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Estimates of Genetic Variability in F₂ Maize Populations¹

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Maize (*Zea mays* L.) breeders emphasize selection within F₂ populations derived from crosses of inbred lines. Studies of the inheritance of quantitative traits in maize have been conducted primarily for genetically broad-based populations. Objectives of our study were to estimate the genetic variability in F₂ populations developed from crosses of related and unrelated lines and to determine the effects of five generations of random intermating of plants within F₂ populations on the estimates of genetic variability. Estimates of additive genetic variability were greater in the unrelated line crosses, but the estimates were not significantly different before and after random intermating within both crosses. Estimates of dominance variance decreased with random mating, suggesting that linkage effects were affecting the estimates. For applied breeding programs, it seems that adequate genetic variability was available in both types of crosses and that five generations of random intermating were not effective for increasing genetic variability.

INDEX DESCRIPTORS: *Zea mays* L., Corn, Quantitative traits, Intermating, Linkage effects, Breeding methods

Information on the genetic variability of breeding populations is important in the choice of effective breeding methods and the expected responses to selection. Estimates of genetic components of variances and average levels of dominance of genes controlling the inheritance of quantitative traits also are useful in the theory of heterosis and its expression in hybrids. Mating designs were developed to provide estimates of genetic components of variance, assuming linkage equilibrium (Comstock and Robinson, 1948, 1952.) These authors emphasized that estimates of additive and dominance genetic variances were biased if the populations were in linkage disequilibrium, and that bias was reduced with genetic recombination in advanced random mating populations.

Estimates of genetic components of variance were summarized by Hallauer and Miranda (1981) for different types of maize (*Zea mays* L.) populations. Additive genetic variance estimates were of greater importance than the dominance variance estimates for 11 traits with the average levels of dominance in the partial to complete dominance range. Linkage disequilibrium, however, biased estimates of genetic variances and average levels of dominance in F₂ populations formed by crossing inbred lines. Few estimates of genetic parameters have been reported in F₂ populations developed from hybrids that exhibited different levels of heterosis. Moreno-Gonzalez and Dudley (1981) estimated genetic effects in crosses of related and unrelated maize lines. Heterosis was greater in crosses of unrelated lines, but the genetic effect estimates were not associated with crosses of either related or unrelated lines.

Objectives of our study were to estimate and compare genetic components of variance and average levels of dominance of genes in two maize populations that descended from a cross of two unrelated lines (B73 × Mo17) and from a cross of two related lines (B73 × B84). B73 and Mo17 are elite lines that represent the 'Reid Yellow Dent' (B73) and 'Lancaster Surecrop' (Mo17) heterotic pattern used in the U.S. Corn Belt. B73 and B84 were developed from BS13, a strain of Iowa Stiff Stalk Synthetic (BSSS) that has been under half-sib recurrent selection (Hallauer et al., 1983). BSSS includes germplasm that is considered representative of Reid Yellow Dent. Estimates of genetic components of variance were obtained for the F₂ populations and after five generations of random intermating within each F₂ population to determine the linkage effects on the estimates of genetic parameters.

MATERIALS AND METHODS

F₂ populations from the B73 × Mo17 and B73 × B84 single-cross hybrids and F₂ synthetic 5 (F₂ Syn. 5) populations obtained after five generations of intermating the F₂ populations were the source materials of the study. B73 and B84 were derived from Iowa Stiff Stalk Synthetic population after five and seven cycles of half-sib recurrent selection, respectively (Hallauer et al., 1983). Mo17 was derived by pedigree selection from the cross, C103 × 187-2; C103 was developed from a strain of Lancaster Surecrop and 187-2 developed from Krug, a selected strain of Reid Yellow Dent. Mo17's performance in hybrids, however, is similar to lines derived from Lancaster Surecrop. Herein, B73 × Mo17 and B73 × B84 are considered unrelated and related line crosses, respectively.

The B73 × Mo17 and B73 × B84 single crosses (F₁'s) were self-pollinated to produce the respective F₂ populations. For each F₂ population, 250 plants were intermated. No tassel was used to pollinate more than two ears, and reciprocal crosses between the same plants were not made. Every plant, where possible, was used either as a male or as a female. All pollinated ears were harvested and equally sampled to form a 250-seed bulk for the next generation of intermating. These procedures were repeated for five generations to produce the F₂ Syn. 5 populations.

The North Carolina Design III mating design was used to develop half-sib and full-sib progenies within each of the two F₂ and two F₂ Syn. 5 populations (Comstock and Robinson, 1952). Randomly chosen plants within each population were used as males and backcrossed to each of the respective parental lines (B73, B84, and Mo17) of the respective F₂ and F₂ Syn. 5 populations. The plants used as males in the backcrosses also were self-pollinated to produce S₁ progenies. Hence, for each randomly chosen plant, there was one pair of backcrosses and one S₁ progeny. Adequate seed for testing was obtained for 40 pairs of backcross progenies and 40 S₁ progenies for each population except for (B73 × Mo17) F₂ Syn. 5, in which 38 pairs were available. The study included, therefore, three inbred lines, two single crosses, two F₂ populations, 316 backcross progenies (158 pairs) from the F₂ and F₂ Syn. 5 populations, and 158 S₁ progenies from the F₂ and F₂ Syn. 5 populations.

