.4	14.3	2.23
Range	34.6	39.3		25.2	29.1	
Stalk lodging, %						
Mean	10.1	6.3	3.70	6.6	6.3	0.44
Range	45.7	21.1		17.1	18.0	
Dropped ears, %						
Mean	1.2	0.8	0.25	1.1	1.7	0.25
Range	9.4	5.7		3.4	5.4	
Days to pollen, no.[c]						
Mean	81.2	83.9	1.80	70.2	74.0	2.3
Range	9.5	10.3		9.5	5.5	

[a]Data for S_2 progenies obtained in three environments and data for testcrosses obtained in six environments for yield and grain moisture and in four environments for root and stalk lodging and dropped ears.

[b]LSD (0.05) was calculated using the genotype x location component of variance from combined analyses of variance to compare means of the two crosses.

[c]Number of days from planting to 50% of plants within plot shedding pollen in two environments for S_2 progenies and one environment for S_2 progeny testcrosses.

progenies and their testcrosses can be considered as genetic covariances. Genetic correlations (r_G) were calculated from entry means over environments for progenies themselves (S1) and their testcrosses (TC) by the formula (Mode and Robinson, 1959);

$$r_G = \sigma_{S1TC}/(\sigma^2_{S1} \times \sigma^2_{TC})^{1/2}.$$

RESULTS

Progeny Evaluation

Differences among S_1 progenies were highly significant ($P \leq 0.01$) for all traits except number of plants for the related (B73 × B84) line cross in the combined analyses (analyses not shown). Orthogonal comparisons between means of unrelated and related line S_1 progenies were highly significant for grain moisture, number of plants, days to pollen shed, and percentage of dropped ears, significant ($P \leq 0.05$) for grain yield, and nonsignificant for percentages of root and stalk lodging. Variability among S_2 progenies within S_1 progenies was highly significant for all traits for both crosses except for percentage of root lodging for unrelated line cross, percentage of dropped ears for related line cross, and number of days to 50% pollen shed for both crosses. Interactions of among- and within-S_1 progenies with environments were highly significant in nearly all instances for all traits except number of plants.

Differences between the means of the S_2 progenies of the two crosses exceeded the calculated LSD (0.05) for all traits (Table 1). The B73 × Mo17 S_2 progenies averaged 0.39 Mg ha^{-1} less yield, 17 g kg^{-1} less grain moisture, 3.4% less root lodging, and flowered 2.7 days earlier than the B73 × B84 S_2 progenies. There was not a consistent trend between crosses in the range of expression for the different traits. Although the average yield of the B73 × Mo17 S_2 progenies was significantly less than for the B73 × B84 S_2 progenies, the range in yield among B73 × Mo17 S_2 progenies was 1.00 Mg ha^{-1} greater. There was no consistent evidence that the variation expected for the different traits would be either greater or less in an unrelated line cross than in a related line cross (Table 1).

Genetic variability among S_1 progenies was significantly greater than among S_2 progenies within S_1 progenies (Table 2). If the genetic differences among progenies were primarily due to additive genetic effects (σ^2_A), it is expected that the genetic differences among S_1 progenies [$\sigma^2_A + (1/4)\sigma^2_D$] would be two times greater than the genetic differences among S_2 progenies [$(1/2\sigma^2_A + (1/2)\sigma^2_D$). Deviations due to dominant effects are expected to be greater among S_2 progenies, but the evidence for maize populations indicates that genetic variability due to additive genetic effects is two to four times greater than dominant effects (Hallauer and Miranda, 1988). Estimates of genetic variability within S_1 progenies were not different from zero for percentage of root lodging and number of days to pollen shed for both crosses. The estimates of components of variance among S_1 progenies exceeded twice their standard errors in both crosses for all traits (Table 2). For grain yield, the variability among S_1 progenies (41.8) was 4.2 times greater than within S_1 progenies (9.9) for the unrelated line cross (B73 × Mo17) and 2.2 times greater for the related line cross (B73 × B84). Variation among S_1 progenies of the unrelated line cross tended to be greater than for the related line cross; e.g., the variation among S_1 progenies of the unrelated line cross was 1.5 times greater than variation among S_1 progenies of related line cross. Although the progeny by environment interactions were generally significant in the analyses of variance, the estimates of the components of variance for the interaction components of variance

Table 2. Estimates of components of genetic variance (σ^2_G) and genetic by environment interaction (σ^2_{GE}) among and within S_1 progenies, experimental error (σ^2), and heritability (h^2) estimates among and within S_1 progenies from combined analyses of variance for S_2 progenies themselves for unrelated (B73 × Mo17) and related (B73 × B84) line crosses.

