Genetic Effects Associated with Reciprocal Recurrent Selection in BSSS and BSCB1 Maize Populations

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ABSTRACT

Reciprocal recurrent selection (RRS) was designed to capitalize on both additive and nonadditive genetic effects for improvement of the cross between two populations by complementary changes in allelic frequencies between populations. Eleven cycles of RRS have been completed in the Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic No. 1 (BSCB1) maize (*Zea mays* L.) populations. The objectives of this study were to partition the response to selection into that due to additive and dominance genetic effects and to evaluate the effects of genetic drift. A population diallel of the C0, C4, C7, C9, and C11 cycles of BSSS(R) and BSCB1(R) and the C8 and C10 interpopulation crosses of BSSS(R) and BSCB1(R) were evaluated. The populations per se selfed and interpopulation crosses selfed of the C0, C4, C7, C8, C9, C10, C11 cycles also were included in the study. The study was evaluated at four locations in 1988 and three locations in 1989. The response of the interpopulation cross for grain yield was 0.28 ± 0.04 Mg ha^{-1} cycle^{-1} and was primarily due to dominance effects. Responses in the populations per se, adjusted for the effects of genetic drift, were similar to the direct effects in the interpopulation cross. Improvement in BSSS(R) was due to both additive and dominance effects, but only dominance effects were important in BSCB1(R). The results showed that selection response occurred at loci with alleles with partial to complete dominance with no evidence for overdominant alleles contributing to selection response. There were no significant changes in grain moisture, and the responses for root and stalk lodging were in the desired direction. It is concluded that RRS was effective for improving the interpopulation cross and inbreeding depression from genetic drift limited the observed response in the populations per se.

RECIPROCAL RECURRENT SELECTION, originally proposed by Comstock et al. (1949), is expected to be effective for simultaneously developing two germplasm sources for hybrid maize breeding programs because selection is based on the performance of the interpopulation cross, in which almost any type of gene action is expressed. Both general and specific combining ability of populations per se should be improved in the advanced cycles of selection, thus increasing the probability of obtaining inbreds with improved combining ability.

A RRS program was initiated in 1949 in Iowa with BSSS BSCB1 maize populations. Reports of progress have been presented periodically (Penny and Eberhart, 1971; Eberhart et al., 1973; Martin and Hallauer, 1980; Smith, 1983; Helms et al., 1989). In general, the direct response to selection in the interpopulation cross was greater than the indirect responses observed in the populations per se. Smith (1983) proposes a model that permits partitioning the response from selection into

components due to additive and dominance genetic effects and also allows estimation of the effect of genetic drift. Smith (1983) used the model to evaluate response to selection in BSSS(R) and BSCB1(R) after seven cycles of RRS, and found that the indirect responses adjusted for the effects of genetic drift were larger than the direct response. Effects of genetic drift due to small population size in BSSS(R) also were detected by Helms et al. (1989). Although genetic drift results in a lack of response in the populations per se, empirical studies have shown that genetic drift does not affect the response of the interpopulation cross, which is the primary objective of a RRS program.

Our study evaluates response to 11 cycles of RRS in BSSS(R) and BSCB1(R). Our objectives were: to (i) partition the response to selection in BSSS(R) and BSCB1(R), using Smith's (1983) model, into that due to additive and dominance genetic effects and to estimate the effect of genetic drift on the indirect response observed in the populations per se and (ii) compare the results for Smith's model with the results from the diverstiy analysis described by Moll and Hanson (1984).

MATERIALS AND METHODS

The details of the first five cycles of RRS with BSSS and BSCB1 were presented by Penny and Eberhart (1971). Details of changes that have been made in the selection program since its inception were described by Keeratinijakal and Lamkey (1993). The primary trait selected has been grain yield, with selection for less grain moisture at harvest and resistance to root and stalk lodging.

