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Population Means and Genetic Variances in Selected and Unselected Iowa Stiff Stalk Synthetic Maize Populations

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Abstract

Recurrent selection is a cyclical breeding procedure that focuses on improving the mean performance of a population by increasing the frequency of favorable alleles while maintaining adequate genetic variability for continued selection response. Iowa Stiff Stalk Synthetic (BSSS) is a maize (*Zea mays* L.) population that has undergone continuous recurrent selection for more than 50 yr as the base population for two independent selection programs (intra- and inter-population). This study was designed to estimate the mean performance and genetic variances in BSSS after seven cycles of half-sib (HS) progeny selection, six cycles of S_2-progeny selection, and 11 cycles of reciprocal recurrent selection (RRS). A Design II (factorial) mating design was constructed to give direct estimates of additive and dominance variance in the individual populations. Fourteen sets of four male × four female matings for each of the four populations were evaluated in a randomized incomplete block experiment grown in six environments. Half-sib progeny and RRS methods have produced the most effective mean performance responses for grain yield in the populations per se, 0.076 and 0.104 Mg ha^{-1} cycle^{-1}, respectively. The S_2-progeny selection procedure in BSSS, with a response of 0.052 Mg ha^{-1} cycle^{-1}, has not performed up to theoretical expectations. Genetic variance component estimates for grain yield supported the suggestion that dominance variance is important in BSSS germplasm. Although additive variance decreased slightly, high heritability estimates suggest that further improvement in population means should be achieved by each selection method. Mean performance and estimated genetic variability for other important agronomic traits (grain moisture, root and stalk lodging, and ear height) generally showed favorable response to selection.

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Joel F. Holthaus and Kendall R. Lamkey*

ABSTRACT

Recurrent selection is a cyclical breeding procedure that focuses on improving the mean performance of a population by increasing the frequency of favorable alleles while maintaining adequate genetic variability for continued selection response. Iowa Stiff Stalk Synthetic (BSSS) is a maize (*Zea mays* L.) population that has undergone continuous recurrent selection for more than 50 yr as the base population for two independent selection programs (intra- and inter-population). This study was designed to estimate the mean performance and genetic variances in BSSS after seven cycles of half-sib (HS) progeny selection, six cycles of S_2-progeny selection, and 11 cycles of reciprocal recurrent selection (RRS). A Design II (factorial) mating design was constructed to give direct estimates of additive and dominance variance in the individual populations. Fourteen sets of four male × four female matings for each of the four populations were evaluated in a randomized incomplete block experiment grown in six environments. Half-sib progeny and RRS methods have produced the most effective mean performance responses for grain yield in the populations per se, 0.076 and 0.104 Mg ha^{-1} cycle^{-1}, respectively. The S_2-progeny selection procedure in BSSS, with a response of 0.052 Mg ha^{-1} cycle^{-1}, has not performed up to theoretical expectations. Genetic variance component estimates for grain yield supported the suggestion that dominance variance is important in BSSS germplasm. Although additive variance decreased slightly, high heritability estimates suggest that further improvement in population means should be achieved by each selection method. Mean performance and estimated genetic variability for other important agronomic traits (grain moisture, root and stalk lodging, and ear height) generally showed favorable response to selection.

R ECURRENT SELECTION is a cyclical breeding procedure used widely in maize breeding programs to enhance maize germplasm resources. Population improvement via recurrent selection methodology focuses on two main objectives: improving the mean performance of a population through an increase in the frequency of favorable alleles and maintaining adequate genetic

variability in the improved population for continued selection and genetic enhancement. Population improvement via recurrent selection increases the probability of developing inbred lines with superior combining ability.

The BSSS maize population was developed in 1934 to 1935 by intermating 16 inbred lines possessing above average stalk quality (Sprague, 1946). Since its development, BSSS has undergone continuous recurrent selection for more than 50 yr as the base population in two independent selection programs (intra- and inter-population). The intra-population program included seven cycles of HS selection [BSSS(HT)Cn] with the double-cross tester Iowa 13, followed by six cycles of S_2-progeny selection [BS13(S)Cn], which continues to date. The inter-population program included 11 cycles of RRS using BSSS, designated BSSS(R)Cn, and Iowa Corn Borer Synthetic #1 [BSCB1(R)Cn] as base populations undergoing simultaneous improvement. As a consequence of these selection programs, BSSS has contributed significantly to maize inbred and hybrid development programs, as evidenced by the production of several widely used inbred lines (B14, B37, B73, and B84) (Hallauer et al., 1983).

Continued advancement in these selection programs would be aided by a knowledge of how the genetic structure of the BSSS populations per se have changed over time. This study was designed to estimate the mean performance and other genetic parameters (additive and dominance variances and their interactions with environments, heritability, and phenotypic and additive genetic correlations) of important agronomic traits in BSSS populations per se. Estimates for grain yield, grain moisture, root and stalk lodging, and ear height were compared following seven cycles of HS progeny selection, six cycles of S_2-progeny selection, and 11 cycles of RRS. The objective was to determine if selection had changed the population parameters.

MATERIALS AND METHODS

Genetic Materials Evaluated

In 1939, HS progeny recurrent selection with the double-cross tester Iowa 13 [(L317 × BL349) × (BL345 × MC410)]

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was initiated in BSSSC0. The procedures for conducting seven cycles of HS selection in this population were described by Eberhart et al. (1973) and Lamkey et al. (1991). After completing seven cycles of selection, the program was changed to S_2-progeny recurrent selection in the population now designated BS13(S)C0. The BS13(S)C0 populations was developed directly from the seventh cycle population of the HS program by imposing minor agronomic selection as detailed by Lamkey (1992). Six cycles of S_2-progeny selection were completed, as summarized by Helms et al. (1989a) and Lamkey (1992), producing the advanced cycle population BS13(S)C6.

