Estimation of genetic variability in two maize populations

ABSTRACT: Reciprocal full-sib selection (FR) for yield improvement was conducted in the BS10 and BS11 maize (*Zea mays* L.) populations. Our objectives were to evaluate the effects of six cycles of reciprocal full-sib selection in BS10 and BS11 and to determine what changes had occurred in the magnitudes of additive and dominance variance resulting from six cycles of selection. Grain yield of full-sib progenies increased 6.3 percent in BS10 and 5.7 percent in BS11 from C0 to C6. Grain yield of S_1 lines increased 11.6 percent in BS10 and 26.3 percent in BS11 from C0 to C6. Estimates of additive genetic variance suggested a decrease from the C0 to C6 of BS10 and BS11 for yield and stalk lodging and an increase for ears per plant from BS10C0 to BS10 (FR) C6. Estimates of dominance variance generally increased, but decreases were observed for yield and stalk lodging in BS11. The changes in the estimates of genetic variances suggest genetic variability was reduced with selection but most of the changes were small and statistically nonsignificant.

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SYSTEMATIC GENETIC improvement of maize (*Zea mays* L.) requires development and improvement of basic breeding populations and extraction of inbred lines and hybrids from the improved populations. Reciprocal full-sib selection is a cyclical breeding method combining both these requirements. The method originally was proposed as a means of developing single-cross hybrids by selecting among and within interpopulation full-sib families to emphasize selection for specific combining ability[4]. Selected lines, when tested as pairs, showed high specific combining ability with their tested mates and also high general combining ability with other selected lines[11].

Hallauer and Eberhart[8] suggested a modification to the single-cross development phase that incorporated population improvement. Both the single-cross development and population improvement phases of reciprocal full-sib selection have been shown to be effective[4,5,7,13].

Our objectives were to evaluate the effects of six cycles of reciprocal full-sib selection in BS10 and BS11 and to determine if changes occurred in the estimates of additive and dominance variances after six cycles of selection.

Materials and Methods

Four maize populations [BS10C0, BS10(FR)C6, BS11C0, and BS11(FR)C6] were evaluated. BS10(FR)C6 and BS11(FR)C6 were developed by six cycles of reciprocal full-sib selection BS10C0 and BS11C0, which was described by Hallauer[4] and Hallauer and Eberhart[8].

Progenies for evaluation in this study were developed within each of the four populations by making reciprocal crosses between randomly chosen pairs of prolific plants. The crosses were made on one ear, and the second ear was self-pollinated. Seed of reciprocal crosses were bulked. Thus, there were twice as many S_1 lines as full-sib families. Within each population, progenies from 50 crosses were evaluated. Thus, 200 full-sib families and 400 S_1 lines were included in this study.

The 600 entries were evaluated in experiments conducted near Ames and Kanawha, Iowa, in 1983 and 1984 (four environments). Each entry was machine-planted in single-row plots 5.44 m long spaced 76.2 cm. All plots were overplanted and later thinned to plant densities of 45 450 and 50 230 plants ha^{-1} in 1983 and 1984, respectively. All plots were hand-harvested with gleaning of dropped ears and ears on broken stalks. Ears were dried to a uniform moisture level of 6 percent and stored for subsequent shelling and yield determinations.

Data were collected on grain yield, number of ears per plant, percentage of root and stalk lodging, plant and ear height, date of 50 percent silking, and tassel branch number.

Because the results were similar for root and stalk lodging and for plant and ear height, the results for root lodging and plant height were not included. Yield was measured in grams plot^{-1} and converted to t ha^{-1} (tons per hectare) for data analysis. Yield and number of ears per plant were measured in all four environments. Stalk lodging was measured during the week before harvest as the number of plants per plot with stalks broken at or below the top ear node and expressed as a percentage of total plants per plot. Percentage of stalk lodging was recorded in the experiments conducted near Kanawha in 1984 and near Ames in 1983 and 1984. Date of 50 percent silking was recorded in the experiments conducted near Ames in 1983 and 1984 as the number of days after planting that 50 percent of the plants in a plot had exposed silk.

The experimental design used in each environment was a modified split plot, with whole plots arranged in incomplete blocks. In the split-plot analysis, the two inbreeding levels, full-sib families or S_1 lines, were whole-plot treatments, and subplot treatments were entries nested within inbreeding levels. This design was used to group entries to avoid competitive effects of different levels of inbreeding.

