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Performance and Inbreeding Depression between a Synthetic and Three Improved Populations of Maize

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Abstract

Effective recurrent selection for a quantitative trait will increase the frequency of favorable alleles in the maize population. As a result, fewer deleterious alleles are expressed for the quantitative trait when inbreeding. This study was conducted to compare performance and inbreeding depression in the original Iowa Stiff Stalk Synthetic (BSSSC0) maize (*Zea mays* L.) population, two improved Iowa Stiff Stalk populations [BSSS(R)C9 and BS13(S)C3], and the cross between the improved populations (C3 × C9). The improved populations of BS13(S)C3 and BSSS(R)C9 yielded similarly to BSSSC0, whereas the S_1 generation of BS13(S)C3 and BSSS(R)C9 yielded significantly greater than the S_1 of BSSSC0. The C3 × C9 population showed high-parent heterosis at the S_0 and S_1 generation levels. Only the BS13(S)C3 population showed significantly less inbreeding depression than did BSSS. Differences among the three improved populations for inbreeding depression of grain yield were not significant.

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Performance and Inbreeding Depression between a Synthetic and Three Improved Populations of Maize

S. P. Walters, W. A. Russell,* K. R. Lamkey, and P. R. White

ABSTRACT

Effective recurrent selection for a quantitative trait will increase the frequency of favorable alleles in the maize population. As a result, fewer deleterious alleles are expressed for the quantitative trait when inbreeding. This study was conducted to compare performance and inbreeding depression in the original Iowa Stiff Stalk Synthetic (BSSSC0) maize (*Zea mays* L.) population, two improved Iowa Stiff Stalk populations [BSSS(R)C9 and BS13(S)C3], and the cross between the improved populations (C3 × C9). The improved populations of BS13(S)C3 and BSSS(R)C9 yielded similarly to BSSSC0, whereas the S_1 generation of BS13(S)C3 and BSSS(R)C9 yielded significantly greater than the S_1 of BSSSC0. The C3 × C9 population showed high-parent heterosis at the S_0 and S_1 generation levels. Only the BS13(S)C3 population showed significantly less inbreeding depression than did BSSS. Differences among the three improved populations for inbreeding depression of grain yield were not significant.

INBREEDING can be described as matings between individuals more closely related than the average relationship within the population. This phenomenon is important to recurrent selection programs because inbreeding occurs naturally in small populations. Recurrent selection that recombines selected individuals will ultimately incur inbreeding depression caused by random genetic drift because, usually, 10 to 20 individuals are selected for recombination (Hallauer and Miranda, 1988). In general, as the population size (number of selected lines) decreases, response to selection is expected to be less and to stop at an earlier cycle at a lower level of gain. Hallauer and Miranda (1988) reported the average estimate of inbreeding depression in maize yields to be 0.05 Mg ha^{-1} per 1% increase in homozygosity. Effects of inbreeding for yield tended to be smaller for Iowa Stiff Stalk Synthetic than other cultivars, but not significantly smaller. The objectives of this study were to compare performances and estimates of inbreeding depression in the original Iowa Stiff Stalk Synthetic, two recycled synthetic populations of maize under different methods of recurrent selection, and the cross between the recycled populations.

MATERIALS AND METHODS

The reference population used in this study was the original Iowa Staff Stalk Synthetic, BSSSC0 (C0). Three other populations studied included BS13(S)C3 (C3), BSSS(R)C9 (C9), and BS13(S)C3 × BSSS(R)C9 (C3 × C9). The C9 was developed from C0 by using nine cycles of reciprocal recurrent selection (RRS) with BSCB1(R) (Helms et al., 1989). The C3 was developed from C0 after seven cycles of half-sib recurrent selection with tester Iowa 13 [(L317 × BL349) × (BL345 × MC401)] followed by three cycles of S_2 progeny recurrent selection (Eberhart et al., 1973). The C3 and C9 per se were random-mated and then crossed to create C3 × C9 (F_1). The F_1 was intermated to create the C3 × C9 (Syn.-2) population. Crosses of earlier cycles for BS13(S) and BSSS(R) had shown significant heterotic expression for yield

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(Russell and Eberhart, 1975; Stangland et al., 1983; Smith, 1983); however, detailed evaluations of the effects of inbreeding germplasm from such crosses have not been done.

