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## Response to Reciprocal Full-sib and Mass Selection in Corn (*Zea mays* L.)<sup>1</sup>

M. M. LANTIN and A. R. HALLAUER<sup>2</sup>

Responses to mass selection for number of ears per plant and reciprocal full-sib selection for grain yield in 2 synthetic varieties of corn (*Zea mays* L.) were determined. Ten cycles of mass selection were effective for increasing number of ears per plant, but no correlated response for grain yield improvement was realized. Reciprocal full-sib selection was effective in increasing grain yield of the 2 parental varieties and their cross and in increasing number of ears per plant. No evidence was obtained that indicated genetic variability decreased in the parent varieties after 4 cycles of reciprocal full-sib selection or after 5 cycles of selection for the interpopulation full-sib crosses. Reciprocal full-sib selection was more effective than mass selection for improvement of other agronomic traits.

INDEX DESCRIPTORS: *Zea Mays* L., maize, mass selection, reciprocal full-sib selection, recurrent selection.

Pedigree breeding methods in developing corn (*Zea mays* L.) lines and hybrids were described by Shull (1908, 1909) and were the primary methods used for deriving lines from the original landrace varieties. Subsequently, pedigree breeding methods were used in F<sub>2</sub> populations produced from crosses of elite lines, originally derived from the landrace varieties. This breeding method is generally referred to as recycling because the objective is to derive lines that include the desirable traits of each parent or to correct specific weaknesses of the original parents (Anonymous, 1980). Sequential pedigree breeding has been successful in developing lines and hybrids that have improved stalks, stronger roots, and greater resistance to pests (Duvick, 1977). The major disadvantages of the pedigree method of recycling lines are the restricted genetic base of the breeding materials and the time between cycles of recombination.

For the past 40 years, breeding methods, designated as recurrent selection, have been proposed for increasing the genetic base of materials included in breeding programs. These methods are useful for improvement of landrace varieties, for improvement of synthetic varieties formed by intermating elite lines, and for adaptation of exotic germplasm. Recurrent selection methods usually are used to improve broad, genetic-base populations for quantitatively inherited traits.

Recurrent selection methods include 3 phases that are conducted in a repetitive manner: development of progenies, evaluation of progenies in replicated trials, and recombination of superior progenies (based on evaluation trials) to form the next cycle population for continued selection (Fig. 1). Objectives of recurrent selection are: 1) to improve the mean performance of the breeding population by increasing the frequency of favorable alleles; and 2) to maintain genetic variability within the breeding population for future selection, which is accomplished by recombination of superior progenies before another cycle of selection is initiated. Because recurrent selection is conducted for quantitative traits, the change in gene frequency from cycle to cycle is expected to be small. Hence, recurrent selection needs to be conducted on a continuing basis to increase gradually the frequency of favorable alleles. Although recurrent selection methods have been advocated for corn improvement, they have not been widely accepted because of the seemingly slow rate of progress and the lack of direct contribution to line development.

Recurrent selection, however, can be adapted for applied breeding programs since improved breeding populations are the foundations for

insuring systematic future genetic advances. Integration of recurrent selection methods with other phases of applied breeding will provide source populations in which pedigree selection can be used for the extraction of new lines. Although the objectives of recurrent selection and pedigree selection are different, they are not independent; one supplements the other. Recycling of lines from use of pedigree selection methods is a form of recurrent selection in populations having a restricted genetic base, longer cycle intervals (8-13 years), and inbreeding is emphasized (Fig. 1). In contrast, recurrent selection methods usually are imposed on populations having a greater genetic base, shorter cycle intervals (2 to 4 years), and minimal inbreeding. Although the 2 methods have different objectives, each can be effectively used for the extraction of improved lines for use in hybrids.

Reciprocal full-sib selection and mass selection are being conducted in two synthetic varieties (BS10 and BS11) adapted to central Iowa. Reciprocal full-sib selection is amenable for improvement of the population cross and for extraction of lines in each cycle of selection; mass selection, however, is limited to improvement of the populations *per se*. Yield improvement was emphasized with reciprocal full-sib selection, and selection for number of ears per plant was emphasized with mass selection. Objectives of our study were to evaluate the response to reciprocal full-sib and mass selection for population improvement, to determine if genetic variability was reduced after four cycles of reciprocal full-sib selection, and to estimate correlated responses for the 2 selection methods. The studies were conducted to show that recurrent selection methods can be used to supplement the traditional pedigree breeding methods.

