

# Responses to Seven Methods of Recurrent Selection in the BS11 Maize Population

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## ABSTRACT

Recurrent selection methods have been effectively used by maize (*Zea mays* L.) breeders to improve the performance of maize populations for quantitatively inherited traits. Although theoretical comparisons of such methods can be easily made, direct comparisons of the efficiencies of methods are time consuming and laborious. Because of these limitations, empirical data comparing multiple recurrent selection methods in the same base population are lacking for maize. Our study was designed to compare the response to selection for seven different methods (six intra- and one inter-population) in the BS11 maize population. A minimum of four cycles of selection were conducted for each of the following methods: mass, modified ear-to-row, half-sib with inbred tester, full-sib,  $S_1$ -progeny,  $S_2$ -progeny, and reciprocal full-sib selection. Selections for all programs except mass and reciprocal full-sib were based on an index composed of grain yield, grain moisture, stalk lodging, and root lodging. Each trait in the selection index was weighted according to its heritability. The populations per se, populations selfed, and testcrosses of the populations to the Cycle 0 population and to inbred B79 were evaluated in our study. Response to selection was measured for grain yield, grain moisture, stalk lodging, and root lodging along with other agronomic traits. All selection methods were successful in significantly improving the population per se performance for grain yield.  $S_2$ -progeny selection had the greatest response for grain yield of 4.5% cycle<sup>-1</sup> and mass selection had the lowest response (0.6 % cycle<sup>-1</sup>). All selection programs in which index selection was practiced, except for modified ear-to-row, were successful in improving the populations per se for all four traits simultaneously. Unlike some previous studies, inbred-progeny selection methods ( $S_1$ ,  $S_2$ ) performed well in BS11 in comparison with other selection methods.

RECURRENT SELECTION METHODS have been used to improve the performance of maize populations for quantitatively inherited traits. Recurrent selection is a cyclical process, which, except for mass selection, includes three phases: (i) development of progenies, (ii) progeny evaluation, and (iii) recombination of selected families or progenies. Although most recurrent selection

methods include these three phases, they vary in types of progenies evaluated (i.e., inbred, full-sib, half-sib, etc.); number of progenies evaluated; number of selected families (i.e., 5, 10, 20, 30, etc.); parental control; and the type of progenies intermated. It is this flexibility in the different types of methods and different parameters that has led to the utilization of a wide range of recurrent selection methods for population improvement with an equally wide range of responses. Even with the diversity of recurrent selection methods, two goals remain common throughout, increasing the mean performance of the population and maintaining the genetic variability in the population to facilitate long-term selection. The focus of our study was to improve the mean performance of a single population with respect to four important agronomic traits via seven different recurrent selection methods.

Grain yield has historically been the most important trait and the trait most frequently used for selection in maize population improvement. Recurrent selection methods have not been widely adopted by maize breeders, although they have been effective for increasing grain yield (Sprague and Eberhart, 1977; Darrah et al., 1978; Darrah, 1986; Hallauer et al., 1988; Hallauer and Miranda, 1988). Previous estimates for grain yield improvement indicate that for different methods of selection in different populations, for the same method in different populations, and for different methods in the same population, one can expect a 2 to 7% increase per cycle in grain yield, depending on the germplasm and selection method (CIMMYT, 1981; Darrah, 1986; Hallauer and Miranda, 1988).

Sprague and Eberhart (1977) summarized results of several different population improvement programs involving different populations and selection methods. They found an average gain cycle<sup>-1</sup> for grain yield of 2.0, 3.1, 3.4, 3.8, and 4.6% cycle<sup>-1</sup> for  $S_2$ -progeny, full-sib, mass, ear-to-row, and  $S_1$ -progeny selection, respectively. Eyherabide and Hallauer (1991) reported a 6.5% cycle<sup>-1</sup> increase in grain yield for the population cross in a reciprocal full-sib selection program between BS10 (for-

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**Abbreviations:** BS10, Iowa Two-ear Synthetic; BS11, Pioneer Two-ear Composite; BSCB1, Iowa Corn Borer Synthetic No. 1; BSSS, Iowa Stiff Stalk Synthetic; C0–C10, Cycle 0 through Cycle 10; FR, reciprocal full-sib; FS, full-sib; GDU, growing degree units, °C; HI, half-sib with inbred tester;  $h^2$ , heritability; MER, modified ear-to-row.

merly 'Iowa Two-ear Synthetic') and BS11 (formerly 'Pioneer Two-ear Composite'). Keeratinjakal and Lamkey (1993) also reported a 7.0% cycle<sup>-1</sup> increase in grain yield in the population cross between 'Iowa Stiff Stalk Synthetic' (BSSS) and 'Iowa Corn Borer Synthetic No. 1' (BSCB1). Lamkey (1992) reported that seven cycles of half-sib selection in BSSS increased grain yield 3.9% cycle<sup>-1</sup> whereas six cycles of S<sub>2</sub>-progeny selection following the seven cycles of half-sib selection gave no response.

The evidence indicates that recurrent selection methods are effective for improving maize population performance, but it is not clear which of the recurrent selection methods are the most efficient. Several summaries of response to selection have been completed for maize, although comparisons of the effectiveness of selection methods have been difficult because in many instances different selection methods were used in different populations for the same traits, the same method was used in different populations for the same traits, or the same method was used in the same population but for different traits. The ideal comparison of selection methods would involve selection for the same traits by using different selection methods in a common base population. These types of data are lacking in maize, however. The objectives of our research were (i) to compare responses to selection for six intra- and one inter-population recurrent selection methods including full-sib (FS), half-sib with an inbred tester (HI), modified ear-to-row (MER), mass, S<sub>1</sub>-progeny, S<sub>2</sub>-progeny, and reciprocal full-sib (FR) in one base population, and (ii) to determine the most effective and efficient method for improving the genetic potential of maize germplasm.

## MATERIALS AND METHODS

### Genetic Material Development

The BS11 population, originally designated as Pioneer Two-ear Composite, was developed by W.L. Brown at Pioneer Hi-Bred Int'l, Inc. It is a genetically broad-based population developed by crossing southern prolific germplasm with U.S. Corn Belt lines (Hallauer, 1967). Because of prior selection for prolificacy and adaptability, BS11 is adapted to the central Corn Belt and has potential as a useful source population from which to derive desirable inbred lines. The BS11 population was chosen for the selection methods study because it is a diverse population and should have adequate additive genetic variance for selection response.

Although winter nurseries were utilized where applicable for selfing or recombination to reduce cycle times, all progeny evaluation trials for each selection method were conducted in central and southern Iowa, the intended area of use for this germplasm. A minimum of four, and in most instances five, cycles of selection were completed for each selection method. Selection of progenies from replicated yield trials for recombination in FS, MER, HI, S<sub>1</sub>-progeny, and S<sub>2</sub>-progeny selection was based on a selection index that included grain yield, grain moisture at harvest, and resistance to stalk and root lodging. Each trait in the selection index was weighted according to its heritability (Smith et al., 1981a,b). Progeny evaluation trials generally were conducted in one year with two replications at each of three locations. A summary of each selection method including cycle times, selection intensities, and testers is given in Table 1.

The BS11 population has a tendency toward prolificacy and was used in 1963 to initiate reciprocal full-sib selection (FR) between BS10 and BS11. Crosses to the reciprocal population and selfs in the FR program were made on different ears of the same plant (Hallauer, 1967). The full-sib families were usually evaluated in one year at two to three locations with two to three replications per location. Remnant S<sub>1</sub> seed of the parents of the selected full-sib families was intermated by using the bulk-entry method (Hallauer, 1985). In the first five cycles of the FR program, selection among progenies was based primarily on grain yield with consideration given to decreased grain moisture and reduced root and stalk lodging. In the first cycle of selection, S<sub>4</sub> families were intermated to form the Cycle 1 population whereas S<sub>1</sub> families were used for all subsequent cycles. Twelve cycles of selection have been completed in the FR program, but only the initial five cycles were evaluated for comparison with the other selection methods.

Mass selection in BS11 was begun in 1967 utilizing the original BS11 Cycle 0 (C<sub>0</sub>) population. The first four cycles of mass selection were conducted by growing plants in the breeding nursery and intermating the second ear on the best two-eared plants to retain prolificacy in the population. Starting with Cycle 5, mass selection was conducted by growing the population in isolation. The field was divided into single-row plots 5.49 m in length. The most desirable plant in each of the most desirable plots was selected based on standability, freedom from disease, etc., and allowed to intermate with all surrounding plants. The selected plants were harvested and seed was bulked to produce the next cycle population. Cycles 2, 4, 6, 8, and 10 were included for our evaluation of progress from mass selection.

Full-sib, modified ear-to-row, half-sib selection with an inbred tester, S<sub>1</sub>-progeny, and S<sub>2</sub>-progeny selection were initiated in the 1977-78 winter nursery by using the same BS11

**Table 1. Selection protocols for each of seven selection methods conducted in the BS11 maize population.**

Selection method	Tester	Cycle time†	No. of progeny		Type of progeny		Selection intensity	Last cycle in study
			Evaluated‡	Recombined	Evaluated	Recombined		
		yr.	no.				%	
Full-sib	BS11	2	100	20	Full-sibs	S <sub>1</sub>	20	5
Half-sib	B79	3	100	20	Testcrosses	S <sub>1</sub>	20	4
Mass	BS11	1	10 000	100	NA§	NA	1	10
Modified ear-to-row	BS11	2	100	20	Half-sibs	S <sub>1</sub>	20	5
Reciprocal full-sib	BS10	2	185	20	Full-sibs	S <sub>1</sub>	10	5
S <sub>1</sub> -progeny	BS11	2	100	20	S <sub>1</sub>	S <sub>1</sub>	20	5
S <sub>2</sub> -progeny	BS11	3	100	20	S <sub>2</sub>	S <sub>1</sub>	20	4

† Based on two nonsimilar seasons per year.

‡ Except for mass, progeny evaluations were generally made by using two replications at each of three locations.

§ Not applicable.

C0 population that was used in 1963 and 1967 to begin the FR and mass selection programs, respectively. Full-sib selection was initiated by making plant-to-plant crosses in the winter nursery to produce full-sib families. The following season in Iowa, approximately 100 full-sib families were evaluated in replicated yield trials, and the best 20 families were selected. Remnant seed of the 20 selected families was planted in the winter nursery, and approximately ten plants per family were selfed to produce  $S_1$ s for cycles 1 to 3; 10 to 15 plants were selfed in subsequent cycles. Self-pollinated ears from the five best plants in each of these 20 selected families were bulked to represent that family for recombination for cycles 1 to 3; all the selfed plants were bulked in cycles 4 and 5. The following season in Iowa, recombination was conducted by making  $S_1 \times S_1$  plant crosses by using the bulk-entry method. Five sets of reciprocal full-sibs per pair in the bulk-entry intermating constituted the full-sib families for evaluation in the next cycle of selection. Thus, after the initial cycle, only three seasons per cycle were needed giving a cycle time of 2 yr.

Modified ear-to-row selection was conducted in a method similar to that described by Compton and Comstock (1976). Selection was for both the male and female gametes, and 2 yr were needed to complete one cycle of selection. Progenies were developed for the first cycle of selection by harvesting open-pollinated ears from the BS11 C0 population grown in isolation. One hundred ears were selected and evaluated the following year in replicated yield trials. The following winter-nursery season was used to self remnant seed of the 20 selected half-sib families. Approximately 10 to 15 plants per family were selfed, and equal quantities of seed from each selfed ear were bulked to represent the selected family during recombination and family formation. The bulked selfs of the 20 selected families were planted in isolation in the following season in Iowa to form families for the next cycle and for recombination. Each family was replicated five times and detasseled before anthesis. Male rows were obtained by bulking equal quantities of selfed seed from each of the 20 selected families. One half-sib plant was harvested from each of the 100 female rows in isolation for the yield trials in the following season. The remaining ears (10–15) from each of the female rows in isolation were harvested and equal quantities of seed were bulked from each ear to form the Syn-1 population. The resulting Syn-1 population was random mated, by chain sibbing 300 to 400 plants to form the Syn-2 population, which was used to represent the population per se for evaluation purposes.