Experiments were conducted at two locations (Agronomy Research Center, Ames, and Ankeny, 1985; Agronomy Research Center, Ames and another location near Ames, 1986) for two years. A randomized incomplete block design was used for each experiment. The genetic materials were assigned to four sets, with each set including an equal number of backcross and S₁ progenies from each of the four populations. The first three sets included 80 backcross (20 from each population) and 40 S₁ (10 from each population) progenies. The fourth set included 76 backcross and 38 S₁ progenies, three inbred

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lines (B73, B84, and Mo17), B73 × Mo17 and B73 × B84 single crosses, and the F₂ populations of B73 × Mo17 and B73 × B84. Each set was partitioned to include subplots of S₁ and backcross progenies to reduce competition effects between the two types of progenies. Each set was replicated twice for each location. Each plot was one row 5.5 m long with 76 cm between plots. Plots were overplanted and thinned to a uniform stand of 50,232 plants ha⁻¹. All plots were hand-harvested except the experiment conducted at Ankeny (1985), which was discarded because of drought conditions. Harvested ears were placed in forced-air dryers and dried to a uniform moisture of 6% before data were recorded for yield and ear components.

Days from planting to 50% silk emergence were recorded for the two experiments conducted at the Agronomy Research Center. Ear height (cm) was measured from ground level to the node bearing the primary ear for five plants within each plot. Ear length (cm) and ear diameter (cm) were measured for 10 ears for each plot and expressed as the average of the 10 measured ears. Number of kernel rows were counted for 10 ears for each of the two experiments conducted in 1986 and expressed on an ear basis. Yield was recorded as the total shelled grain weight of all harvested ears and converted to t ha⁻¹. Plot means (days to flower, ear height, ear length and diameter, and number of kernel rows), and plot totals (yield) were used in the analyses of variance.

A split-plot analysis of variance was calculated for each set within each environment. An analysis that included pooling over sets for the backcross and S₁ progenies for each trait was calculated within each environment. Finally, the pooled analyses for each environment were combined over environments to permit estimation of genotype by environment interactions for the backcross and S₁ progenies.

The genetic model used for estimation of genetic components of variance for the backcross progenies was the Design III model developed by Comstock and Robinson (1952). Two components of variance are estimable from the backcross analyses: variation among males (σ_m^2), which is the covariance of half sibs or (1/4) σ_A^2 (additive genetic variance), and interaction of males with the two parent lines (σ_{mp}^2) or σ_D^2 (variance due to dominance deviations). Average level of dominance (\bar{d}) of genes controlling the expression of the trait was estimated as $(\sigma_{mp}^2/2\sigma_m^2)^{1/2}$. Analyses of the S₁ progenies also provide estimates of σ_A^2 and σ_D^2 . Because F₂ populations were sampled, the expected gene frequencies of the loci segregating for alleles affecting the traits are 0.5. Expected genetic components of variance among S₁ progenies for gene frequencies of 0.5 are $\sigma_A^2 + (1/4)\sigma_D^2$. The same expressions are expected for the F₂ Syn. 5 populations, provided that sampling did not change gene frequencies after five generations of random mating. If linkages among loci controlling the traits are present, linkage would bias the estimates of σ_A^2 positively with coupling-phase linkages and negatively with repulsion-phase linkages. Estimates of σ_D^2 are positively biased for both linkage phases. The effects of linkages are expected to be greatest in the F₂ generation and gradually reduce with subsequent generations of genetic recombination. Estimates of average levels of dominance are expected to decrease from the F₂ to the F₂ Syn. 5 if repulsion-phase linkages are important.

Estimates of the σ_m^2 , σ_{mp}^2 , and σ_{S1}^2 components of variance were translated to the expected genetic (σ_A^2 and σ_D^2) components of variance to estimate σ_A^2 , σ_D^2 , and \bar{d} for each population for the backcross and S₁ progenies. Because only one genetic parameter can be obtained from the S₁ analyses, the variation among S₁ progenies estimates $\sigma_A^2 + (1/4)\sigma_D^2$. Estimates of σ_A^2 and σ_D^2 , their interactions with environments, and experimental error also were determined by the method of least squares by using the mean squares from the backcross and S₁ progenies analyses of variance. Expectations for each of the mean squares for both analyses were determined for σ_A^2 , σ_{AE}^2 , σ_D^2 , σ_{DE}^2 , and σ^2 (experimental error) and expressed in matrix notation that included the σ_m^2 , σ_{mp}^2 , σ_{S1}^2 , σ_{me}^2 , σ_{mpe}^2 , σ_{S1E}^2 , and σ^2 components of variance.