In 1949, RRS was initiated in the BSSS and BSCB1 maize populations. The base population, BSSSC0, used in this program is identical to the original BSSS population used in the intra-population selection program. Details of 11 cycles of RRS were outlined by Penny and Eberhart (1971) and Keeratinijakal and Lamkey (1993a). The Cycle 11 population of BSSS was designated BSSS(R)C11.

In all selection programs, grain yield was the primary trait under selection, with secondary selection pressure to maintain low grain moisture at harvest and increase resistance to root and stalk lodging. Beginning with C9 of RRS and C3 of S_2-progeny selection, progenies were selected using a selection index weighted by the heritabilities of grain yield, grain moisture, root lodging, and stalk lodging. The selection intensities averaged 9.7% for HS selection, 15.6% for S_2-progeny selection, and 12.1% for RRS. The harmonic mean of the number of progenies recombined in each selection program is 10 for HS selection, 15 for S_2-progeny selection, and 11.6 for RRS. Assuming an effective population size of $2n$, where n is the number of progenies recombined, the estimated inbreeding level of the four populations due to small effective population size is 0% for BSSSC0, 29% for BS13(S)C0, 45% for BS13(S)C6, and 37% for BSSS(R)C11.

The genetic materials evaluated in this study were produced from BSSSC0 and three populations derived from BSSSC0 by selection: BS13(S)C0, BS13(S)C6, and BSSS(R)C11. Starting in the 1989 breeding nursery, a North Carolina Design II (factorial) mating design was developed within each of the four populations. A series of half- and full-sib progenies were developed within each population by crossing four males (S_0 plants) to each of four females (S_1 progenies). The S_1 progenies were developed in the 1988 breeding nursery by selfing random S_0 plants from each population. Each male was crossed to several plants within a S_1 progeny and the resulting seed was bulked to obtain a representative sample of the gametic array of the original S_0 female plant (Hallauer and Miranda, 1988). The average number, variance, and range of S_1 plants sampled per female within each population were, respectively, 9, 11.1, and 1 to 19 for BSSSC0; 9, 8.4, and 4 to 19 for BS13(S)C0; 13, 7.8, and 4 to 20 for BS13(S)C6; and 13, 7.5, and 5 to 20 for BSSS(R)C11. Thus, each set of four × four matings produced progenies from a sampling of eight random plants within each population. To achieve a reasonable sample of individuals, 14 sets of four × four matings were constructed within each population, yielding a total sampling of 112 random S_0 plants from each population. Therefore, a total of 224 full-sib progenies (14 sets of 16 progenies) from each population were produced for field evaluation.

Experimental Design and Procedures

The 896 entries (full-sib progenies) were evaluated in 14 sets of a replications-within-sets randomized incomplete block experiment (Comstock and Robinson, 1948). Because of insufficient seed supply, eight entries were replaced with hybrid filler in all environments. Each set consisted of 16 full-sib

progenies from each of the four individual populations completely randomized within each of two replications. The entries were grown at Ames, Ankeny, and Crawfordsville, IA, in 1992 and Ames, Ankeny, and Martinsburg, IA, in 1993. Each location × year combination was considered a different random environment. A plot consisted of two machine-planted rows 5.49 m long with 0.76 m between rows. Plots were overplanted and thinned to a uniform plant density of approximately 62 165 plants ha^{-1}. All experiments were machine-cultivated and/or hand weeded as necessary for proper weed control.

Data were collected for machine-harvestable grain yield (Mg ha^{-1}) adjusted to 155 g kg^{-1} grain moisture, grain moisture (g kg^{-1}) at harvest, stand (plant ha^{-1}), root lodging (% of plants leaning more than 30° from vertical), stalk lodging (% of plants broken at or below the primary ear node), and ear height (cm). Ear heights were calculated as the average measurement of 10 competitive plants per plot, measured as the distance from the soil surface to the highest ear-bearing node. All traits were evaluated at each environment, except for ear height, which was not recorded at Ankeny or Martinsburg in 1993. Because uniform plant stands were not achieved, grain yield data were adjusted for plant population by covariance analysis.

Statistical Methods

Analyses for all traits were calculated on the basis of plot mean data. The data for each trait were analyzed by pooling over sets and combining across environments in the general analyses, with all effects in the model considered random. The sums of squares among entries, among entries by environments, and pooled error were partitioned into sources of variation among and within populations. Because of the missing entries, within population degrees of freedom were adjusted appropriately. The variances of the population means were calculated as the mean square for genotypes within population within sets for the appropriate population divided by the total number of observations in the mean. The among population sums of squares were then further partitioned into three contrasts (one non-orthogonal and two orthogonal) to compare the effect of seven cycles of HS progeny selection [BSSSC0 vs. BS13(S)C0], six cycles of S_2-progeny selection [BS13(S)C0 vs. BS13(S)C6], and 11 cycles of RRS [BSSSC0 vs. BSSS(R)C11]. Contrast mean squares were tested for significance by using the corresponding interaction with environments mean squares.

Analyses for individual populations pooled over sets and combined across environments were calculated to partition the within population variation for each population into male, female, and male × female interaction sources of variation. Because the missing entries caused some of the four × four sets to be unbalanced, the appropriate male or female was deleted, yielding some three × four balanced sets. Because the mean squares for the male and female sources of variation have the same genetic expectation, their degrees of freedom and sums of squares were pooled to give more precise estimates of the variation among half-sib families. The within population × environment interaction degrees of freedom and sums of squares were partitioned similarly. Within population error mean squares were used to test the significance of the within population × environment interaction sources of variation. The appropriate interaction mean square terms were then used for testing the within population components. Because direct tests of the male, female, and pooled components were not available, Satterthwaite's (1946) approximation was used to construct the appropriate F-test.