In the 1987 breeding nursery, a population diallel was produced among C0 (Cycle 0), C4, C7, C9, and C11 of BSSS(R) and BSCB1(R). In addition, the C8 and C10 interpopulation crosses of BSSS(R) and BSCB1(R) were produced. Seed of C0, C4, C7, C8, C9, C10, and C11 of BSSS(R) and BSCB1(R) populations per se and populations per se selfed were also produced. Selfed seed of the C0, C4, C7, C8, C9, C10, and C11 interpopulation crosses was produced in the 1988 nursery. The populations per se, populations per se selfed, and interpopulation crosses selfed were produced by intercrossing or selfing ≈ 100 plants. The population crosses were produced by reciprocally crossing 50 plants from each population.

Data were collected at three Iowa locations in 1988 and four Iowa locations in 1989 for grain yield (Mg ha^{-1} at 155 g kg^{-1} grain moisture), grain moisture (g kg^{-1}), stand (plants ha^{-1}), stalk lodging (% plants broken below the ear node), root lodging (% plants inclined more than 30° from vertical), ear height (cm), plant height (cm), silking date (days after planting), and pollen date (days after planting). Details of the experimental design, environmental design, and data collection procedures were given by Keeratinijakal and Lamkey (1993).

Means over environments for the 82 noninbred and inbred genotypes were combined into one data set (Table 1). This data set was used to estimate genetic parameters in the model described by Smith (1983). The model was used to estimate the contribution of additive and dominance genetic effects to the mean of the *I*th population (AOI and DOI), the contribution of additive and dominance genetic effects to the response to

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Abbreviations: BSCB1, Iowa Corn Borer Synthetic no. 1; BSSS, Iowa Stiff Stalk Synthetic; C*n*, *n*th cycle of selection; RRS, reciprocal recurrent selection. **, Significant at the 0.01 probability level.

Table 1. Mean grain yields across environments for the BSSS(R)Cn and BSCB1(R)Cn maize populations and population crosses, and (in parentheses) their S_1 generations.

	BSSS(R)							BSCB1(R)						
	C0	C4	C7	C8	C9	C10	C11	C0	C4	C7	C8	C9	C10	C11
							Mg ha⁻¹							
BSSS(R)C0	3.55†‡ (2.40)													
BSSS(R)C4	4.00	3.76 (2.88)												
BSSS(R)C7	4.54	4.60	4.24 (2.83)											
BSSS(R)C8	—§	—	—	4.34 (3.34)										
BSSS(R)C9	4.92	4.98	4.47	—	4.25 (3.39)									
BSSS(R)C10	—	—	—	—	—	3.98 (3.22)								
BSSS(R)C11	4.84	4.69	4.41	—	4.07	—	3.92 (3.28)							
BSCB1(R)C0	4.24† (3.41)	4.16	5.10	—	5.20	—	5.51	3.21† (2.55)						
BSCB1(R)C4	4.37	4.94† (4.40)	5.36	—	5.64	—	5.66	3.48	3.16 (2.83)					
BSCB1(R)C7	4.96	5.74	6.08† (5.13)	—	6.63	—	6.35	4.14	3.95	3.61 (2.52)				
BSCB1(R)C8	—	—	—	6.59† (5.39)	—	—	—	—	—	—	3.30 (2.62)			
BSCB1(R)C9	5.50	6.32	6.42	—	6.94† (5.38)	—	6.70	4.92	4.28	3.96	—	3.87 (2.74)		
BSCB1(R)C10	—	—	—	—	—	6.84† (5.47)	—	—	—	—	—	—	3.59 (2.92)	
BSCB1(R)C11	5.86	6.62	6.62	—	6.95	—	6.76† (5.09)	4.81	4.39	4.02	—	4.02	—	3.76 (2.80)

† Mean of duplicated entries.
‡ SE of means are 0.24 for S_0 population, 0.17 for S_1 population, 0.21 for S_1 population cross, and 0.17 for duplicated entries of S_0 population.
§ Not included in the study.

