

1998

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## Abstract

The number of lines recombined in a recurrent selection program affects the genetic variation remaining after selection as well as the selection intensity. Both of these variables are important in establishing and maintaining a desirable rate of progress from recurrent selection. Little empirical evidence is available in maize (*Zea mays* L.) to establish the appropriate effective population size for recurrent selection programs. The objective of this study was to compare the response to S<sub>i</sub>-progeny selection in four selection programs (5-S<sub>1</sub>, 10-S<sub>1</sub>, 20-S<sub>1</sub>, and 30-S<sub>1</sub>). Each program had different numbers of individuals intermated (5, 10, 20, or 30, respectively) with a common selection intensity of 20%. Four cycles of selection were completed for the 5-S<sub>1</sub>, 10-S<sub>1</sub>, and 30-S<sub>1</sub> programs and five cycles of selection were completed for the 20-S<sub>1</sub> program. Grain yield increased significantly for the 10-S<sub>1</sub>, 20-S<sub>1</sub>, and 30-S<sub>1</sub> programs, and there were no significant differences in rates of response among programs. Grain yield decreased significantly in the 5-S<sub>1</sub> program. All four programs improved significantly for grain yield of testcrosses with 'Pioneer Two-ear Composite', Cycle 0 (BS11CO) and the inbred B79. These results suggest that drift becomes a stronger force in altering allele frequencies than selection when fewer than 10 lines are recombined. There does not seem to be an advantage, at least in the short term, of recombining more than 10 lines per cycle of selection.

## Disciplines

Agricultural Science | Agronomy and Crop Sciences | Plant Breeding and Genetics

## Comments

This article is published as Weyhrich, Roger A., Kendall R. Lamkey, and Arnel R. Hallauer. "Effective population size and response to S<sub>1</sub>-progeny selection in the BS11 maize population." *Crop science* 38, no. 5 (1998): 1149-1158. doi: [10.2135/cropsci1998.0011183X003800050008x](https://doi.org/10.2135/cropsci1998.0011183X003800050008x). Posted with permission.

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## Effective Population Size and Response to S<sub>1</sub>-Progeny Selection in the BS11 Maize Population

Roger A. Weyhrich, Kendall R. Lamkey,\* and Arnel R. Hallauer

### ABSTRACT

The number of lines recombined in a recurrent selection program affects the genetic variation remaining after selection as well as the selection intensity. Both of these variables are important in establishing and maintaining a desirable rate of progress from recurrent selection. Little empirical evidence is available in maize (*Zea mays* L.) to establish the appropriate effective population size for recurrent selection programs. The objective of this study was to compare the response to S<sub>1</sub>-progeny selection in four selection programs (5-S<sub>1</sub>, 10-S<sub>1</sub>, 20-S<sub>1</sub>, and 30-S<sub>1</sub>). Each program had different numbers of individuals intermated (5, 10, 20, or 30, respectively) with a common selection intensity of 20%. Four cycles of selection were completed for the 5-S<sub>1</sub>, 10-S<sub>1</sub>, and 30-S<sub>1</sub> programs and five cycles of selection were completed for the 20-S<sub>1</sub> program. Grain yield increased significantly for the 10-S<sub>1</sub>, 20-S<sub>1</sub>, and 30-S<sub>1</sub> programs, and there were no significant differences in rates of response among programs. Grain yield decreased significantly in the 5-S<sub>1</sub> program. All four programs improved significantly for grain yield of testcrosses with 'Pioneer Two-ear Composite', Cycle 0 (BS11C0) and the inbred B79. These results suggest that drift becomes a stronger force in altering allele frequencies than selection when fewer than 10 lines are recombined. There does not seem to be an advantage, at least in the short term, of recombining more than 10 lines per cycle of selection.

RECURRENT SELECTION METHODS have been widely used by maize breeders for population improvement and for genetic experiments to compare empirical results with those of quantitative genetic theory. Maize breeders using recurrent selection methods have two goals in mind, (i) improvement of population mean performance and (ii) maintenance of genetic variation for continued selection. Recurrent selection is a cyclical breeding system involving three steps (development of

progenies, evaluation and selection of progenies, and recombination of selected progenies), each of which is vitally important and can dramatically influence progress toward goals of the recurrent selection program. The number of individuals recombined in each cycle of selection has been one of the major concerns of long-term recurrent selection programs.

The number of individuals recombined in the recurrent selection program, along with the breeding structure of the population, directly impacts the effective population size. The effective size of a population of individuals was described in Falconer and Mackay (1996) as "the number of individuals that would give rise to the calculated sampling variance, or rate of inbreeding, if they bred in the manner of the idealized population." Or, as described by Kimura and Crow (1963), the effective population size is "the number in an idealized population in which each individual has an equal number of expected progeny." In this manner, the effective population size is directly related to the true population size and the breeding structure of the individuals. The concepts and consequences of effective population size have been previously discussed (Robertson, 1960; Baker and Curnow, 1969; Vencovsky, 1978; Enfield, 1980). With finite population sizes, the danger exists that an allele might become fixed in a population by chance even though there was a more desirable allele present in the population (Robertson, 1960). Problems associated with finite population sizes, such as the fixation of undesirable alleles due to random genetic drift, have been demonstrated theoretically and empirically to affect response to selection and ultimately, the limit to selection response (Robertson, 1960; Frankham et al., 1968; Baker and Curnow, 1969; Enfield, 1980). The key for the plant breeder is to use an appropriate population size that will maximize both short- and long-term responses. The balance would be to recombine few enough individuals that a reasonable response could be

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**Abbreviations:** BS11C0, Pioneer Two-ear Composite, Cycle 0; GDU, growing degree units (°C);  $h^2$ , heritability; S, selection differential; 5-S<sub>1</sub>, 10-S<sub>1</sub>, 20-S<sub>1</sub>, and 30-S<sub>1</sub>, S<sub>1</sub> progeny selection where 5, 10, 20, and 30 individuals were recombined, respectively.

expected in the short term, but not too few that a sharp decrease in genetic variance would compromise long-term genetic progress. Also, if too few individuals were intermated, the primary force changing allele frequency would be random genetic drift rather than selection.

Traditionally, maize breeders have recombined between 10 and 25 individuals in recurrent selection programs. In recurrent selection programs where only 10 lines were recombined, random genetic drift has been shown to be a significant factor in limiting the response to selection (Smith, 1983, 1984; Helms et al., 1989). However, even in recurrent selection programs where drift has been shown to be an important factor, significant progress has been made without exhausting genetic variance (Holthaus and Lamkey, 1995; Labate et al., 1997). Garay et al. (1996) reported on recurrent selection experiments where 10 lines were recombined and found that drift was not a significant factor. Rawlings (1980) suggested that an effective population size of 30 would be reasonably adequate for most genetic systems to achieve a balance between short- and long-term goals and that maintenance of genetic variation should only be a concern if it doesn't compromise response to selection. Baker and Curnow (1969) suggested that recombining at least 16 individuals would not result in selection limitations in less than 30 generations, while there was no point in using more than 16 individuals when short-term genetic progress was the main concern. Frankham et al. (1968), however, found that larger population sizes gave more response to selection and warned that the effects of finite population size should not be ignored even in the short term. Hallauer (1992), after reviewing literature on effective population sizes, suggested that approximately 25 to 35 progenies should be intermated for maize recurrent selection programs.