The covariances of relatives, provided by the analysis of variance, were translated into appropriate genetic components

of variance given the inbreeding coefficient (F) of the parents is zero (Comstock and Robinson (1948)). Additive genetic (σ_A^2), dominance genetic (σ_D^2), additive × environment (σ_{AE}^2), dominance × environment (σ_{DE}^2), and error (σ_e^2) variance component estimates were calculated by equating the observed mean squares to the expected mean squares and solving the resulting system of equations. Additive and additive × environment variance components estimates were calculated using the male and female pooled and its interaction with environments mean squares, respectively. Approximate 90% confidence intervals were calculated for each variance component estimate according to the procedures of Burdick and Graybill (1992). Variance component estimates were declared significantly different from zero if the approximate 90% confidence interval did not bracket zero. Comparisons of variance component estimates between populations were declared significant if their confidence intervals did not overlap. Heritabilities and their exact 90% confidence intervals (Knapp and Bridges, 1987) were estimated on a half-sib progeny mean basis for individual traits within each population. Phenotypic and additive genetic correlations among traits within populations were calculated from the appropriate covariance components (Mode and Robinson, 1959).

RESULTS

The average grain yield across all environments was 4.56 Mg ha^{-1} with a mean coefficient of variation (CV) of 15.4%. Mean grain yields ranged from 2.18 Mg ha^{-1} (Martinsburg, 1993) to 7.75 Mg ha^{-1} (Ankeny, 1992) and mean CVs ranging from 9.2% (Ames, 1992) to 22.3% (Martinsburg, 1993). Mean grain moisture ranged from 191 g kg^{-1} (Ames, 1992) to 283 g kg^{-1} (Ames, 1993) with CVs consistently below 7.0%. Because of excessive rainfall and below normal temperatures at all locations during the 1993 growing season, grain yields were less than 50% of the 1992 averages and grain moistures were approximately 25% higher at harvest. The data were combined cross years, despite these differences between years, because there was no indication that the data from 1 yr were superior to the data from the other year. Root and stalk lodging averaged 2.5 and 10.5%, respectively, across all environments. Mean ear heights ranged from 90 cm (Crawfordsville, 1992) to 121 cm (Ankeny, 1992).

Among Population Analysis and Means

The differences among populations for grain yield, grain moisture, root lodging, stalk lodging, and ear height were all highly significant ($P \leq 0.01$). Grain yield comparisons in the populations before and after selection were highly significant for each of the selection programs: seven cycles of HS progeny selection [BSSSC0 vs. BS13(S)C0], six cycles of S$_2$-progeny selection [BS13(S)C0 vs. BS13(S)C6], and eleven cycles of RRS [BSSSC0 vs. BSSS(R)C11] (Table 1). Seven cycles of HS progeny selection in BSSS produced a mean grain yield increase of 0.53 Mg ha^{-1} or 1.9% cycle^{-1}. Six cycles of S$_2$-progeny selection in the same program resulted in an additional mean grain yield increase of 0.31 Mg ha^{-1} or 1.2% cycle^{-1}. Total grain yield gain in the intra-population selection program was, therefore, 0.84 Mg ha^{-1} or 1.6% cycle^{-1}. After 11 cycles of RRS, BSSS

Table 1. Means, error variances, and coefficients of variation from the combined analyses of variance across six environments of five traits measured in four BSSS populations.

Trait†	Population	Mean ± SE	$\hat{\sigma}_e^2$	CV (%)
Grain yield (Mg ha^{-1})	BSSSC0	3.93 ± 0.04	0.383	15.80
	BS13(S)C0	4.46 ± 0.03	0.411	14.40
	BS13(S)C6	4.77 ± 0.03	0.450	14.10
	BSSS(R)C11	5.07 ± 0.03	0.384	12.20
Grain moisture (g kg^{-1})	BSSSC0	226 ± 1	168.5	5.70
	BS13(S)C0	225 ± 1	185.2	6.00
	BS13(S)C6	221 ± 1	149.1	5.50
	BSSS(R)C11	234 ± 1	166.3	5.50
Root lodging (%)	BSSSC0	1.9 ± 0.1	9.95	162.90
	BS13(S)C0	4.5 ± 0.2	25.20	112.70
	BS13(S)C6	3.4 ± 0.1	16.74	119.50
	BSSS(R)C11	0.5 ± 0.0	1.70	246.80
Stalk lodging (%)	BSSSC0	12.6 ± 0.3	41.92	51.20
	BS13(S)C0	9.8 ± 0.2	31.81	57.30
	BS13(S)C6	12.4 ± 0.2	41.88	52.30
	BSSS(R)C11	7.1 ± 0.1	17.93	59.80
Ear height (cm)	BSSSC0	118 ± 0.5	37.9	5.20
	BS13(S)C0	111 ± 0.5	36.0	5.40
	BS13(S)C6	105 ± 0.5	35.3	5.60
	BSSS(R)C11	98 ± 0.4	32.4	5.80

† Grain yield, grain moisture, root lodging, and stalk lodging were measured in six environments, whereas ear height was measured in only four environments.

population per se grain yield increased at a rate of 2.6% cycle^{-1}, for a total gain of 1.14 Mg ha^{-1}. Mean grain yield increases of two-thirds to two phenotypic standard deviations were accompanied by a reduction in the range of the distribution of approximately two phenotypic standard deviations, while maintaining approximate normality (Fig. 1).