The experiment grown in each environment was divided into 10 incomplete blocks, herein referred to as sets, with two replications within each set. One replication of a set included 60 of the 600 entries for an experiment. The 60 entries within each set included 5 full-sib families from BS10C0, BS10(FR)C6, BS11C0, and BS11(FR)C6, and 10 S_1 lines from the same parents as the full-sib families. In each replication of each set, entries were randomized within whole

plots, and whole plots were randomized within replications and sets.

Analyses of variance were performed separately for full-sib families and S_1 lines to partition sums of squares due to genotypes within inbreeding levels, interactions between genotypes within inbreeding levels and environments, and experimental error into components due to full-sib families and S_1 lines. The variation among full-sib families and S_1 lines was partitioned to obtain sums of squares attributable to genotypes within the four populations and comparisons between populations. The effects of environments, sets, replications, and genotypes were considered random, and the effects of inbreeding levels were considered fixed.

The ratio of the larger component of experimental error to the smaller component was compared with tabulated values of the F-ratio with numerator and denominator degrees of freedom corresponding to the degrees of freedom of the appropriate components of the experimental error. When the calculated ratio exceeded the tabulated F-value, the components of experimental error due to either full-sib families or S_1 lines were used as separate estimates of experimental error. Otherwise, estimates of full-sib family and S_1 line experimental error were pooled.

Analyses of covariance between full-sib families and S_1 lines, pooled over sets and combined over environments were calculated. Plot values for each full-sib family and the mean of the two S_1 lines from the parents of that full-sib family were treated as covariates. Sums of cross products due to genotypes within sets were partitioned in the same manner as those sources of variation in combined analyses of variance.

Components of variance and covariance

were estimated by solving the set of simultaneous linear equations that resulted from equating the observed values of mean squares and mean products with their expectations. Standard errors of estimates of variance and covariance components were calculated by using the procedures described by Anderson and Bancroft[1] and Mode and Robinson[15].

Additive and dominance variances and their interactions with environments were estimated within BS10C0, BS10(FR)C6, BS11C0, and BS11(FR)C6. Estimates of genetic parameters were obtained by solving the set of simultaneous linear equations that resulted from equating the observed values of genetic and genotype × environment components of variance and covariance with their genetic expectations. The method of weighted least squares was used to correct for unequal variances of the components.

Results and Discussion

Environmental conditions during 1983 and 1984 were generally good for maize production. A wet, cool spring provided excellent early growth in 1983. Despite severe heat and drought stress encountered during silking and pollination, particularly in the experiment conducted near Ames, overall mean grain yields of 4.40 and 4.51 t ha^{-1} were obtained in the experiments conducted in 1983 near Kanawha and Ames, respectively. Coefficients of variation for grain yield averaged 14.3 percent for the two experiments conducted near Kanawha and 13.7 percent for the two experiments conducted near Ames.

Analyses of variance, pooled over sets and combined over environments (not shown), in-

Table I. Population means, standard errors (SE), LSDs, coefficients of variation (CV) for six traits of the C0 and C6 populations of BS10 and BS11

Family type	Trait	Population and cycle means				SE	LSD (0.05)	CV (%)
		BS10C0	BS10(FR)C6	BS11C0	BS11(FR)C6			
Full-sib								
	Yield (t ha^{-1})	5.42	5.76	5.60	5.92	0.04	0.12	13.7
	Ears per plant (no.)	1.03	1.17	1.08	1.21	0.01	0.02	109.7
	Ear height (cm)	114.2	113.5	132.6	121.8	0.48	1.34	8.0
	Stalk lodging (%)	38.8	27.2	39.6	30.6	0.78	2.16	39.4
	Days-to-50%-silking (no.)	75.3	75.2	78.8	76.8	0.08	0.23	1.8
	Tassel branches (no.)	17.6	18.5	22.1	17.2	0.14	0.38	12.2
S_1								
	Yield (t ha^{-1})	3.79	4.23	3.39	4.28	0.03	0.07	16.1
	Ears per plant (no.)	1.00	1.20	1.02	1.24	0.01	0.02	132.4
	Ear height (cm)	99.1	101.8	113.7	104.8	0.29	0.80	7.6
	Stalk lodging (%)	33.1	24.5	32.9	24.8	0.61	1.70	45.2
	Days-to-50%-silking (no.)	77.7	77.5	81.3	78.8	0.07	0.19	2.1
	Tassel branches (no.)	16.2	16.6	19.6	15.8	0.09	0.25	13.5

dicated that effects of inbreeding levels were significant ($P \leq 0.05$) for percentage of stalk lodging and highly significant ($P \leq 0.01$) for grain yield. A highly significant inbreeding levels × environments interaction was detected for grain yield, indicating inconsistencies in performance of the two inbreeding levels over environments.