RESULTS AND DISCUSSION

Differences between backcross and S₁ progenies and their interactions with environments were highly significant ($P \leq 0.01$) for each trait within each of the four populations (analyses not shown). The mean squares for backcrosses and S₁ progenies, averaged for all traits, were 87.7 and 89.5% greater, respectively, than the backcross and S₁ progeny by environment mean squares. Differences between the average of the two sets of backcross progenies and the mean of the S₁ progenies also were highly significant for all traits. Differences among males pooled over sets and combined over environments were highly significant for each trait for each population except for days to flower in the (B73 × B84) F₂ population. The male by parent line interaction was highly significant for each trait in each population except for the following instances: a significant ($P \leq 0.05$) difference was detected for ear diameter for the (B73 × B84) F₂ population and number of kernel rows for the (B73 × Mo17) F₂ and (B73 × Mo17) F₂ Syn. 5 populations, and nonsignificant differences were detected for ear height for the (B73 × B84) F₂ and (B73 × B84) F₂ Syn. 5 populations, days to flower for the (B73 × B84) F₂ population, and number of kernel rows for the (B73 × B84) F₂ and (B73 × B84) F₂ Syn. 5 populations. Each of the four nonsignificant differences occurred in the populations derived from the related line cross. The analyses of variance indicated that significant genetic differences occurred among the progenies to permit the estimation of genetic components of variance.

Means for the pairs of backcross progenies and the S₁ progenies for each trait for each population are listed in Table 1. Orthogonal comparisons of the pairs of backcross progeny means for the F₂ vs. F₂ Syn. 5 populations were either significant or highly significant for each trait, and backcross progeny means for the (B73 × Mo17) populations vs. the (B73 × B84) populations were significant for all except plant height. Orthogonal comparisons between S₁ progeny means were either significant or highly significant for all comparisons except grain yield for (B73 × B84) F₂ vs. (B73 × B84) F₂ Syn. 5. Comparisons of the means of the backcross progenies with those for the S₁ progenies were used as an estimate of inbreeding depression (Table 1). Estimates of inbreeding depression were similar for the F₂ and F₂ Syn. 5 populations for both crosses, which would be expected if no significant changes in gene frequency occurred with random mating. S₁ progenies of the (B73 × Mo17) populations tended to have greater inbreeding depression than the S₁ progenies for the B73 × B84 populations, particularly for grain yield. Greater inbreeding depression would be expected in crosses of unrelated lines. The relative means and estimates of inbreeding depression agree with the a priori choice of inbred lines used in the crosses.

Estimates of components of variance from the combined analyses of variance of the backcross (Design III, Table 2) and S₁ progenies (Table 3) for each trait measured within each population show that the estimates of the components of genetic variances were greater than their respective interactions with environments. The estimates of σ_A^2 were numerically greater than the estimates of σ_D^2 in all instances except for grain yield for the (B73 × B84) F₂ population (Table 2). If one considers twice the standard errors of the estimates for judging significance between the estimates of σ_A^2 and σ_D^2 , the estimates of σ_A^2 were not significantly greater than the estimates of σ_D^2 in all instances [e.g., estimates of σ_A^2 and σ_D^2 for grain yield for the (B73 × Mo17) F₂ population, Table 2]. Additive effects, however, were of greater importance than the dominance effects for each trait for each population. There were no indications that the five generations of random intermating of plants within the F₂ populations increased genetic variability because of genetic recombination. It was expected a priori that the (B73 × Mo17) F₂ population (cross of unrelated lines) would have greater genetic variability than the (B73 × B84) F₂ population (cross of related lines). Although not statistically significant in all

Table 1. Progeny (BC1, BC2, and S1) means of six traits for four maize populations averaged over replications, sets, and environments.

Population	Progeny ^a	Traits					
		Yield	Height	Length	Diameter	Days to flower ^b	Kernel-row number
		t ha ⁻¹		cm		no.	
(B73 × Mo17) F ₂	BC1	7.70	104	16.4	4.7	85.3	16.4
	BC2	7.51	97	19.2	4.3	85.3	13.3
	S1	5.40	87	16.0	4.3	85.9	14.5
	I (%) ^c	-29.0	-13.4	-10.1	-4.4	0.7	-2.4
(B73 × Mo17) F ₂ Syn. 5	BC1	7.75	102	16.5	4.7	85.1	16.5
	BC2	7.72	98	19.2	4.3	84.8	13.5
	S1	5.50	87	16.3	4.3	85.3	14.7
	I (%) ^c	-28.9	-13.0	-8.7	-4.4	0.4	-2.0
(B73 × B84) F ₂	BC1	6.28	104	15.0	4.7	87.2	17.6
	BC2	6.48	104	15.8	4.6	87.9	16.2
	S1	5.26	93	14.6	4.6	87.8	16.5
	I (%) ^c	-17.6	-10.6	-5.2	-1.1	0.3	-2.4
(B73 × B84) F ₂ Syn. 5	BC1	6.80	102	15.1	4.7	86.7	17.7
	BC2	6.66	100	16.1	4.6	87.0	16.5
	S1	5.43	88	14.7	4.4	87.0	16.9
	I (%) ^c	-19.3	-12.9	-5.8	-5.4	-0.2	-1.2
SE (BC means)		0.04	0.28	0.04	0.006	0.07	0.03
SE (S ₁ means)		0.05	0.41	0.06	0.009	0.11	0.05
C.V. BC (%)		10.9	6.1	5.1	2.8	5.7	3.6
C.V. S ₁ (%)		13.2	7.1	5.9	3.0	4.1	4.1

^aBC1 is the backcross to B73, BC2 is the backcross to either Mo17 or B84, and S1 is the progenies after one generation of selfing.