### MATERIALS AND METHODS

Reciprocal full-sib selection (FR) was initiated in BS10 and BS11 in 1963 with grain yield as the primary trait of selection (Hallauer, 1967). Reciprocal full-sib selection procedures are similar to those described by Comstock et al. (1949) for reciprocal recurrent selection except full-sib progenies rather than half-sib progenies are evaluated. Reciprocal full-sib selection was developed to integrate the features of reciprocal recurrent selection with line development necessary for applied breeding programs (Hallauer and Eberhart, 1970). As originally proposed, reciprocal full-sib selection required populations that produced seed on two ears of individual plants. Modifications, however, can be made to conduct reciprocal full-sib selection with populations that include plants that produce seed on only one ear per plant (Hallauer, 1973).

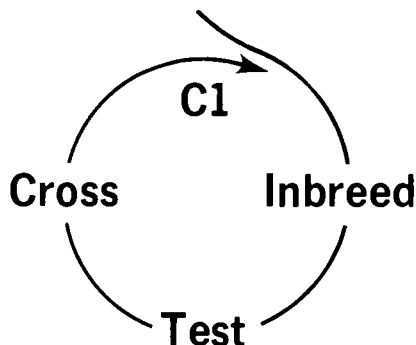
The BS10 and BS11 populations include plants that produce seed on 2 ears per plant. Plants of each population were planted in alternate rows in the breeding nursery where plant-to-plant crosses (full-sib progenies) and selfed progenies of each plant included in the crosses were made (Hallauer, 1967). Full-sib progenies were evaluated in replicated yield trials to determine which progenies to recombine to form the next cycle of selection; this phase of selection was for the

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### PEDIGREE SELECTION

Population C0  
(Narrow-genetic base, e.g., F<sub>2</sub>)



### RECURRENT SELECTION

Population C0  
(Broad-genetic base; e.g., variety)

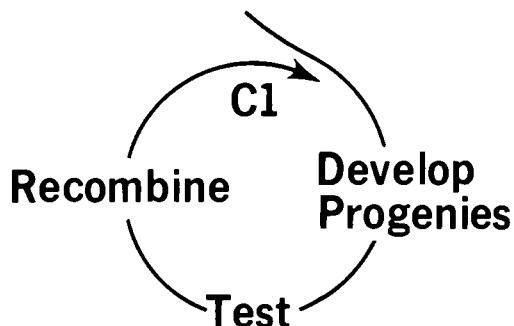


Fig. 1. Sequence of breeding methods for pedigree and recurrent selection.

improvement of the population cross. Selfed progenies of the superior full-sib progenies were included in the breeding nurseries for additional inbreeding, crossing, and testing for the development of new lines with superior performance in hybrids. If winter nurseries are available, one cycle of reciprocal full-sib selection can be completed in 2 years. Reciprocal full-sib selection for population improvement is conducted independently from the line development phase, but each cycle of reciprocal full-sib selection generates a new set of lines for the breeding nursery. Hence, reciprocal full-sib selection combines the long-term objectives of population improvement with the short-term objectives of line development. Four cycles of reciprocal full-sib selection in BS10

and BS11 were completed in 1977. Trials to evaluate response to reciprocal full-sib selection included 15 entries: C0, C1, C2, C3, and C4 cycles of BS10 and BS11 and the population crosses between each of the cycle populations.

In addition to reciprocal full-sib selection, mass selection (M) for increased ears per plant also was conducted in BS10 and BS11. Methods of selection within each isolation planting of BS10 and BS11 were similar to those described by Gardner (1961). Each population was grown in isolation, with a plant density of 49,000 plants per hectare. At the time of selection, each isolation field was subdivided into about 100 40-plant subplots of competitive standing plants. Final selection included 3 ears from each subplot for a selection intensity of 7.5%. Equal quantities of seed were saved from each ear, and 2 bulk samples were formed; the first was for planting the next cycle of selection, and the second was put in cold storage for future use. Ten cycles of mass selection were completed by 1976. In 1976, seed of the C2, C4, C6, C8, and C9 cycles (cycle 10 was lost in 1975) of mass selection were planted in the nurseries for seed increase and to produce the cycle crosses of BS10 and BS11. Cycle 10 of BS10 and BS11 was obtained from 1976 mass selection fields and included in the evaluation trials. The mass selection phase also included 15 entries.