Our study was designed to compare the responses to  $S_1$ -progeny selection conducted by using four effective population sizes with the same selection intensity. Maize breeders are interested in determining which effective population size and selection method will give the greatest response to selection. In other words, how many individuals should be intermated to provide the best compromise between selection response, loss of genetic variance, and inbreeding depression due to random genetic drift. Comparisons of this type have been made for flour beetle [*Tribolium castaneum* (Herbst)] (Enfield, 1980), turnip (*Brassica rapa* L.) (Lascoux et al., 1994), fruit fly (*Drosophila melanogaster* L.) (Frankham et al., 1968), and maize (Darrah, 1986). Additional information comparing response to selection conducted by using a range of effective population sizes in maize is needed. Hence, the objective of our study was to compare the response to  $S_1$ -progeny selection conducted while intermating four different numbers of individuals with equal selection intensities.

## 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 Intl. It is a genetically broad-based population developed

by crossing southern prolific germplasm with U.S. Corn Belt lines (Hallauer, 1967). After 10 cycles of mass selection for adaptation and prolificacy, BS11 is adapted to the central Corn Belt and has potential as a source population from which to derive inbred lines.

The effective population-size study described herein was conducted and evaluated as a portion of a larger recurrent selection methods experiment (Weyhrich et al., 1998). Four separate  $S_1$ -progeny selection programs were conducted with BS11C0 in which 5, 10, 20, or 30 lines were intermated to form the next cycle of selection. The programs in which 5, 10, 20, or 30 lines were recombined are referred to as 5-S1, 10-S1, 20-S1, and 30-S1, respectively.

A cycle of selection in the 5-S1 program was conducted by growing the population per se in winter nursery and selfing 25 to 50  $S_0$  plants. Ears from the 25 most desirable plants were harvested. The following season in Iowa, the 25  $S_1$  lines were grown in replicated yield trials generally at three locations with two replications per location. Based on yield trial results, the best five lines were selected for recombination. Selection of progenies for recombination from replicated yield trials was based on a selection index composed of grain yield, grain moisture at harvest, and resistance to stalk and root lodging. The index was weighted by the heritabilities of each of the four traits (Smith et al., 1981a,b). Remnant  $S_1$  seed from the selected lines was planted in winter nursery and recombined using the bulk-entry method (Hallauer, 1985). 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.

Selection was conducted for the 10-S1 program in a manner similar to that described above for 5-S1 except that 50  $S_1$  lines were evaluated in replicated trials and 10 lines were recombined each cycle. Likewise, 20-S1 selection was conducted by evaluating 100  $S_1$  lines with 20 lines selected each cycle for recombination. Selections in the 30-S1 program were made from replicated trials consisting of 150  $S_1$  lines with 30 lines being recombined each cycle. Thus, although the number of lines evaluated and intermated varied among the four programs, the selection intensity for all four selection programs was 20%. Four cycles of selection in 5-S1, 10-S1, and 30-S1 and five cycles of selection in 20-S1 were completed and were included in our evaluation. Index selection was used for all programs except for the first two cycles of 5-S1, 10-S1, and 30-S1 where selection was conducted only for grain yield adjusted to 155 g kg<sup>-1</sup> grain moisture.

### Effective Population-Size Program Evaluation and Procedures

In the 1991 breeding nursery, seed of the populations per se and populations per se selfed were produced for the C0 to C5 of 20-S1 and C0 to C4 of 5-S1, 10-S1, and 30-S1. Each of the populations per se was also topcrossed to BS11C0 and inbred B79 in isolation plots. Seed of the populations per se and populations per se selfed was produced by chain sibbing or selfing  $\approx$ 160 plants. The topcross seed was produced by using  $\approx$ 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.

The entries included in the noninbred experiment were the populations per se for all cycles of selection of each effective size program, population crosses to BS11C0, and the population crosses to inbred B79. Multiple entries of BS11C0 (20 per replication) and BS11C0 × B79 (10 per replication) were included to give a more precise estimate of the starting point for the effective population-size selection programs and to minimize correlations among regression coefficients. The entries were evaluated in a 13 by 13 partially balanced lattice design with five replications at each location and year combination (environment), except for Chariton in 1994, where only four replications were evaluated.

The inbred experiment included multiple entries of BS11C0 selfed (10 per replication) and the populations per se selfed for each cycle for all selection programs. The inbred materials were evaluated in a 7 by 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  $\approx 62\,124$  plants  $\text{ha}^{-1}$ . All experiments were machine cultivated and 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 plants  $\text{ha}^{-1}$ ), root lodging (percentage of plants leaning  $>30^\circ$  from vertical), stalk lodging (percentage of plants broken at or below the primary ear node), and the percentage of dropped ears. Plant, ear, and top height were measured on two replications at 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 per plot 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). Due to 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, root and stalk 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 or 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 regression groups based on common C0 genotypes. Group 1 included all cycles of selection of the populations per se and the population crosses to the C0 since they all have BS11C0 as their common C0 genotype. Group 2 included all of the populations crossed to B79 that have BS11C0 × B79 as the common C0 genotype. The third group included all of the selfed populations per se that have BS11C0

selfed as the common C0 genotype. The sums of squares for each group were partitioned in a manner similar to the procedure described by Eberhart (1964). Responses for all four selection methods were fit simultaneously through the common C0 intercept by weighted least squares regression 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 later cycle means having equal weight for all methods. Standard errors for the regression coefficients were obtained by taking the square root of the appropriate diagonal element of the  $(\mathbf{X}'\mathbf{W}^{-1}\mathbf{X})^{-1}$  matrix where  $\mathbf{W}$  is a matrix with the variance of cycle means on the diagonal and zeros on the off-diagonal and  $\mathbf{X}$  is a matrix of the number of cycles of selection conducted for each method. Estimates of the average response per cycle were obtained from the linear regression coefficients from the model containing only the linear term for each method. Average response per year was calculated by dividing the average response per cycle by the number of years required to complete a cycle of selection. The percentage of response per cycle was calculated as the ratio of the linear regression coefficient to the estimated C0 intercept and multiplied by 100.