Mean grain yield of BS10 and BS11 increased significantly from the C0 to C6 when either full-sib families or S_1 lines were evaluated (Table I). Population means of full-sib families increased 6.3 percent in BS10 and 5.7 percent in BS11 from the C0 to the C6. The observed increase in mean grain yield of the S_1 lines from C0 to C6 was 11.6 percent for BS10 and 26.3 percent for BS11. Observed gains in grain yield were less than those reported in BS10 and BS11 by Hallauer[5]. Discrepancies in response to selection between studies may be the result of either sampling errors or genotype by environment interaction.

No conclusive evidence of inadequate sampling of reference populations or decreased genetic variability was obtained in this study. Inbreeding depression may have played a role in the limited response to selection observed. By assuming that effective population size was approximately the same as the number of lines recombined, coefficients of inbreeding of BS10(FR)C6 and BS11(FR)C6 were estimated to be 0.137 and 0.143, respectively. From multiplying these values by the decrease in grain yield per 1 percent increase in the coefficient of inbreeding calculated from the C0 data in Table I, the expected decrease in grain yield due to inbreeding depression would be 0.46 t ha^{-1} in BS10(FR)C6 and 0.63 t ha^{-1} in BS11(FR)C6.

Differences between grain yield of S_1 lines in BS10 and BS11 and between cycles (C0 vs. C6) were significant in all instances (Figure 1). Reciprocal full-sib selection was effective in increasing mean S_1 line yield of both populations. Variability among S_1 lines, however, was significantly reduced in BS10 [66 ± 11 for BS10 vs. 33 ± 6 for BS10(FR)C6] and indicated that the same trend was occurring in BS11 [57 ± 6 for BS11C0 vs. 42 ± 7 for BS11(FR)C6].

Reciprocal full-sib selection, as practiced in BS10 and BS11, provides indirect selection pressure for prolificacy in addition to direct selection pressure for yield. Indirect selection was effective in increasing the population mean of ears per plant in both BS10 and BS11 (Table I). Ears per plant increased 13.6 percent in BS10 and 12.0 percent in BS11 from C0 to C6 for the full-sib families. For populations evaluated as S_1 lines, there

was a 20.0 percent increase in ears per plant from C0 to C6 of BS10 and a 21.6 percent increase from C0 to C6 of BS11.