Experiments that included 30 entries were conducted at 5 Iowa locations (Kanawha, Ames Research Center, Ames Atomic Energy Farm, Nashua, and Martinsburg) in 1978 and 3 (Nashua, Ames, and Ankeny) in 1979. Experimental design was a randomized complete block with 3 replications at each location. Two-row plots 5.1 m long and spaced 76 cm were used at all locations except one (Martinsburg), at which rows were spaced 96 cm. Data were obtained at each location on each plot for grain yield, ears per plant, percentage of root (leaning more than 30° from vertical) and stalk (breakage below ear) lodging, dropped ears (ears not retained on plants at harvest), and stand (plants per plot converted to plants per hectare). Days from planting to mid-silk were recorded at three locations (two locations in 1978 and one in 1979). All plots were overplanted and thinned to a final stand of 44,000 plants per hectare. The 1979 Ankeny experiment was discarded before harvest because of wind damage and poor plant development. Hence, data were available for 7 experiments. Analyses of variance were conducted on plot means for each experiment and combined over experiments. In the combined analyses, sums of squares for the 30 entries were partitioned into three groups: 1) response of BS10 to reciprocal full-sib and mass selection; 2) response of BS11 to reciprocal full-sib and mass selection; and 3) response of BS10 and BS11 population crosses to reciprocal full-sib and mass selection. Linear and quadratic (where appropriate) regression coefficients were estimated for each group of entries for response to reciprocal full-sib and mass selection.

Evaluation trials to determine if there was a change in genetic variability after 4 cycles of reciprocal full-sib selection included 400 unselected S<sub>1</sub> lines; 100 from each of BS10C0, BS10C4, BS11C0, and BS11C4 populations. Unselected S<sub>0</sub> plants of the original (C0) and improved (C4) populations of BS10 and BS11 were selfed in 1977. The 400 S<sub>1</sub> lines were grown at 2 locations (Kanawha and Ames Research Center) in 1978 and 1979. The 400 S<sub>1</sub> lines were partitioned into 10 sets of 40 lines. Each set included 10 entries of the 2 C0 and C4 populations replicated twice. Lines were randomized within each population and populations randomized within each replication. One-row plots 5.0 m long and spaced 76 cm were used at each location. All plots were overplanted and thinned to a final stand of 44,000 plants per hectare. Data were collected on all plots at all locations for grain yield, stand, and ears per plant. Days from planting to mid-silk were recorded on all plots in 1978 and 1979 at the Ames Research Center.

Analyses of variance were conducted on plot means for each experiment and combined over experiments for each trait. Table 1 includes the partitioning of the sources of variation among S<sub>1</sub> lines for each

Table 1. Analysis of variance for 100 S<sub>1</sub> lines for the C0 and C4 populations of BS10 and BS11 combined over experiments.

Source	df	E(MS)
Experiments (E)	3	
Sets (S)	9	
E × S	27	
Replications/S/E	40	
Lines/S	390	$\hat{\sigma}^2 + 2\hat{\sigma}_{LE}^2 + 8\hat{\sigma}_L^2$
BS10C0/S	90	
BS10C4/S	90	
BS11C0/S	90	
BS11C4/S	90	
(BS10C0 vs BS10C4)/S	10	
(BS11C0 vs BS11C4)/S	10	
(BS10 vs BS11)/S	10	
(Lines × E)/S	1170	$\hat{\sigma}^2 + 2\hat{\sigma}_{LE}^2$
Pooled error	1560	$\hat{\sigma}^2$
Total	3199	

population. The same partitions were made for the line-experiment interaction. F-tests were made to determine if the variation among S<sub>1</sub> progenies, means between C0 and C4, BS10 and BS11, and their interactions with experiments were different from zero. S<sub>1</sub> line components of variance were calculated for C0 and C4 for each population by equating expected mean squares with observed mean squares. Random effects were assumed for experiments and entries in determining the expected mean squares. S<sub>1</sub> line components of variance were used to calculate genetic coefficients of variation and heritabilities and to make comparisons between original (C0) and improved (C4) populations. If we assume dominance effects were zero, variation among S<sub>1</sub> lines is equivalent to the additive genetic variance of the respective populations. If gene frequency of segregating alleles was 0.5, variation among S<sub>1</sub> lines is equivalent to the additive genetic variance and 0.25 of the dominance variance. Hence, most of the variation among S<sub>1</sub> lines is additive. Heritabilities (h<sup>2</sup>) were calculated on a progeny mean basis as  $\hat{\sigma}_g^2 / (\hat{\sigma}_g^2/8 + \hat{\sigma}_{ge}^2/4 + \hat{\sigma}_e^2)$ , where  $\hat{\sigma}_g^2$ ,  $\hat{\sigma}_{ge}^2$ , and  $\hat{\sigma}_e^2$  are estimates of experimental error, S<sub>1</sub> line-experiment interaction, and genetic variation among S<sub>1</sub> lines, respectively.