Half-sib selection with an inbred tester was initiated by selfing 300 to 400 plants in the winter nursery. The resulting  $S_1$  lines were grown the following season in the Iowa breeding nursery and infested with European corn borer [*Ostrinia nubilalis* (Hübner)] larvae. Approximately 30 to 50% of the lines were discarded before anthesis on the basis of evaluation of resistance to whorl-leaf feeding. Two plants in the remaining  $S_1$  lines were simultaneously selfed and crossed to four plants of the inbred tester B79. Inbred B79 was derived from the BS10 population, which was used as the reciprocal population for BS11 in the FR program (Russell and Hallauer, 1976). At harvest, seed from the best of the two selfed plants was placed in storage and the corresponding testcross seed was bulked for replicated evaluation. The following season in Iowa, the 100 testcrosses were evaluated in replicated yield trials and the superior 20 testcrosses were selected. In the following winter nursery, remnant  $S_1$  seed of the male parent of the 20 selected testcrosses was recombined by the bulk-entry method. The resulting Syn-1 population was random mated by chain sibbing 300 to 400 plants to form the Syn-2 population. The next cycle was initiated by selfing the Syn-2 population in the winter nursery.

Progenies were developed for  $S_1$ -progeny selection by selfing 300 to 400  $S_0$  plants in the winter nursery. Ears from the more desirable 100 to 150 plants were harvested. The following season in Iowa, 100  $S_1$  lines were grown in replicated yield trials, and the best 20 lines were selected. The selected lines, planted from remnant  $S_1$  seed, were recombined in the winter nursery using the bulk-entry method. The resulting Syn-1 population was random mated by chain sibbing 300 to 400 plants, to form the Syn-2 population. The Syn-2 population was used to initiate the next cycle of selection.

$S_2$ -progeny selection was conducted by selfing 300  $S_0$  plants in the winter nursery. The  $S_1$  lines were grown ear-to-row the following season in the Iowa breeding nursery. All rows were artificially infested with European corn borer larvae and rated for resistance to whorl-leaf feeding before anthesis. Generally 30 to 50% of the lines were discarded before anthesis on the basis of whorl-leaf feeding as well as other agronomic traits, such as plant type, tillering, lodging, plant and ear height, and maturity. Three to five plants were self-pollinated in the remaining  $S_1$  lines. At harvest, 100  $S_2$  progenies were selected for replicated evaluation, each derived from a single plant in a different  $S_1$  line. Criteria for choosing among pollinated plants within rows included seed set, ear diseases, and lodging. The following season in Iowa, the  $S_2$  lines per se were evaluated in replicated trials. In the following winter nursery, the 20 selected families, planted from remnant  $S_1$  seed, were recombined by the bulk-entry method to form the Syn-1 population. The Syn-1 population was random mated by chain sibbing 300 to 400 plants to form the Syn-2 population. The next cycle was initiated by selfing  $S_0$  plants in the Syn-2 population.

#### Selection Method Evaluation and Procedures

In the 1991 Iowa breeding nursery, seed of the populations per se and populations per se selfed was produced for the C0 to C5 of  $S_1$ -progeny, FR, MER, and FS selection methods, C0 to C4 of HI and  $S_2$ -progeny selection methods, and C2, C4, C6, C8, and C10 of mass selection. Each of the populations per se was also topcrossed to BS11C0 and B79 in isolation plots. Seed of the populations per se and populations per se selfed was produced by chain sibbing or selfing 160 plants. The topcross seed was produced by using 160 plants of the populations as females and the testers as males. Equal quantities of seed were bulked from each ear to form all types of populations.

The noninbred ( $S_0$ -populations per se, testcrosses to BS11C0, and testcrosses to B79) and inbred ( $S_1$ -populations selfed) materials were evaluated in separate experiments grown in central and southern Iowa. Both experiments were conducted at Ames, Ankeny, Crawfordsville, and Martinsburg, IA, in 1992 and 1993, as well as Ames, Chariton, Crawfordsville, and Fairfield, IA, in 1994. Because of poor stands, data were not obtained for the inbred experiment at Chariton in 1994.

Entries included in the noninbred experiment were the populations per se for all cycles of selection and each method, population crosses to the BS11C0, and the population crosses to inbred B79. Multiple entries of BS11C0 (20 per replication) and BS11C0  $\times$  B79 (10 per replication) were included to give a more precise estimate of the BS11C0 mean and to minimize correlations among regression coefficients. The entries and three hybrid checks were evaluated in a  $13 \times 13$  partially balanced lattice design with five replications for each environment (location  $\times$  year combination) except for Chariton in 1994 where only four replications were evaluated. The inbred experiment included multiple entries of BS11C0 selfed (10 per replication) along with the populations per se selfed for

each cycle of selection for all methods. The inbred entries and one inbred line check were evaluated in a  $7 \times 8$  rectangular lattice with five replications per environment.

For both experiments, a plot consisted of two machine-planted rows 5.49 m in length with 0.76 m between rows. Plots were overplanted and thinned to a uniform stand density of approximately 62 124 plants  $\text{ha}^{-1}$ . All experiments were machine cultivated and/or hand weeded as necessary to maintain proper weed control. All plots were machine harvested with no gleaning of dropped ears.

Data were collected on all replications for machine-harvestable grain yield ( $\text{Mg ha}^{-1}$ ) adjusted to 155  $\text{g kg}^{-1}$  grain moisture, grain moisture ( $\text{g kg}^{-1}$ ) at harvest, final stand (1000 plant  $\text{ha}^{-1}$ ), root lodging (percentage of plants leaning greater than  $30^\circ$  from vertical), stalk lodging (percentage of plants broken at or below the primary ear node), and dropped ears (%). Plant, ear, and top height were measured on two replications in each environment except for Ames in 1993 in the noninbred experiment, which was not measured. Plant and ear height were recorded as the average of measurements on 10 competitive plants  $\text{plot}^{-1}$  and measured as the distance from the soil surface to the node of the flag leaf and to the highest ear-bearing node, respectively. Top height was calculated as the difference between plant height and ear height. Growing degree units (GDU,  $^\circ\text{C}$ ) to 50% silk emergence were recorded on two replications at Ames in 1992, 1993, and 1994. Growing degree units were calculated as  $[(\text{Daily maximum temperature} - \text{daily minimum temperature})/2] - 10$ , where the maximum and minimum limits for calculation purposes were 30 and  $10^\circ\text{C}$ , respectively (Shaw, 1988). Because of excessive lodging, root lodging, stalk lodging, and dropped ears were not measured at Ames in 1992 in the noninbred experiment. Also, data for grain yield, grain moisture, lodging, and dropped ears were recorded on only three replications for the inbred experiment at Martinsburg in 1992.

### Statistical Analysis

The analyses of variance for individual environments were calculated according to the analysis for a square and rectangular lattice for the noninbred and inbred experiments, respectively. Entry means in each environment, adjusted for lattice block effects, were used to compute an unweighted analysis of variance combined over environments. For further analysis, the populations per se, population crosses, and selfed populations were separated into three groups for regression based on common C0 genotypes. Group one included all cycles of selection of the populations per se and the population crosses to the C0, which had BS11C0 as their common C0 genotype. Group two included all of the populations crossed to B79, which had BS11C0  $\times$  B79 as the common C0 genotype. The third group included all of the selfed populations per se, which had BS11C0 selfed as the common C0 genotype. The sums of squares for each group were partitioned to simultaneously fit regression lines for all seven selection methods through the common C0 intercept (Eberhart, 1964). Weighted least squares regression was utilized with the weight being the variance of cycle means from the combined analysis of variance. Multiple C0 entries for each regression group allowed the common C0 intercept to be weighted more heavily than all other points, with the selected-cycle means having equal weight for all selection methods. Standard errors for the regression coefficients were obtained by taking the square root of the appropriate diagonal element of the  $(X'W^{-1}X)^{-1}$  matrix where  $W$  is a matrix with the variance of cycle means on the diagonal and zeros on the off-diagonal and  $X$  is a matrix of the number of cycles of selection conducted for each method.

Estimates of the average response cycle $^{-1}$  were obtained from the linear regression coefficients from the model containing only the linear term for each method. Average response year $^{-1}$  was calculated by dividing the average response cycle $^{-1}$  by the number of years required to complete a cycle for each method of selection. Percentage response cycle $^{-1}$  was calculated as the ratio of the linear regression coefficient to the estimated C0 intercept and multiplied by 100.

Inbreeding depression in absolute units was calculated by using cycle means from those environments where the trait of interest was measured on both the  $S_0$  and  $S_1$  experiments. Inbreeding depression in absolute units was calculated as the  $S_0$  minus  $S_1$  cycle means. Percentage inbreeding depression was calculated by dividing inbreeding depression in absolute units by the noninbred mean and multiplying by 100. Standard errors for inbreeding depression in absolute units were calculated as the square root of the sum of the variance of noninbred and inbred cycle means (Lamkey and Smith, 1987). Significance of inbreeding depression was tested by a  $t$ -test with the degrees of freedom associated with the  $t$ -statistic approximated as given by Satterthwaite (1946).

Cumulative selection differentials were calculated by summing the selection differentials from progeny evaluation trials over all cycles of selection. Predicted gain was calculated by multiplying heritability ( $h^2$ ) by the selection differential for each cycle and summing this product over all cycles of selection. When  $h^2$  for an individual cycle and method was not available, the mean  $h^2$  over all cycles was substituted in the calculation of predicted gain. Realized heritabilities were calculated by regressing the cycle means or cumulative responses, on to the cumulative selection differential (Falconer, 1954; Hill, 1972; Nyquist, 1991). Weighted least squares regression was utilized and, since no replicate programs were conducted, the standard errors for the realized heritabilities were calculated in the same manner as the standard errors for the regression coefficients for linear responses to selection. Realized  $h^2$  was not calculated for a trait where inconsistencies in sign of the selection differential caused the cumulative selection differential to fluctuate in sign as well.

An economic analysis of the selection methods was carried out by assuming direct costs of \$10 for an average nursery row, \$15 per winter nursery row, \$10 per yield trial plot, and a cost of \$350 for an average-size isolation. The cost per unit of gain was calculated by taking the cost cycle $^{-1}$  divided by the gain cycle $^{-1}$  estimated for each selection method. The number of years to achieve one unit gain ( $1 \text{ Mg ha}^{-1}$ ) was calculated by multiplying the inverse of the gain cycle $^{-1}$  by the number of years to complete one cycle of selection. The cost  $\text{yr}^{-1}$  was calculated by dividing the cost cycle $^{-1}$  by the number of years required to complete one cycle. The gain per investment was calculated by dividing the gain cycle $^{-1}$  by the cost cycle $^{-1}$ .