Although the contrasts for each selection method were highly significant for grain moisture, only the change observed with RRS was agronomically meaningful (Table 1). The average grain moisture remained relatively constant after 13 cycles of intra-population selection and increased only slightly (8 g kg^{-1}) with 11 cycles of RRS. For root lodging, BSSSC0 vs. BS13(S)C0 and BSSSC0 vs. BSSS(R)C11 comparisons were highly significant, whereas the BS13(S)C0 vs. BS13(S)C6 comparison was significant ($P \leq 0.05$). Mean root lodging increased with HS progeny selection, but decreased with S$_2$-progeny and RRS (Table 1). All population comparisons for stalk lodging were highly significant, with mean stalk lodging decreasing with HS progeny and RRS, and increasing with S$_2$-progeny selection. Although all population means for root and stalk lodging were statistically different, the magnitude of the differences was not agronomically important. Population comparisons for ear height were all highly significant, with the BSSSC0 vs. BSSS(R)C11 comparison producing a mean square seven times greater than the other comparisons. All three selection methods resulted in decreasing mean ear height, with decreases of 1.0 and 1.8 cm cycle^{-1} for the intra- and inter-population methods, respectively (Table 1).

Within Population Analysis and Estimated Genetic Variances

For all traits, the within population mean squares for male, female, male and female pooled, male × female, and their interactions with environments were generally significant or highly significant. The interactions with
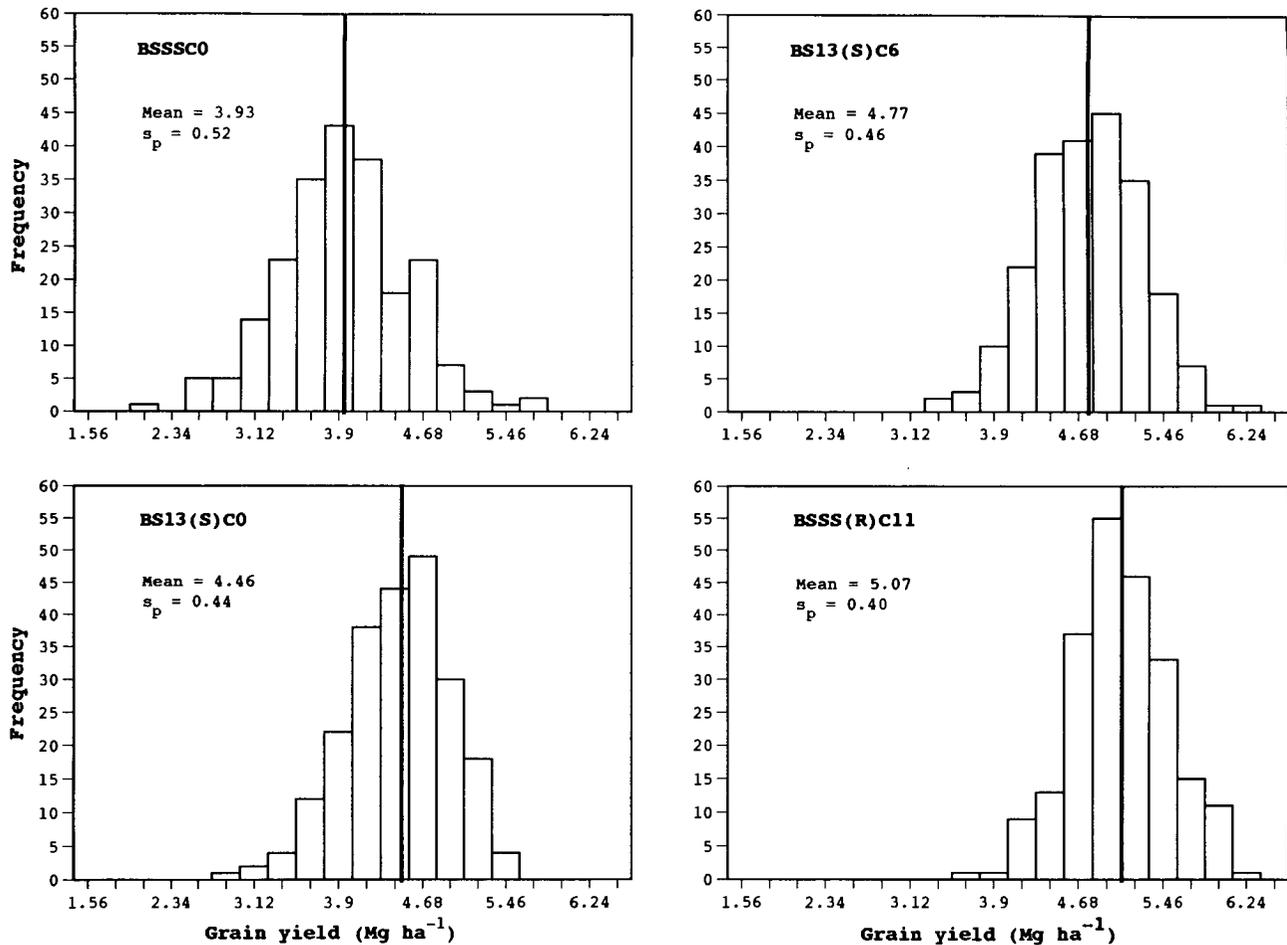
Fig. 1. Frequency distribution, mean, and phenotypic standard deviation for grain yield of full-sib progenies from BSSSC0, BS13(S)C0, BS13(S)C6, and BSSS(R)C11 maize populations. Distances between class intervals are one half of a phenotypic standard deviation of the BSSSC0 population. Vertical lines represent the population means.

environments were generally much smaller than the main effects, however. The within population sources of variation suggested that significant genetic variation among the half-sib and full-sib progenies was present in each population for all traits.

Of 16 genetic variance component estimates for grain yield in the four BSSS populations, only the estimate of the dominance × environment component in BSSS(R)C11 was not significantly different from zero (Table 2). In the original BSSS population, additive and dominance variance contributed equally to the total genetic variation. The only significant change in component estimates after seven cycles of HS progeny selection in BSSS was a 91% increase in additive × environment interaction variance. Additive and dominance variance component estimates were reduced by a nonsignificant 32 and 50%, respectively, however. Six cycles of S_2-progeny selection produced no significant changes in any of the variance component estimates. Dominance variance increased by approximately 51%, however. Although all variance component estimates were reduced after 11 cycles of RRS, the virtual depletion of dominance and dominance × environment interaction variance (76 and 91% decreases, respectively) were the only significant changes.