## RESULTS

**Populations and population crosses:** Differences among entries were significant for all traits except percentage of dropped ears. Differences among the three groups of entries were significant for grain yield, ears per plant, and days from planting to 50% silking. Observed variations for most traits were explained by their regressions on cycles of reciprocal full-sib and mass selection. Significant quadratic responses for ears per plant and days from planting to 50% silk were detected, but no quadratic response over cycles for yield was indicated. Yield responses for reciprocal full-sib and mass selection for each population and population cross are presented in Fig. 2 on a per-year basis. Yield response was positive in all instances for reciprocal full-sib selection and negative in all instances for mass selection for ears per plant (prolificacy).

Mass selection for prolificacy did not produce a correlated response for yield improvement in BS10 and BS11 (Fig. 2). Mass selection, however, was effective for increasing number of ears per plant, but the direct response was similar to that for reciprocal full-sib selection,

which emphasized yield (Table 2). Although BS10(M)C10 had a 1.7% greater grain yield than BS10C0 (Table 2), the average response to selection was -0.17 (Fig. 2). Similar responses for yield were obtained for mass selection in BS11 and the population cross. Although mass selection for prolificacy was effective for increasing ear number, reduction in either ear or kernel size must have been sufficient to cause no significant increase in grain yield. Days from planting to 50% silking were significantly later in the mass-selected population of BS10 and the population cross.

Direct response to reciprocal full-sib selection for grain yield in the population cross was realized, but the response was significant and similar for BS10 (4.2 q/ha), BS11 (4.6 q/ha), and the population cross (4.8 q/ha) after 4 cycles of reciprocal full-sib selection. Grain yield increase was about 7% in all instances, and heterosis of the population cross was 11.2% before selection and 12.8% after 4 cycles of selection. Reciprocal full-sib selection had a correlated response of increased ear number that was similar to the direct response of mass selection for greater ear number (Table 2). Four cycles of reciprocal full-sib selection significantly decreased days from planting to 50% silking in BS10 and BS11, whereas mass selection for prolificacy significantly increased days from planting to 50% silking in BS10 and the population cross.

There was no consistent evidence of significant correlated response from mass selection for prolificacy and reciprocal full-sib selection for root and stalk lodging and dropped ears (not shown). None of the differences for dropped ears was significant for either selection method for BS10, BS11, and their crosses. Stalk lodging decreased for each group of entries from reciprocal full-sib selection, but the differences were significant for only BS11. Mass selection significantly increased stalk lodging in BS10, with no changes in BS11 and the population crosses. No consistent trends were observed among selection methods for root lodging.

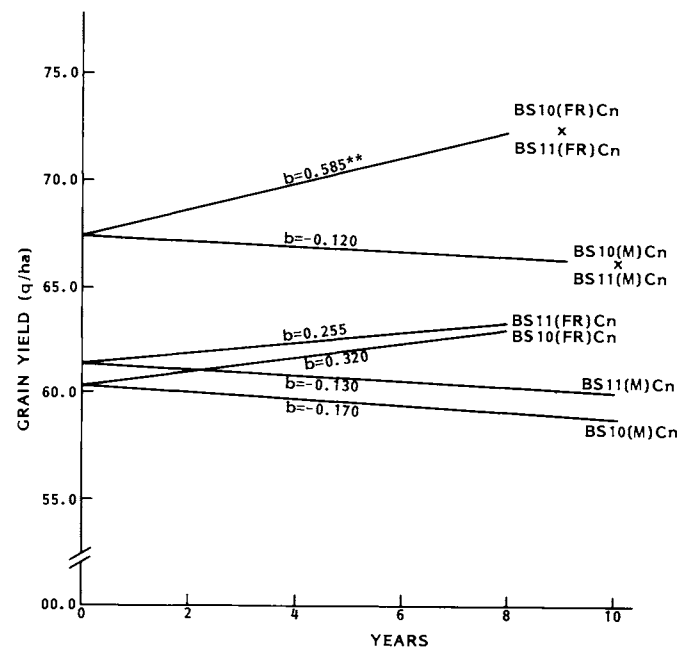


Fig. 2. Yield response of BS10, BS11, and their crosses from four cycles of reciprocal full-sib selection for yield and 10 cycles of mass selection for number of ears per plant.

FULL-SIB AND MASS SELECTION IN CORN

Table 2. Mean performance of original and selected populations of BS10 and BS11, their populations crosses, and S<sub>1</sub> lines extracted from original and selected reciprocal full-sib populations of BS10 and BS11.