For the purposes of calculating inbreeding depression in absolute units and its associated parameters, cycle means were combined for only those environments where the particular trait of interest was measured on both the inbred and noninbred experiments. Inbreeding depression in absolute units was calculated as the  $S_0$  minus the  $S_1$  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 ( $S$ ) were calculated by summing the  $S$ 's over all cycles of selection. Predicted gain was calculated by multiplying heritability ( $h^2$ ) by the  $S$  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 as proposed by Falconer (1954) and later reviewed by Hill (1972) and Nyquist (1991), where the cycle means, or cumulative responses, were regressed on the cumulative  $S$ . Again, weighted least squares regression was used and because 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.

## RESULTS AND DISCUSSION

### Selection Trial Results

Mean heritabilities for grain yield in the selection trials were consistent among the four  $S_1$ -progeny programs ranging from 68.5 (20-S1) to 74.9% (5-S1) (Table 1). Mean  $S$ 's for grain yield were high and ranged from 0.70 (20-S1) to 1.26 (5-S1)  $\text{Mg ha}^{-1}$ . The  $S$  was the smallest for 20-S1 for all cycles of selection except for Cycle 3. Heritabilities and  $S$ 's for grain moisture, stalk lodging, and root lodging are not given for the first two cycles of 5-S1, 10-S1, and 30-S1 programs because these

**Table 1. 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 are unpublished data obtained from the Annual Reports of the Cooperative Federal-State Corn Breeding Investigations, Ames, IA, 1977 through 1989.**

Trait	Population	Cycle 0		Cycle 1		Cycle 2		Cycle 3		Cycle 4		Mean $h^2$	Mean S
		$h^2$	S	$h^2$	S	$h^2$	S	$h^2$	S	$h^2$	S		
Grain yield (Mg ha <sup>-1</sup> )	5-S1	79.0	1.70	66.6	1.75	83.4	0.82	70.6	0.78	-†	-	74.9	1.26
	10-S1	79.0	1.97	66.6	1.30	86.2	0.98	57.7	0.39	-	-	72.4	1.16
	20-S1	84.6	1.12	60.3	1.00	57.3	0.28	71.7	0.61	68.4	0.51	68.5	0.70
	30-S1	79.0	1.63	66.6	1.45	70.5	0.55	64.5	0.49	-	-	70.2	1.03
Grain moisture (g kg <sup>-1</sup> )	5-S1	-‡	-	-	-	79.6	12.0	68.2	1.0	-	-	73.9	6.5
	10-S1	-	-	-	-	72.9	-4.0	77.0	-10.0	-	-	75.0	-7.0
	20-S1	80.6	-1.0	72.9	-5.0	60.4	-1.0	78.9	-1.0	81.6	-8.0	74.9	-3.2
	30-S1	-	-	-	-	82.2	-9.0	83.4	-4.0	-	-	82.8	-6.5
Stalk lodging (%)	5-S1	-	-	-	-	78.6§	-8.1	56.4	-2.1	-	-	67.5	-5.1
	10-S1	-	-	-	-	82.3§	-6.3	58.7	-3.7	-	-	70.5	-5.0
	20-S1	75.1	-4.1	52.7	-3.3	74.3	-8.6	64.6§	-4.3	70.8	-5.5	67.5	-5.2
	30-S1	-	-	-	-	73.4§	-6.9	77.1	-6.1	-	-	75.3	-6.5
Root lodging (%)	5-S1	-	-	-	-	-11.0§	-15.5	47.7	-1.5	-	-	18.4	-8.5
	10-S1	-	-	-	-	73.1§	-20.2	68.2	-5.6	-	-	70.7	-12.9
	20-S1	63.8	-0.7	37.9	-0.4	45.8	-9.8	86.7§	-7.7	37.7	-0.6	54.4	-3.8
	30-S1	-	-	-	-	79.4§	-23.5	65.2	-2.0	-	-	72.3	-12.8

† Cycle not completed for inclusion in study.

‡ Data not available.

§ Because of severe lodging at two locations, these traits were only measured in one environment and therefore may be biased with genotype × environment interaction.

traits were not measured. Mean heritabilities for grain moisture ranged from 73.9 (5-S1) to 82.8% (30-S1). Average S's for grain moisture in the 10-S1, 20-S1, and 30-S1 programs were all in the desired direction and as high as -7.0 g kg<sup>-1</sup>, while the average S for the 5-S1 program was 6.5 g kg<sup>-1</sup> and moving in the wrong direction. Average heritabilities for stalk lodging were similar over all programs (67.5 to 75.3) and mean S's were also similar, ranging from -5.0 to -6.5%. Mean heritabilities for root lodging in the selection trials were erratic and varied from 18.4 (5-S1) to 72.3% (30-S1), mean S's ranged from -3.8 (20-S1) to -12.9% (10-S1). Differ-

ences between the S's in 20-S1 and 10-S1 can be explained by the selection in the Cycle 2 populations where S's were large in the 5-S1, 10-S1, and 30-S1 programs and relatively small in the 20-S1 program. The differences between S's may be because the 20-S1 program was not evaluated for selection in the same years each cycle as the 5-S1, 10-S1, and 30-S1 programs.

### Responses to Direct Selection

Selection differentials and heritabilities indicate that significant response to selection for grain yield was ex-

**Table 2. Observed mean grain yields for each cycle of four selection methods and least squares estimates of response to selection in the BS11 maize population. Data were 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#	% Response††	
		C0	C1	C2	C3	C4		C5	$b_0$	$b_1$			$b_q$
Mg ha <sup>-1</sup>													
S <sub>0</sub> populations per se	5-S1	4.69	4.26	4.14	4.20	3.92	-‡‡	0.13	4.73	-0.22 ± 0.02**	-	-0.11 ± 0.01**	-4.6
	10-S1	4.65	5.12	5.27	5.26	-	-			0.15 ± 0.02**	-	0.07 ± 0.01**	3.1
	20-S1	5.02	4.81	4.96	5.11	5.21	-			0.09 ± 0.02**	*	0.05 ± 0.01**	1.9
	30-S1	4.98	4.97	5.06	5.25	-	-			0.13 ± 0.02**	-	0.06 ± 0.01**	2.7
Testcrosses to BS11 C0	5-S1	4.69	4.73	4.97	5.21	5.12	-		4.73	0.12 ± 0.02**	-	0.06 ± 0.01**	2.4
	10-S1	4.85	5.09	5.32	5.46	-	-			0.18 ± 0.02**	-	0.09 ± 0.01**	3.9
	20-S1	4.89	4.82	5.14	5.28	5.20	-			0.11 ± 0.02**	-	0.06 ± 0.01**	2.3
	30-S1	4.95	5.40	5.42	5.51	-	-			0.22 ± 0.02**	-	0.11 ± 0.01**	4.7
Testcrosses to inbred B79	5-S1	6.25	5.88	6.16	6.48	6.57	-		6.15	0.08 ± 0.03**	*	0.04 ± 0.01**	1.3
	10-S1	5.97	6.61	6.59	6.50	-	-			0.12 ± 0.03**	-	0.06 ± 0.01**	1.9
	20-S1	6.21	6.07	6.01	6.43	6.73	-			0.06 ± 0.02**	**	0.03 ± 0.01**	1.0
	30-S1	6.35	6.22	6.36	6.64	-	-			0.10 ± 0.03**	-	0.05 ± 0.01**	1.6
S <sub>1</sub> populations per se	5-S1	3.20	3.27	2.94	2.79	2.93	-	0.10	3.25	-0.11 ± 0.02**	-	-0.05 ± 0.01**	-3.3
	10-S1	3.16	3.72	3.86	4.15	-	-			0.21 ± 0.02**	-	0.12 ± 0.01**	6.5
	20-S1	3.52	3.58	3.64	3.69	3.75	-			0.12 ± 0.02**	-	0.06 ± 0.01**	3.6
	30-S1	3.64	3.82	3.75	4.08	-	-			0.21 ± 0.02**	-	0.11 ± 0.01**	6.6