The majority of the total genetic variance for grain moisture in all four BSSS populations was additive with all variance component estimates significantly different from zero, except for the estimate of dominance × environment variance in BSSSC0. Dominance, additive × environment, and dominance × environment variance component estimates were of relatively unimportant magnitude, however. The only significant change in variance component estimates after seven cycles of HS progeny selection was a 76% increase in additive × environment interaction variance. Six cycles of S_2-progeny selection produced no significant changes in any of the variance component estimates. Additive and dominance variance component estimates were reduced by a nonsignificant 28 and 32%, respectively, however. Eleven cycles of RRS significantly increased the amount of additive and dominance × environment interaction variance.

Six of 16 variance component estimates for root lodging were not significantly different from zero. Total genetic variance was composed of mainly additive variance, with dominance variance virtually zero in all four BSSS populations. Genetic variance × environment interactions were generally larger than their genetic variance counterparts. Additive, additive × environment, and dominance × environment variance increased sig-

Table 2. Estimates of genetic components of variance, their interactions with environments, and the ratio of additive and dominance variances from the combined analyses of variance across six environments of five traits measured in four BSSS populations.

Trait‡	Genetic components of variance†				
	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_{AE}$	$\hat{\sigma}^2_{DE}$	$\hat{\sigma}^2_A/\hat{\sigma}^2_D$
Grain yield (Mg ha⁻¹)					
BSSSC0	0.319 (0.208,0.479)§	0.334 (0.234,0.472)	0.154 (0.097, 0.217)	0.333 (0.217, 0.463)	1.05
BS13(S)C0	0.218 (0.140,0.331)	0.166 (0.103,0.249)	0.294 (0.232,0.366)	0.198 (0.093,0.312)	0.76
BS13(S)C6	0.228 (0.145,0.347)	0.251 (0.173,0.356)	0.200 (0.145,0.261)	0.144 (0.035,0.263)	1.10
BSSS(R)C11	0.247 (0.178,0.350)	0.080 (0.041,0.137)	0.106 (0.067,0.148)	0.029 (−0.060,0.123)	0.33
Grain moisture (g kg⁻¹)					
BSSSC0	354.2 (264.0,490.1)	118.3 (85.1,164.7)	81.5 (61.1,104.6)	0.0 (−38.9,42.9)	0.33
BS13(S)C0	403.9 (301.8,555.9)	135.7 (97.8,167.6)	143.1 (114.5,176.0)	71.0 (25.1,120.7)	0.34
BS13(S)C6	291.7 (218.1,401.2)	92.6 (65.0,130.3)	96.2 (75.1,120.4)	55.7 (18.8,95.6)	0.32
BSSS(R)C11	670.0 (518.5,897.4)	62.7 (37.6,96.6)	64.7 (43.7,88.2)	92.9 (49.0,140.8)	0.09
Root lodging (%)					
BSSSC0	2.23 (1.29,3.60)	0.51 (−0.38,1.68)	3.98 (2.76,5.35)	2.33 (−0.17, 5.03)	0.23
BS13(S)C0	10.60 (6.67,16.31)	2.72 (0.16,6.08)	22.88 (18.57,27.86)	12.26 (5.82,19.25)	0.26
BS13(S)C6	4.90 (3.02,7.61)	1.16 (−0.42,3.20)	8.49 (6.29,10.97)	7.38 (3.16,11.97)	0.24
BSSS(R)C11	0.12 (0.04,0.22)	0.07 (−0.06,0.24)	0.09 (−0.05,0.23)	−0.02 (−0.41,0.39)	0.62
Stalk lodging (%)					
BSSSC0	25.30 (17.26,37.25)	10.37 (5.40,17.15)	24.06 (18.44,30.48)	3.74 (−6.42,14.65)	0.41
BS13(S)C0	18.84 (13.60,26.61)	1.72 (−1.12,5.40)	10.99 (7.36,15.04)	11.84 (3.97,20.34)	0.09
BS13(S)C6	22.17 (15.96,31.38)	−0.34 (−3.59,3.78)	15.43 (10.65,20.78)	13.05 (2.88,24.02)	−0.02
BSSS(R)C11	2.36 (1.32,3.82)	0.55 (−0.79,2.28)	1.57 (0.11,3.14)	0.78 (−3.27,5.09)	0.23
Ear height (cm)					
BSSSC0	92.5 (68.7,128.2)	34.7 (24.2,49.3)	6.4 (1.8,11.6)	3.1 (−8.3,15.7)	0.38
BS13(S)C0	96.0 (73.1,130.1)	15.3 (8.2,24.5)	10.3 (5.3,15.9)	12.3 (1.3,24.7)	0.16
BS13(S)C6	103.1 (79.1,138.9)	15.8 (9.3,24.4)	5.8 (1.8, 10.2)	1.9 (−8.1,12.8)	0.15
BSSS(R)C11	93.4 (71.6,126.1)	12.0 (6.4,19.3)	7.6 (3.7,12.0)	1.0 (−8.2,11.0)	0.13

† σ^2_A, σ^2_D, σ^2_{AE}, and σ^2_{DE} are the additive, dominance, additive by environment interaction, and dominance by environment interaction components of variance, respectively.

‡ Grain yield, grain moisture, root lodging, and stalk lodging were measured in six environments, whereas ear height was measured in only four environments.

§ Values in parentheses are the approximate upper and lower 90% confidence interval bounds, respectively, for the variance components estimates calculated according to the procedures of Burdick and Graybill (1992).

nificantly with HS progeny selection. The additive × environment variance decreased significantly after S₂-progeny selection. Additive and additive × environment interaction variances were virtually depleted with RRS.