Trait	Populations	Populations and crosses		S <sub>1</sub> Lines		Inbreeding <sup>a</sup>
		Means	% of C0	Means	% of C0	
Yield	BS10C0	q/ha		q/ha		%
	BS10(FR)C4	59.9	—	46.3	—	77.1
	BS10(M)C10	64.1	107.0	50.9	109.9	79.4
	BS11C0	60.9	101.7	—	—	—
	BS11(FR)C4	58.2	—	42.9	—	73.7
	BS11(M)C10	62.8	107.9	52.4	122.1	83.4
	BS10C0 × BS11C0	59.1	101.6			
	BS10(FR)C4 × BS11(FR)C4	68.0	—			
	BS10(M)C9 × BS11(M)C9	72.8	107.1			
	LSD (0.05)	65.8	96.8	3.8	7.5	
Ears per plant	BS10C0	no.		no.		%
	BS10(FR)C4	1.1	—	1.2	—	109.1
	BS10(M)C10	1.5	136.4	1.8	150.0	120.0
	BS11C0	1.5	136.4	—	—	—
	BS11(FR)C4	1.2	—	1.3	—	108.3
	BS11(M)C10	1.4	116.7	1.7	130.8	121.4
	BS10C0 × BS11C0	1.5	125.0			
	BS10(FR)C4 × BS11(FR)C4	1.2	—			
	BS10(M)C9 × BS11(M)C9	1.5	125.0			
	LSD (0.05)	1.6	133.3	0.1	0.3	
Days to silk <sup>b</sup>	BS10C0	no.		no.		%
	BS10(FR)C4	74.8	—	83.1	—	111.1
	BS10(M)C10	73.0	97.6	83.7	100.7	114.7
	BS11C0	77.1	103.1	—	—	—
	BS11(FR)C4	79.5	—	87.4	—	109.9
	BS11(M)C10	77.4	97.4	84.8	97.0	109.6
	BS10C0 × BS11C0	79.3	99.8			
	BS10(FR)C4 × BS11(FR)C4	75.8	—			
	BS10(M)C9 × BS11(M)C9	75.8	100.0			
	LSD (0.05)	77.5	102.2	1.2	1.9	

<sup>a</sup>Mean performance of S<sub>1</sub> lines expressed as percentage of population per se.

<sup>b</sup>Days from planting to 50% silking.

*S<sub>1</sub> progenies:* Mean performance of S<sub>1</sub> progenies from the C0 and C4 populations of BS10 and BS11 (Table 2) and estimates of S<sub>1</sub> components of variance (Table 3) showed that grain yield and ears per plant significantly increased without significant reduction in genetic variance. Days from planting to 50% silking decreased for BS11 (87.4 to 84.8) with a trend for reduced genetic variability. All estimates of genetic variability ( $\sigma^2_g$ , Table 3) were significantly greater than zero for grain yield, ears per plant, and days from planting to 50% silking. Estimates of interactions of S<sub>1</sub> lines with experiments were significant for each trait for each cycle, but the estimates of heritability were greater than 81% in all instances. Genetic coefficients of variation also showed that, relative to the mean, genetic variation was not substantially reduced with selection.

S<sub>1</sub> line means of the C0 and C4 populations showed that reciprocal full-sib selection was effective for increasing the frequency of favorable dominant alleles for grain yield: 1) mean performance increased in both populations (9.9% for BS10 and 21.1% for BS11); and 2) the effects of inbreeding were reduced (Table 2). Either frequency of favorable alleles was lower in BS11 than BS10 or selection was more effective in BS11 than BS10 because S<sub>1</sub> mean performance of BS11 has a greater increase in grain yield from C0 to C4 and reduced inbreeding effects (10.1%). Although effects of reciprocal full-sib selection for grain yield were similar for population performance (7.0% for BS10 and 7.9% for BS11), a significantly greater response to selection was realized in the S<sub>1</sub> generation for BS11 (22.1% for BS11 vs. 9.9% for BS10). For ears per plant and days from planting to 50% silk, mean

Table 3. Estimates of components of variance, heritability ( $h^2$ ), and genetic coefficient of variation (G.C.V.) for yield, ears per plant, and days to silk in each population of  $S_1$  lines.