## RESULTS

### Selection Trial Results

Mean heritabilities for grain yield ranged from 47.1 (HI) to 86.7% ( $S_2$ -progeny), and the average selection differentials ranged from 0.67 to  $1.19 \text{ Mg ha}^{-1}$  (Table 2). The mean heritabilities over cycles of selection are consistent with data published by Lamkey and Hallauer (1987). They summarized heritabilities for numerous recurrent selection programs into three broad groups including some of the earlier cycles from these selection programs. Group one of our experiment would only

**Table 2. Heritabilities ( $h^2$ ) and selection differentials (S) from progeny evaluation trials conducted in the BS11 maize population to select desirable lines to form the next cycle of selection. Heritabilities and selection differentials were unpublished data obtained from the Annual Reports of the Cooperative Federal-State Corn Breeding Investigations, Ames, IA, 1963 through 1989.**

Trait	Selection method	Cycle 0		Cycle 1		Cycle 2		Cycle 3		Cycle 4		Mean	
		$h^2$	S	$h^2$	S	$h^2$	S	$h^2$	S	$h^2$	S	$h^2$	S
Grain yield (Mg ha <sup>-1</sup> )	Full-sib	54.0	0.78	80.8	1.05	62.7	0.90	66.0	0.48	62.9	0.59	65.3	0.76
	Half-sib	45.0	0.76	61.9	0.83	29.0	0.51	52.3	0.59	-	-	47.1	0.67
	Modified ear-to-row	54.0	0.78	59.7	0.70	57.5	0.67	54.0	0.68	54.5	0.55	55.9	0.68
	Reciprocal full-sib	81.0	0.63	40.0	1.17	60.1	1.27	62.0	1.11	67.0	1.13	62.0	1.06
	S <sub>1</sub> -progeny	84.6	1.12	60.3	1.00	57.0	0.28	71.7	0.61	68.4	0.51	68.4	0.70
	S <sub>2</sub> -progeny	86.7	1.59	86.2	1.02	90.0	1.06	83.7	1.07	-	-	86.7	1.19
Grain moisture (g kg <sup>-1</sup> )	Full-sib	71.1	-4.0	86.0	-7.0	61.0	-1.0	67.0	-8.0	86.2	-4.0	74.3	-4.8
	Half-sib	89.4	-5.0	62.7	0.0	75.0	1.0	76.4	6.0	-	-	75.9	0.5
	Modified ear-to-row	71.1	-4.0	76.1	-1.0	77.8	-4.0	76.0	-11.0	66.2	-7.0	73.4	-5.4
	Reciprocal full-sib	-	-13.0	83.9	2.0	75.9	0.0	73.1	1.0	30.4	-2.0	65.8	-2.4
	S <sub>1</sub> -progeny	80.6	-1.0	72.9	-5.0	60.0	-1.0	78.9	-1.0	81.6	-8.0	74.8	-3.2
	S <sub>2</sub> -progeny	88.2	-1.0	87.0	-4.0	88.0	-14.0	84.4	-10.0	-	-	86.9	-7.3
Stalk lodging (%)	Full-sib	61.4	-3.6	52.7	-1.5	66.0	-6.6	68.0	-11.4	60.9	-3.3	61.8	-5.3
	Half-sib	46.9	-5.5	39.1	-1.1	71.0	-6.9	60.4	-8.7	-	-	54.4	-5.6
	Modified ear-to-row	61.4	-3.6	49.9	-1.1	59.7	-4.8	39.0	-6.5	59.7†	-3.2	53.9	-3.8
	Reciprocal full-sib	-	1.9	65.1	-4.0	56.3	-11.6	55.4	-0.8	59.8	1.8	59.2	-2.5
	S <sub>1</sub> -progeny	75.1	-4.1	52.7	-3.3	74.0	-8.6	64.6†	-4.3	70.8	-5.5	67.4	-5.2
	S <sub>2</sub> -progeny	67.8	-10.0	76.2	-8.8	78.0	-2.8	58.4	-4.1	-	-	70.1	-6.4
Root lodging (%)	Full-sib	39.6	-3.9	75.2	-5.7	37.6	-2.7	23.0	-2.8	60.5	-2.5	47.2	-3.5
	Half-sib	38.4	-9.6	49.6	-1.4	73.0	-3.9	14.4	-1.2	-	-	43.9	-4.0
	Modified ear-to-row	39.6	-3.9	59.4	-5.4	45.4	-0.5	0.0	-0.5	59.0†	-9.4	40.7	-3.9
	Reciprocal full-sib	-	1.2	-	0.3	31.4	0.2	53.3	-0.7	50.3	-1.7	45.0	-0.1
	S <sub>1</sub> -progeny	63.8	-0.7	37.9	-0.4	46.0	-9.8	86.7†	-7.7	37.7	-0.6	54.4	-3.8
	S <sub>2</sub> -progeny	80.4	-6.5	59.3	-3.1	72.0	-4.9	66.9	-1.5	-	-	69.7	-4.0

† These estimates may be biased because the traits were only measured in one environment because of severe lodging in the other environments.

include the FS program. Group two includes the HI, FR, and MER programs, and group three includes both inbred-progeny selection methods. Their group heritabilities averaged 65.5 (Group 1), 55.7 (Group 2), and 78.6% (Group 3), whereas corresponding averages for our experiment were 65.3, 55.0, and 77.6%. Average heritabilities for grain moisture were high for all selection methods ranging from 65.8 (FR) to 86.9% (S<sub>2</sub>-progeny). The average heritabilities in the selection trials were high for stalk lodging as well, ranging from 53.9 (MER) to 70.1% (S<sub>2</sub>-progeny) selection. Heritabilities for root lodging were slightly lower in selection trials ranging from 40.7 (MER) to 69.7% (S<sub>2</sub>-progeny).

### General Results of Evaluation Trials

Two of the years in which these materials were evaluated (1992 and 1994) represented near optimum growing conditions for maize and resulted in record yields throughout much of the Corn Belt; however, extremely high rainfall and a cool growing season resulted in lower grain yields in 1993. The average grain yield across all environments was 5.53 Mg ha<sup>-1</sup> for the S<sub>0</sub> experiment and 3.43 Mg ha<sup>-1</sup> for the S<sub>1</sub> experiment. Mean grain yields in individual environments ranged from 2.64 to 7.37 Mg ha<sup>-1</sup> for the S<sub>0</sub> material and ranged from 1.58 to 5.03 Mg ha<sup>-1</sup> for the S<sub>1</sub> material. Grain yield in 1993 was 51 (S<sub>0</sub> experiments) and 46% (S<sub>1</sub> experiments) less than the average for 1992 and 1994.

Means for grain moisture ranged from 19.4 to 33.7% for the S<sub>0</sub> experiment and from 18.2 to 28.8% for the S<sub>1</sub> experiment. Substantial amounts of stalk lodging were found in this material. Mean stalk lodging at individual environments ranged from 6.3 to 35.7% for S<sub>0</sub> materials and from 5.2 to 26.0% for the S<sub>1</sub> experiment. Root

lodging was erratic among individual environments. Mean root lodging for individual environments ranged from 0.5 to 9.8% and from 0.5 to 13.3% for the S<sub>0</sub> and S<sub>1</sub> experiments, respectively.

### Traits under Direct Selection

It is evident from the selection differentials and heritabilities for grain yield that each method would be expected to respond to selection (Table 2). For all seven recurrent selection methods, grain yield increased significantly in the populations per se (Table 3 and Fig. 1A). Responses in the populations per se ranged from 0.03 Mg ha<sup>-1</sup> cycle<sup>-1</sup> (0.6%) for mass selection to 0.21 Mg ha<sup>-1</sup> cycle<sup>-1</sup> (4.5%) for S<sub>2</sub>-progeny selection. The response to selection in the S<sub>2</sub>-progeny selection program was not significantly greater than the 0.17 Mg ha<sup>-1</sup> cycle<sup>-1</sup> in the MER program; however, the response for S<sub>2</sub>-progeny was significantly greater than that for all other methods. When put on a per year basis, MER gave the greatest response per year of 0.09 Mg ha<sup>-1</sup> yr<sup>-1</sup> followed by S<sub>2</sub>-progeny selection with 0.07 Mg ha<sup>-1</sup> yr<sup>-1</sup>. Mass and HI had the least responses of 0.03 Mg ha<sup>-1</sup> yr<sup>-1</sup>.

Responses for grain yield in the testcrosses to the C0 population were also significant for all selection methods ranging from 0.04 to 0.25 Mg ha<sup>-1</sup> cycle<sup>-1</sup> for mass and S<sub>2</sub>-progeny selection, respectively. The response for S<sub>2</sub>-progeny selection was significantly greater than the responses for all other selection methods. Grain yield in testcrosses to inbred B79 did not respond to mass selection, whereas MER, HI, FR, and S<sub>2</sub>-progeny methods all had statistically equivalent increases in grain yield when crossed to B79. Unlike the previous three population types, the selfed populations had varying

Table 3. Observed mean grain yields for each cycle of seven selection methods and least squares estimates of response to selection in BS11 maize population. Data combined over 12 environments for S<sub>0</sub> populations per se and testcrosses, and 11 environments for the S<sub>1</sub> populations.†

Population type	Selection method	Cycle of selection					S.E. of mean‡	Regression coefficients§			Response per year	Percentage response#	
		C0	C1	C2	C3	C4		C5	b <sub>0</sub>	b <sub>1</sub>			b <sub>q</sub>
Mg ha <sup>-1</sup>													
S <sub>0</sub> population per se	Full-sib	4.69	4.72	4.76	5.13	5.17	4.87	0.13	4.73	0.07 ± 0.02**	-	0.03 ± 0.01**	1.4
	Half-sib		5.14	5.07	4.86	4.93	-††			0.08 ± 0.02**	**	0.03 ± 0.01**	1.6
	Mass‡‡		4.75	4.98	4.67	4.96	5.12			0.03 ± 0.01**	-	0.03 ± 0.01**	0.6
	Modified ear-to-row		4.89	5.08	5.28	5.51	5.50			0.17 ± 0.02**	-	0.09 ± 0.01**	3.6
	Reciprocal full-sib		4.64	5.36	5.34	5.20	5.13			0.12 ± 0.02**	**	0.06 ± 0.01**	2.6
	S <sub>1</sub> -progeny		5.02	4.81	4.96	5.11	5.21			0.09 ± 0.02**	*	0.05 ± 0.01**	1.9
	S <sub>2</sub> -progeny		4.91	5.50	5.14	5.59	-			0.21 ± 0.02**	-	0.07 ± 0.01**	4.5
Testcrosses to BS11 C0	Full-sib	4.69	4.95	4.92	5.18	5.16	5.28		4.73	0.12 ± 0.02**	-	0.06 ± 0.01**	2.5
	Half-sib		4.98	5.02	5.01	5.23	-			0.12 ± 0.02**	-	0.04 ± 0.01**	2.6
	Mass		4.72	4.87	5.05	5.10	4.98			0.04 ± 0.01**	-	0.04 ± 0.01**	0.8
	Modified ear-to-row		4.92	4.96	5.19	5.34	5.56			0.16 ± 0.02**	-	0.08 ± 0.01**	3.3
	Reciprocal full-sib		5.34	5.33	5.25	5.28	5.59			0.18 ± 0.02**	**	0.09 ± 0.01**	3.8
	S <sub>1</sub> -progeny		4.89	4.82	5.14	5.28	5.20			0.11 ± 0.02**	-	0.06 ± 0.01**	2.3
	S <sub>2</sub> -progeny		4.69	5.53	5.43	5.67	-			0.25 ± 0.02**	-	0.08 ± 0.01**	5.2
Testcrosses to inbred B79	Full-sib	6.25	6.21	6.12	6.59	6.42	6.16		6.15	0.04 ± 0.02*	-	0.02 ± 0.01*	0.7
	Half-sib		6.44	6.34	6.30	6.66	-			0.11 ± 0.03**	-	0.04 ± 0.01**	1.7
	Mass		6.34	6.06	5.74	6.40	6.44			0.01 ± 0.01	*	0.01 ± 0.01	0.2
	Modified ear-to-row		6.24	6.54	6.72	6.62	6.69			0.13 ± 0.02**	-	0.07 ± 0.01**	2.1
	Reciprocal full-sib		5.28	6.61	6.56	6.35	6.69			0.09 ± 0.02**	*	0.04 ± 0.01**	1.4
	S <sub>1</sub> -progeny		6.21	6.07	6.01	6.43	6.73			0.06 ± 0.02**	**	0.03 ± 0.01**	1.0
	S <sub>2</sub> -progeny		6.14	6.54	6.48	6.35	-			0.09 ± 0.03**	-	0.03 ± 0.01**	1.4
S <sub>1</sub> populations per se	Full-sib	3.20	3.18	3.16	3.35	3.32	3.53	0.10	3.25	0.03 ± 0.02*	-	0.02 ± 0.01*	1.0
	Half-sib		3.29	3.40	2.96	3.23	-			-0.02 ± 0.02	-	-0.01 ± 0.01	-0.6
	Mass		3.29	3.28	3.22	2.95	3.16			-0.01 ± 0.01	-	-0.01 ± 0.01	-0.4
	Modified ear-to-row		3.19	3.26	3.73	3.54	3.58			0.08 ± 0.02**	-	0.04 ± 0.01**	2.4
	Reciprocal full-sib		3.29	3.93	3.74	3.49	3.81			0.12 ± 0.02**	**	0.06 ± 0.01**	3.7
	S <sub>1</sub> -progeny		3.52	3.58	3.64	3.69	3.75			0.12 ± 0.02**	-	0.06 ± 0.01**	3.6
	S <sub>2</sub> -progeny		3.48	3.86	3.79	3.89	-			0.19 ± 0.02**	*	0.06 ± 0.01**	5.8