Decreases in population means of percentage of stalk lodging were observed in both populations at both inbreeding levels. From the C0 to C6 of BS10, stalk lodging decreased from 38.8 to 27.2 percent among full-sib progenies and from 33.1 to 24.5 percent among S_1 progenies (Table I). In BS11, population means for stalk lodging decreased from 39.6 to 30.6 percent among full-sib families and from 32.9 to 24.8 percent among S_1 lines. Resistance to stalk lodging was im-
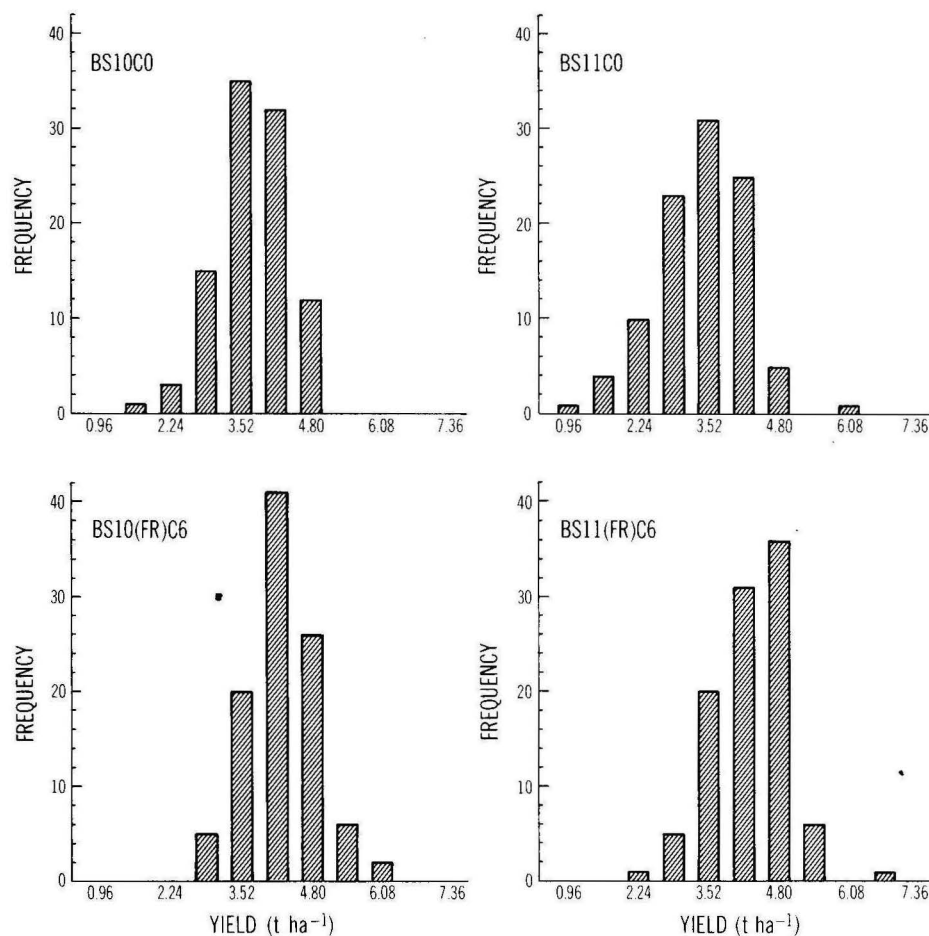

FIGURE 1 Frequency distributions of S_1 progenies for the BS10C0, BS10(FR)C6, BS11C0, and BS11(FR)C6 populations evaluated in two replications at four environments.

Table II. Inbreeding depression expressed as the reduction in the S_1 generation mean as a percentage of the S_0 generation mean, averaged over trials in 1983 and 1984

Trait	Populations and cycles			
	BS10C0	BS10(FR)C6	BS11C0	BS11(FR)C6
	%			
Yield (t ha^{-1})	30.1	26.6	39.5	27.7**
Ears per plant (no.)	2.9	−2.6	5.6	−2.5
Ear height (cm)	13.2	10.1*	14.2	13.9
Stalk lodging (%)	14.9	9.9	16.9	19.4
Days-to-50%-silking (no.)	−8.9	−8.6	−8.4	−7.0*
Tassel branches (no.)	8.3	10.4	11.5	8.4*

*, ** Significant differences between estimates of inbreeding depression in the C0 and C6 populations within BS10 or BS11 at the 0.05 and 0.01 probability levels, respectively

proved because of selection among full-sib progenies and the implementation, after the first cycle of selection, of machine harvesting of yield trials. Population means for percentage of stalk lodging in BS10 and BS11 seemed higher than in many single-eared populations, which is consistent with the photosynthetic stress-translocation balance hypothesis proposed by Dodd[2].

Days-to-silk of the full-sib families and S_1 lines were unchanged in response to reciprocal full-sib selection in BS10. Significant decreases in number of days-to-silk were observed among progeny types from BS11C0 to BS11(FR)C6, with full-sib families decreasing by 6.3 percent and S_1 lines decreasing by 7.5 percent. The reduction in number of days-to-silk from BS11C0 to BS11(FR)C6 resulted from nicking between the earliest plants in BS11 and a more representative sample of plants from BS10 when reciprocal full-sib progenies were developed for testing.

Observed inbreeding depression after one generation of self-pollination was less for the C6 populations than for the C0 populations (Table II). The values are the reduction in the mean of the S_1 generation expressed as a percentage of the S_0 (full-sib) generation mean. A highly significant reduction in inbreeding depression for grain yield was found between BS11C0 and BS11(FR)C6. The C6 population of BS11 showed 29.8 percent less inbreeding depression that the C0 population. An 11.7 percent reduction in inbreeding depression for grain yield was detected between BS10C0 and BS10(FR)C6. However,

the difference between inbreeding depression in the C0 and C6 populations of BS10 was not significant for grain yield. Reciprocal full-sib selection was effective for increasing the frequency of favorable alleles for the traits evaluated. Negative values of inbreeding depression were obtained for ears per plant and date of silking because S_1 line means were greater than means of full-sib families. Greater prolificacy after inbreeding also has been reported in the C0 and C4 populations of BS10 and BS11[13] and in Iowa Stiff Stalk Synthetic[3]. Harris et al.[10] concluded that the potential for prolificacy was conditioned by recessive alleles. Hallauer[6] indicated that prolificacy fit the description of a threshold trait because environmental and genetic effects seem to be continuous, whereas phenotypic expression was discrete.