selection in the Ith population (ALI and DLI), the effect of loss of heterozygotes due to genetic drift or selection in the Ith population (DQI), a dominance term that is a function of the change in allelic frequencies in the Ith population at loci where the Ith and I'th populations differ in allelic frequency (DLII'), heterosis in the cross of the Ith and I'th populations (HII'), and a heterosis term that is a quadratic function of changes in allelic frequencies and dominance in the cross of the Ith and I'th populations (HQII'). When effective population size is <20, DQI is predominately an estimate of the loss of heterozygotes due to genetic drift (Smith, 1983). Although a bias from selection exists, it is expected to be small, especially with small effective population size. Hanson (1987) pointed out that DQI reflects heterosis between the base population and the nth cycle of selection and that failure to obtain the expected heterosis could reflect genetic drift. Because effective population size is <20 for BSSS(R) and BSCB1(R), we will assume that DQI in our analysis is an estimate of the loss of heterozygotes due to random genetic drift.

The genetic parameters from Smith's (1983) model (β) were calculated by using weighted least squares: $\beta = (X'W^{-1}X)^{-1}X'W^{-1}Y$, where the elements of the Y-matrix are the entry means and the elements of the X-matrix are functions of cycle number and the coefficients of the genetic parameters. The matrix W contains the variances of the entry means on the diagonal and zeros on the off diagonal. Standard errors of the parameter estimates were calculated as the square root of the corresponding diagonal element (C_{ii}) of the $(X'W^{-1}X)^{-1}$ matrix.

The data from the 10-parent diallel among C0, C4, C7, C9, and C11 of BSSS(R) and BSCB1(R) were used to calculate the diversity analysis described by Moll and Hanson (1984). The diversity analysis makes use of the population per se and population cross data from the diallel to estimate additive-associated (D_a) and dominance-associated (D_d) distances between population. For D_a to be nonzero, there must be differences in frequencies of alleles between populations having

additive effects, and for D_d to be nonzero, there must be dominance at the locus level and differences in allelic frequencies between populations. Hanson (1987) showed that D_a provides information similar to ALI from Smith's (1983) model, although there is no comparable term from Smith's model for D_d. Hanson (1987) proposed using D_d as a relative measure of genetic diversity but did present experimental evidence. The modification of principal component analysis described by Hanson and Moll (1986) was used to graphically depict the spatial divergence represented by the dominance-associated distances.

RESULTS AND DISCUSSION

Additive (AOI) and dominance (DOI) effects for grain yield were significantly different from zero ($P \leq 0.05$) for BSSS(R) and BSCB1(R), but the dominance effects were smaller than the additive effects (Table 2). These estimates suggest that grain yield was largely controlled by alleles with additive effects. The positive estimates of ALI and DLI in BSSS(R) indicates that RRS effectively increased the frequency of favorable alleles for grain yield in BSSS(R) with additive and dominance effects. The changes in allelic frequencies due to selection in BSCB1(R) occurred mainly at loci having alleles with dominance effects, because the estimate of ALI was nonsignificant. The estimates of ALI and DLI in BSCB1(R) were consistent with the results from Keeratinijakal and Lamkey (1993), in that the improvement in grain yield of BSCB1(R), 0.06 Mg ha⁻¹ cycle⁻¹ was greater than improvement in the BSCB1(R) population selfed, 0.02 Mg ha⁻¹ cycle⁻¹.

The effect of loss of heterozygotes in the populations per se due to genetic drift (DQI) was identical in both populations (−0.012** Mg ha⁻¹ cycle⁻¹). The negative

Table 2. Least squares estimates of genetic model parameters (Smith, 1983) for yield and other agronomic traits in the BSSS(R) and BSCB1(R) maize populations.