	Traits					
	Grain		Lodging		Dropped	Days to
Parameter	Yield	Moisture	Root	Stalk	ears	flower
	Mg ha^{-1} (x 10)[a]	g ha^{-1} (x 10^{-1})[b]	----------%----------		(x 10)[a]	no.
B73 × Mo17 —						
σ^2_G: Among	41.8±9.8	17.0±3.4	21.5±5.2	18.2±6.5	5.5±2.3	2.8±0.5
Within	9.9±4.4	2.1±1.2	−0.4±2.7	13.2±4.6	5.1±1.9	−0.2±0.2
σ^2_{GE}: Among	17.1±5.4	2.0±1.3	7.4±4.1	16.8±5.0	4.1±1.9	0.3±0.3
Within	28.2±5.5	6.1±1.6	16.8±5.0	29.5±4.9	5.6±2.3	2.1±0.4
h^2: Among	76±18	83±16	65±15	63±22	46±19	89±18
Within	37±17	30±17	−3±19	47±16	43±16	−23±24
B73 × B84 —						
σ^2_G: Among	28.5±9.2	14.4±3.2	27.7±7.3	2.9±1.6	3.5±1.6	1.2±0.4
Within	12.8±5.2	3.4±1.4	−2.4±3.8	2.9±1.6	0.1±1.0	−0.3±0.2
σ^2_{GE}: Among	28.1±7.0	2.8±1.4	15.1±6.5	0.4±1.6	7.3±2.0	0.9±0.3
Within	31.9±6.1	5.8±1.6	36.2±7.2	3.7±2.3	1.1±1.9	1.6±0.3
h^2: Among	63±20	79±18	66±17	35±19	32±15	65±20
Within	42±17	42±17	−13±20	31±17	2±17	−41±27
Overall —						
σ^2_G: Among	37.0±6.9	22.0±3.1	24.9±4.6	11.8±3.4	5.2±1.4	3.6±0.5
Within	11.3±3.4	2.7±0.9	−1.3±2.3	8.2±2.3	2.7±1.1	−0.3±0.2
σ^2_{GE}: Among	24.5±4.5	4.3±1.1	17.7±4.1	18.3±3.0	5.6±1.4	1.1±0.3
Within	30.0±4.2	5.9±1.2	26.2±4.4	17.1±2.6	3.5±1.6	1.8±0.2
σ^2:	44.8±2.0	17.3±0.8	56.0±2.5	31.7±1.4	30.1±1.4	0.8±0.1
h^2: Among	70±13	84±12	62±12	51±15	43±12	83±12
Within	39±12	36±12	−8±14	43±12	30±12	−30±18

[a]Estimates of components of variance multiplied by 10.
[b]Estimates of components of variance divided by 10.

were generally smaller than the S_1 progeny components of variance. This relation for estimates within progenies was the reverse. In all instances, except for percentage of stalk lodging in the related line cross, the estimates of the within-S_1 progeny by environment interaction component of variance was greater than the within-S_1 progeny component of variance.

Heritability estimates (h^2) among and within S_1 progenies indicate that selection would be more effective among S_1 progenies than among S_2 progenies within S_1 progenies. Greater additive genetic variability among S_1 progenies and less interaction of S_1 progenies with environments would contribute to the greater h^2 estimates among S_1 progenies. Estimates of σ^2_A and σ^2_D and their interactions

Table 3. Estimates of genetic gain[a] for among and within S_1 progeny selection within related (B73 × B84) and unrelated (B73 × Mo17) line crosses expressed as a percentage of individual trait means.