\*,\*\* 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 Cycle 0 are S.E./20<sup>0.5</sup> for BS11C0 and S.E./10<sup>0.5</sup> for BS11C0 × B79 and for BS11C0 S<sub>1</sub>.

§  $b_0$  is an estimate of the C0 mean;  $b_1$  is an estimate of the average rate of response per cycle;  $b_q$  is included to indicate when the quadratic term was significant.

# Response per year was calculated as the response per cycle divided by 2, the number of years required to complete a cycle of selection.

†† The percentage response per cycle was calculated as the ratio of  $b_1$  to the predicted C0 intercept and multiplied by 100.

‡‡ Cycle not included in study.

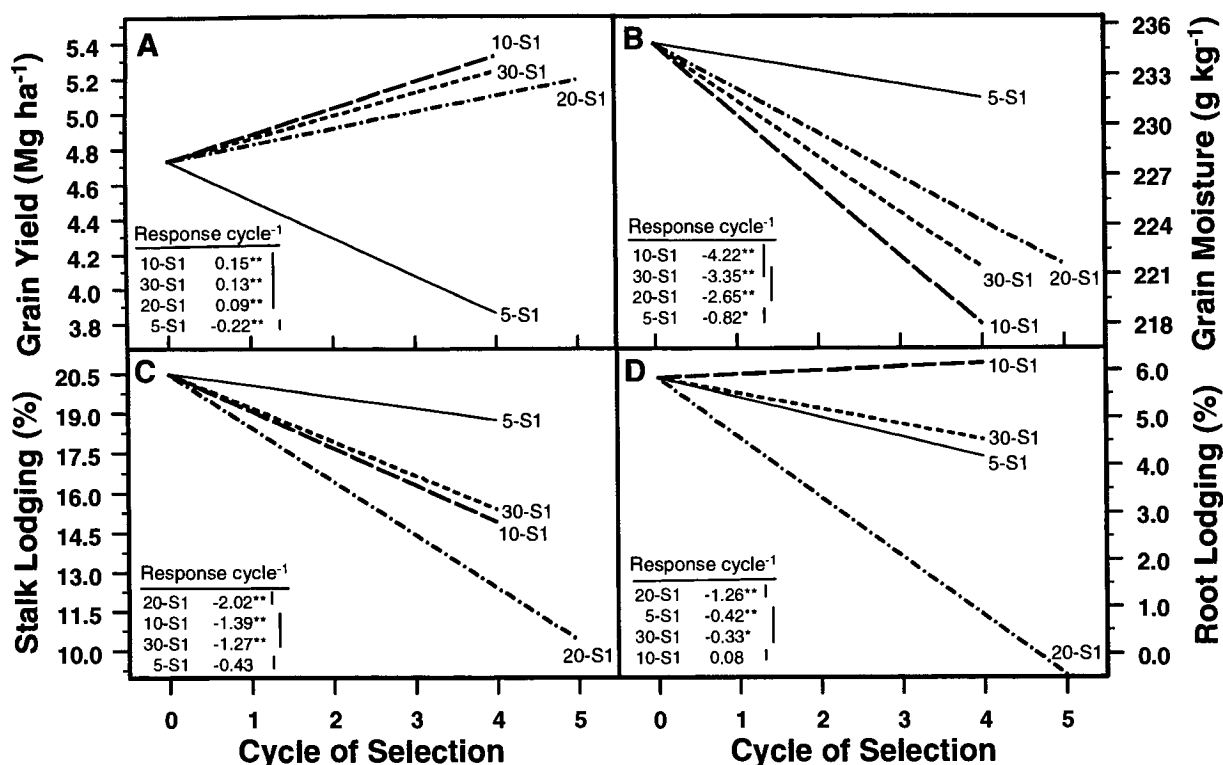


Fig. 1. Responses to selection in the populations per se for (A) grain yield, (B) grain moisture at harvest, (C) stalk lodging, and (D) root lodging for four selection methods in BS11. \* and \*\* indicate significance of the linear response ( $H_0: b_1 = 0$ ) at the 0.05 and 0.01 probability levels,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

pected in each of the selection programs (Table 1). There were significant increases in grain yield for the S<sub>0</sub> populations per se over cycles of selection (0.09 to 0.15 Mg ha<sup>-1</sup>) for 10-S1, 20-S1, or 30-S1 selection programs (Table 2, Fig. 1A). The responses for these three programs were not significantly different from each other. When only five superior lines were intermated (5-S1), the result was a significant decrease in grain yield of  $-0.22$  Mg ha<sup>-1</sup> cycle<sup>-1</sup> or a 4.6% decrease cycle<sup>-1</sup>.

In testcrosses to the BS11C0, all four programs showed significant increases in grain yield, ranging from 0.11 (20-S1) to 0.22 (30-S1) Mg ha<sup>-1</sup> cycle<sup>-1</sup> (Table 2). Testcrossing to BS11C0 removes the effects of genetic drift by restoring heterozygosity to those loci that may have become fixed in the population by drift. These crosses show that progress has been made in the 5-S1 program even though the effects of drift have most likely overwhelmed any progress made from selection in the population per se. All four selection programs showed significant and statistically equivalent increases in B79 testcross response (0.06–0.12 Mg ha<sup>-1</sup>). The populations selfed represent the direct response to S<sub>1</sub>-progeny selection. Grain-yield responses in the selfed populations were significant in the desirable direction for the 10-S1, 20-S1, and 30-S1 programs, while a significant decrease of  $-0.11$  Mg ha<sup>-1</sup> was found for the 5-S1 program.

Grain moisture decreased significantly in the populations per se for all four selection programs (Table 3, Fig. 1B). Intermating only five lines resulted in the smallest response for grain moisture while intermating either

10 or 30 lines resulted in significant decreases in grain moisture  $\geq -3.35$  g kg<sup>-1</sup> cycle<sup>-1</sup>. The responses in the BS11C0 testcrosses were in the desired direction for the 10-S1, 20-S1, and 30-S1 programs and were similar. The BS11C0 testcross of the 5-S1 populations to the C0 revealed a trend for an increase in grain moisture over cycles of selection of 2.55 g kg<sup>-1</sup> cycle<sup>-1</sup>. The trends for grain moisture responses in the testcrosses to B79 and the selfed populations likewise followed the same pattern as those for the crosses to the C0.