Trait	Population	Components of variance <sup>a</sup>			$\hat{h}^2$	G.C.V. <sup>b</sup>
		$\hat{\sigma}_e^2$	$\hat{\sigma}_{ge}^2$	$\hat{\sigma}^2$		
Yield	BS10C0	55.0 ± 9.5	8.9 ± 3.9	57.3 ± 4.2	85	16
	BS10(FR)C4	55.3 ± 10.1	23.6 ± 4.9	57.1 ± 4.2	81	15
	BS11C0	72.1 ± 12.4	14.5 ± 4.9	68.1 ± 5.1	86	20
	BS11(FR)C4	82.4 ± 13.7	14.2 ± 4.1	54.0 ± 4.0	89	17
Ears/plant <sup>c</sup>	BS10C0	0.5 ± 0.1	0.1 ± 0.0	0.5 ± 0.1	86	18
	BS10(FR)C4	1.2 ± 0.2	0.2 ± 0.1	1.0 ± 0.1	87	19
	BS11C0	1.0 ± 0.2	0.1 ± 0.0	0.8 ± 0.1	89	23
	BS11(FR)C4	0.8 ± 0.1	0.1 ± 0.0	0.8 ± 0.1	85	17
Days to silk	BS10C0	7.2 ± 1.2	0.9 ± 0.2	1.4 ± 0.2	89	10
	BS10(FR)C4	4.2 ± 0.7	0.4 ± 0.2	1.2 ± 0.1	88	7
	BS11C0	7.8 ± 1.3	1.3 ± 0.4	2.3 ± 0.2	86	9
	BS11(FR)C4	5.3 ± 0.9	0.5 ± 0.2	1.6 ± 0.2	89	8

<sup>a</sup> $\hat{\sigma}_e^2$ ,  $\hat{\sigma}_{ge}^2$ , and  $\hat{\sigma}^2$  are  $S_1$  line,  $S_1$  line-experiment interaction, and experimental error components of variance, respectively.

<sup>b</sup>G.C.V. is the genetic coefficient of variation.

<sup>c</sup>Variance components multiplied by 10.

Table 4. Summary of components of variance, heritabilities ( $h^2$ ), and genetic coefficients of variation (G.C.V.) for the original and five cycles of reciprocal full-sib selection in BS10 and BS11 for grain yield.

Cycle	Year	Number of			Yield q/ha	Components of variance			$h^2, \%$	G.C.V., %
		Reps	Locations	Entries		2 $\sigma$	2 $\sigma_{ge}$	2 $\sigma_g$		
0	1964	2	2	144	52.5	31.2 ± 2.6	-0.2 ± 2.2	32.2 ± 6.8	80	11.3
1	1971	2	3	181	67.4	154.9 ± 9.0	18.8 ± 8.4	26.4 ± 6.6	45	7.6
2	1973	2	3	248	65.1	134.8 ± 6.9	29.0 ± 6.9	48.4 ± 7.4	60	10.7
3	1975	2	2	223	70.4	88.0 ± 6.1	-1.6 ± 4.9	33.9 ± 7.6	60	7.6
4	1977	2	2	159	49.1	60.1 ± 4.8	0.6 ± 4.1	31.1 ± 7.5	67	11.4
5	1979	2	3	156	73.3	114.0 ± 7.6	16.6 ± 6.8	32.8 ± 6.5	57	7.8
Average		2	2.5	185	63.0	97.2 ± 6.2	10.5 ± 5.6	34.1 ± 7.1	62	9.7

response in the  $S_1$  generation was greater in BS10 for ears per plant and greater in BS11 for days to 50% silk. Estimates of inbreeding depression, however, were similar for both sets of  $S_1$  progenies. Observed response for  $S_1$  generations of C4 populations reflects traits of the C0 populations; BS11C0 was lower yielding, had more ears per plant, and was later silking than BS10C0. The population that had lowest C0  $S_1$  progeny means for grain yield (BS11) and ears per plant (BS10) had the greatest response as C4  $S_1$  progeny means. For days from planting to 50% silking, there was no change in  $S_1$  progeny means of BS10 from C0 to C4, but the BS11C4  $S_1$  progeny mean was significantly earlier than the C0. The change in the  $S_1$  progeny means reflected the selection pressures of the methods used for reciprocal full-sib selection: 1) only

plants that produced seed on 2 ears were retained; and 2) selection for simultaneous flowering was necessary to make the full-sib crosses between BS10 and BS11. Hence, experimental techniques increased selection pressure for number of ears in BS10 and for earlier flowering in BS11 to produce the full-sib crosses.