\*,\*\* Significant linear or quadratic response at the 0.05 and 0.01 probability levels, respectively.

† Check means, in Mg ha<sup>-1</sup>: B79 × B77 = 6.30; B79 × Mo17 = 7.63; B73 × B95 = 5.95; B73 × Mo17 = 7.17; B79 = 1.67.

‡ Standard errors for C0s are S.E./20<sup>1/2</sup> for BS11C0 and S.E./10<sup>1/2</sup> for BS11C0 × B79 and for BS11C0 S<sub>1</sub>.

§ b<sub>0</sub> is an estimate of the C0 mean; b<sub>1</sub> is an estimate of the average rate of response per cycle; b<sub>q</sub> is included to indicate when the quadratic term was significant.

|| Response per year calculated based on number of years to complete each cycle given previously.

# The percentage response per cycle was calculated as the ratio of b<sub>1</sub> to the estimated C0 intercept and multiplied by 100.

†† Cycle not included in study.

‡‡ C1, C2, C3, C4, and C5 correspond to cycles 2, 4, 6, 8, and 10 for mass selection only.

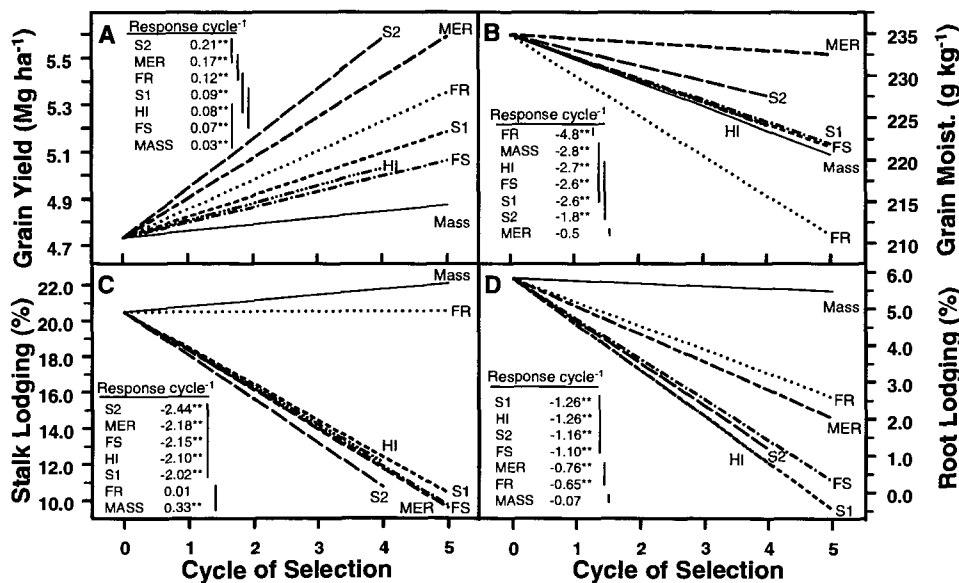


Fig. 1. Responses to selection for grain yield (A), grain moisture at harvest (B), stalk lodging (C), and root lodging (D) for seven selection methods in BS11. \* and \*\* indicate significance of the linear response ( $H_0: b_1 = 0$ ) at = 0.05 and 0.01, respectively. Responses are sorted in order of greatest response in the desirable direction to least response. Responses for each method connected by the same vertical line do not differ significantly at = 0.05.

**Table 4.** Observed mean grain moisture for each cycle of seven selection methods and least squares estimates of response to selection in the BS11 maize population. Data combined over 12 environments for S<sub>0</sub> populations per se and testcrosses, and 11 environments for the S<sub>1</sub> populations.†

Population type	Selection method	Cycle of selection					S.E. of mean‡	Regression coefficients§			Response per year¶	Percentage response#	
		C0	C1	C2	C3	C4		C5	b <sub>0</sub>	b <sub>1</sub>			b <sub>q</sub>
g kg <sup>-1</sup>													
S <sub>0</sub> populations per se	Full-sib	237	228	227	231	224	222	2.08	234.9	-2.58 ± 0.30**	-	-1.29 ± 0.15**	-1.1
	Half-sib	233	231	219	229	-	-††			-2.68 ± 0.40**	-	-0.89 ± 0.13**	-1.1
	Mass‡‡	225	226	206	215	211				-2.84 ± 0.15**	**	-2.84 ± 0.15**	-1.2
	Modified ear-to-row	232	244	233	237	226				-0.47 ± 0.30	**	-0.23 ± 0.15	-0.2
	Reciprocal full-sib	200	215	220	220	218				-4.78 ± 0.30**	**	-2.39 ± 0.15**	-2.0
	S <sub>1</sub> -progeny	231	233	225	225	221				-2.65 ± 0.30**	-	-1.32 ± 0.15**	-1.1
	S <sub>2</sub> -progeny	236	239	228	224	-				-1.82 ± 0.40**	**	-0.61 ± 0.13**	-0.8
Testcrosses to BS11 C0	Full-sib	237	234	238	234	230	226		234.9	-1.10 ± 0.30**	*	-0.55 ± 0.15**	-0.5
	Half-sib	235	241	232	234	-				0.02 ± 0.40	-	0.01 ± 0.13	0.0
	Mass	232	232	218	231	230				-0.90 ± 0.15**	**	-0.90 ± 0.15**	-0.4
	Modified ear-to-row	238	241	242	239	233				0.80 ± 0.30**	**	0.40 ± 0.15**	0.3
	Reciprocal full-sib	214	224	227	230	229				-2.09 ± 0.30**	**	-1.04 ± 0.15**	-0.9
	S <sub>1</sub> -progeny	235	225	228	226	225				-2.27 ± 0.30**	-	-1.13 ± 0.15**	-1.0
	S <sub>2</sub> -progeny	235	239	229	231	-				-0.82 ± 0.40**	-	-0.27 ± 0.13**	-0.3
Testcrosses to inbred B79	Full-sib	240	235	238	233	230	221		238.7	-2.65 ± 0.31**	*	-1.33 ± 0.16**	-1.1
	Half-sib	239	238	230	242	-				-0.47 ± 0.41	*	-0.16 ± 0.14	-0.2
	Mass	239	234	220	236	230				-1.09 ± 0.16**	**	-1.09 ± 0.16**	-0.5
	Modified ear-to-row	243	246	242	238	232				-0.14 ± 0.31	**	-0.07 ± 0.16	-0.1
	Reciprocal full-sib	211	227	231	228	233				-2.65 ± 0.31**	**	-1.33 ± 0.16**	-1.1
	S <sub>1</sub> -progeny	235	225	228	226	225				-1.58 ± 0.31**	-	-0.79 ± 0.16**	-0.7
	S <sub>2</sub> -progeny	235	239	229	231	-				-1.37 ± 0.41**	-	-0.46 ± 0.14**	-0.6
S <sub>1</sub> populations per se	Full-sib	223	218	223	222	216	204	2.47	221.9	-2.08 ± 0.37**	**	-1.04 ± 0.18**	-0.9
	Half-sib	220	219	208	221	-				-1.76 ± 0.49**	*	-0.59 ± 0.16**	-0.8
	Mass	218	216	195	211	213				-1.67 ± 0.18**	**	-1.67 ± 0.18**	-0.8
	Modified ear-to-row	225	232	229	225	219				0.78 ± 0.37*	**	0.39 ± 0.18*	0.4
	Reciprocal full-sib	187	201	208	207	205				-4.77 ± 0.37**	**	-2.38 ± 0.18**	-2.1
	S <sub>1</sub> -progeny	222	222	216	212	214				-1.75 ± 0.37**	-	-0.87 ± 0.18**	-0.8
	S <sub>2</sub> -progeny	228	227	219	217	-				-0.39 ± 0.49	**	-0.13 ± 0.16	-0.2

\*,\*\* Significant linear or quadratic response at the 0.05 and 0.01 probability levels, respectively.

† Check means, in g kg<sup>-1</sup>: B79 × B77 = 2.38; B79 × Mo17 = 212; B73 × B95 = 222; B73 × Mo17 = 211; B79 = 210.

‡ Standard errors for C0s are S.E./20<sup>1/2</sup> for BS11C0 and S.E./10<sup>1/2</sup> for BS11C0 × B79 and for BS11C0 S<sub>1</sub>.

§ b<sub>0</sub> is an estimate of the C0 mean; b<sub>1</sub> is an estimate of the average rate of response per cycle; b<sub>q</sub> is included to indicate when the quadratic term was significant.

¶ Response per year calculated based on number of years to complete each cycle given previously.

# The percentage response per cycle was calculated as the ratio of b<sub>1</sub> to the estimated C0 intercept and multiplied by 100.

†† Cycle not included in study.

‡‡ C1, C2, C3, C4, and C5 correspond to cycles 2, 4, 6, 8, and 10 for mass selection only.

responses to the selection methods for grain yield. A nonsignificant decrease in grain yield over cycles of selection was found in the selfed populations for both the HI and mass selection programs. Selection increased the grain yield for the selfed populations for the other five methods with the greatest response per cycle for S<sub>2</sub>-progeny selection of 0.19 Mg ha<sup>-1</sup> (5.8%). Modified ear-to-row, FR, and S<sub>1</sub>-progeny selection had similar and significant increases in grain yield. On a per year basis, FR, S<sub>1</sub>, and S<sub>2</sub> progeny selection had equivalent increases in grain yield of 0.06 Mg ha<sup>-1</sup> yr<sup>-1</sup> in the selfed populations.