^bDays from planting to 50% silk emergence.

^cEstimate of inbreeding depression calculated as $1 - [S1 / (BC1 + BC2) / 2] \times 100$.

instances, genetic variability was greater in the population developed from the cross of unrelated lines.

Specific comparisons of the relative magnitude of the variance component estimates and levels of dominance will be discussed for grain yield and plant height for the two crosses. Estimates of σ_A^2 , averaged for the F₂ and F₂ Syn. 5 populations, for yield and plant height were 2.4 and 2.1 times greater, respectively, for the B73 × Mo17 cross than for the B73 × B84 cross. Estimates of σ_B^2 were 2.7 times greater in the B73 × Mo17 cross for plant height than the B73 × B84 cross. Thus, the genetic variability in the unrelated line cross for additive and dominance effects was at least twice the genetic variability in the related line cross. If repulsion-phase linkages were important, they would be expected to cause a negative bias in the estimates of σ_A^2 . Random intermating would be expected to reduce the frequency of repulsion phase linkages and, subsequently, reduce the negative bias in the estimates of σ_A^2 . On the basis of the estimates obtained for the F₂ and F₂ Syn. 5 populations for both crosses, it does not seem that repulsion-phase linkages had a large affect on the estimates of σ_A^2 . If linkage occurs equally often in coupling and repulsion, the bias in σ_A^2 also is likely to be small. Linkages have a positive bias on the estimates of σ_B^2 regardless of the linkage phases. The greatest changes in the estimates of σ_B^2 occurred for grain yield in both crosses, suggesting dominance effects were greater than for the other traits (Table 2).

Estimates of the levels of dominance were less in the F₂ Syn. 5 populations relative to the F₂ populations in both crosses for all traits except number of kernel rows for the B73 × Mo17 cross and ear height for the B73 × B84 cross (Table 2). The effects of dominance were greater for grain yield than for the other traits, and the bias due to linkages also was greater. In both crosses, the estimates of levels of dominance were in the overdominance range for the F₂ populations.

After five generations of intermating, the estimates of average levels of dominance were in the partial to complete dominance range. Dominance effects were of lesser importance for the expression of ear height in both crosses, and the effects of random intermating had less effect in changing the estimates.

Estimates of levels of dominance for the other traits were intermediate to those for grain yield and ear height. Estimates of levels of dominance and the biases due to linkage effects for the two crosses were similar to those reported for other F₂ populations of maize (Hallauer and Miranda, 1981).

Estimates of genetic variability among the S₁ progenies had a trend similar to those obtained from the Design III analyses (Table 3). Estimates of variability among S₁ progenies for the B73 × Mo17 cross were greater than those for the B73 × B84 cross, and five generations of random intermating did not have a consistent effect on the estimates. The trends in the relative magnitude of the estimates for S₁ progenies and the estimates of σ_A^2 from the Design III analyses were similar except for grain yield for the (B73 × B84) F₂ and F₂ Syn. 5 populations, which were reversed (Tables 2 and 3). The estimates of variation among S₁ progenies tended to be greater than the estimates of σ_A^2 from the Design III analyses, but this would be expected because variance among S₁ ($\sigma_{S_1}^2$) progenies is $\sigma_A^2 + (1/4)\sigma_B^2$ for F₂ populations. If dominance effects were not important, $\sigma_{S_1}^2 = \sigma_A^2$. The estimates of $\sigma_{S_1}^2$, averaged for the F₂ and F₂ Syn. 5 populations, were 135.1 for B73 × Mo17 and 49.1 for B73 × B84 for grain yield (Table 3). The estimates of σ_A^2 and σ_B^2 , averaged for the F₂ and F₂ Syn. 5 populations, were 106.2 for σ_A^2 and 66.9 for σ_B^2 for B73 × Mo17 (Table 2) and 44.2 for σ_A^2 and 24.5 σ_B^2 for B73 × B84; $\sigma_A^2 + (1/4)\sigma_B^2$ is 122.9 for B73 × Mo17 and 50.3 for B73 × B84, which are similar to the estimates of $\sigma_{S_1}^2$ for B73 × Mo17 (135.1, Table 3) and B73 × B84 (49.1, Table 3). The estimates of genetic variability for grain yield

were consistent for both crosses. Assuming only additive and dominance effects, the total genetic variability in the B73 × Mo17 populations was 2.5 times greater than in the B73 × B84 populations, for both the estimates from Design III (Table 2) and the S₁ progenies (Table 3). Dominance effects were important in both crosses, accounting for 38.6 (B73 × Mo17) and 35.7% (B73 × B84) of the total genetic variability.