For stalk lodging, five of 16 variance component estimates were not significantly different from zero. Additive variance represented the largest portion of total genetic variance in all four BSSS populations. Dominance and additive × environment variances were reduced significantly with HS selection. There were no significant changes in variance component estimates with S₂-progeny selection. Eleven cycles of RRS significantly decreased the additive, dominance, and additive × environment interaction variances.

Total genetic variance for ear height was represented mainly by additive variance in all four BSSS populations, with three of four dominance × environment interaction component estimates not significantly different from zero. Dominance variance was reduced significantly with HS progeny selection and RRS. Variance component estimates were unchanged with S₂-progeny selection.

Heritability Estimates

Heritability estimates measured in the four BSSS populations, on a half-sib progeny mean basis, for grain yield, grain moisture, root lodging, stalk lodging, and ear height were all significantly different from zero (Table 3). Heritability estimates were a direct reflection of the importance of additive genetic variance for the trait and population of interest. Heritability estimates for grain yield and moisture decreased with HS progeny selection and

increased with RRS. However, only the increase in heritability after RRS was significant. Heritability for both root and stalk lodging decreased after 11 cycles of RRS, although the differences were not significant. Heritability estimates for ear height remained constant after all selection methods.

Phenotypic and Additive Genetic Correlations

There were significant phenotypic correlations between grain yield and grain moisture in BSSS(R)C11, between grain yield and root and stalk lodging in BS13(S)C6, and between grain yield and ear height in BS13(S)C0 and BSSS(R)C11 (Table 4). Root lodging was correlated with stalk lodging in BSSSC0 and ear height in all four BSSS populations. The highly significant phenotypic correlation between root lodging and ear height was the only correlation to show a consistent trend across populations. Genetic correlations generally mirrored phenotypic correlation results with no obvious trends or patterns developing across the three selection methods.

DISCUSSION

Effects of Selection on Population Mean Performance

Measurement of the average linear response to selection of the various traits was based on population per se performance. Therefore, changes measured in HS and RRS programs are indirect responses to selection,

Table 3. Estimates of heritability (h^2) on a half-sib progeny mean basis from the combined analyses of variance across six environments of five traits measured in four BSSS populations.

| Trait† | h^2 | 90% Confidence interval‡ | |
		Lower	Upper
Grain yield			
BSSSC0	0.664	0.537	0.760
BS13(S)C0	0.621	0.495	0.722
BS13(S)C6	0.621	0.489	0.724
BSSS(R)C11	0.775	0.694	0.837
Grain moisture			
BSSSC0	0.857	0.805	0.897
BS13(S)C0	0.841	0.788	0.884
BS13(S)C6	0.844	0.791	0.886
BSSS(R)C11	0.938	0.916	0.955
Root lodging			
BSSSC0	0.559	0.398	0.683
BS13(S)C0	0.599	0.469	0.704
BS13(S)C6	0.590	0.450	0.701
BSSS(R)C11	0.399	0.153	0.576
Stalk lodging			
BSSSC0	0.705	0.602	0.787
BS13(S)C0	0.777	0.698	0.838
BS13(S)C6	0.773	0.692	0.835
BSSS(R)C11	0.550	0.370	0.681
Ear height			
BSSSC0	0.854	0.796	0.897
BS13(S)C0	0.892	0.852	0.922
BS13(S)C6	0.912	0.879	0.937
BSSS(R)C11	0.912	0.878	0.937

† Grain yield, grain moisture, root lodging, and stalk lodging were measured in six environments, whereas ear height was measured in only four environments.

‡ Exact 90% confidence intervals were calculated according to the procedures of Knapp and Bridges (1987).

whereas those measured in S_2-progeny selection programs are direct responses to selection.

Half-Sib Progeny Selection

Half-sib progeny selection was effective for improving the mean grain yield in the BSSS population per se. Seven cycles of HS progeny selection resulted in an indirect response of 0.076 Mg ha^{-1} cycle^{-1}. These find-

ings are similar to the results of 0.074 Mg ha^{-1} cycle^{-1} reported by Eberhart et al. (1973) and 0.091 Mg ha^{-1} cycle^{-1} reported by Smith (1979). However, estimates of 0.344 Mg ha^{-1} cycle^{-1} reported by Helms et al. (1989a) and 0.164 Mg ha^{-1} cycle^{-1} reported by Lamkey (1992) do not agree particularly well with our results. Differences among studies in the average linear rate of response may be a function of the environments in which the materials were evaluated and differences in methods of calculating response. Population per se performance estimates in our study were confounded with the effects of inbreeding because of small effective population size, whereas the estimates provided by Helms et al. (1989a) were adjusted for these effects. These findings support the fact that HS selection in BSSS has effectively increased the frequency of favorable alleles for grain yield.

Responses to HS selection of the agronomic traits undergoing secondary selection pressure were generally in a favorable direction. Grain moisture at harvest and percentage stalk lodged plants remained relatively constant or decreased slightly with selection, which was generally the trend with other evaluation studies (Eberhart et al., 1973; Helms et al., 1989a; and Lamkey, 1992). Percentage of root lodged plants increased slightly as a consequence of the direction of the selection differential as reported by Lamkey (1992), however. Average ear height decreased significantly (1 cm cycle^{-1}) with HS selection, even though no selection pressure was applied to the trait. The decrease in ear height could have resulted as a correlated response to selection or because of inbreeding due to small effective population size.

S_2 Progeny Selection

Average linear direct response to selection for grain yield in BS13 after six cycles of S_2-progeny selection was 0.052 Mg ha^{-1} cycle^{-1}, which was between the estimates of 0.009 Mg ha^{-1} cycle^{-1} and 0.226 Mg ha^{-1}

Table 4. Phenotypic (above diagonal) and additive genetic (below diagonal) correlations of half-sib progeny from the combined analyses of variance across six environments among five traits measured in four BSSS populations.