Response for grain moisture was in the desirable direction for all methods of selection (Table 4 and Fig. 1B). Grain moisture decreased for the populations per se at the greatest rate in the FR program (-4.8 g kg<sup>-1</sup> cycle<sup>-1</sup>). Significant decreases were also found for all other selection methods except MER, which had a nonsignificant response for grain moisture. In the testcrosses to the C0 population, all selection methods, except for HI and MER, resulted in significantly decreased grain moisture. S<sub>1</sub>-progeny selection had the greatest response of -2.3 g kg<sup>-1</sup> cycle<sup>-1</sup> or -1.1 g kg<sup>-1</sup> yr<sup>-1</sup>. Similar to the C0 crosses, testcrosses to B79 decreased in grain moisture for all selection methods with FS and FR having the greatest responses of -2.7 g kg<sup>-1</sup> cycle<sup>-1</sup>. An

evaluation of the selfed populations showed that FR selection, similar to the populations per se, had the greatest response in the desirable direction of -4.8 g kg<sup>-1</sup> cycle<sup>-1</sup>, whereas MER selection significantly increased in grain moisture (0.8 g kg<sup>-1</sup> cycle<sup>-1</sup>).

Selection response for stalk lodging was also generally in the desired direction. Stalk lodging in BS11C0 averaged 20%, and five of the seven selection methods effectively reduced this by nearly 50% after only four or five cycles of selection (Table 5 and Fig. 1C). Mass selection had a significant increase in stalk lodging of 0.3% cycle<sup>-1</sup>, and FR selection was not effective in changing the stalk lodging in the population per se. S<sub>2</sub>-progeny selection had the greatest decrease of -2.4% cycle<sup>-1</sup> in the populations per se and was slightly more effective than MER, which decreased -2.2% cycle<sup>-1</sup> of selection. For both the population crosses to the C0 and to inbred B79, stalk lodging decreased significantly for all selection methods except for mass selection. In both population types, stalk lodging was reduced at the greatest rate with S<sub>2</sub>-progeny selection (-1.8% cycle<sup>-1</sup> for crosses to the C0 and B79). Likewise, S<sub>2</sub>-progeny selection resulted in the greatest decrease in stalk lodging in the selfed populations (-2.6% cycle<sup>-1</sup>).

Root lodging was the fourth trait under direct selection in most of the programs. In all instances (all types

**Table 5. Observed mean stalk lodging for each cycle of seven selection methods and least squares estimates of response to selection in the BS11 maize population. Data combined over 11 environments for all population types.†**

Population type	Selection method	Cycle of selection						S.E. of mean‡	Regression coefficients§			Response per year¶	Percentage response#
		C0	C1	C2	C3	C4	C5		b <sub>0</sub>	b <sub>1</sub>	b <sub>q</sub>		
%													
S <sub>0</sub> populations per se	Full-sib	20.0	18.8	15.3	15.8	11.4	9.3	1.14	20.5	-2.15 ± 0.16**	-	-1.08 ± 0.08**	-10.5
	Half-sib		19.6	18.3	13.8	11.1	-††			-2.10 ± 0.22**	*	-0.70 ± 0.07**	-10.2
	Mass‡‡		22.1	21.2	22.1	23.0	24.1			0.33 ± 0.08**	-	0.33 ± 0.08**	1.6
	Modified ear-to-row		19.3	14.1	13.6	11.5	10.6			-2.18 ± 0.16**	-	-1.09 ± 0.08**	-10.7
	Reciprocal full-sib		22.1	19.3	17.5	20.2	22.8			0.01 ± 0.16	*	0.01 ± 0.08	0.1
	S <sub>1</sub> -progeny		18.8	18.9	13.6	13.1	9.3			-2.02 ± 0.16**	-	-1.01 ± 0.08**	-9.9
	S <sub>2</sub> -progeny		18.7	13.3	13.1	11.8	-			-2.44 ± 0.22**	-	-0.81 ± 0.07**	-11.9
	Testcrosses to BS11 C0	Full-sib	20.0	19.1	19.3	17.2	17.3	13.8		20.5	-1.09 ± 0.16**	-	-0.54 ± 0.08**
	Half-sib		18.6	18.7	16.1	15.2	-			-1.33 ± 0.22**	-	-0.44 ± 0.07**	-6.5
	Mass		20.0	21.7	21.8	21.7	19.2			0.04 ± 0.08	-	0.04 ± 0.08	0.2
	Modified ear-to-row		19.5	18.5	15.3	15.0	16.0			-1.18 ± 0.16**	-	-0.59 ± 0.08**	-5.8
	Reciprocal full-sib		18.9	18.3	19.5	18.2	18.7			-0.49 ± 0.16**	-	-0.25 ± 0.08**	-2.4
	S <sub>1</sub> -progeny		18.3	20.8	15.8	15.3	14.8			-1.18 ± 0.16**	-	-0.59 ± 0.08**	-5.8
	S <sub>2</sub> -progeny		18.8	13.9	15.4	14.8	-			-1.76 ± 0.22**	*	-0.59 ± 0.07**	-8.6
Testcrosses to inbred B79	Full-sib	20.7	19.1	16.6	16.6	13.9	14.9		20.8	-1.45 ± 0.17**	-	-0.73 ± 0.09**	-7.0
	Half-sib		19.8	18.8	15.1	15.1	-			-1.50 ± 0.23**	-	-0.50 ± 0.08**	-7.2
	Mass		20.5	21.2	22.2	21.4	21.6			0.10 ± 0.09	-	0.10 ± 0.09	0.5
	Modified ear-to-row		21.3	17.3	17.6	16.4	14.4			-1.19 ± 0.17**	-	-0.60 ± 0.09**	-5.7
	Reciprocal full-sib		19.8	18.3	17.8	19.0	16.7			-0.78 ± 0.17**	-	-0.39 ± 0.09**	-3.7
	S <sub>1</sub> -progeny		19.7	18.4	16.6	15.2	13.1			-1.44 ± 0.17**	-	-0.72 ± 0.09**	-6.9
	S <sub>2</sub> -progeny		18.2	16.4	15.6	13.8	-			-1.83 ± 0.23**	-	-0.61 ± 0.08**	-8.8
S <sub>1</sub> populations per se	Full-sib	18.5	17.4	17.6	12.1	9.0	8.9	0.97	18.9	-2.08 ± 0.14**	-	-1.04 ± 0.07**	-11.0
	Half-sib		16.2	14.0	11.8	10.2	-			-2.29 ± 0.19**	-	-0.76 ± 0.06**	-12.1
	Mass		16.9	21.1	21.5	18.3	18.3			0.04 ± 0.07	-	0.04 ± 0.07	0.2
	Modified ear-to-row		16.6	13.7	11.0	11.2	11.8			-1.87 ± 0.14**	**	-0.93 ± 0.07**	-9.9
	Reciprocal full-sib		21.9	16.8	13.2	18.8	17.0			-0.51 ± 0.14**	-	-0.26 ± 0.07**	-2.7
	S <sub>1</sub> -progeny		16.4	17.7	11.4	11.5	8.9			-1.95 ± 0.14**	-	-0.97 ± 0.07**	-10.3
	S <sub>2</sub> -progeny		16.9	10.9	10.8	10.2	-			-2.57 ± 0.19**	*	-0.86 ± 0.06**	-13.6

\*,\*\* Significant linear or quadratic response at the 0.05 and 0.01 probability levels, respectively.

† Check means, in %: B79 × B77 = 18.6; B79 × Mo17 = 15.3; B73 × B95 = 11.2; B73 × Mo17 = 7.2; B79 = 9.4.

‡ Standard errors for C0s are S.E./20<sup>1/2</sup> for BS11C0 and S.E./10<sup>1/2</sup> for BS11C0 × B79 and for BS11C0 S<sub>1</sub>.

§ b<sub>0</sub> is an estimate of the C0 mean; b<sub>1</sub> is an estimate of the average rate of response per cycle; b<sub>q</sub> is included to indicate when the quadratic term was significant.

¶ Response per year calculated based on number of years to complete each cycle given previously.

# The percentage response per cycle was calculated as the ratio of b<sub>1</sub> to the estimated C0 intercept and multiplied by 100.

†† Cycle not included in study.

‡‡ C1, C2, C3, C4, and C5 correspond to cycles 2, 4, 6, 8, and 10 for mass selection only.

of populations and all selection methods), selection response for root lodging was in the desirable direction (Table 6 and Fig. 1D). S<sub>1</sub>-progeny and HI selection were the most effective methods for decreasing root lodging in the population per se (-1.3% cycle<sup>-1</sup>). By the final cycle of S<sub>1</sub>-progeny and HI selection, root lodging decreased from 6.1% in the C0 to 1.0% or less. S<sub>1</sub>-progeny selection was the most effective method for reducing root lodging in the C0 and B79 testcrosses and in the selfed populations. Root lodging showed no significant response to mass selection in any of the four population types evaluated.

### Correlated Responses

Selection based on grain yield, grain moisture, stalk lodging, and root lodging also resulted in significant changes in other agronomic traits (Table 7). Plant and ear height in the populations per se were significantly reduced with all selection methods except for mass. Inconsistent responses among selection methods were found for top height. Although significant responses for top height were found in both directions, they rarely exceeded a 1-cm decrease or increase cycle<sup>-1</sup>.

The percentage of plants with dropped ears showed little-to-no response to selection. Only two significant responses associated with S<sub>1</sub>-progeny selection in the

populations per se and the B79 testcrosses were detected. The mean percentage of dropped ears for the C0 was 1%; the equivalent of less than one dropped ear per plot. The overall experiment mean in the various environments ranged from 0.1 to 2.2% dropped ears.

The number of GDUs required to reach mid-silk decreased significantly in the populations per se for all selection methods and ranged from -2.10 (mass) to -16.30 GDU cycle<sup>-1</sup> (S<sub>1</sub>-progeny) (Table 7). Populations developed with S<sub>1</sub> and S<sub>2</sub>-progeny selection methods required 16 and 12 fewer GDU to reach mid-silk with each cycle of selection, respectively. Assuming an average of 13 GDU day<sup>-1</sup> in July, the responses in S<sub>1</sub> and S<sub>2</sub>-progeny selection would be equivalent to decreasing time to mid-silk by 1 d with each cycle of selection. Cycle 5 of S<sub>1</sub>-progeny selection and C4 of S<sub>2</sub>-progeny selection are 6.0 and 4.5 d earlier than the C0, respectively (data not shown). Although responses in GDU requirement for the other selection methods were significant, they amounted to less than a 1-d reduction in GDU cycle<sup>-1</sup>. Responses for GDU in the BS11C0 and B79 testcrosses were inconsistent among selection methods. The FS, FR, S<sub>1</sub>, and S<sub>2</sub>-progeny selection methods also had significant decreases in the GDU to mid-silk for the testcrosses. The selfed populations were later-maturing and on average required a greater number of GDU to reach mid-silk compared with the S<sub>0</sub> popula-



**Table 6. Observed mean root lodging for each cycle of seven selection methods and least squares estimates of response to selection in the BS11 maize population. Data combined over 11 environments for all population types.†**