Because five generations of random intermating did not have a consistent effect on the estimates of genetic variability within the F₂ and F₂ Syn. 5 populations, the best estimates of genetic variability in the F₂ populations would be those that included all sources (Table 4). The estimates of σ_A^2 , σ_D^2 , and their interactions with environments were similar to those for the respective backcross and S₁ analyses. Intermating within the F₂ populations was not effective in changing the estimates of σ_A^2 , but the estimates of σ_D^2 and the ratio (σ_D^2/σ_A^2) tended to decrease with intermating. Greater genetic variability was present in the unrelated cross and did not change with intermating.

The parental lines used in the crosses to produce the F₂ populations were selected on the basis of their presumed genetic divergence. The parent lines and their respective F₁, F₂, and F₃ (bulk of S₁ progenies) generations were included in set 4 to compare the means of the different generations for the two crosses (Table 5). The estimates of heterosis (H) and inbreeding depression (I) for grain yield were greater

for the cross (B73 × Mo17) of unrelated lines, indicating a greater frequency of heterozygous loci. Except for number of kernel rows, the estimates of H and I agree with the expected genetic differences among the lines used for the two crosses. The estimates of genetic variability were greater in the unrelated line cross, suggesting greater potential responses to selection (Tables 2, 3, and 4). But these types of crosses may not be the more desirable because of the confounding effects of germplasm for maintaining the heterotic pattern (Reid Yellow Dent × Lancaster Surecrop) emphasized in the U.S. Corn Belt. Use of unrelated line crosses for developing recovered lines may require more extensive testing to determine the crosses that maximize the heterotic response in hybrids.

Random intermating plants within F₂ populations did not increase the genetic variability in either related or unrelated crosses. The current practice of sampling F₂ populations without additional genetic recombination by random mating has been used successfully, and our data suggest that the additional time and effort of random intermating are not necessary. The effects of random intermating within F₂ populations have been examined theoretically and empirically. Bos (1977) and Pederson (1974) determined theoretically that there were no advantages to intermating F₂ plants in autogamous crop species. Hanson (1959) suggested that 3 to 5 generations of intermating were necessary to establish linkage equilibrium before initiating

Table 2. Estimates of additive (σ_A^2) and dominance (σ_D^2) components of variance, their interactions (σ_{AE}^2 and σ_{DE}^2) with environments, experimental errors, and levels of dominance for six traits obtained from the Design III analysis pooled over sets and combined over environments for four maize populations.