Responses to selection for decreased stalk lodging were in the desired direction in all four programs and for all population types (Table 4). In the populations per se, the 20-S1 program showed the greatest response to selection ( $-2.02\%$  cycle<sup>-1</sup>) while the 10-S1 and 30-S1 programs showed significant decreases as well. The 5-S1 program showed no response to selection for reduced stalk lodging and, similar to grain moisture in the 5-S1 program, lagged behind the other three programs. The BS11C0 testcrosses resulted in significant decreases in stalk lodging with the 20-S1 having a significantly greater response than the other three programs, while the 30-S1 program showed no response. In both the B79 testcrosses and the selfed populations, all selection programs had significant decreases in stalk lodging.

Root-lodging responses were erratic among the four selection programs and four population types (Table 5). The 5-S1, 20-S1, and 30-S1 programs resulted in significant decreases in root lodging in the populations per se of  $-0.42$ ,  $-1.26$ , and  $-0.33\%$  cycle<sup>-1</sup>, respec-

**Table 3. Observed mean grain moisture for each cycle of four selection methods and least squares estimates of response to selection in the BS11 maize population. Data were 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#	% 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	5-S1	237	227	221	233	239	—‡‡	2.08	234.8	-0.82 ± 0.40*	**	-0.41 ± 0.20*	-0.3
	10-S1		236	222	226	216	—			-4.22 ± 0.40**	—	-2.11 ± 0.20**	-1.8
	20-S1		231	233	225	225	221			-2.65 ± 0.30**	—	-1.32 ± 0.15**	-1.1
	30-S1		232	225	222	225	—			-3.35 ± 0.40**	*	-1.67 ± 0.20**	-1.4
Testcrosses to BS11 C0	5-S1	237	238	234	245	246	—		234.8	2.55 ± 0.40**	—	1.28 ± 0.20**	1.1
	10-S1		237	231	230	225	—			-1.98 ± 0.40**	—	-0.99 ± 0.20**	-0.8
	20-S1		235	225	228	226	225			-2.27 ± 0.30**	—	-1.13 ± 0.15**	-1.0
	30-S1		236	231	230	225	—			-2.02 ± 0.40**	—	-1.01 ± 0.20**	-0.9
Testcrosses to inbred B79	5-S1	240	237	235	242	245	—		238.7	0.86 ± 0.41*	**	0.43 ± 0.21*	0.4
	10-S1		238	240	237	231	—			-1.14 ± 0.41**	—	-0.57 ± 0.21**	-0.7
	20-S1		239	235	232	231	233			-1.58 ± 0.31**	—	-0.79 ± 0.16**	-0.5
	30-S1		240	238	236	239	—			-0.24 ± 0.41	—	-0.12 ± 0.21	-0.1
S <sub>1</sub> populations per se	5-S1	223	222	208	224	231	—	2.47	221.9	0.51 ± 0.49	**	0.25 ± 0.25	0.2
	10-S1		225	222	221	213	—			-1.16 ± 0.49*	*	-0.58 ± 0.25*	-0.5
	20-S1		222	222	216	212	214			-1.75 ± 0.37**	—	-0.87 ± 0.18**	-0.8
	30-S1		228	220	216	216	—			-1.29 ± 0.49*	—	-0.65 ± 0.25*	-0.6

\*,\*\* 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 = 238; B79 × Mo17 = 212; B73 × B95 = 222; B73 × Mo17 = 211; B79 = 210.

‡ Standard errors for Cycle 0 are S.E./20<sup>0.5</sup> for BS11C0 and S.E./10<sup>0.5</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 was calculated as the response per cycle divided by 2, the number of years required to complete a cycle of selection.

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

‡‡ Cycle not included in study.

tively. The 10-S1 program showed no response to selection in any of the four population types. The only program that resulted in a significant decrease in root lodging in the BS11C0 and B79 testcrosses was the 20-S1 program. Intermating 20 to 30 lines resulted in significant decreases in root lodging in the populations selfed as well.

## Correlated Responses

S<sub>1</sub>-progeny selection for increased grain yield, reduced grain moisture, reduced stalk lodging, and reduced root lodging resulted in significant changes in other important agronomic traits as well (Table 6). Index selection resulted in significant decreases in plant and ear height in the populations per se for all selection

**Table 4. Observed mean stalk lodging for each cycle of four selection methods and least squares estimates of response to selection in the BS11 maize population. Data were combined over 11 environments for all population types.†**

Population type	Selection method	Cycle of selection					S.E. of mean‡	Regression coefficients§			Response per year#	% 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	5-S1	20.0	22.2	24.3	16.9	17.6	—‡‡	1.15	20.49	-0.43 ± 0.22	**	-0.22 ± 0.11	-2.1
	10-S1		21.8	19.9	15.3	13.9	—			-1.39 ± 0.22**	**	-0.70 ± 0.11**	-6.8
	20-S1		18.8	18.9	13.6	13.1	9.3			-2.02 ± 0.16**	—	-1.01 ± 0.08**	-9.9
	30-S1		19.1	18.7	16.2	15.4	—			-1.27 ± 0.22**	—	-0.64 ± 0.11**	-6.2
Testcrosses to BS11 C0	5-S1	20.0	20.8	21.4	15.6	17.0	—		20.49	-0.88 ± 0.22**	—	-0.44 ± 0.11**	-4.3
	10-S1		21.3	18.7	16.4	17.8	—			-0.86 ± 0.22**	—	-0.43 ± 0.11**	-4.2
	20-S1		18.3	20.8	15.8	15.3	14.8			-1.18 ± 0.16**	—	-0.59 ± 0.08**	-5.8
	30-S1		20.6	20.2	18.9	18.7	—			-0.41 ± 0.22	—	-0.21 ± 0.11	-2.0
Testcrosses to inbred B79	5-S1	20.7	19.8	18.7	18.0	17.9	—		20.80	-0.84 ± 0.23**	—	-0.42 ± 0.11**	-4.0
	10-S1		19.4	19.8	15.5	15.4	—			-1.36 ± 0.23**	—	-0.68 ± 0.11**	-6.6
	20-S1		19.7	18.4	16.6	15.2	13.1			-1.44 ± 0.17**	—	-0.72 ± 0.09**	-6.9
	30-S1		22.1	19.2	17.7	17.1	—			-0.87 ± 0.23**	—	-0.43 ± 0.11**	-4.2
S <sub>1</sub> populations per se	5-S1	18.5	20.0	20.4	13.7	13.9	—	0.97	18.91	-1.05 ± 0.19**	**	-0.53 ± 0.10**	-5.6
	10-S1		17.4	15.4	10.9	11.0	—			-2.14 ± 0.19**	—	-1.07 ± 0.10**	-11.3
	20-S1		16.4	17.7	11.4	11.5	8.9			-1.95 ± 0.14**	—	-0.97 ± 0.07**	-10.3
	30-S1		18.6	16.4	13.6	12.3	—			-1.59 ± 0.19**	—	-0.79 ± 0.10**	-8.4

\*,\*\* 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 Cycle 0 are S.E./20<sup>0.5</sup> for BS11C0 and S.E./10<sup>0.5</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 was calculated as the response per cycle divided by 2, the number of years required to complete a cycle of selection.