Population	Parameter†	Grain		Lodging		Height		Date	
		Yield	Moisture	Root	Stalk	Ear	Plant	Silking	Pollen
		Mg ha⁻¹	g kg⁻¹	%		cm		d after planting	
BSSS(R)	AOI	1.568**	214.1**	4.68	1.40	66.97**	146.96**	93.47**	88.16**
	DOI	0.921**	−1.6	0.72	9.38**	22.60**	33.56**	−2.33**	−1.55**
	ALI	0.080**	0.6	−0.09	−0.15	0.30	1.28**	−0.01	0.02
	DLI	0.068**	−0.9	0.04	−0.16	−0.51	−0.91*	−0.27**	−0.24**
	DLII'	−0.015	0.2	−0.06	0.09	0.05	0.10	−0.03	0.04
	2(ALI + DLI)‡	0.295**	−0.6	−0.11	−0.62*	−0.43	0.73	−0.56**	−0.44**
	ALI + DLI + 2DLII'§	0.118**	0.20	−0.17	−0.13	−0.11	0.57*	−0.34**	−0.14**
	DQI	−0.012**	0.0	−0.01	0.00	−0.02	−0.05**	0.01*	0.01**
BSCB1(R)	AOI	2.236**	187.3**	6.01	6.31*	65.66**	152.72**	92.05**	85.59**
	DOI	0.373*	−6.2	3.65	17.64**	19.07**	25.56**	−4.18**	−2.98**
	ALI	0.001	0.6	0.03	−0.45*	−0.09	−0.12	0.05	0.10
	DLI	0.147**	−0.6	−0.55	−1.10**	0.31	1.21**	0.06	0.08
	DLII'	0.009	0.1	0.11	0.32*	−0.02	−0.20	−0.09**	−0.06*
	2(ALI + DLI)‡	0.297**	1.0	−1.05**	−3.10**	0.42	2.18**	0.24*	0.36**
	ALI + DLI + 2DLII'§	0.166**	0.3	−0.30	−0.91	0.18	0.69**	−0.07	0.06
	DQI	−0.012**	0.0	0.02	−0.00	−0.07**	−0.13**	−0.00	−0.00
BSSS(R) × BSCB1(R)	HII'	0.457**	−3.0**	0.11	−1.45	2.92**	4.17**	−0.01	−0.34*
	HQII'	0.000	0.0	0.01	−0.02	0.01	0.02	0.01**	0.00
R^2		99.5	99.9	94.5	98.4	99.9	99.9	99.9	99.9

*,** Significant at the 0.05 and 0.01 probability levels, respectively.
† AOI and DOI, contribution of additive and dominant genetic effects to the mean of the *k*th population; ALI and DLI, contribution of additive and dominance genetic effects to the response to selection in the *k*th population; DLII', change in allelic frequency in the *k*th population at loci where the *k*th and *l*'th the populations differ in allelic frequency; DQI, estimate of loss of heterozygotes due to genetic drift; HII', heterosis in the cross of the *k*th and *l*'th populations; HQII', a heterosis term that is a quadratic function of changes in allelic frequencies and dominance in the cross of the *k*th and *l*'th populations.
‡ Response in the population per se adjusted for genetic drift.
§ Contribution of the population to response in the interpopulation cross.

estimates of DQI indicate that inbreeding due to genetic drift limited improvement in grain yield in the populations per se. At C11, the estimated loss in grain yield due to effects of genetic drift was 2.90 Mg ha⁻¹ for both populations. The accumulated inbreeding would not only depress mean performance, but also reduce the genetic variance in the populations. Thus, the maximum potential of the populations will never be realized. The change to intermating 20 selected lines rather than 10 selected lines for the last three cycles was done to reduce the cumulative effects of genetic drift. Intermating more than 20 lines would further reduce the effect of genetic drift, but more testcross progenies also would be needed for evaluation to maintain the same selection intensity.

Estimates of DLII' for grain yield were not significant for either population, which indicates that improvement in the population cross was largely dependent on the improvement in the populations per se (ALI + DLI). The effect due to heterosis (HII') was significant ($p \leq 0.01$), indicating both directional dominance for grain yield and a difference in the frequency of alleles affecting grain yield between the original populations. The estimate of HQII' for grain yield was equal to zero. HQII' is equal to $\Delta p \Delta p' d$, where Δp and $\Delta p'$ are the changes in the frequencies of favorable alleles in BSSS(R) and BSCB1(R), respectively, and d is the dominance effect. If directional dominance does not exist, then HQII' would equal zero. The significant estimates of DOI, DLI, and HII' in the populations, however, support the existence of directional dominance for grain yield. A zero estimate for HQII' would also result if the change in allelic frequencies in either or both populations was equal to zero

or if changes in allelic frequencies were such that HQII' was positive for some loci and negative for other loci, canceling each other out when HQII' was summed over loci. (Tanner and Smith, 1987). The zero estimate of HQII' indicates that RRS selected favorable alleles with dominance effects at different loci in each population and that overdominance was not important for grain yield. The steady increase in inbreeding depression and heterosis observed in the interpopulation crosses with cycles of selection also supports selection of favorable alleles at different loci in each population (Keeratinijakal and Lamkey, 1993).