### DISCUSSION

Two distinctly different recurrent selection methods were imposed on two synthetic varieties of corn adapted to central Iowa with selection for two different traits: 1) mass selection (the simplest method of population improvement) for prolificacy, a trait relatively easy to

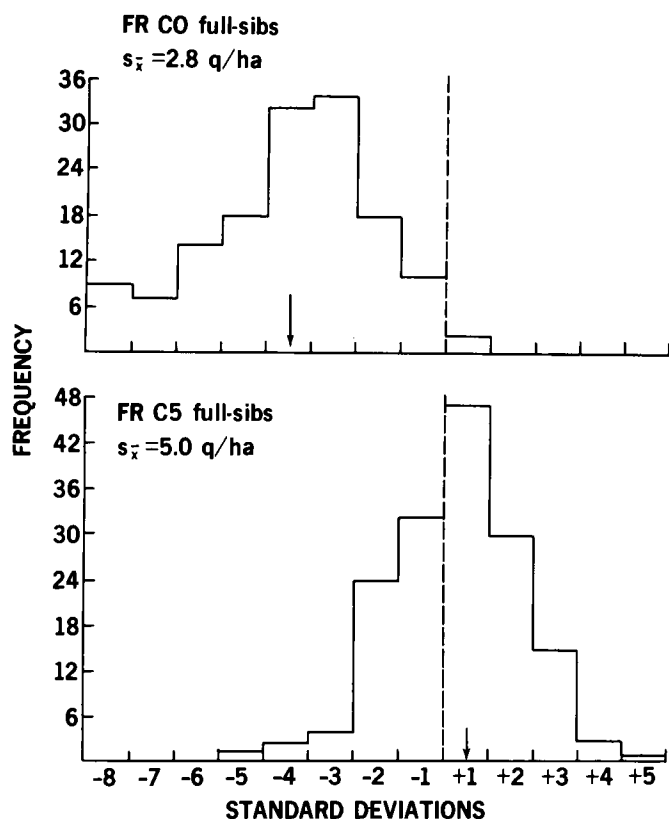


Fig. 3. Frequency distributions of C0 and C5 cycle full-sib progenies from reciprocal full-sib (FR) selection with BS10 and BS11. Dotted vertical line indicates mean of five check hybrids and arrow indicates mean of full-sib progenies.

measure; and 2) reciprocal full-sib selection (one of the more complex methods of population improvement) for grain yield, a trait whose expression can best be measured in replicated trials repeated over environments. Mass selection is a method of intrapopulation selection where the primary objective is to improve the population itself. Reciprocal full-sib selection is imposed on two populations, and the primary response of selection is directed to the population cross. Indirect responses (i.e., cross performance for mass selection and population performance per se for reciprocal full-sib selection) could be realized, however, if selection was primarily for additive genetic effects. Response to mass selection is primarily dependent on additive genetic effects, whereas reciprocal full-sib selection emphasizes selection for nonadditive genetic effects as well as additive genetic effects. Because mass selection is based on individual, nonreplicated plants, its use is usually restricted to those traits that have relatively high heritabilities. More complex selection methods that produce progenies for evaluation in replicated trials are used for traits that have lower heritabilities.

Heritability estimates for yield and prolificacy on an individual plant basis were not greatly different. When the mass selection study for prolificacy in BS10 and BS11 was initiated, it was assumed prolificacy had a higher heritability than grain yield. Lonquist (1967) reported that the indirect response for grain yield improvement was greater with mass selection for prolificacy than the direct response with mass selection for grain yield. Lonquist's results suggested that mass selection

for greater ear number was more effective than mass selection for grain yield; i.e., ear number had a higher heritability than grain yield. Because ear number per plant is relatively easy to measure, mass selection would be appropriate. Heritability estimates obtained for segregating populations suggest that the heritability of ear number (prolificacy) on an individual plant basis is not as high as originally assumed; i.e., about 24.2% (Hallauer, 1974) and inherited in a recessive manner (Harris et al., 1976). In comparison, heritability estimates for grain yield on an individual plant basis are about 20% (Hallauer and Miranda, 1981). Hence, the heritabilities of grain yield and prolificacy on an individual plant basis are not greatly different.

Response to mass selection for prolificacy was positive, but indirect response for grain yield improvement was not realized. Seed was harvested only from plants that had 2 or more ears. No grain yield measurements were made for the ears selected. Ten cycles of mass selection increased ear number, but there must have been unfavorable effects on other components of grain yield (ear length, kernel size, and kernel depth), which were not measured. Hence, ear number increased, but there was no indirect response for grain yield improvement. The effects of mass selection for number of ears per plant are similar to those reported by Cortez and Hallauer (1979) for ear length. Mass selection for ear length was effective, but no correlated response for grain yield was realized because kernel depth was reduced.