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

‡‡ Cycle not included in study.



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

Population type	Selection method	Cycle of selection					S.E. of mean‡	Regression coefficients§			Response per year#	% 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	5-S1	6.1	6.4	6.9	4.3	3.2	-‡‡	0.77	5.84	-0.42 ± 0.15**	*	-0.21 ± 0.07**	-7.1
	10-S1		6.4	7.2	7.7	4.2	-			0.08 ± 0.15	**	0.04 ± 0.07	1.3
	20-S1		3.8	2.7	0.9	0.9	0.6			-1.26 ± 0.11**	**	-0.63 ± 0.05**	-21.5
	30-S1		6.2	9.2	4.0	3.0	-			-0.33 ± 0.15*	*	-0.16 ± 0.07*	-5.6
Testcrosses to BS11 C0	5-S1	6.1	5.8	5.4	4.7	5.6	-		5.84	-0.18 ± 0.15	-	-0.09 ± 0.07	-3.0
	10-S1		5.5	6.8	5.4	3.9	-			-0.25 ± 0.15	-	-0.12 ± 0.07	-4.3
	20-S1		4.5	3.2	3.3	1.3	1.5			-0.98 ± 0.11**	-	-0.49 ± 0.05**	-16.8
	30-S1		6.6	5.6	4.7	6.4	-			-0.03 ± 0.15	-	-0.01 ± 0.07	-0.5
Testcrosses to inbred B79	5-S1	2.5	3.6	3.6	2.4	2.1	-		2.73	-0.03 ± 0.15	-	-0.01 ± 0.08	-1.1
	10-S1		2.6	3.6	2.3	2.2	-			-0.06 ± 0.15	-	-0.03 ± 0.08	-2.2
	20-S1		2.6	1.2	1.4	1.0	0.6			-0.45 ± 0.11**	-	-0.22 ± 0.06**	-16.5
	30-S1		4.0	4.6	3.2	2.5	-			0.18 ± 0.15	*	0.09 ± 0.08	6.7
S <sub>1</sub> populations per se	5-S1	5.9	9.9	6.5	5.6	3.3	-	0.97	6.33	-0.35 ± 0.19**	**	-0.17 ± 0.10	-5.5
	10-S1		7.1	8.1	6.3	4.4	-			-0.12 ± 0.19	*	-0.06 ± 0.10	-1.8
	20-S1		4.1	5.5	0.8	0.7	0.6			-1.30 ± 0.14**	-	-0.65 ± 0.07**	-20.6
	30-S1		10.2	7.6	3.9	2.8	-			-0.50 ± 0.19*	*	-0.25 ± 0.10*	-7.9

\*\*, 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 Cycle 0 are S.E./20<sup>0.5</sup> for BS11C0 and S.E./10<sup>0.5</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 was calculated as the response per cycle divided by 2, the number of years required to complete a cycle of selection.

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

‡‡ Cycle not included in study.

programs. The greatest reduction in plant and ear height was -8.07 and -6.52 cm cycle<sup>-1</sup> for the 20-S1 program. This population also showed the greatest favorable response for root and stalk lodging. Top height increased significantly in the 5-S1 and 10-S1 selection programs, while it decreased significantly in both the 20-S1 and 30-S1 programs. These same trends for plant, ear, and top height held for the BS11C0 and B79 testcrosses as well as for the selfed populations. The percentage of dropped ears was erratic for each program with the exception of the 5-S1 program. In the 5-S1 program, the percentage of dropped ears significantly increased

over cycles of selection for the populations per se, testcrosses, and the populations selfed (Table 6). This increase cycle<sup>-1</sup> in dropped ears was as high as 17.3% of the C0 mean for the B79 testcrosses (Table 6). With selection, all of the populations per se became significantly earlier in reaching mid silk. The C5 population of the 20-S1 program was 6 d earlier than the C0 assuming 13 GDU d<sup>-1</sup> at flowering or the equivalent of becoming ≈1 d earlier with each cycle of selection. Likewise, the 20-S1 program also showed the greatest response in GDU required to reach mid silk in the selfed populations. Selfed 5-S1 populations became later in flowering

**Table 6. Least squares estimates of response per cycle to four selection methods for five agronomic traits in the BS11 maize population. Values in parentheses are per cycle responses as a percent of the predicted C0 mean.†**

Population type	Selection method	Height			Dropped ears	Growing degree units					
		Plant	Ear	Top							
cm											
S <sub>0</sub> populations per se	5-S1	-3.59**	(-1.5)	-4.72**	(-3.6)	1.13**	(1.0)	0.10*	(9.9)	-2.38*	(-0.3)
	10-S1	-3.33**	(-1.4)	-4.11**	(-3.1)	0.80**	(0.7)	-0.09*	(-9.7)	-7.17**	(-0.8)
	20-S1	-8.07**	(-3.3)	-6.52**	(-4.9)	-1.59**	(-1.4)	-0.09**	(-9.3)	-16.30**	(-1.8)
	30-S1	-5.12**	(-2.1)	-4.35**	(-3.3)	-0.72**	(-0.6)	-0.08	(-8.6)	-9.79**	(-1.1)
Testcrosses to BS11 C0	5-S1	1.75**	(0.7)	0.01	(0.0)	1.74**	(1.5)	0.13**	(13.3)	-0.53	(-0.1)
	10-S1	-0.40	(-0.2)	-1.13**	(-0.9)	0.75**	(0.7)	-0.04	(-3.8)	-3.47**	(-0.4)
	20-S1	-3.81**	(-1.6)	-3.54**	(-2.7)	-0.27	(-0.2)	-0.04	(-3.7)	-10.39**	(-1.2)
	30-S1	-1.85**	(-0.8)	-1.99**	(-1.5)	0.15	(0.1)	-0.10*	(-10.7)	-7.16**	(-0.8)
Testcrosses to inbred B79	5-S1	0.97**	(0.4)	-0.70*	(-0.5)	1.66**	(1.6)	0.14**	(17.3)	-3.03*	(-0.4)
	10-S1	0.42	(0.2)	-0.72*	(-0.6)	1.09**	(1.0)	-0.02	(-2.1)	-1.50	(-0.2)
	20-S1	-2.97**	(-1.3)	-2.89**	(-2.3)	-0.13	(-0.1)	-0.07*	(-8.9)	-6.71**	(-0.8)
	30-S1	-1.36**	(-0.6)	-1.49**	(-1.2)	0.12	(0.1)	-0.09	(-11.0)	-3.68**	(-0.4)
S <sub>1</sub> populations per se	5-S1	-0.64	(-0.3)	-2.71**	(-2.5)	2.09**	(2.1)	0.08**	(11.8)	2.13	(0.2)
	10-S1	-0.11	(-0.1)	-1.03**	(-1.0)	1.00**	(1.0)	-0.02	(-2.5)	-4.20**	(-0.5)
	20-S1	-5.94**	(-2.8)	-4.92**	(-4.6)	-0.95**	(-0.9)	-0.03	(-4.7)	-10.53**	(-1.2)
	30-S1	-2.60**	(-1.2)	-2.22**	(-2.1)	-0.38	(-0.4)	-0.08*	(-11.5)	-8.82**	(-1.0)

\*\*, 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 predicted C0 intercept and multiplied by 100.