Population type	Selection method	Cycle of selection						S.E. of mean‡	Regression coefficients§			Response per year¶	Percentage response#
		C0	C1	C2	C3	C4	C5		b <sub>0</sub>	b <sub>1</sub>	b <sub>q</sub>		
%													
S <sub>0</sub> populations per se	Full-sib	6.1	2.9	3.6	1.7	0.8	1.7	0.77	5.8	-1.10 ± 0.11**	**	-0.55 ± 0.05**	-18.9
	Half-sib		5.7	3.2	1.5	1.0	-††			-1.26 ± 0.15**	-	-0.42 ± 0.05**	-21.6
	Mass‡‡		7.2	4.8	4.0	5.9	5.5			-0.07 ± 0.05	-	-0.07 ± 0.05	-1.2
	Modified ear-to-row		4.9	2.7	4.2	2.3	2.7			-0.76 ± 0.11**	-	-0.38 ± 0.05**	-13.1
	Reciprocal full-sib		2.0	3.6	2.7	3.5	4.1			-0.65 ± 0.11**	**	-0.33 ± 0.05**	-11.1
	S <sub>1</sub> -progeny		3.8	2.7	0.9	0.9	0.6			-1.26 ± 0.11**	*	-0.63 ± 0.05**	-21.5
	S <sub>2</sub> -progeny		3.4	2.7	1.6	2.5	-			-1.16 ± 0.15**	**	-0.39 ± 0.05**	-19.9
Testcrosses to BS11 C0	Full-sib	6.1	4.6	4.3	3.4	3.0	2.4		5.8	-0.73 ± 0.11**	-	-0.37 ± 0.05**	-12.5
	Half-sib		4.8	5.2	3.4	2.0	-			-0.83 ± 0.15**	-	-0.28 ± 0.05**	-14.3
	Mass		6.6	5.3	3.6	5.4	6.7			-0.04 ± 0.05	*	-0.04 ± 0.05	-0.7
	Modified ear-to-row		5.8	4.6	4.8	5.0	3.1			-0.41 ± 0.11**	-	-0.21 ± 0.05**	-7.1
	Reciprocal full-sib		2.8	3.8	3.6	3.7	4.3			-0.55 ± 0.11**	**	-0.27 ± 0.05**	-9.4
	S <sub>1</sub> -progeny		4.5	3.2	3.3	1.3	1.5			-0.98 ± 0.11**	-	-0.49 ± 0.05**	-16.8
	S <sub>2</sub> -progeny		6.3	4.3	2.9	3.0	-			-0.76 ± 0.15**	-	-0.25 ± 0.05**	-13.0
Testcrosses to inbred B79	Full-sib	2.5	2.5	2.6	1.8	1.7	1.1		2.7	-0.28 ± 0.11*	-	-0.14 ± 0.06*	-10.4
	Half-sib		2.7	1.2	1.4	1.4	-			-0.41 ± 0.15*	-	-0.14 ± 0.05*	-15.1
	Mass		2.4	2.7	2.5	3.3	2.1			-0.02 ± 0.06	-	-0.02 ± 0.06	-0.6
	Modified ear-to-row		2.8	2.0	2.5	2.1	2.4			-0.11 ± 0.11	-	-0.06 ± 0.06	-4.2
	Reciprocal full-sib		1.7	2.0	2.7	1.6	1.6			-0.23 ± 0.11	-	-0.12 ± 0.06	-8.5
	S <sub>1</sub> -progeny		2.6	1.2	1.4	1.0	0.6			-0.45 ± 0.11**	-	-0.22 ± 0.06**	-16.5
	S <sub>2</sub> -progeny		3.2	1.1	1.9	2.0	-			-0.27 ± 0.15	-	-0.09 ± 0.05	-10.0
S <sub>1</sub> populations per se	Full-sib	5.9	5.1	4.0	4.1	1.7	1.5	0.97	6.3	-1.00 ± 0.14**	-	-0.50 ± 0.07**	-15.9
	Half-sib		4.0	3.2	2.4	2.3	-			-1.22 ± 0.19**	-	-0.41 ± 0.06**	-19.2
	Mass		6.1	6.6	2.9	5.4	5.9			-0.14 ± 0.07	-	-0.14 ± 0.07	-2.3
	Modified ear-to-row		6.5	4.6	4.7	3.8	3.4			-0.60 ± 0.14**	-	-0.30 ± 0.07**	-9.5
	Reciprocal full-sib		3.2	4.8	3.1	5.3	3.1			-0.66 ± 0.14**	-	-0.33 ± 0.07**	-10.4
	S <sub>1</sub> -progeny		4.1	5.5	0.8	0.7	0.6			-1.30 ± 0.14**	-	-0.65 ± 0.07**	-20.6
	S <sub>2</sub> -progeny		4.8	2.4	3.1	1.9	-			-1.23 ± 0.19**	-	-0.41 ± 0.06**	-19.4

\*,\*\* Significant linear or quadratic response at the 0.05 and 0.01 probability levels, respectively.

† Check means, in %: B79 × B77 = 1.5; B79 × Mo17 = 0.9; B73 × B95 = 3.8; B73 × Mo17 = 2.7; B79 = 1.9.

‡ Standard errors for C0s are S.E./20<sup>1/2</sup> for BS11C0 and S.E./10<sup>1/2</sup> for BS11C0 × B79 and for BS11C0 S<sub>1</sub>.

§ b<sub>0</sub> is an estimate of the C0 mean; b<sub>1</sub> is an estimate of the average rate of response per cycle; b<sub>q</sub> is included to indicate when the quadratic term was significant.

¶ Response per year calculated based on number of years to complete each cycle given previously.

# The percentage response per cycle was calculated as the ratio of b<sub>1</sub> to the estimated C0 intercept and multiplied by 100.

†† Cycle not included in study.

‡‡ C1, C2, C3, C4, and C5 correspond to cycles 2, 4, 6, 8, and 10 for mass selection only.

tions. Responses for the selfed populations were in the negative direction, but were not significant for the HI, mass, and MER selection methods. Growing degree unit changes year<sup>-1</sup> were the greatest for S<sub>1</sub>-progeny selection in all four population types.

### Inbreeding Depression

Significant inbreeding depression was found for grain yield for all cycles of selection and for each selection method (Table 8). There was no clear trend over cycles of selection for changes in inbreeding depression with any selection method when expressed in either absolute units or as a percentage of the noninbred mean. Significant inbreeding depression was found for grain moisture at harvest for most cycles of most selection methods. No trend in relative magnitude of inbreeding depression was found for grain moisture, with the exception of the HI selection method. For the HI selection method, there was a decrease in the amount of inbreeding depression over cycles of selection expressed in both absolute units and as a percentage of the noninbred mean. Inbreeding depression for stalk lodging was inconsistent among cycles of selection and methods and no trends for inbreeding depression were evident. Inbreeding depression for root lodging was significant for only S<sub>1</sub>-progeny selection, and no trends were evident among selection methods.

### Realized Heritability

Realized heritabilities were calculated to determine the amount of the cumulative selection differential realized in each of the selection programs (Table 9). The cumulative selection differentials were large for grain yield as were the predicted gains from selection. The cumulative selection differential was smallest for the HI program (2.69 Mg ha<sup>-1</sup>). Because of a lower heritability (47.1%) in the selection trials, the HI program had the least predicted gain (1.31 Mg ha<sup>-1</sup>). The S<sub>2</sub>-progeny selection method had the greatest predicted gain (4.11 Mg ha<sup>-1</sup>) for grain yield because of a larger cumulative selection differential (4.74 Mg ha<sup>-1</sup>) and a greater average h<sup>2</sup> in the selection trials (86.7%). Realized heritabilities for grain yield, in the populations per se, were small and ranged from 9.3 (FS) to 25.6% (MER).

Realized heritabilities for grain moisture at harvest ranged from 0.0 (S<sub>2</sub>-progeny) to 41.6% (FS). Realized heritability for stalk lodging in the populations per se ranged from 26.7 (HI) to 54.9% (MER). Realized heritability for root lodging was similar to stalk lodging and ranged from 5.7 (HI) to 27.9% (S<sub>1</sub>-progeny).

### Relative Economic Gain

In a comparison of selection methods, not only rates of genetic improvement should be compared but also

**Table 7. Least squares estimates of response per cycle to seven selection methods for five agronomic traits in the BS11 maize population. Values in parentheses are percentage responses per cycle.†**

Population type	Selection method	Height			Dropped ears	Growing degree units to mid-silk
		Plant	Ear	Top		
		cm			%	°C
S <sub>0</sub> populations per se	Full-sib	-5.75** (-2.4)	-6.11** (-4.6)	0.38** (0.3)	-0.06 (-5.9)	-8.08** (-0.9)
	Half-sib	-5.07** (-2.1)	-4.74** (-3.6)	-0.34** (-0.3)	-0.01 (-0.7)	-8.94** (-1.0)
	Mass	-0.18 (-0.1)	0.02 (0.0)	-0.18 (-0.2)	0.00 (-0.3)	-2.10** (-0.2)
	Modified ear-to-row	-1.05** (-0.4)	-2.17** (-1.6)	1.10** (1.0)	0.01 (1.4)	-3.68** (-0.4)
	Reciprocal full-sib	-2.85** (-1.2)	-2.23** (-1.7)	-0.64** (-0.6)	0.03 (2.9)	-9.85** (1.1)
	S <sub>1</sub> -progeny	-8.07** (-3.3)	-6.52** (-4.9)	-1.59** (-1.4)	-0.09** (-9.3)	-16.30** (-1.8)
	S <sub>2</sub> -progeny	-3.60** (-1.5)	-3.87** (-2.9)	0.27** (0.2)	0.10** (10.6)	-12.16** (-1.4)
Testcrosses to BS11 C0	Full-sib	-2.16** (-0.9)	-2.66** (-2.0)	0.47** (0.4)	0.02 (1.7)	-3.78** (-0.4)
	Half-sib	-1.20** (-0.5)	-1.90** (-1.4)	0.73** (0.7)	0.02 (1.7)	-1.55 (-0.2)
	Mass	0.64** (0.3)	0.41** (0.3)	0.25** (0.2)	0.00 (0.3)	0.14 (0.0)
	Modified ear-to-row	0.61* (0.2)	-0.34 (-0.3)	0.96** (0.9)	0.02 (2.5)	0.26 (0.0)
	Reciprocal full-sib	-0.53* (-0.2)	-1.10** (-0.8)	0.61** (0.5)	0.05 (5.5)	-4.90** (-0.6)
	S <sub>1</sub> -progeny	-3.81** (-1.6)	-3.54** (-2.7)	-0.27 (-0.2)	-0.04 (-3.7)	-10.39** (-1.2)
	S <sub>2</sub> -progeny	-0.82* (-0.3)	-1.53** (-1.2)	0.72** (0.6)	0.08 (7.8)	-4.57** (-0.5)
Testcrosses to inbred B79	Full-sib	-2.00** (-0.9)	-2.59** (-2.0)	0.59** (0.6)	-0.01 (-1.0)	-3.47** (-0.4)
	Half-sib	-0.75* (-0.3)	-1.78** (-1.4)	1.02** (1.0)	-0.01 (-1.3)	-2.47* (-0.3)
	Mass	0.31* (0.1)	0.07 (0.1)	0.22* (0.2)	-0.02 (-2.5)	0.19 (0.0)
	Modified ear-to-row	0.90** (0.4)	0.06 (0.0)	0.83** (0.8)	-0.01 (-1.0)	-0.09 (0.0)
	Reciprocal full-sib	-0.33 (-0.1)	-0.64* (-0.5)	0.30 (0.3)	0.04 (4.7)	-3.44** (-0.4)
	S <sub>1</sub> -progeny	-2.97** (-1.3)	-2.89** (-2.3)	-0.13 (-0.1)	-0.07** (-8.9)	-6.71** (-0.8)
	S <sub>2</sub> -progeny	-0.13 (-0.1)	-1.43** (-1.1)	1.32** (1.3)	0.02 (2.9)	-3.48** (-0.4)
S <sub>1</sub> populations per se	Full-sib	-3.02** (-1.4)	-3.77** (-3.5)	0.73** (0.7)	-0.05 (-7.1)	-5.53** (-0.6)
	Half-sib	-2.40** (-1.2)	-2.31** (-2.1)	0.00 (0.0)	-0.03 (-4.8)	-1.62 (-0.2)
	Mass	-0.07 (0.0)	-0.09 (-0.1)	0.01 (0.0)	-0.01 (-1.6)	-0.11 (0.0)
	Modified ear-to-row	1.30** (0.6)	-0.01 (0.0)	1.32** (1.3)	-0.02 (-2.1)	-0.12 (0.0)
	Reciprocal full-sib	-1.70** (-0.8)	-1.20** (-1.1)	-0.45* (-0.4)	-0.03 (-4.7)	-6.14** (-0.7)
	S <sub>1</sub> -progeny	-5.94** (-2.8)	-4.92** (-4.6)	-0.95** (-0.9)	-0.03 (-4.7)	-10.53** (-1.2)
	S <sub>2</sub> -progeny	-2.04** (-1.0)	-2.53** (-2.3)	0.54 (0.5)	0.02 (2.8)	-11.15** (-1.2)

\*,\*\* Significant linear response at the 0.05 and 0.01 probability levels, respectively.