Estimates of σ_A^2 were significantly greater than zero (exceeding twice the standard error) in all populations for all traits (Table III). No estimate of σ_D^2 was greater than twice its standard error, and these estimates were generally substantially smaller than estimates of σ_A^2. However, estimates of σ_D^2 were greater than estimates of σ_A^2 for grain yield in BS10C0 and BS10(FR)C6. The estimate of σ_{AE}^2 was significantly greater than zero for percentage of stalk lodging, and the estimate of σ_{DE}^2 was significantly greater than zero for silk date in BS10C0. The estimate of σ_{DE}^2 for ears per plant was significantly less than zero for ears per plant in BS10C0. The magnitude of the estimates of σ_A^2 was similar to those reported for other populations adapted to the

U.S. Corn Belt, but the estimates of σ_D^2 tended to be greater[9].

Nearly 21 percent of the estimates of σ_D^2, σ_{AE}^2, and σ_{DE}^2 were negative, and one negative estimate was significantly different from zero. By definition, a variance component is always positive. However, Searle[17] indicated that there is nothing intrinsic to the analysis of variance to prevent negative estimates of variance components from occurring. Negative estimates of variance components can arise because of several factors, including inadequate genetic or statistical models, inadequate sampling of reference populations, sampling errors in estimation, and poor experimental techniques. Assortative mating may have occurred during the development of experimental progenies relative to time of flowering. High frequencies of negative estimates of σ_D^2 in two maize populations were reported by Lindsey et al.[14]. They attributed the occurrence of negative estimates to assortative mating during the development of experimental progenies and obtained evidence supporting this hypothesis.

Inadequate sampling of the reference populations may have played a role in negative estimates of variance components obtained in this study. Kearsey[12] studied the size of experiments necessary to detect dominance variance and concluded that, in most situations, the minimum experimental size required was too large to make comparisons among populations practical.

Means and coefficients of variation indicated that experimental techniques used in

Table III. Weighted least squares estimates of additive ($\hat{\sigma}_A^2$), dominance ($\hat{\sigma}_D^2$), additive × environments ($\hat{\sigma}_{AE}^2$), and dominance × environments ($\hat{\sigma}_{DE}^2$) components of variance and their standard errors in the C0 and C6 populations of BS10 and BS11