Trait†	Population	Grain yield	Grain moisture	Root lodging	Stalk lodging	Ear height
Grain yield (Mg ha^{-1})	BSSSC0		−0.10	−0.12	−0.07	0.02
	BS13(S)C0		0.13	0.19	0.03	0.32*
	BS13(S)C6		0.01	0.30*	−0.31*	0.18
	BSSS(R)C11		0.34**	0.22	−0.04	0.35**
Grain moisture (g kg^{-1})	BSSSC0	−0.16		0.09	−0.02	−0.01
	BS13(S)C0	0.13		0.10	−0.13	0.19
	BS13(S)C6	−0.11		0.01	0.01	−0.04
	BSSS(R)C11	0.39		−0.07	0.00	0.15
Root lodging (%)	BSSSC0	−0.22	0.13		0.35**	0.54**
	BS13(S)C0	0.30	0.15		0.22	0.57**
	BS13(S)C6	0.51	0.03		−0.07	0.35**
	BSSS(R)C11	0.37	−0.13		0.12	0.45**
Stalk lodging (%)	BSSSC0	0.01	−0.03	0.48		0.25
	BS13(S)C0	0.17	−0.11	0.27		0.11
	BS13(S)C6	−0.27	0.06	−0.09		−0.03
	BSSS(R)C11	−0.07	−0.01	0.23		0.19
Ear height (cm)	BSSSC0	0.00	−0.01	0.67	0.30	
	BS13(S)C0	0.40	0.19	0.57	0.11	
	BS13(S)C6	0.20	−0.05	0.39	−0.07	
	BSSS(R)C11	0.40	0.16	0.71	0.24	

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

† Grain yield, grain moisture, root lodging, and stalk lodging were measured in six environments, whereas ear height was measured in only four environments.

cycle^{-1} obtained by Lamkey (1992) and Helms et al. (1989a), respectively. The response seen in our study and that of Lamkey (1992) does not support the theoretical superiority of S$_2$-progeny selection method. As Lamkey (1992) suggested, the lack of response in this selection program could be a result of random genetic drift because the estimated level of inbreeding in BS13(S)C6 is approximately 45%. The results of Helms et al. (1989a), which were adjusted for the effects of inbreeding because of small effective population size, show much greater response to selection.

The selection responses for grain moisture (-0.7 g kg^{-1} cycle^{-1}) and percentage of root lodging (-0.15% cycle^{-1}) were in the desired direction, a trend consistent with the results of Helms et al. (1989a) and Lamkey (1992). Percentage of stalk lodging, however, increased with selection at a rate of 0.4% cycle^{-1}, which was not considered agronomically important. Ear height decreased with S$_2$-progeny selection at the same rate as was found in the HS selection program (1 cm cycle^{-1}).

Reciprocal Recurrent Selection

Reciprocal recurrent selection was effective for improving the mean grain yield of the BSSS population per se. After 11 cycles of RRS, average indirect response in the population per se was 0.104 Mg ha^{-1} cycle^{-1}, compared with 0.060 Mg ha^{-1} cycle^{-1} reported by Keeratinijakal and Lamkey (1993a) and 0.356 Mg ha^{-1} cycle^{-1} reported by Helms et al. (1989a). The expected response to RRS in the populations per se is low for two reasons. First, change in per se performance of populations undergoing RRS methods is an indirect response to selection. Second, BSSS(R)C11 is approximately 37% inbred because of small effective population size. The estimate of population per se performance is increased when response is adjusted for the effects of inbreeding (Smith, 1979; Helms et al., 1989a; Keeratinijakal and Lamkey, 1993b). Therefore, random genetic drift is largely responsible for the small response to selection observed in the population per se. Our study, however, produced a grain yield response that was more favorable than previous studies in which response was not adjusted for random genetic drift. Our results suggest that RRS has been effective at increasing the frequency of favorable alleles for grain yield in the population per se.

Grain moisture in the BSSS population per se increased significantly with RRS (0.7 g kg^{-1} cycle^{-1}). Smith (1983) and Keeratinijakal and Lamkey (1993a) reported little or no effect of selection for grain moisture, whereas Helms et al. (1989a) found an increase of 1.2 g kg^{-1} cycle^{-1}. In agreement with the results of Keeratinijakal and Lamkey (1993a), our study showed favorable response to selection for root and stalk lodging, -0.1% cycle^{-1} and -0.5% cycle^{-1}, respectively. Decreasing ear height in the population per se is also consistent with the report of Keeratinijakal and Lamkey (1993a).

Effects of Selection on Genetic Parameters

Favorable changes in the mean performance of the populations with selection suggest an increase in the frequency of favorable alleles. Under a model of complete dominance, increasing the frequency of the favorable allele through selection to a level greater than 0.25 would lead to a decrease in additive variance (Falconer, 1989). Dominance variance decreases gradually at allelic frequencies greater than 0.5. In addition, additive and dominance variance can only be equal when allelic frequency is greater than 0.5. The changes in additive and dominance variance for grain yield found in our study tend to support this theory. Additive and dominance variance for grain yield in BSSS were generally of equal importance. For other agronomic traits in BSSS, additive genetic variance seemed to be much more important than dominance variance. Additive × environment and dominance × environment interaction variance-component estimates were generally of little importance.

Half-Sib Progeny Selection

Half-sib progeny selection produced changes in the genetic variance components for grain yield that were consistent with the results reported by Stucker and Hallauer (1992). Additive variance was reduced slightly, whereas additive × environment interaction variance increased significantly. Dominance and dominance × environment interaction variances tended to decrease at a greater rate than the additive variance. Helms et al. (1989b) reported a small decrease in the total genetic variance among S$_2$ progenies after HS selection and attributed the reduction to the increased level of inbreeding because of small effective population size. This may also explain the decrease in total genetic variance that was observed in our study. Half-sib selection has been effective at increasing the frequency of favorable alleles, as determined by significant increases in population per se performance, which may also contribute to a loss in genetic variation.