Direct response to reciprocal full-sib selection was effective for grain yield improvement in BS10, BS11, and their cross (about 7%). In addition, a significant indirect response for ear number was realized. Reciprocal full-sib selection was based on replicated trials of full-sib families. A summary of 5 cycles of reciprocal full-sib selection showed that the heritability for grain yield for full-sib families averaged 62% (Table 4). Estimates of the full-sib progeny component of variance ( $\sigma_g^2$ , Table 4) showed that the variation among full-sib progenies had not decreased with selection (32.2 for C0 vs. 32.8 for C5). Results from selection trials supported the estimates of variance among  $S_1$  progenies obtained for the C0 and C4 cycles (Table 3). Distributions of the C0 and C5 cycle full-sib progenies were similar (Fig. 3). Although the relative distributions of the C0 and C5 cycle full-sib progenies were similar, the mean of the distributions relative to the mean of 6 check hybrids increased from four standard deviations below the mean of check hybrids to 1 standard deviation above the mean of check hybrids. Five cycles of reciprocal full-sib selection improved the mean of BS10, BS11, and their cross (Table 3) and maintained the same level of genetic variability for further selection. Hence, the 2 objectives of recurrent selection were realized.

Indirect response to reciprocal full-sib selection for grain yield, for number of ears per plant and days to 50% silk was as effective as mass selection for increased ear number and more effective than mass selection for flowering. Days from planting to 50% silking were significantly reduced in BS10 and BS11 and remained the same for their cross (Table 2). Selection in the breeding nursery and grain moisture measurements in the grain yield trials were effective in maintaining similar maturity. Breeding procedures used in reciprocal full-sib selection required seed set on 2 ears (Hallauer, 1967), which increased the frequency of plants producing seed on more than 1 ear. Although number of ears per plant was not recorded in the full-sib progeny trials, individual plant selection was used in producing the progenies. Consequently, response for number of ears per plant increased at the same rate as mass selection for ear number. But grain yield response was realized with reciprocal full-sib selection, whereas no grain yield response was realized with mass selection for ear number.

Reciprocal full-sib selection and mass selection in BS10 and BS11 were initiated to satisfy the long- (mass selection), intermediate- (reciprocal full-sib selection), and short-term (line development) goals of corn breeding. Mass selection was conducted to form back-up populations for BS10 and BS11 if evidence indicated genetic variability was

reduced from use of reciprocal full-sib selection. Our study showed equivalent levels of genetic variability after 4 cycles of selection for BS10 and BS11 themselves and after 5 cycles for the interpopulation full-sib progenies. Except for greater number of ears per plant, the results of mass selection were not encouraging; grain yield was maintained at the same level but at the expense of later flowering. It seems other measurements are required in addition to number of ears per plant to increase grain yield by mass selection. Results from reciprocal full-sib selection were positive, and response should be realized from future selection. Because reciprocal full-sib selection is adaptable for applied breeding programs, the method seems useful for developing new lines from each cycle of selection for possible use in hybrids.

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## In Memoriam

### Dr. Cameron L. Christensen 1931-1980

Dr. Cameron L. Christensen died of a heart attack at home in Lehigh, Iowa on August 6, 1980. He is survived by his wife Deloris and three daughters, Julia, Christy, and Tracy. Born in Goldfield, Iowa on August 3, 1931, he received his baccalaureate degree at the University of Iowa in 1953, the same year he married.

From 1953-1958, Cameron taught high school at Coggon and Manchester, Iowa. In 1958 he received a fellowship at Washington University in St. Louis where he completed an MS in Botany in 1959. He spent most of the next 8 years teaching in Rockwell City after a summer of teaching at Iowa Wesleyan. In 1963 he was awarded the honor of "Outstanding Biology Teacher in Iowa." A charter faculty member of Iowa Central Community College, he headed the Life Sciences Department from its inception in 1967 and stayed there for the remainder of his career. For 15 years he pursued a Ph.D., mostly during the summers, at various universities until he was awarded the Ph.D. degree in 1975 from Kentucky Christian University.

Dr. Christensen was active in numerous state and national professional societies. He served one year as treasurer of the Iowa Academy of Science. His publications included articles on general biology, education, and diatoms.

"Chris" or "Cam," as he was widely known, had two great passions, teaching and research. He gave many high school and college undergraduate students their only chance to know and appreciate the fascinating world of biology around them. To those who knew him, his booming voice and swashbuckling manner, which surfaced on occasion, only belied that compassionate, sympathetic, and sharing mind that touched so many other minds.

Charles W. Reimer