Population	Generation	Trait	Variance component estimates				σ^2	Level of dominance
			σ_A^2	σ_{AE}^2	σ_D^2	σ_{DE}^2		
B73 × Mo17	F ₂	Yield (t ha ⁻¹) ^a	104.3 ± 30.8	17.1 ± 9.0	85.0 ± 23.0	13.9 ± 5.2	60.1 ± 2.8	1.28
	F ₂ Syn. 5		108.0 ± 32.6	17.6 ± 9.2	48.8 ± 14.2	2.3 ± 4.0	60.1 ± 2.8	0.95
	F ₂	Ear height (cm)	85.1 ± 22.9	2.9 ± 4.6	12.9 ± 4.3	-2.6 ± 2.0	38.3 ± 1.8	0.55
	F ₂ Syn. 5		127.1 ± 33.1	0.3 ± 4.2	14.7 ± 4.7	-4.4 ± 1.9	38.3 ± 1.8	0.48
	F ₂	Ear length (cm)	11.5 ± 3.4	1.4 ± 1.0	3.8 ± 1.3	1.4 ± 1.1	7.3 ± 0.3	0.81
	F ₂ Syn. 5		11.5 ± 3.5	1.3 ± 1.0	3.5 ± 1.0	0.6 ± 0.5	7.3 ± 0.3	0.78
	F ₂	Ear diameter (cm) ^a	3.4 ± 0.9	-0.1 ± 0.2	1.0 ± 0.3	0.0 ± 0.1	1.6 ± 0.1	0.78
	F ₂ Syn. 5		2.5 ± 0.7	-0.1 ± 0.2	0.6 ± 0.2	-0.1 ± 0.1	1.6 ± 0.1	0.72
	F ₂	Days to flower (no.)	26.2 ± 5.8	7.4 ± 3.6	4.7 ± 1.3	0.1 ± 1.2	14.3 ± 0.8	0.60**
	F ₂ Syn. 5		19.4 ± 3.8	-3.3 ± 3.3	3.0 ± 0.7	-4.5 ± 0.5	14.3 ± 0.8	0.56**
B73 × B84	F ₂	Kernels rows (no.) ^c	20.8 ± 3.4	-0.1 ± 0.3	0.8 ± 0.3 ^c	0.8 ± 0.4	3.3 ± 0.2	0.28**†
	F ₂ Syn. 5		6.0 ± 1.4	2.0 ± 1.8	0.1 ± 0.0	0.1 ± 0.0	3.3 ± 0.2	0.53*†
	F ₂	Yield (t ha ⁻¹) ^a	32.9 ± 11.6	-7.7 ± 5.3	38.3 ± 10.8	-4.6 ± 3.1	60.1 ± 2.8	1.53*
	F ₂ Syn. 5		55.4 ± 17.9	2.5 ± 6.8	10.7 ± 5.2	1.6 ± 3.8	60.1 ± 2.8	0.62*
	F ₂	Ear height (cm)	55.1 ± 15.9	1.2 ± 4.3	1.9 ± 3.0	9.0 ± 3.3	38.3 ± 1.8	0.26**
	F ₂ Syn. 5		45.8 ± 14.6	8.1 ± 5.3	3.2 ± 2.6	1.2 ± 2.4	38.3 ± 1.8	0.38**
	F ₂	Ear length (cm) ^b	6.2 ± 2.1	0.9 ± 0.9	1.9 ± 0.7	-0.6 ± 0.4	7.3 ± 0.3	0.78
	F ₂ Syn. 5		8.1 ± 2.6	1.1 ± 1.0	1.3 ± 0.6	-0.6 ± 0.4	7.3 ± 0.3	0.57**
	F ₂	Ear diameter (cm) ^a	0.7 ± 0.4	0.5 ± 0.2	0.4 ± 0.1	0.4 ± 0.1	1.6 ± 0.1	1.06
	F ₂ Syn. 5		1.5 ± 0.4	-0.2 ± 0.1	0.3 ± 0.1	-0.3 ± 0.1	1.6 ± 0.1	0.64*
F ₂	Days to flower (no.) ^b	6.0 ± 4.6	26.6 ± 13.3	1.8 ± 1.5	6.0 ± 2.1	14.3 ± 0.8	0.77	
F ₂ Syn. 5		12.5 ± 2.8	-3.1 ± 3.8	3.3 ± 0.9	-2.3 ± 0.8	14.3 ± 0.8	0.73	
F ₂	Kernel rows (no.) ^c	10.6 ± 2.0	1.1 ± 1.5	0.8 ± 0.3	0.7 ± 0.4	3.3 ± 0.2	0.38**	
F ₂ Syn. 5		9.1 ± 1.7	0.1 ± 1.1	0.3 ± 0.2	-0.3 ± 0.2	3.3 ± 0.2	0.27**	

^aEstimates were multiplied by 10².

^bEstimates were multiplied by 10.

^cDays from planting to 50% silk emergence.

* and ** indicate that levels of dominance were different from complete dominance at 0.01 and 0.05 probability levels, respectively.

† and § indicate that derivations from no dominance were different from no dominance at 0.01 and 0.05 probability levels, respectively.

Table 4. Estimates of additive (σ_A^2) and dominance (σ_D^2) variance components from S_1 and Design III combined analyses Pooled over sets and combined over environments for six traits for four maize populations.