	Trait						
	Grain		Lodging		Dropped	Days to	
Groups	Yield	Moisture	Root	Stalk	ears	pollen shed	Average
	----------%----------						
B73 × Mo17							
Among	19.1	9.0	115.4	39.8	40.3	3.0	37.8
Within	11.7	5.8	68.0	20.1	20.2	1.8	21.3
Ratio[b]	1.6	1.6	1.7	2.0	2.0	1.7	1.7
B73 × B84							
Among	12.2	7.3	82.6	14.7	76.0	1.9	32.4
Within	7.3	4.6	47.4	7.1	45.3	1.1	18.8
Ratio[b]	1.7	1.6	1.7	2.1	1.7	1.7	1.7
Overall							
Among	16.2	10.6	95.8	36.2	65.0	3.5	33.6
Within	9.9	6.6	56.8	19.8	38.0	2.2	20.0
Ratio[b]	1.6	1.6	1.7	1.7	1.6	1.7	1.7

[a]Genetic gains were estimated with a parental control (C = 1) of one, a selection intensity of 20% (k = 1.40), and negative estimates of components of variance were assumed to be zero.
[b]Ratio was calculated as among divided by within.

with environments were calculated from the components of variance for among- and within-S_1 progenies. The estimates of σ^2_A exceeded twice their standard erors for all traits in both crosses (estimates not shown). The estimates of σ^2_D were frequently negative, and all positive estimates were smaller than their respective standard errors. For the S_2 progenies evaluated for these two crosses, it seems that additive genetic effects were of greater importance.

Relative genetic gains expected by among- and within-S_1 progeny selection were similar for both crosses (Table 3). The greatest differences between among- and within-S_1 progeny selection were for percentages of root and stalk lodging, which is because of the lower estimates of within-S_1 progeny variability for these two traits. Expected genetic gain,on the average, was 70% greater among S_1 progenies.

Testcross Evaluation

Differences among testcrosses were highly significant for all traits except stand in the combined analyses of variance of the six environments (analyses not shown). The testcross sum of squares was partitioned for among-S_1 progeny testcrosses (S_1) and within-S_1 progeny testcrosses (S_2/S_1) for the related and unrelated line crosses. Differences among S_1 progeny testcrosses were not significant for percentage of dropped ears, significant for percentage of stalk lodging, and highly significant for the other traits for the unrelated line cross. Highly significant differences for grain moisture and significant differences were detected for the other traits of the related line cross. More significant differences were detected among S_1 progeny testcrosses for the unrelated line cross. Similar trends for levels of significance occurred for the within S_1 progeny testcross for the different traits. Relatively little genetic variation for yield was present within-S_1 progeny testcrosses of the related line cross. Mean squares for among-S_1 progeny testcross × environment interaction were highly significant for all traits except for percentage of stalk lodging, which was significant. Interactions of percentage of root and stalk lodging and dropped ears with environments were generally significant both for among- and within-S_1 progeny testcrosses. Testcrosses were not consistent in their performance across environments because of the different conditions at the different locations in 1986 and 1987. Both years were good for grain production, but a severe windstorm on July 29, 1986 caused excessive lodging at the three locations.

Means and ranges for the testcross traits for the related and unrelated line crosses show that average yield of the related line testcrosses was 13% greater than that of unrelated line testcrosses, but the related line testcrosses had a 6% lower range in yield (Table 1). The related line testcrosses had greater yield, more grain moisture at harvest, greater root lodging, and more days to pollen shed than the unrelated line crosses; the differences were significant by the LSD. There were no trends that a greater range among testcrosses would be expected in either the related or the unrelated line testcrosses.