| Component | Populations and cycles | Trait | | | | | |
		yield t ha^{-1}	no. ears per plant	ear height (cm)	% stalk lodging	no. days to 50% silking	no. tassel branches
$\hat{\sigma}_A^2$	BS10C0	23.7 ± 11.5	0.75 ± 0.18	132.2 ± 29.4	120.8 ± 42.4	4.2 ± 1.2	11.1 ± 2.8
	BS10(FR)C6	17.7 ± 8.8	2.88 ± 0.68	102.6 ± 29.4	91.3 ± 38.0	3.9 ± 0.9	9.7 ± 2.4
	BS11C0	45.8 ± 14.2	2.53 ± 0.61	185.6 ± 55.7	104.6 ± 38.5	6.0 ± 1.7	12.3 ± 3.3
	BS11(FR)C6	29.8 ± 9.7	1.88 ± 0.52	112.5 ± 39.8	81.7 ± 28.9	6.6 ± 1.6	4.0 ± 1.8
$\hat{\sigma}_D^2$	BS10C0	47.8 ± 33.5	−0.74 ± 0.44	−82.5 ± 94.2	31.1 ± 114.2	1.5 ± 4.3	0.4 ± 9.2
	BS10(FR)C6	49.1 ± 31.4	0.15 ± 2.09	20.3 ± 102.1	47.2 ± 137.7	−1.1 ± 2.9	−4.1 ± 8.0
	BS11C0	35.6 ± 48.9	−0.61 ± 1.72	65.0 ± 201.8	99.2 ± 130.4	1.0 ± 5.9	−0.6 ± 11.0
	BS11(FR)C6	17.6 ± 31.9	0.27 ± 1.60	104.9 ± 148.5	25.4 ± 93.0	0.5 ± 5.5	5.4 ± 6.6
$\hat{\sigma}_{AE}^2$	BS10C0	5.2 ± 5.0	0.07 ± 0.11	1.7 ± 12.7	83.7 ± 29.8	−0.66 ± 0.43	−0.6 ± 0.8
	BS10(FR)C6	−0.3 ± 5.0	0.24 ± 0.18	8.5 ± 11.6	53.9 ± 28.7	−0.34 ± 0.35	0.7 ± 1.1
	BS11C0	2.6 ± 5.7	0.41 ± 0.22	10.9 ± 12.2	39.2 ± 22.4	0.48 ± 0.50	−0.4 ± 1.3
	BS11(FR)C6	2.1 ± 5.6	0.28 ± 0.25	6.1 ± 10.4	35.9 ± 21.7	0.04 ± 0.27	0.3 ± 0.6
$\hat{\sigma}_{DE}^2$	BS10C0	7.2 ± 19.3	−1.41 ± 0.36	5.3 ± 51.2	2.8 ± 109.3	3.56 ± 1.51	1.1 ± 3.3
	BS10(FR)C6	20.7 ± 20.0	0.07 ± 0.62	−15.6 ± 45.8	74.5 ± 107.5	1.31 ± 1.32	0.6 ± 4.4
	BS11C0	29.8 ± 22.4	0.71 ± 0.75	−8.5 ± 47.3	−10.4 ± 83.2	1.26 ± 1.65	7.9 ± 5.0
	BS11(FR)C6	22.5 ± 22.6	1.61 ± 0.89	−28.0 ± 41.4	−19.1 ± 81.3	−1.10 ± 0.99	−4.0 ± 2.2

this study were good. However, the restricted randomization used to avoid competition between full-sib families and S_1 lines may have influenced the occurrence of negative estimates of variance components. Nelder[16] indicated that, with split-plot designs, negative estimates of variance components could arise when the correlation between subplots in the same whole plot is less than the correlation between subplots in different whole plots.

The magnitudes of total estimated genetic variance, $\hat{\sigma}^2_A$ and $\hat{\sigma}^2_D$, are functions of gene frequencies, and the magnitudes of genetic variances are expected to change in response to selection. Changes in genetic variability are influenced by several factors, including selection intensity, initial amounts of actual and potential variability, linkage disequilibrium, and rates of recombination[9].

For most traits evaluated in this study, estimates of σ^2_A showed some decrease in magnitude from the C0 to C6 populations of BS10 and BS11. However, the magnitude of $\hat{\sigma}^2_A$ for ears per plant increased from BS10C0 to BS10(FR)C6. Generally, estimates of σ^2_D tended to increase in magnitude from the C0 to C6 of BS10 and BS11. Decreases in the magnitude of $\hat{\sigma}^2_D$ were observed for grain yield and percentage of stalk lodging from BS11C0 to BS11(FR)C6. Because the 95 percent confidence intervals of estimates of variance components from the C0 and C6 overlapped in many instances, seeming changes in magnitudes of genetic components of variance may have been the results of sampling. If changes in genetic variances

have occurred, they were small. Although the response to reciprocal full-sib selection in BS10 and BS11 has been positive, the changes in gene frequency were not great enough to affect the relative magnitude of the genetic components of variance and the relative proportions of $\hat{\sigma}^2_A$ and $\hat{\sigma}^2_D$ in BS10 and BS11.

Reciprocal full-sib selection was designed to improve the cross performance of BS10 and BS11 with emphasis on grain yield. Continued improvement is dependent on the genetic variance within each of the populations. Response to reciprocal full-sib selection has been realized, both in the population crosses (direct response) and the populations themselves (indirect response)[7]. Although the differences in the estimates of σ^2_A between C0 and C6 of BS10 and BS11 were not significantly different, there were trends that suggested that the genetic variability was less in the C6 than in the C0 populations (Table III). The same trends were observed in the variation among full-sib (16 for C0 vs. 18 for C6 of BS10, and 30 for C0 vs. 14 for C6 of BS11) and S_1 (66 for C0 vs. 33 for C6 of BS10, and 57 for C0 vs. 42 for C6 of BS11) progenies. The evidence suggests that genetic variability was reduced after six cycles of reciprocal full-sib selection.

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