The realized gains for grain yield in the populations per se [2(ALI + DLI)], which are the indirect responses to selection adjusted for the effects of genetic drift, were significant for both BSSS(R) and BSCB1(R). The direct effects of selection (ALI + DLI + 2DLII') were significant in BSSS(R) and BSCB1(R), indicating that improvement in the interpopulation cross was contributed by both populations. The estimated realized gain in the interpopulation cross, calculated from the sum of the direct effects of both populations, was 0.284 ± 0.035 Mg ha⁻¹ cycle⁻¹. Fifty-eight percent of the realized gain in the interpopulation cross was contributed by BSCB1(R). The realized gains for the populations per se [2(ALI + DLI)] were not significantly different from the realized gain for the interpopulation cross.

The results from the diversity analysis for grain yield showed that by C7 the estimated additive- and dominance-associated divergence for both populations from their C0 differed significantly from zero (Table 3). Estimated distances based on dominance-associated genetic

Table 3. Estimated distances for grain yield (Mg ha^{-1}) between populations based on additive-associated (above diagonal) and dominance-associated (below diagonal) genetic effects following 11 cycles of reciprocal recurrent selection within the BSSS(R) and BSCB1(R) maize populations.

	Population									
	BSSS(R)					BSCB1(R)				
Population	C0	C4	C7	C9	C11	C0	C4	C7	C9	C11
BSSS(R)C0		0.953**	1.597**	2.328**	1.939**	0.592**	0.483**	0.838**	1.945**	2.224**
BSSS(R)C4	0.710		0.634**	1.369**	0.978**	1.556**	1.448**	0.050	0.984**	1.264**
BSSS(R)C7	1.621**	1.093**		0.723**	0.326**	2.199**	2.091**	0.749**	0.332**	0.618**
BSSS(R)C9	2.486**	1.845**	—†		0.375**	2.930**	2.822**	1.483**	0.369**	0.021
BSSS(R)C11	2.526**	1.972**	—	—		2.540**	2.433**	1.093**	—	0.266**
BSCB1(R)C0	1.983**	2.927**	3.665**	4.348**	4.419**		0.033	1.442**	2.547**	2.825**
BSCB1(R)C4	2.975**	4.040**	4.533**	5.182**	5.234**	0.747		1.334**	2.439**	2.718**
BSCB1(R)C7	4.312**	5.412**	5.795**	6.447**	6.442**	2.488**	1.231*		1.099**	1.378**
BSCB1(R)C9	4.791**	5.911**	6.155**	6.787**	6.755**	3.140**	1.927**	—		0.259**
BSCB1(R)C11	5.110**	6.192**	6.401**	6.994**	6.971**	3.392**	2.204**	0.270	—	

*,** Significant at the 0.05 and 0.01 probability level, respectively.
† Distance estimates were less then zero.

effects increased with selection at a faster rate than distances based on additive-associated genetic effects. These results demonstrate that selection has increased the frequency of favorable alleles in both populations and is consistent with the results obtained from Smith's (1983) model (Table 2). The BSCB1(R) population seems to have been more responsive to selection as evidenced from the larger changes in additive- and dominance-associated genetic effects.