Estimates of the components of variance and heritabilities among- and within-S_1 progeny testcrosses (Table 4) were not as great as those among and within S_1 progenies themselves (Table 2). Because of the masking effects of the testers, the genetic variability among S_1 testcrosses ($0.25\sigma^2_A$) would not be expected to be as great as the genetic variability among S_1 progenies (σ^2_A) themselves, assuming only additive genetic effects. Except for percentage of dropped ears of

Table 4. Estimates of components of genetic variance (σ^2_G) and genetic by environment interaction (σ^2_{GE}) among- and within-S_1 progeny testcrosses, experimental error, and heritability (h^2) estimates among- and within-S_1 testcrosses from combined analyses of variance of testcrosses for unrelated (B73 × Mo17) and related (B73 × B84) line crosses.

	Traits					
	Grain		Lodging		Dropped	Days to
Parameter	Yield	Moisture	Root	Stalk	ears	pollen shed
	Mg ha^{-1} (x 10)[a]	g kg^{-1} (x 10^{-1})[b]	----------%----------		(x 10)[a]	no.
B73 × Mo17 —						
σ^2_G: Among	7.7±2.7	2.6±0.7	4.5±1.8	2.1±1.0	−0.1±0.1	0.7±0.2
Within	6.2±2.1	1.6±0.5	3.9±1.7	2.0±1.0	1.3±0.8	0.4±0.1
σ^2_{GE}: Among	6.0±2.5	0.8±0.5	2.5±1.8	0.5±1.1	0.3±1.0	- - -
Within	−8.9±3.5	−0.7± −0.7	−9.4±2.6	5.2±1.6	−4.6±1.6	- - -
h^2: Among[c]	44±15	60±16	33±13	41±19	0±12	
Within[c]	45±16	52±15	38±16	32±16	26±16	
B73 × B84 —						
σ^2_G: Among	1.3±2.2	3.2±0.8	7.2±4.2	−0.1±0.6	2.3± 1.5	0.1±0.1
Within	3.2±2.8	0.9±0.5	5.6±3.2	1.3±0.8	2.2±1.3	0.1±0.1
σ^2_{GE}: Among	2.5±4.4	0.0±0.6	23.2±5.4	1.9±1.0	7.7±2.0	- - -
Within	26.5±5.9	2.5±0.9	19.4±5.2	1.0±1.3	2.3±2.2	- - -
h^2: Among[c]	12±20	66±16	33±19	0±18	25±17	
Within[c]	19±17	31±16	29±17	29±17	29±17	
Overall —						
σ^2_G: Among	32.1±4.8	13.2±1.6	28.4±1.9	0.9±0.6	1.7±0.8	4.2±0.5
Within	4.8±1.7	1.3±0.3	4.7±1.7	1.7±0.6	1.8±0.8	0.2±0.1
σ^2_{GE}: Among	15.2±2.8	1.5±0.4	29.4±3.4	1.8±0.8	6.0±1.1	- - -
Within	8.2±3.5	0.9±0.6	4.5±2.9	3.2±1.1	−1.3±1.4	- - -
σ^2:	108.1±3.4	19.4±0.6	70.4±2.8	23.7±0.9	39.8±1.6	1.0±0.1
h^2: Among[c]	74±11	87±11	64±11	21±13	21±10	90±0.4
Within[c]	31±11	42±11	32±11	31±12	28±12	89±0.7

[a]Estimates of components of variance multiplied by 10.
[b]Estimates of components of variance divided by 10.
[c]Heritabilities expressed as percentages.

Table 5. Product-moment correlations between traits of the S_2 progenies and their testcrosses for the unrelated (B73 × Mo17) and related (B73 × B84, in parentheses) line crosses calculated from the among-S_1 progeny components of variance and covariance.

S_2 progeny traits	Testcross traits: Grain Yield	Grain Moisture	Lodging Root	Lodging Stalk	Dropped ears
Grain yield	0.15 (0.08)	0.08 (0.09)	0.04 (0.01)	0.05 (−0.10)	−0.06 (0.09)
Grain moisture	0.10 (0.09)	0.47** (0.48)**	0.23** (0.05)	0.08 (0.02)	0.04 (−0.07)
Root lodging	−0.05 (0.07)	0.01 (0.16)*	0.49** (0.36)**	0.15* (−0.14)	0.05 (−0.08)
Stalk lodging	0.16** (−0.14)	−0.14 (−0.17)*	0.13 (0.06)	0.48** (0.08)*	0.04 (0.18)*
Dropped ears	−0.30** (−0.01)	−0.01 (−0.01)	−0.05 (−0.05)	−0.07 (0.05)	0.16* (0.31)**