The S_0 and S_1 composite entries from each of the four populations (C0, C3, C9, C3 × C9) and the F_1 of C3 × C9 were included in the experiment. The four S_0 entries were sampled from bulks of each population. Each S_1 composite was obtained by sampling an equal number of selfed seeds from 125 random S_0 plants in a population. Separate randomizations were assigned to S_0 and S_1 entries. The four S_0 and the F_1 of C3 × C9 entries were grown adjacent to the four S_1 entries within a replicate with appropriate border rows to eliminate unequal competition. Thus, there were nine entries in each of five replicates in the experiment, which was grown in seven environments from 1986 to 1988. The locations used were the Agronomy and Agricultural Engineering Research Center located near Ames, IA; another research area near Ames; and the Iowa State Research Farm near Ankeny, IA. Single-row plots were 0.76 m wide by 5.04 m long, planted with 32 kernels. Plots were later hand thinned at the four- to six-leaf stage to 21 plants plot^{-1}. Plant density was ≈54 140 plants ha^{-1}. All plots were cultivated, with further weed control by herbicides and hand weeding.

Data were collected for 12 plant, ear, and grain traits. Five traits were measured before harvest: (i) Days to anthesis, or the number of days after June 30 until 50% of the plants in a plot had shed pollen; (ii) days to silk emergence, or the number of days after June 30 until 50% of the plants in a plot showed silk emergence; (iii) pollen-silk interval, or the difference between days to anthesis and days to silk; (iv) plant height (cm) measured from the ground to the flag leaf node on five similarly spaced plants plot^{-1}; (v) and ear height (cm), measured from the ground to the primary-ear node of five similarly spaced plants plot^{-1}. All plots were hand harvested by removing all ears from 10 similarly spaced plants plot^{-1}. The numbers of primary and secondary ears and the number of barren plants were recorded for each plot. Harvested ears were dried to a uniform moisture (ca. 100 g kg^{-1}), and data were obtained for the following ear and grain traits: average number of kernel rows on primary ears, average ear length (primary and secondary), average primary ear diameter, average kernel depth for the primary ears, average grain yield per plot expressed in tonnes (Mg) per hectare, and average weight (g) of 300 kernels plot^{-1}.

Statistical analyses were performed according to the randomized complete-block design for data combined from seven environments. Plot values for each trait were used in the analyses of variance. The model assumed was mixed, where environments were random and entries were fixed. The eight entry degrees of freedom and sums of squares were partitioned into: among S_0 and F_1 entries (df = 4), among S_1 composites (df = 3), and S_0 entries vs. S_1 composites (df = 1). The degrees of freedom and sums of squares for entries × environments and pooled error were partitioned similarly. LSD values were calculated by using the appropriate error mean square or genotype × environment ($g \times e$) mean square if significant. To compare S_0 means vs. S_1 means, an LSD was calculated by using the S_0 error term (or $g \times e$ if significant), the S_1 error term (or $g \times e$ if significant), and an approximate t value (Steel and Torrie, 1980).

Two measures of inbreeding depression were calculated for each trait. The first measure was in absolute units, calculated as the noninbred (S_0) minus the inbred (S_1) generation means. The standard error of inbreeding depression in absolute units was calculated as the square root of the sum of the variance of the inbred and noninbred generation means. The second measure was percentage of inbreeding depression, calculated as the S_0 minus the S_1 generation means divided by the S_0 generation mean and multiplied by 100.

RESULTS AND DISCUSSION

The combined analyses of variance (not shown) indicated significant differences ($P < 0.05$) among entries for all traits evaluated. Significant differences were observed among S_0 and F_1 entries for all traits except pollen–silk interval and among S_1 composites for all traits except ear diameter and 300-kernel weight. S_0 entries vs. S_1 composites showed significant differences for all traits except pollen–silk interval and ears per plant. The genotype × environment interaction was not significant ($P > 0.05$) for plant height, ear diameter, kernel depth, number of kernel rows, ears per plant, and 300-kernel weight.

The C3 × C9 (F_1) was significantly different from BSSSC0 for all traits except pollen-silk interval, plant height, kernel depth, number of kernel rows, and 300-kernel weight (Table 1). Significant decreases were ob-

Table 1. S_0, F_1, and S_1 means for 12 traits for each of four Iowa Stiff Stalk Synthetic (BSSS) populations evaluated in seven environments.†