In contrast to the populations per se, additive effects were of much less importance than dominance effects in the population crosses (comparison of BSSS(R)Cn vs. BSCB1(R)Cn). Additive effects initially increased from BSSS(R)C0 vs. BSCB1(R)C0 (0.59) to BSSS(R)C4 vs. BSCB1(R)C4 (1.45) and then decreased to BSSS(R)C11 vs. BSCB1(R)C11 (0.27). The additive-associated distance between the rth and r'th population may be expressed in terms of single-locus effects as $[n(\Sigma_i(P_{ri} - P_{r'i} + \Delta_{ri} - \Delta_{r'i})a_i)^2]^{1/2}$, where n is the number of alleles per locus, P_{ri} is the frequency of the ith allele in the rth base (C0) population, Δ_{ri} is the change in frequency of the ith allele in the rth population (Cn), and a_i is half the deviation of the mean of the ith homozygote from the mean of all homozygotes in the population (Hanson, 1987). If the rth or the r'th population has not undergone selection, then the appropriate Δ values are set to zero. The decrease in additive-associated distances observed with selection between BSSS(R)Cn vs. BSCB1(R)Cn can only be explained by a greater change in allelic frequencies in one population than in the other.

The estimated distances between populations based on dominance-associated gene effects were plotted according to the first two principal components (Fig. 1). The spatial arrangement of the populations reflect relative genetic diversity and are used to assess interrelationships among populations (Hanson, 1987). The two principal components together accounted for 98.3% of the dominance-associated variation among populations. The first principal component accounted for 91.8% of the variation and reflected primarily divergence between the BSSS(R)Cn and the BSCB1(R)Cn populations. The second principal component reflected primarily divergence of the selected populations from their respective base populations. Distances between populations based on dominance-associated gene effects steadily increased from BSSS(R)C0 vs. BSCB1(R)C0 (1.98) to BSSS(R)C11 vs.

BSCB1(R)C11 (6.97) (Table 3). The largest estimates of dominance-associated divergence were 6.99 for BSSS(R)C9 vs. BSCB1(R)C11 and 6.97 for BSSS(R)C11 vs. BSCB1(R)C11.

Hanson and Moll (1986) and Hanson (1987) calculated the ratio of dominance-associated distances, $D = d_{34} / (d_{12} + d_{13} + d_{24})$, where the subscripts 1, 2, 3, and 4 refer to BSSS(R)C0, BSCB1(R)C0, BSSS(R)Cn, and BSCB1(R)Cn, respectively. They showed that, under an overdominance model, the ratio should increase with cycles of selection; with partial to complete dominance, the ratio should decrease with cycles of selection. The ratios for C4, C7, C9, and C11 were 1.17. 0.95, 0.89, and 0.88, respectively, indicating that selection has been for complementary loci with partial to complete dominance. Hanson (1987) completed a similar analysis for C4 and C7 of RRS in BSS(R) and BSCB1(R) by using
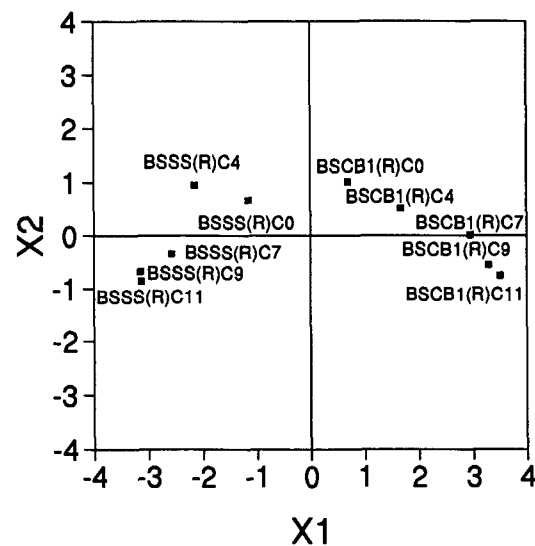

Fig. 1. Two-dimensional representation (principal components) of diversity among maize populations resulting from 11 cycles of reciprocal recurrent selection in the Iowa Stiff Stalk Synthetic (BSSS) and Iowa Corn Borer Synthetic no. 1 (BSCB1) maize populations based on dominance-associated gene effects. The first (X1) and second (X2) principal components accounted for 91.8 and 6.5% of the variation, respectively. Distances were measured in megagrams per hectare.

Smith's (1983) data and reached the same conclusion, that there is no evidence for overdominance for grain yield in these populations.