Additive and dominance variance estimates for grain moisture remained unchanged with HS selection, whereas their interactions with environments increased slightly in magnitude. Stucker and Hallauer (1992) reported a significant decrease in both additive and dominance variance for grain moisture. Helms et al. (1989b) showed a nonsignificant decrease in total genetic variance after HS selection. All variance component estimates for root lodging were very small, although significant increases in additive, additive × environment, and dominance × environment components were found in our study. A significant increase in total genetic variation for root lodging was also reported by Helms et al. (1989b). Dominance and additive × environment interaction components of variance for stalk lodging decreased significantly in our study. A decreasing trend was reported by Stucker and Hallauer (1992) for all variance component estimates. No significant changes in variance component estimates for ear height were detected; however, a decrease in dominance variance approached significance.

S₂-Progeny Selection

S_2-progeny selection produced unexpected changes in the genetic variance component estimates for grain yield. Additive variance remained unchanged whereas dominance variance increased with selection. Helms et al. (1989b) reported a nonsignificant increase in total genetic variance for grain yield after three cycles of selection. In an evaluation of cycles zero through five of the S_2-progeny selection program, Lamkey (1992) found that the estimates of genetic variance for each cycle were significantly different from zero. The changes in genetic variance and observed response to selection suggest that S_2-progeny selection has not been able to capitalize on the additive genetic variance in BS13. Iowa Stiff Stalk Synthetic is unique relative to other maize populations because the additive and dominance variance contribute equally to the total genetic variance (Hallauer and Miranda, 1988). It is not clear if this unique variance component structure is responsible for the lack of progress from S_2-progeny selection. Inbreeding because of small effective size has increased from 29% in BS13(S)C0 to 45% in BS13(S)C6, but the expected reductions in the genetic variance components due to inbreeding were not observed.

All variance component estimates for grain moisture showed a declining trend with S_2-progeny selection, but none of the changes were significant. Total genetic variance in the study of Helms et al. (1989b) also showed a slight decrease over selection cycles. A decrease in additive $\times$ environment interaction variance was the only significant change in variance component estimates for root lodging in our study. Helms et al. (1989b) reported a near significant decrease in genetic variance for this trait. No significant changes were detected with the estimated variance components for stalk lodging, although no dominance variance remained for this trait after selection. A slight increase in genetic variance was found by Helms et al. (1989b). Variance component estimates for ear height showed no significant changes over cycles of S_2-progeny selection.

Reciprocal Recurrent Selection

All variance component estimates for grain yield in the BSSS population per se were reduced after 11 cycles of RRS. Dominance and dominance $\times$ environment interaction variances were reduced significantly. The estimate of dominance variance was near zero and the dominance $\times$ environment interaction variance was not significantly different from zero. Hallauer (1971) found similar trends after four cycles of selection. Helms et al. (1989b) reported a near significant decrease in total genetic variance in BSSS after nine cycles of selection. A rather large decrease in total genetic variance (approximately 50%) in the population per se was accompanied by only moderate mean performance increases. A significant loss of heterozygotes in the population per se because of the effects of random genetic drift was reported by Keeratinijakal and Lamkey (1993b) as an explanation for limited im-

provement of grain yield in the population per se. They also reported that RRS increased the level of heterozygosity in the population cross by selection for complementary loci with alleles in the partial to complete dominance range. Selection for complementary sets of loci and random genetic drift would result in an increase in heterozygosity of the population cross and a decrease in heterozygosity of the population per se, as has been observed by Keeratinijakal and Lamkey (1993a,b). The decrease we observed in dominance variance in BSSS after 11 cycles of RRS is in agreement with these findings.

Additive genetic variance for grain moisture increased significantly with selection. The additive variance was at least seven times greater than any of the other variance component estimates. Keeratinijakal and Lamkey (1993b) also reported that grain moisture was mainly controlled by additive effects. Reciprocal recurrent selection, however, has not been effective at improving the mean performance of the population per se for grain moisture. Helms et al. (1989b) reported an overall reduction in the total genetic variance for grain moisture after nine cycles of selection. All variance component estimates for root and stalk lodging in the BSSS(R)C11 population per se were either near or not significantly different from zero. A significant decrease in dominance variance was the only change observed for variance component estimates of ear height. Additive variance seems to be the most important source of variation for ear height, a result consistent with those of Keeratinijakal and Lamkey (1993b).

Implications

The results from our study showed that HS progeny and RRS methods have been more effective than S_2-progeny selection for improving the mean performance for grain yield of the BSSS populations per se. Genetic theory suggests that per se selection methods, such as S_2-progeny selection, should be more effective than other methods of recurrent selection in populations where overdominant gene action is not important for the traits of interest. Overdominant loci have not been found to contribute significantly to grain yield in maize populations (Hallauer and Miranda, 1988). Response of grain yield in BSSS populations to S_2-progeny selection in our study and Lamkey (1992) has not followed theoretical expectations. Our study supports the results of other researchers that in BSSS dominance variance plays a more important role in grain yield than in other maize populations (Hallauer and Miranda, 1988), however. The importance of dominance variance in BSSS provides for more effective response from selection with testcross selection methods that can take advantage of dominance genetic effects. Half-sib progeny and RRS methods were found to be more effective in improving the mean performance in BSSS populations. However, Helms et al. (1989) reported that when selection responses were adjusted for the level of inbreeding, all three selection methods produced similar grain yield responses.

With adequate levels of available additive genetic variance remaining and high heritability estimates for all

traits, future response from selection should be achieved from each selection method. However, HS progeny and RRS methods have the ability to take advantage of dominance genetic effects and may be more appropriate in BSSS maize populations. Secondary selection pressure on important agronomic traits, when the primary trait under selection is grain yield, was effective for maintaining or improving their level in the advanced populations.

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