* and ** indicate significance at the 5 and 1% levels, respectively.

the related line testcrosses, the estimates of variability among S_1 progenies were more than four times greater than the variability among S_1 testcrosses, suggesting that the testers (H99 × A619 for unrelated line cross and Mo17 × MBS2040 for related line cross) affected the expression of differences among S_1 progenies. Both testers included elite lines whose alleles seemingly masked the expression of the alleles of the S_1 progenies. The tester for the related line cross (B73 × B84) included lines of the opposite heterotic group and would be expected to possess either different alleles or the same alleles at different frequencies than for B73 and B84. The tester for the unrelated line cross (B73 × Mo17) was a compromise for the widely used heterotic group, and the differences in allele frequencies between tester and S_1 progenies were not expected to be as great as between the B73 × B84 and Mo17 × MBS2040. Hallauer and Lopez-Perez (1979) reported that the tester (Mo17) from the opposite heterotic group was an effective tester for an unselected group of lines derived from Iowa Stiff Stalk Synthetic. It seems that the variability among S_1 progenies of B73 × B84 was as great as among unselected lines of Iowa Stiff Stalk Synthetic or that MBS2040 included more alleles in common with B73 and B84. Estimates of the components of variance among testcrosses were similar for related and unrelated lines, with similar estimates among- and within-S_1 progeny testcrosses. Except for grain yield for B73 × B84, estimates of components of variance and heritabilities indicate selection among-S_1 testcrosses would be more effective (Table 4).

Correlations Between S_1 Progenies and Testcrosses

Correlations between the performance of S_2 progenies themselves and their respective testcrosses were less than 0.5 in all instances. Greater correlations were obtained for grain moisture and percentage of root and stalk lodging with no association for grain yield between S_2 progenies themselves and their testcrosses (Table 5). The correlations are similar to those reported for other studies (Hallauer and Miranda, 1988) and those expected theoretically (Smith, 1986).

DISCUSSION

Estimates of additive genetic variance (σ^2_A), deviations due to dominant effects (σ^2_D), and their interactions with environments (σ^2_{AE} and σ^2_{DE}) were determined from the components of variance among and within S_1 progenies (Table 2). Estimates of σ^2_A exceeded twice their standard errors in both crosses for most traits, whereas the estimates of σ^2_D were negative in both crosses but within the range of zero relative to their standard errors (estimates not shown). Estimates of σ^2_A for yield were greater in the unrelated line cross (49.1 ± 13.4) than for the related line cross (29.4 ± 12.8), but σ^2_D was not significant in either cross. Except for percentages of root lodging and dropped ears, the same trends for the estimates of σ^2_A and σ^2_D were similar for other traits. Differences among progenies, therefore, were due to additivity of effects within and among loci, with no evidence that dominant effects had a significant role.

Because the differences among testcrosses for each cross (Table 4) were smaller than the differences among lines (Table 2), the masking effects of the tester were evident in both crosses. Better discrimination among testcrosses might have been attained with use of inbred lines instead of single-cross testers. Horner et al. (1973) reported that variation among testcrosses to an inbred line would be twice the variation among testcrosses to a genetically broad-based tester. The testers (H99 × A619 and Mo17 × MBS2040) were crosses of lines expected to have some level of commonality. The variation among testcrosses to inbred lines would be expected to be greater than among testcrosses to single crosses, but the differences would not be as great for the comparisons made by Horner et al. (1973). Comstock (1979) emphasized, however, that the choice of an inbred line to use as tester is dependent on the relative frequency of alleles relative to the materials tested. It seems that a poor choice of testers was used for the S_1 progenies for both crosses, although, based on pedigree, the testers seemed logical choices.