**Table 7. Inbreeding depression in actual units and percent (in parenthesis) of four S<sub>1</sub> progeny selection programs in the BS11 maize population for nine agronomic traits.**

Trait	Cycle	Selection program							
		5-S1		10-S1		20-S1		30-S1	
Grain yield (Mg ha <sup>-1</sup> )	C0	1.33**	(29.4)†						
	C1	0.82**	(20.0)	1.31**	(29.3)	1.33**	(27.4)	1.18**	(24.5)
	C2	1.04**	(26.1)	1.26**	(25.3)	1.03**	(22.3)	0.96**	(20.1)
	C3	1.24**	(30.8)	1.21**	(23.9)	1.19**	(24.6)	1.17**	(23.8)
	C4	0.93**	(24.1)	0.97**	(18.9)	1.25**	(25.3)	1.01**	(19.8)
	C5	-	-	-	-	1.38**	(26.9)	-	-
Grain moisture (g kg <sup>-1</sup> )	C0	17.0**	(7.1)						
	C1	8.0*	(3.5)	13.0**	(5.5)	12.0**	(5.1)	7.0*	(3.0)
	C2	16.0**	(7.1)	3.0	(1.3)	13.0**	(5.5)	7.0*	(3.1)
	C3	11.0**	(4.7)	8.0*	(3.5)	11.0**	(4.8)	8.0*	(3.6)
	C4	10.0**	(4.1)	5.0	(2.3)	15.0**	(6.6)	11.0**	(4.8)
	C5	-	-	-	-	10.0**	(4.5)	-	-
Stalk lodging (%)	C0	3.3**	(15.9)						
	C1	4.2**	(18.1)	5.6**	(25.2)	4.4**	(22.0)	2.0	(10.0)
	C2	4.9**	(20.2)	5.8**	(27.9)	3.3*	(16.6)	3.7*	(19.1)
	C3	3.8*	(21.6)	5.6**	(34.4)	3.0*	(20.8)	4.5**	(26.3)
	C4	4.3**	(23.6)	3.9*	(26.4)	3.3*	(23.2)	5.0**	(30.5)
	C5	-	-	-	-	1.9	(19.2)	-	-
Root lodging (%)	C0	0.4	(6.3)						
	C1	-3.2*	(-47.1)	-0.5	(-7.5)	-0.2	(-5.0)	-3.6**	(-54.5)
	C2	1.0	(13.3)	-1.3	(-18.3)	-2.7*	(-93.1)	1.5	(16.1)
	C3	-1.5	(-34.1)	1.3	(16.9)	0.1	(11.1)	0.1	(2.6)
	C4	0.0	(0.0)	-0.5	(-12.2)	0.1	(12.5)	0.4	(12.5)
	C5	-	-	-	-	0.2	(28.6)	-	-
Plant height (cm)	C0	34.9**	(14.3)						
	C1	27.8**	(11.6)	24.3**	(10.1)	30.0**	(12.9)	29.1**	(12.2)
	C2	23.2**	(10.0)	26.1**	(11.1)	23.0**	(10.1)	25.2**	(10.9)
	C3	25.3**	(10.9)	25.2**	(10.8)	26.7**	(12.3)	22.8**	(10.4)
	C4	24.2**	(10.5)	21.9**	(9.5)	21.3**	(10.4)	26.2**	(11.5)
	C5	-	-	-	-	28.4**	(13.7)	-	-
Ear height (cm)	C0	24.8**	(18.7)						
	C1	21.6**	(17.0)	16.8**	(13.2)	21.4**	(17.2)	18.7**	(14.6)
	C2	16.7**	(14.1)	17.8**	(14.3)	18.4**	(15.0)	15.9**	(13.2)
	C3	17.0**	(14.6)	13.1**	(11.2)	19.0**	(17.1)	17.2**	(14.9)
	C4	17.4**	(15.3)	11.2**	(9.9)	15.0**	(14.8)	15.3**	(13.3)
	C5	-	-	-	-	17.0**	(17.0)	-	-
Top height (cm)	C0	9.8**	(8.8)						
	C1	7.0**	(6.3)	7.9**	(6.9)	8.5**	(7.8)	10.9**	(9.9)
	C2	6.5**	(5.8)	7.9**	(7.1)	4.6**	(4.4)	9.3**	(8.5)
	C3	8.3**	(7.1)	11.6**	(10.1)	7.3**	(6.9)	5.6**	(5.4)
	C4	6.8**	(5.8)	10.9**	(9.4)	6.1**	(5.9)	11.3**	(10.0)
	C5	-	-	-	-	10.9**	(10.1)	-	-
Dropped ears (%)	C0	0.3**	(30.0)						
	C1	0.2	(15.4)	0.4	(40.0)	0.3	(30.0)	0.8**	(57.1)
	C2	0.4	(36.4)	0.2	(28.6)	-0.2	(-40.0)	0.5	(50.0)
	C3	0.4	(28.6)	0.2	(22.2)	0.3	(33.3)	-0.3	(-100.0)
	C4	0.3	(23.1)	-0.1	(-14.3)	0.2	(25.0)	0.3	(42.9)
	C5	-	-	-	-	0.0	(0.0)	-	-
Growing degree units (°C)	C0	-18.8**	(-2.1)						
	C1	-29.9**	(-3.4)	-52.1**	(-6.1)	-36.3**	(-4.2)	-41.6**	(-4.8)
	C2	-35.1**	(-4.0)	-39.0**	(-4.5)	-31.9**	(-3.7)	-29.3**	(-3.4)
	C3	-20.4*	(-2.3)	-43.1**	(-5.0)	-45.3**	(-5.4)	-26.7**	(-3.1)
	C4	-51.3**	(-5.9)	-15.2	(-1.7)	-50.4**	(-6.2)	-20.0**	(-2.3)
	C5	-	-	-	-	-45.4**	(-5.5)	-	-

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

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

than the C0 selfed population, albeit <1 d after four cycles of selection.