Population	Trait	Component of variance estimates						σ_D^2/σ_A^2
		σ_A^2	σ_{AE}^2	σ_D^2	σ_{DE}^2	σ^2		
B73 × Mo17	F ₂	Yield (t ha ⁻¹) ^a	112.9±3.6	34.8± 9.2	85.5± 3.9	19.5± 9.6	48.6±10.3	0.76
	F ₂ Syn. 5		118.8±3.4	22.0± 8.3	49.5± 3.7	5.3± 9.2	52.2± 9.8	0.42
	F ₂	Ear height (cm)	69.6±6.0	-0.3±15.4	11.9± 6.5	-7.8±15.9	49.5±17.1	0.17
	F ₂ Syn. 5		102.2±9.2	-2.4±23.7	13.2±10.0	-11.5±24.5	54.2±26.3	0.13
	F ₂	Ear length (cm) ^b	15.1±1.5	3.2± 3.7	4.0± 1.6	2.4± 3.9	5.0± 4.2	0.26
	F ₂ Syn. 5		12.2±0.3	1.3± 0.7	3.6± 0.3	0.5± 0.7	7.3± 0.8	0.30
	F ₂	Ear diameter (cm) ^a	4.0±0.3	0.6± 0.8	1.1± 0.3	0.3± 0.8	1.0± 0.9	0.28
	F ₂ Syn. 5		1.4±0.4	-0.2± 1.1	0.6± 0.4	-0.4± 1.7	2.3± 1.2	0.43
	F ₂	Days to flower (no.) ^{bc}	11.6±0.2	3.5± 5.8	2.8± 2.4	-3.0± 6.1	20.9± 6.5	0.24
	F ₂ Syn. 5		13.1±2.8	12.0± 7.3	2.0± 3.1	-1.3± 7.5	9.4± 8.1	0.15
(B73 × B84)	F ₂	Kernels rows (no.) ^b	12.4±0.4	1.2± 1.1	0.5± 0.5	0.1± 1.1	3.9± 1.2	0.04
	F ₂ Syn. 5		3.7±0.4	-0.7± 1.0	0.5± 0.4	-0.1± 1.1	4.8± 1.2	0.14
	F ₂	Yield (t ha ⁻¹) ^a	51.4±8.1	7.5±20.8	39.4± 8.8	5.8±21.6	39.0±23.2	0.77
	F ₂ Syn. 5		35.0±7.5	8.2±19.3	9.5± 8.1	-1.1±20.0	67.1±21.5	0.27
	F ₂	Ear height (cm)	59.3±1.5	0.4± 3.8	2.2± 1.6	9.5± 3.9	36.9± 4.2	0.04
	F ₂ Syn. 5		46.4±1.7	-1.6± 4.4	3.3±1.8	-2.0± 4.5	43.7± 4.8	0.07
	F ₂	Ear length (cm) ^b	10.3±1.7	2.9± 4.3	2.0± 1.8	0.7± 4.4	4.6± 4.8	0.19
	F ₂ Syn. 5		8.8±0.3	1.1± 0.6	1.3± 0.3	-0.7± 0.7	7.4±0.7	0.15
	F ₂	Ear diameter (cm) ^a	1.0±0.1	0.1± 0.2	0.4± 0.1	0.3± 0.2	1.8± 0.2	0.40
	F ₂ Syn. 5		0.3±0.4	-0.4± 1.1	0.2± 0.5	-0.7± 1.2	2.4± 1.3	0.67
F ₂	Days to flower (no.) ^{bc}	6.1±3.2	-2.1± 8.4	1.3± 3.6	-0.9± 8.7	25.8± 9.4	0.21	
F ₂ Syn. 5		7.5±0.6	-2.1± 1.7	2.2± 0.7	-3.0± 1.7	16.1± 1.8	0.29	
F ₂	Kernel rows (no.) ^b	4.9±0.9	-0.2± 2.3	0.4± 1.0	-0.3± 2.4	5.4± 2.4	0.08	
F ₂ Syn. 5		5.5±2.5	0.0± 0.5	0.2± 0.2	-0.6± 0.5	3.9± 0.5	0.04	

^aEstimates were multiplied by 10².^bEstimates were multiplied by 10.^cDays from planting to 50% silk emergence.Table 5. Means and estimates of heterosis and inbreeding depression of six traits for inbred lines and their F₁, F₂ and F₃ generations measured in three environments.

Trait	Generations					I (%) ^b			Generations					I (%) ^b		
	B73	Mo17	F ₁	F ₂	F ₃	H (%) ^a	F ₂ /F ₁	F ₃ /F ₁	B73	B84	F ₁	F ₂	F ₃	H (%) ^a	F ₂ /F ₁	F ₃ /F ₁
Yield (t ha ⁻¹)	3.44	4.14	10.87	9.01	5.76	187	-17	-47	3.43	4.45	7.21	6.49	4.85	83	-10	-33
Ear height (cm)	98	87	109	110	90	17	2	-17	98	83	103	101	89	14	-2	-14
Ear length (cm)	12.3	13.5	20.8	17.3	16.0	61	-17	-23	12.3	17.4	18.2	15.1	14.3	23	-17	-21
Ear diameter (cm)	4.3	4.1	4.9	4.9	4.4	17	0	-10	4.3	3.6	4.4	4.5	4.4	11	2	0
Days to flower (no.) ^c	89	91	83	86	86	-8	4	4	89	89	86	87	88	-3	1	2
Kernel rows (no.)	19.7	14.2	15.3	17.6	14.6	-10	15	-5	19.7	11.1	14.7	16.9	16.4	1	15	12

^aH is heterosis estimate calculated as $(F_1 - \bar{P})\bar{P}^{-1} \times 100$ where \bar{P} is average of parent lines.MILLER, P. A., and J. O. RAWLINGS. 1967. Breakup of initial linkage blocks through intermating in a cotton breeding population. *Crop Sci.* 7:199-204.MORENO-GONZALEZ, M., and J. W. DUDLEY. 1981. Epistasis in related and unrelated maize hybrids determined by three methods. *Crop Sci.* 21:644-651.

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Table 3. Estimates of variance components among S_1 progenies ($\sigma_{S_1}^2$), their interactions with environments ($\sigma_{S_1E}^2$), and experimental error for six traits for four maize populations evaluated in three environments.