Grain moisture has been one of the traits considered in the selection program. Estimates of AOI for grain moisture were significant, and estimates of DOI were nonsignificant for both populations, suggesting that grain moisture was mainly controlled by additive effects (Table 2). The nonsignificant estimates of 2(ALI + DLI) indicate that there were no changes in allelic frequencies at loci affecting grain moisture. This was expected, because high-yielding testcross progenies in the evaluation trials that were average or below average for grain moisture at harvest were selected in each cycle of selection. Our results show that RRS successfully maintained grain moisture while increasing grain yield. Although dominance effects were unimportant in the base populations, there was a difference in allelic frequencies between the base populations and some level of directional dominance resulting in a significant estimate of HII'.

All estimates of individual genetic parameters for root lodging were nonsignificant for both populations (Table 2). The linear decreases observed for root lodging in BSSS(R) and BSCB1(R), however, suggests that selection reduced the frequency of unfavorable alleles for root lodging selection reduced the frequency of unfavorable alleles for root lodging (Keeratinijakal and Lamkey, 1992). The estimate of 2(ALI + DLI) for BSCB1(R) was significant and negative, indicating realized gain for root lodging in BSCB1(R) (Table 2). The estimated realized gain in the population cross was $-0.47 \pm 0.36\%$ cycle^{-1}.

Dominance effects were of primary importance for stalk lodging in BSSS(R) and BSCB1(R) (Table 2). There was significant realized gain in BSSS(R) resulting in a reduction in stalk lodging with selection. The reduction in stalk lodging in BSCB1(R) was caused primarily by the contributions of heterozygotes (DLI > ALI). The realized gain for stalk lodging was significantly greater in BSCB1(R) than in BSSS(R), which may be expected because BSCB1(R)C0 had approximately two times as much stalk lodging as BSSS(R)C0. The estimated realized gain in the population cross for stalk lodging was $-1.04 \pm 0.33\%$ cycle $^{-1}$. Most of the improvement for stalk lodging in the population cross was contributed by BSCB1(R).

Responses to selection for ear and plant heights and silking and pollen dates are correlated responses to selection. Additive effects for the four traits were of more importance in the base populations than dominance effects. The correlated response to selection in the populations per se [2(ALI + DLI)] was significant for plant height in BSCB1(R). When crossed, both populations contributed to taller plants in the interpopulation cross, with a realized gain of 1.26 ± 0.36 cm cycle^{-1}.

The correlated responses in the populations per se for silking and pollen dates were negative for BSSS(R) and positive for BSCB1(R) (Table 2). The correlated responses to selection in the interpopulation cross were significant for silking and pollen dates in BSSS(R). The BSSS(R) population contributed earliness in flowering

dates to the interpopulation cross, whereas BSCB1(R) tended to delay the flowering dates in the interpopulation cross. The estimated direct response for silking date in the interpopulation cross was -0.41 ± 0.08 d cycle^{-1}, but the direct response for pollen date was not significant.

The results from our study demonstrate that RRS was effective for improving grain yield of the population cross. The results from Smith's (1983) model and Moll and Hanson's (1984) diversity analysis showed that selection response occurred at complementary loci in BSSS(R) and BSCB1(R), with alleles in the partial to complete dominance range. There was no evidence for overdominant alleles contributing to selection response. Because selection response occurred at loci having alleles with partial to complete dominance, improvement was expected in the populations per se. The lack of improvement in the populations per se reported by Keeratinijakal and Lamkey (1992) is attributed to inbreeding depression resulting from random genetic drift, because both Smith's model and Moll and Hanson's diversity analysis revealed improvement in the frequencies of alleles with additive and dominance effects. Significant estimates of DQI, a measure of random genetic drift, were also obtained from Smith's model, supporting this conclusion. There were no significant genetic changes for grain moisture, and the genetic changes that occurred for root and stalk lodging were in the desired direction. In conclusion, RRS has been an effective method for the genetic improvement of the interpopulation cross, but inbreeding depression from genetic drift has limited the observed responses in the populations per se.

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