Maize breeders select among and within segregating progenies as the progenies are advanced to greater homozygosity by self-pollination. Our results agree, as expected, with the theoretical parameters that greater variation exists among S_1 progenies than within S_1 progenies, particularly if additive genetic effects are of greater importance. Our primary objective was to determine if differences among and within S_1 progenies of different types of crosses (related vs. unrelated) were sufficiently different to modify selection strategies for particular crosses. Although the estimate of additive genetic variance for yield was 67% greater in the unrelated cross, dominance effects were not important in either cross. Hence, greater genetic gains would be expected with selection among progenies for both types of crosses.

Estimates of genetic gains for among-progeny selection were greater than within-progeny selection in all instances (Table 3). Average genetic gains were greater among and within S_1 progenies for the unrelated line cross (B73 × Mo17), but the same relative trends for among- and within-S_1 progeny selection existed for both crosses. On the average, among-S_1 progeny selection will have 70.7% greater genetic gain than within-S_1 progeny selection. Greater differences in genetic gain for among- vs. within-S_1 progeny selection occur for

percentages of root and stalk lodging and dropped ears, which are traits that have lower individual plant heritabilities. Selection strategies that emphasize selection among progenies will result in greater genetic gains for all traits. Testcrosses, particularly in the earlier generations of inbreeding (S_1 and S_2), also should be emphasized among progenies because the differences for within-progeny testcrosses were smaller. The proper choice, however, is critical in determining the relative combining ability of lines, and use of two or more inbred lines seems preferable to use of single-cross testers.

REFERENCES

ANDERSON, R.L., and T.A. BANCROFT. 1952. Statistical theory in research. McGraw-Hill, Inc., New York.

CASLER, M.D. 1982. Genotype x environment intereaction bias to parent-offspring regression heritability estimates. Crop Sci. 22:540-542.

COMSTOCK, R.E. 1979. Inbred lines versus the populations as testers in reciprocal recurrent selection. Crop Sci. 19:881-886.

DICKERSON, G.E. 1969. Techniques for research in quantitative animal genetics. p. 36-79. *In* Techniques and procedures in Animal Science Research. Am. Soc. Anim. Sci., Albany, NY.

FALCONER, D.S. 1981. Introduction to Quantitative Genetics. 2nd ed. Longman, Inc., New York.

HALLAUER, A.R., and E. LOPEZ-PEREZ. 1979. Comparisons among testers for evaluating lines of corn. Proc. Annu. Hybrid Corn Ind. Res. Conf. 34:57-75.

HALLAUER, A.R., and J.B. MIRANDA, Fo. 1988. Quantitative Genetics in Maize Breeding. Iowa State Univ. Press. 2nd ed. Ames, IA.

HORNER, E.S., H.W. LUNDY, M.C. LUTRICK, and W.H. CHAPMAN. 1973. Comparison of three methods of recurrent selection in maize. Crop Sci. 13:485-489.

MATHER, K., and J.L. JINKS. 1971. Introduction to biometrical genetics. Cornell Univ. Press, Ithaca, NY.

MODE, C.J., and H.F. ROBINSON. 1959. Pleiotropism and the genetic variance and covariance. Biometrics 15:518-537.

RAWLINGS, J.O., and D.L. THOMPSON. 1962. Performance level as criterion for choice of maize testers. Crop Sci. 2:217-220.

RUSSELL, W.A. 1972. Registration of B70 and B73 parental lines of maize. Crop Sci. 12:721.

RUSSELL, W.A. 1979. Registration of B84 parental line of maize. Crop Sci. 19:566.

RUSSELL, W.A., and A.R. HALLAUER. 1980. Corn. p. 299-312. *In* W.F. Fehr and H.H. Hadley (eds.) Hybridication of Crop Plants. Am. Soc. Agron., Madison, WI.

SMITH, O.S. 1986. Covariance between line per se and testcross performance. Crop Sci. 26:540-543.

SPRAGUE, G.F. 1946. Early testing of inbred lines of corn. J. Am. Soc. Agron. 38:108-117.

ZUBER, M.S. 1973. Registration of 20 maize parental lines. Crop Sci. 13:799-780.