### Inbreeding Depression

Highly significant ( $P < 0.01$ ) inbreeding depression for grain yield was found for all cycles of selection in each of the four selection programs (Table 7). No trends toward a decrease in inbreeding depression were observed among the 5-S1, 20-S1, and 30-S1 selection programs. There was a slight trend for a decrease in in-

breeding depression in the 10-S1 program, however. Significant inbreeding depression also was detected for grain moisture in most of the cycles in each of the four programs. There was no clear trend in inbreeding depression for grain moisture over cycles of selection. Likewise, inbreeding depression was significant for most cycles of each population for stalk lodging. No significant inbreeding depression was found for root lodging with the exception of the C1 for 5-S1 and 30-S1 and the C2 of the 20-S1 programs (Table 7). Plant, ear, and top height had highly significant inbreeding-depression

**Table 8. Grain yield, cumulative selection differentials (Cumulative S), predicted gain, realized heritabilities (italics), and correlated heritabilities for four S<sub>i</sub>-progeny selection programs in the BS11 maize population each with a different effective population size.**

Selection program	Cumulative S	Predicted gain†	Populations per se	Realized heritability		
				Crosses to		Populations selfed
				BS11 C0	B79	
	Mg ha <sup>-1</sup>					
5-S1	5.05	3.74	-15.1 ± 1.8	-8.8 ± 1.8	5.3 ± 1.8	-7.3 ± 1.5
10-S1	4.64	3.49	11.4 ± 1.8	14.0 ± 1.8	8.6 ± 1.9	15.6 ± 1.6
20-S1	3.52	2.50	12.6 ± 2.4	14.9 ± 2.4	7.5 ± 2.5	16.1 ± 2.1
30-S1	4.12	2.96	11.3 ± 2.1	19.8 ± 2.1	7.9 ± 2.2	18.8 ± 1.8

† Calculated by taking the heritability multiplied by selection differential for each cycle and summed over cycles.

effects for all cycles of selection in each of the four programs. Although it is difficult to determine any clear trends for inbreeding depression for plant, ear, and top height, all selected cycles have lower inbreeding depression for plant and ear height than the C0. Although the C0 and the C1 of 30-S1 suffered significant inbreeding depression for percentage of dropped ears, the advanced cycles in the four programs displayed no significant inbreeding depression. All selection programs suffered significant inbreeding depression for the number of GDU required to reach mid silk. There was no trend for a decrease in inbreeding depression for mid silk, and several of the selected cycles had greater inbreeding depression than the C0 population.

### Realized Heritability

The cumulative S's for grain yield (Table 8) were large for all selection programs, ranging from 3.52 (20-S1) to 5.05 (5-S1) Mg ha<sup>-1</sup>. Likewise, the predicted gains also were large for each program, ranging from 2.50 (30-S1) to 3.74 (5-S1) Mg ha<sup>-1</sup>. The cumulative S of 5.05 Mg ha<sup>-1</sup> was larger in the 5-S1 program than in any of the other three programs. If five random lines were recombined in this population without selection, the population yields per se would most likely have decreased at a higher rate than in our study. Realized heritabilities (Table 8) were similar and low for 10-S1, 20-S1, and 30-S1 programs. The realized heritability for 5-S1 was negative because the cumulative S increased, but the grain yield decreased over cycles of selection. The trend for realized heritabilities was to increase with increasing effective population size. Frankham et al. (1968) also reported the trend for an increase in realized heritability with increased population size.

### DISCUSSION

From our results of selected traits (primarily grain yield), it seems that the point at which genetic drift no longer dominated progress from selection in the population per se had been reached when 10 lines were recombined. After this point, there seemed to be no advantage, at least in the short term, for selecting and intermating an additional 10 to 20 progenies (i.e., no additional increase in response was found for 20-S1 and 30-S1 vs. 10-S1). That is not to say that genetic variance has not been impacted differently in these programs, however. Darrah (1986) reported a greater selection response per cycle for ear-to-row selection when 100

individuals were evaluated vs. 49 individuals at 10% selection intensity. Our result is also in contrast to that of Frankham et al. (1968), who found that the larger population sizes at the same selection intensity resulted in greater responses to selection. The discrepancy between our results and those of Frankham et al. (1968) could be because *short term* in our study is four or five cycles, whereas their response was evaluated over 12 cycles. Therefore, in our study, recombining an additional 10 or 20 progenies did not contribute enough favorable alleles to the population to have an impact on the short-term response. A possibility for improving the response would be to increase the selection intensity for a given effective population size. Frankham et al. (1968) found that higher selection intensity at the same population size gave better responses even in the short term (12 generations). Our data agree with the conclusion of Baker and Curnow (1969) that there is no additional gain in the short term by having an effective population size >16.

Based on population per se and selfed-population data, intermating 20 lines was an optimal number for maximizing stalk- and root-lodging response. However, because the 20-S1 program was selected in each cycle for these traits, while the other three were not, the 20-S1 program probably had a distinct advantage in this study. If the responses are calculated for these traits, based on the number of cycles in which selection was practiced for those specific traits and not based on the number of overall cycles of selection, the rates of response for stalk and root lodging are as high in the 5-S1, 10-S1, and 30-S1 programs as in the 20-S1 program. A compromise between long-term and short-term goals in the recurrent selection program discussed above is most likely more of a theoretical result than a real limitation to the breeding program. Recurrent selection programs have been conducted for many cycles with finite population sizes without the exhaustion of genetic variance (Holthaus and Lamkey, 1995; Labate et al., 1997). A simulation study conducted by Lacy (1987) also showed that even with a population size of 20, genetic variation remained in the population for nearly 100 generations in the absence of directional selection. He showed that strong directional selection in a finite population is more likely to quickly deplete the genetic variance than genetic drift. The concern over the loss of genetic variation only need be relevant in a closed population such as those used for genetic studies. In practice, breeding programs using recurrent selection for improv-

ing populations to derive inbred lines need not remain closed to the introduction of new individuals (genotypes) from outside the population. Lacy (1987) clearly showed that new individuals from outside the population every other generation or so can counter the depletion of genetic variation by random genetic drift. Therefore, in practice, if it is concluded that genetic variation is being depleted in a program, an individual can be added to the population from other source germplasm. Nevertheless, it is critical that caution be given to the introduction of new individuals into a population. Although there may be a plethora of individuals from which to choose to introduce into the population to increase the genetic variation, many of those individuals also may reduce the selection response already obtained in the population.

#### ACKNOWLEDGMENTS

The authors are indebted to Dr. O.S. Smith who had the foresight to conceptualize and plan the effective population-size study in the late 1970s. We gratefully acknowledge funding for the selection-methods study provided by a USDA Competitive Grant no. 85-CRCR-1-1567. The evaluation phase of the study described herein was funded by USDA Competitive Grant no. 90-37140-5578.

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