Population	Generation	Trait	Variance component estimates			h^2
			$\sigma_{S_1}^2$	$\sigma_{S_1E}^2$	σ^2	
B73 × Mo17	F ₂	Yield (t ha ⁻¹) ^a	136.4 ± 36.3	38.3 ± 10.7	50.1 ± 3.3	0.87 ± 0.23
	F ₂ Syn. 5		133.8 ± 35.3	21.6 ± 8.0	50.1 ± 3.3	0.90 ± 0.24
	F ₂	Ear height (cm)	68.7 ± 17.7	4.2 ± 4.2	39.8 ± 2.6	0.90 ± 0.23
	F ₂ Syn. 5		99.3 ± 25.4	5.2 ± 4.5	39.8 ± 2.6	0.92 ± 0.24
	F ₂	Ear length (cm)	17.0 ± 4.4	2.1 ± 1.0	8.1 ± 0.5	0.89 ± 0.21
	F ₂ Syn. 5		13.3 ± 3.5	1.0 ± 0.9	8.1 ± 0.5	0.89 ± 0.27
	F ₂	Ear diameter (cm) ^a	4.5 ± 1.1	-0.3 ± 0.2	1.8 ± 0.1	0.88 ± 0.22
	F ₂ Syn. 5		1.2 ± 0.4	0.4 ± 0.2	1.8 ± 0.1	0.74 ± 0.17
	F ₂	Days to flower (no.) ^{bc}	17.5 ± 3.6	4.0 ± 3.3	19.8 ± 1.6	0.72 ± 0.16
	F ₂ Syn. 5		20.5 ± 4.9	9.5 ± 4.6	19.8 ± 1.6	0.67 ± 0.17
	F ₂	Kernels rows (no.) ^b	18.3 ± 3.1	1.5 ± 0.8	4.2 ± 0.3	0.92 ± 0.15
	F ₂ Syn. 5		5.6 ± 1.0	0.8 ± 0.4	4.2 ± 0.3	0.80 ± 0.13
B73 × B84	F ₂	Yield (t ha ⁻¹) ^a	65.9 ± 17.3	2.9 ± 4.9	50.1 ± 3.3	0.88 ± 0.23
	F ₂ Syn. 5		32.3 ± 11.1	19.2 ± 7.5	50.1 ± 3.3	0.69 ± 0.24
	F ₂	Ear height (cm)	60.9 ± 15.6	0.6 ± 3.6	39.8 ± 2.6	0.90 ± 0.23
	F ₂ Syn. 5		47.3 ± 12.2	-2.2 ± 3.2	39.8 ± 2.6	0.88 ± 0.23
	F ₂	Ear length (cm) ^b	11.9 ± 3.1	1.1 ± 0.9	8.1 ± 0.5	0.88 ± 0.23
	F ₂ Syn. 5		9.3 ± 2.5	0.5 ± 1.1	8.1 ± 0.5	0.85 ± 0.23
	F ₂	Ear diameter (cm) ^a	1.2 ± 0.3	0.0 ± 0.2	1.8 ± 0.1	0.67 ± 0.20
	F ₂ Syn. 5		1.2 ± 0.3	-0.1 ± 0.1	1.8 ± 0.1	0.67 ± 0.20
	F ₂	Days to flower (no.) ^{bc}	10.5 ± 2.1	-3.6 ± 1.6	19.8 ± 1.6	0.67 ± 0.19
	F ₂ Syn. 5		11.8 ± 2.3	-4.1 ± 1.6	19.8 ± 0.19	0.70 ± 0.19
	F ₂	Kernel rows (no.) ^b	6.6 ± 1.2	-0.5 ± 0.6	4.2 ± 0.3	0.88 ± 0.15
	F ₂ Syn. 5		8.2 ± 1.4	-0.2 ± 0.5	4.2 ± 0.3	0.89 ± 0.16

^aEstimates were multiplied by 10².

^bEstimates were multiplied by 10.

^cDays from planting to 50% silk emergence.

^d $\sigma_{S_1}^2$ has an expected value of $\sigma_A^2 + (1/4)\sigma_D^2$ for allele frequency of 0.05.

^e h^2 is the heritability estimate for S_1 progenies calculated as $\sigma_{S_1}^2 / (\sigma_{S_1E}^2/e + \sigma_{S_1}^2)$.

selection. Inter-mating followed by selection could increase the chances of obtaining useful recombinants compared with selection without inter-mating. Empirical studies in cotton (*Gossypium hirsutum* L.) tobacco (*Nicotiana tabacum* L.), sorghum [*Sorghum bicolor* (L.) Moench], and wheat (*Triticum aestivum* L.) suggested that increased genetic recombination resulted from random inter-mating (Miller and Rawlings, 1967; Humphrey et al., 1969; Meredith and Bridge, 1971; Verna et al., 1979; Yunus and Paroda, 1982; Nordquist et al., 1973). Altman and Busch (1984), however, concluded from a study in spring wheat that the benefits of recombination were inadequate to justify random inter-mating of F_2 populations of single crosses as a primary breeding procedure before selection. Similar studies have not been reported in allogamous crop species except to determine the linkage biases in the estimation of average levels of dominance of genes controlling the expression of quantitative traits (Hallauer and Miranda, 1981).

Random inter-mating within two F_2 maize-populations included in our study agree with theoretical conclusions for autogamous crop species. Although the two F_2 populations were developed from lines based on level of genetic relationships, the effects of random inter-mating were similar; random mating did not increase genetic variability. Linkage effects, both coupling and repulsion, were evident in the F_2 populations because the estimates of average levels of dominance generally were reduced after five generations of random inter-mating.

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