† The percentage response per cycle was calculated as the ratio of b<sub>1</sub> to the estimated C0 intercept and multiplied by 100.

the costs of obtaining the improvement. Estimates of costs presented in Table 10 serve only as a guide to the relative costs of conducting these selection methods. Estimates of the cost cycle<sup>-1</sup> are completely independent

of time for one unit of gain and, likewise, the time to achieve one unit of gain is independent of cost per unit of gain. The average cost to conduct a cycle of selection ranged from \$350 (Mass) to \$14 300 (HI). Av-

**Table 8. Inbreeding depression in actual units and percentage (in parentheses) for seven selection methods in the BS11 maize population for four traits upon which selection was practiced.**

Trait	Cycle	Selection method						
		Full-sib	Half-sib	Mass†	Modified ear-to-row	Reciprocal full-sib	S <sub>1</sub> progeny	S <sub>2</sub> progeny
Grain yield (Mg ha <sup>-1</sup> )	C0	1.33** ‡(29.4)						
	C1	1.39** (30.4)	1.67** (33.7)	1.24** (27.4)	1.54** (32.6)	1.13** (25.6)	1.33** (27.4)	1.20** (25.6)
	C2	1.44** (31.3)	1.41** (29.3)	1.45** (30.7)	1.66** (33.7)	1.33** (25.3)	1.03** (22.3)	1.42** (26.9)
	C3	1.59** (32.2)	1.80** (37.8)	1.27** (28.3)	1.43** (27.7)	1.39** (27.1)	1.19** (24.6)	1.27** (25.1)
	C4	1.71** (34.0)	1.53** (32.1)	1.85** (38.5)	1.78** (33.5)	1.57** (31.0)	1.25** (25.3)	1.58** (28.9)
C5	1.17** (24.9)	-	1.70** (35.0)	1.74** (32.7)	1.11** (22.6)	1.38** (26.9)	-	
Grain moisture (g kg <sup>-1</sup> )	C0	17** (7.1)						
	C1	13** (5.6)	16** (6.8)	10** (4.4)	9** (3.8)	15** (7.4)	12** (5.1)	11** (4.6)
	C2	5 (2.2)	15** (6.4)	12** (5.3)	14** (5.7)	16** (7.4)	13** (5.5)	15** (6.2)
	C3	11** (4.7)	13** (5.9)	13** (6.3)	6 (2.6)	15** (6.7)	11** (4.8)	11** (4.8)
	C4	10** (4.4)	9** (3.9)	6 (2.8)	14** (5.9)	15** (6.8)	15** (6.6)	10** (4.4)
C5	20** (8.9)	-	1 (0.5)	10** (4.4)	16** (7.2)	10** (4.5)	-	
Stalk lodging (%)	C0	3.3* (15.9)						
	C1	3.4* (17.3)	5.5** (26.7)	6.6** (28.2)	4.6** (22.4)	3.1* (13.3)	4.4** (22.0)	3.3* (16.9)
	C2	-0.2 (-1.3)	5.5** (28.8)	2.7 (12.3)	1.2 (8.3)	4.2** (20.6)	3.3** (16.6)	3.3* (23.6)
	C3	4.6** (28.4)	3.3* (22.6)	2.8 (12.3)	4.0** (27.4)	6.1** (32.6)	3.0* (20.8)	2.3 (17.4)
	C4	3.3* (27.5)	1.9 (15.7)	6.1** (25.4)	0.8 (6.7)	3.9* (18.1)	3.3* (23.2)	2.9 (23.2)
C5	1.0 (10.1)	-	8.5** (32.9)	-0.3 (-2.7)	7.5** (31.9)	1.9 (19.2)	-	
Root lodging (%)	C0	0.4 (6.3)						
	C1	-2.2 (-71.0)	2.1 (35.0)	1.9 (25.0)	-1.5 (-30.0)	-1.0 (-45.5)	-0.2 (-5.0)	-1.1 (-29.7)
	C2	0.0 (0.0)	0.0 (0.0)	-1.9 (-40.4)	-1.3 (-43.3)	-1.1 (-29.7)	-2.7* (-93.1)	0.7 (24.1)
	C3	-2.1 (-116.7)	-0.8 (-50.0)	1.6 (37.2)	-0.2 (-4.5)	-0.2 (-6.9)	0.1 (11.1)	-1.2 (-66.7)
	C4	-0.9 (-112.5)	-1.2 (-109.0)	0.8 (13.1)	-1.7 (-77.3)	-1.6 (-42.1)	0.1 (12.50)	0.8 (29.6)
C5	0.4 (22.2)	-	0.0 (0.0)	-0.4 (-14.8)	1.6 (35.6)	0.2 (28.6)	-	

\*,\*\* Significant at the 0.05 and 0.01 probability level, respectively.

† C1, C2, C3, C4 and C5 correspond to cycles 2, 4, 6, 8, and 10 for mass selection only.

‡ The percentage inbreeding depression was calculated by dividing inbreeding depression in absolute units by the noninbred mean and multiplying by 100.

**Table 9. Cumulative selection differentials (Cum. S), predicted gain, realized heritabilities (underscored), and correlated heritabilities of six selection methods and four progeny types in the BS11 maize population.**

Trait	Method	Cum. S	Predicted gain†	Populations per se	Realized heritability		
					Crosses to		Populations selfed
					C0	B79	
					%		
Grain yield (Mg ha <sup>-1</sup> )	Full-sib	3.80	2.52	<u>9.3 ± 2.3</u>	15.1 ± 2.3	5.9 ± 2.4	4.6 ± 2.0
	Half-sib	2.69	1.31	<u>12.4 ± 3.5</u>	18.5 ± 3.5	<u>15.1 ± 3.7</u>	-1.5 ± 3.0
	Modified ear-to-row	3.38	1.89	<u>25.6 ± 2.6</u>	23.2 ± 2.6	<u>18.8 ± 2.8</u>	11.9 ± 2.3
	Reciprocal full-sib	5.31	3.19	<u>12.6 ± 1.8</u>	17.4 ± 1.8	9.0 ± 1.9	12.1 ± 1.5
	S <sub>1</sub> -progeny	3.52	2.50	<u>12.6 ± 2.4</u>	14.9 ± 2.4	7.5 ± 2.5	16.1 ± 2.1
	S <sub>2</sub> -progeny	4.74	4.11	<u>18.0 ± 2.0</u>	20.6 ± 2.0	7.0 ± 2.1	<u>16.1 ± 1.7</u>
Grain moisture (g kg <sup>-1</sup> )	Full-sib	-24.0	-18.3	<u>41.6 ± 6.2</u>	24.6 ± 6.2	45.4 ± 6.3	25.3 ± 7.5
	Half-sib	2.0	0.9	‡	-	-	-
	Modified ear-to-row	-27.0	-19.7	<u>2.4 ± 6.2</u>	-9.7 ± 6.2	0.2 ± 6.3	-25.8 ± 7.4
	Reciprocal full-sib	-13.0	-6.8	NA§	NA	NA	NA
	S <sub>1</sub> -progeny	-16.0	-12.4	<u>73.2 ± 10.9</u>	85.4 ± 10.9	38.9 ± 11.1	<u>30.1 ± 13.1</u>
	S <sub>2</sub> -progeny	-29.0	-25.1	<u>24.4 ± 6.1</u>	17.8 ± 6.1	16.2 ± 6.2	<u>-0.9 ± 7.4</u>
Stalk lodging (%)	Full-sib	-26.4	-17.1	<u>40.1 ± 3.2</u>	18.3 ± 3.2	25.5 ± 3.3	39.1 ± 2.8
	Half-sib	-22.2	-13.2	<u>39.8 ± 4.4</u>	22.7 ± 4.4	26.7 ± 4.5	41.7 ± 3.8
	Modified ear-to-row	-19.2	-10.1	<u>54.9 ± 4.4</u>	27.3 ± 4.4	<u>28.5 ± 4.6</u>	45.5 ± 3.9
	Reciprocal full-sib	-13.8	-7.4	NA	NA	NA	NA
	S <sub>1</sub> -progeny	-25.8	-17.9	<u>38.2 ± 3.3</u>	20.6 ± 3.3	26.1 ± 3.4	36.3 ± 2.9
	S <sub>2</sub> -progeny	-25.7	-18.1	<u>31.9 ± 3.1</u>	22.2 ± 3.1	23.1 ± 3.2	<u>33.6 ± 2.7</u>
Root lodging (%)	Full-sib	-17.6	-9.0	<u>26.9 ± 2.9</u>	18.8 ± 2.9	4.5 ± 3.0	19.9 ± 3.8
	Half-sib	-16.1	-7.4	<u>22.6 ± 3.1</u>	16.1 ± 3.1	<u>5.7 ± 3.2</u>	19.4 ± 4.1
	Modified ear-to-row	-19.7	-10.5	<u>18.9 ± 3.1</u>	11.7 ± 3.1	<u>0.3 ± 3.3</u>	9.9 ± 4.1
	Reciprocal full-sib	-1.0	-0.5	NA	NA	NA	NA
	S <sub>1</sub> -progeny	-19.2	-12.0	<u>28.2 ± 2.8</u>	23.5 ± 2.8	8.5 ± 2.9	27.9 ± 3.6
	S <sub>2</sub> -progeny	-16.0	-11.6	<u>24.4 ± 3.3</u>	16.2 ± 3.3	3.2 ± 3.5	<u>20.7 ± 4.3</u>

† Calculated by multiplying  $h^2 \times S$  (Table 1) for each cycle and summing over cycles. When  $h^2$  was not given, the value for the mean  $h^2$  for the particular selection method was used.

‡ Values not reported because of inconsistent direction of selection differential among cycles causing random fluctuation of cumulated S around zero over cycles of selection.

§ Selection was not directly practiced for these traits in the FR program causing random fluctuations of the cumulated S.

erage costs year<sup>-1</sup> ranged from \$350 (Mass) to \$6050 (FR). The cost year<sup>-1</sup> of the FR selection method was so high partly because nearly double the number of families were evaluated in yield trials in comparison with other selection methods (Table 1). This increased cost would be expected to be partly offset by the increased gain cycle<sup>-1</sup> from a higher selection intensity.

More important than the cost cycle<sup>-1</sup> is the investment needed to achieve a given amount of gain. In our study, a 1 Mg ha<sup>-1</sup> increase in grain yield would be equivalent to a 21% increase over the C0. The cost unit<sup>-1</sup> gain ranged from \$12 122 (Mass) to \$190 058 (HI). The length

of time required to achieve a 1 Mg ha<sup>-1</sup> increase in grain yield ranged from 12 (MER) to 40 (HI) yr.

## DISCUSSION

It is clear from the results of our study, and from previous studies, that recurrent selection methods can be successfully utilized for the improvement of maize populations. Empirical data are lacking for the direct comparison of more than a few recurrent selection methods in any given maize population, however. Darrah (1986) reported on a comparison of five recurrent

**Table 10. Gain cycle<sup>-1</sup> and year<sup>-1</sup> for the populations per se along with costs for a one unit increase in grain yield and the number of years needed to achieve this increase. All costs and times are based on rates of gain and selection techniques used for the BS11 maize population presented in our study only.**

Selection method	Gain per cycle	Gain year <sup>-1</sup>	Ave. cost cycle <sup>-1</sup>	Ave. cost year <sup>-1</sup> †	Cost unit <sup>-1</sup> of gain‡	Time to achieve one unit of gain§	Return on investment¶
	Mg ha <sup>-1</sup>	Mg ha <sup>-1</sup>	\$Cycle <sup>-1</sup>	\$Yr. <sup>-1</sup>	\$#	Yr.	Mg ha <sup>-1</sup> \$ <sup>-1</sup> × 10 <sup>5</sup>
Full-sib	0.067	0.033	6 700	3 350	100 250	30	1.00
Half-sib	0.075	0.025	14 300	4 767	190 058	40	0.53
Mass	0.029	0.029	350	350	12 123	35	8.25
Modified ear-to-row	0.172	0.086	6 650	3 325	38 721	12	2.58
Reciprocal full-sib	0.124	0.062	12 100	6 050	97 213	16	1.03
S <sub>1</sub> -progeny	0.091	0.046	7 300	3 650	79 888	22	1.25
S <sub>2</sub> -progeny	0.212	0.071	10 300	3 433	48 530	14	2.06

† Calculated by taking cost cycle<sup>-1</sup> divided by the number of years required to complete one cycle.

‡ One unit of Gain is equal to a one Mg ha<sup>-1</sup> increase in grain yield. Calculated as the cost divided by the gain cycle<sup>-1</sup>.

§ Calculated as the inverse of gain cycle<sup>-1</sup> multiplied by the number of years required per cycle.

¶ Calculated by taking gain cycle<sup>-1</sup> divided by the total cost cycle<sup>-1</sup>.

# All calculations were made assuming a cost of \$10 per nursery row, \$15 per winter nursery row, \$10 per yield trial plot, and a cost of an average size isolation of \$350.

selection methods for grain yield with several variations of each basic method. Likewise, Stojsin and Kannenberg (1994) compared four selection methods in each of five populations. Our study compares seven methods of recurrent selection within the same base population.

An important result of our study is the success of many recurrent selection methods for improving several traits simultaneously. In some instances, selection for agronomic traits, such as insect resistance alone, has caused yield reductions, or selection for yield alone has caused undesirable responses in other agronomic traits, such as lodging or grain moisture (Rehn and Russell, 1986; Nyhus et al., 1989). In our study, most selection methods showed significant progress in the desired direction for all four traits included in the selection index (Fig. 1). The only exception was the nonsignificant decrease in grain moisture for MER. Additionally, significant improvements in the desirable direction also were made in the populations per se for correlated agronomic traits.

No published reports exist describing progress from recurrent selection in BS11 with the exception of the FR program (Hallauer, 1984; Eyherabide and Hallauer, 1991). Thus, comparison of results with previous reports in the BS11 population must be confined to the FR program. Eyherabide and Hallauer (1991) reported an increase in grain yield in the BS11 population per se of  $0.08 \text{ Mg ha}^{-1} \text{ cycle}^{-1}$  after eight cycles of FR selection. Rodriguez and Hallauer (1988) reported a  $0.04 \text{ Mg ha}^{-1} \text{ cycle}^{-1}$  increase in grain yield in the BS11 population per se after seven cycles of FR selection. Our results showed a slightly higher increase in grain yield with only five cycles of selection ( $0.12 \text{ Mg ha}^{-1} \text{ cycle}^{-1}$ ). Eyherabide and Hallauer (1991) reported an increase in grain yield and a decrease in grain moisture, stalk lodging, root lodging, and ear height in the BS11 population per se. Our data agree with the trends reported for each of these traits with the exception of stalk lodging. Our data show no significant change in stalk lodging whereas Eyherabide and Hallauer (1991) showed a decrease of 1.1% per cycle. Possible explanations for this discrepancy are that the evaluations were made in a different set of environments and our evaluations were confined to only the first five cycles whereas Eyherabide and Hallauer (1991) evaluated eight cycles of selection.

Comstock (1964) concluded that in the absence of overdominance, inbred progeny selection was expected to be superior to other recurrent selection methods for improvement of the population per se. Choo and Kannenberg (1979) conducted a simulation study comparing mass, ear-to-row, and  $S_1$ -progeny selection, and they concluded that  $S_1$ -progeny selection would give superior improvement with both an additive and a complete dominance model. Wright's (1980) conclusions agree with the expected superiority of  $S_1$ -progeny selection. Although the theoretical comparison among selection methods is known, results from previous studies comparing recurrent selection methods for population improvement have been inconsistent. An evaluation of half-sib selection with a double-cross tester and  $S_1$ -progeny selection by Burton et al. (1971) showed that  $S_1$ -

progeny selection had greater improvement in grain yield than the half-sib method. A later evaluation of the same program after further selection showed no differences among these methods for observed grain yield response, however (Tanner and Smith, 1987). Results of Stojsin and Kannenberg (1994) also showed that the most significant responses were obtained with selfed progeny selection vs. other methods. Conversely, Horner et al. (1973) compared  $S_2$ -progeny selection with testcross selection with a genetically broad-based tester and with an inbred tester. Improvements in the populations per se for grain yield were significantly greater for both testcross methods than for  $S_2$ -progeny selection after five cycles of selection. Selfed populations of each of these programs showed no differences among the three methods. Horner et al. (1989) also compared  $S_2$  progeny selection with testcross selection with an inbred line from a reciprocal population. Their results showed that although both methods resulted in significant improvement for grain yield, topcross selection was superior to  $S_2$ -progeny selection. Darrah (1986) completed a study in which multiple recurrent selection methods were compared. He concluded that the most consistent improvement was obtained by using ear-to-row selection. Darrah (1986) also showed that although  $S_1$ -progeny selection resulted in significant yield improvement, it was not as high as would be predicted and was less than the gain obtained with ear-to-row selection. Holthaus and Lamkey (1995) also found a lack of response to inbred progeny selection vs. other forms of reciprocal recurrent and half-sib selection in BSSS. Variance component estimates in BSSS show the dominance and additive genetic variances are roughly equivalent ( $\sigma_D^2/\sigma_A^2 = 1.05$ ; Holthaus and Lamkey, 1995). The importance of dominance variance in BSSS could be a possible reason for inbred progeny selection methods to either not respond to selection or not to be superior to alternate selection methods in BSSS. If additive genetic variance is of great importance in a population relative to the magnitude of dominance variance, then inbred-progeny selection would be expected to be superior to other methods under most genetic situations.

Our data differ from the reports by Horner et al. (1973 and 1989), Darrah (1986), Lamkey (1992), and Holthaus and Lamkey (1995) because inbred progeny methods were superior to the other selection methods and had the greatest per cycle selection response if all four traits under selection were taken into account. Responses for grain yield in the populations per se were consistent within the range of previously reported responses summarized by Hallauer and Miranda (1988). Estimates of variance components in the BS11 population by Reeder et al. (1987) showed that dominance variance estimates were never greater than twice their standard errors and were substantially smaller than estimates of the additive genetic variance. The large additive genetic variance relative to dominance variance may explain why inbred progeny methods were superior in BS11 and not in some previous studies. Additionally, based on the agronomic characteristics of the BS11C0, (i.e., relatively lower yield, higher stalk lodging, etc.),

the load in this population (number of individuals suffering genetic death due to their deleterious alleles; Falconer and Mackay, 1996) may be greater than for other maize populations. Inbred progeny methods would uncover deleterious recessive alleles and expose them to the effects of selection. Inbred progeny selection may not necessarily increase mean performance by acting directly to increase the frequency of favorable alleles, but by directly decreasing the frequency of deleterious recessive alleles. Selection methods such as MER and FS, which use the population per se as the tester, would be expected to uncover deleterious recessive alleles more effectively than methods using unrelated inbred or population testers, which could potentially mask the effects of deleterious recessive alleles. Thus, based on the relative performance of the methods for all agronomic traits, it seems evident from our experiment that the best tester for population per se improvement in BS11 is the population itself.

Inbreeding depression for grain yield in BS11 shows that with all selection methods there remains significant inbreeding depression (Table 8). There seems to be no trend toward a decrease in inbreeding depression with selection. This fact would seem to indicate that the frequency of favorable alleles has not increased to fixation at very many of the loci controlling grain yield. Similar results were obtained for grain moisture, stalk lodging, and root lodging. The only emerging trend for a decrease in inbreeding depression over cycles was with grain moisture and stalk lodging in the HI program.

Predicted gains for many of the selection methods in BS11 were large, whereas observed gains were low in comparison. The discrepancy, however, between predicted and realized gain is not unique to our study. There are two possible reasons for this discrepancy and both involve the possible overestimation of heritability in the progeny evaluation trials. Lamkey and Hallauer (1987) showed that when heritability is estimated from the variance among families in the selection trials, heritabilities may be biased upwards and represent an upper bound of the heritability for certain progeny types. Likewise, heritability based on single-year data, such as the case in the selection trials, is biased upwards because of genotype  $\times$  year interactions being confounded in the numerator (Comstock and Moll, 1963). Another possible reason for the lack of relationship between predicted and realized gain is the potential for the genotype  $\times$  environment interactions experienced in the selection environments to not be representative of the genotype  $\times$  environments interactions that occurred in the multi-year evaluation trials (Comstock and Moll, 1963).

Although all methods of selection showed significant increases in grain yield in the populations per se, realized heritability estimates for all selection methods were low. This disturbing result occurs because the cumulative selection differentials for all the selection methods were extremely large, attaining 5.31 Mg ha<sup>-1</sup> after only five cycles of selection (Table 9). With reasonable heritabilities in the selection trials, predicted gains from selection were as great as 4.11 Mg ha<sup>-1</sup>, with never more

than 26% being realized based on estimates given in Table 9. Realized heritabilities lower than heritabilities calculated based on additive genetic variances seem to be a common occurrence (Comstock, 1996). Published reports on realized heritability calculated from recurrent selection methods in maize are inadequate to determine whether our realized heritabilities are unrealistically low.

In a discussion of selection-method efficiency and maize improvement, the topic of economics inevitably arises. Estimates of cost to conduct recurrent selection based on the manner in which each method was conducted resulted in a wide range of costs cycle<sup>-1</sup> among selection methods. The costs unit<sup>-1</sup> of gain varied among selection methods. Because costs for each phase of a selection program will vary among breeding programs, an attempt was made to determine what effect changing the initial costs would have on the cost unit<sup>-1</sup> of gain. To assess this, costs of the four main components were varied to evaluate possible rank changes among methods. Each cost (i.e., cost per winter nursery row, cost per isolation, etc.) was reduced by 50% and doubled with all other costs remaining equal. Although the relative magnitude among selection methods changed, varying costs did not change the rank among the selection methods for the cost unit<sup>-1</sup> of gain. For our study, HI selection, although in many instances a desired method, was costly per unit gain in part because of its relatively low rate of gain and its additional costs per cycle for tester rows in nurseries. Taking into account both cost unit<sup>-1</sup> gain and length of time required, both MER and S<sub>2</sub>-progeny selection provided reasonably high rates of gain at moderate investment and would be expected to increase grain yield by 21% in 12 or 14 yr, respectively. The greatest return on investment would be expected from MER and S<sub>2</sub>-progeny selection.

#### ACKNOWLEDGMENTS

The authors are indebted to Dr. O.S. Smith who had the foresight to conceptualize and plan the selection methods study in the late 1970s. We gratefully acknowledge funding for the selection methods study provided by a USDA Competitive Grant #85-CRCR-1-1567. The evaluation phase of the study described herein was funded by USDA Competitive Grant #90-37140-5578.

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