Population	Mid-anthesis	Mid-silk emergence	Pollen–silk interval	Height		Ear		Kernel		Ears	300-kernel weight	Grain yield
				Plant	Ear	Length	Diameter	Depth	Rows			
	— d after 30 June —		d	——— cm ———					——— no. ———		g	Mg ha^{-1}
S_0												
BSSSC0	13.9	16.6	2.6	210.0	108.1	13.3	4.4	0.8	17.1	0.9	74.1	5.57
BS13(S)C3	13.1	14.5*	1.4*	192.9*	97.9*	15.2*	4.2*	0.7*	14.4*	1.0*	72.8	5.55
BSSS(R)C9	11.1*	13.1*	2.0	207.9	98.0*	14.6*	4.3*	0.7*	17.2	1.0*	68.4*	5.61
C3 × C9	10.7*	12.8*	2.0	204.6*	99.6*	15.9*	4.4	0.8	16.3*	1.0*	72.2	6.51*
C3 × C9 (F_1)	10.4*	12.4*	2.0	206.9	101.0*	17.4*	4.5*	0.8	16.6	1.0*	75.6	7.78*
LSD‡ (0.05)	0.9	1.4	0.8	4.2	3.5	0.9	0.1	0.1	0.6	0.1	3.4	0.78
S_1												
BSSSC0	14.1	17.3	3.2	189.5	95.1	10.9	4.1	0.8	16.4	0.8	68.4	3.65
BS13(S)C3	13.8	15.6*	1.7*	177.2*	85.1*	14.1*	4.1	0.6*	14.4*	1.0*	68.7	4.54*
BSSS(R)C9	11.7*	14.2*	2.5*	190.5	87.9*	13.0*	4.1	0.7*	16.7	0.9*	66.7	4.31*
C3 × C9	12.2*	14.2*	2.0*	187.9	90.8*	14.3*	4.2	0.7*	16.1	1.0*	71.0	5.08*
LSD§ (0.05)	1.0	1.4	0.6	5.3	3.5	1.0	–	0.1	0.8	0.1	–	0.48
LSD¶ (0.05)	0.9	1.4	0.7	4.8	3.5	–	0.1	0.1	0.7	–	3.4	0.64

* Significantly different from BSSSC0 at the 0.05 level of probability.

† Plant height and ear height were evaluated in six environments; days to anthesis and silk emergence and pollen–silk interval were evaluated in five environments; and kernel row number was evaluated in four environments.

‡ LSD used to compare among S_0 and F_1 means.

§ LSD used to compare among S_1 means.

¶ LSD used to compare S_0 means vs. S_1 means.

Table 2. Differences between S_0 and S_1 means and percentages (in parentheses) of inbreeding depression for each of four Iowa Stiff Stalk Synthetic (BSSS) populations evaluated in seven environments.†

				Height		Ear		Kernel				
Population	Mid-anthesis	Mid-silk emergence	Pollen–silk interval	Plant	Ear	Length	Diameter	Depth	Rows	Ears	300-kernel weight	Grain yield
	— d after 30 June —		d	——— cm ———					——— no. ———		g	Mg ha^{-1}
C0	−0.2	−0.7	−0.6	20.5*	13.0*	2.4*	0.3*	0	0.7*	0.1*	5.7*	1.92*
	(−1.4)	(−4.2)	(−23.1)	(9.8)	(12.0)	(18.0)	(6.8)	(0)	(4.1)	(11.1)	(7.7)	(34.5)
C3	−0.7	−1.1	−0.3	15.7*	12.8*	1.1*	0.1*	0.1*	0	0	4.1*	1.01*
	(−5.3)	(−7.6)	(−21.4)	(8.1)	(13.1)	(7.2)	(2.4)	(14.3)	(0)	(0)	(5.6)	(18.2)
C9	−0.6	−1.1	−0.5	17.4*	10.1*	1.6*	0.1*	0	0.5	0.1*	1.7	1.30*
	(−5.4)	(−8.4)	(−25.0)	(8.4)	(8.4)	(10.9)	(4.7)	(0)	(2.9)	(10.0)	(2.5)	(23.2)
C3 × C9	−1.5*	−1.4*	0	16.7*	8.8*	1.6*	0.2*	0.1*	0.2	0	1.2	1.43*
	(−14.0)	(−10.9)	(0)	(8.1)	(8.1)	(10.1)	(4.5)	(12.5)	(1.2)	(0)	(1.7)	(22.0)
(C3 × C9) F_1 vs. (C3 × C9) S_1	−1.8*	−1.8*	0	19.0*	10.2*	3.1*	0.3*	0.1*	0.5	0	4.6*	2.70*
	(−17.3)	(−14.5)	(0)	(9.2)	(9.2)	(17.8)	(6.7)	(12.5)	(3.0)	(0)	(6.1)	(34.7)
LSD‡ (0.05)	1.4	2.0	1.4	6.8	4.9	1.3	0.14	0.08	0.8	0.08	4.9	0.90

† Indicates a significant inbreeding depression at the 0.05 probability level.

† Plant height and ear height were evaluated in six environments; days to anthesis and silk emergence and pollen–silk interval were evaluated in five environments; and kernel row number was evaluated in four environments.

‡ LSD used to compare inbreeding depression between populations.

served from the C3 × C9 (F_1) to the C3 × C9 (S_0) for ear length, ear diameter, 300-kernel weight, and grain yield. Among S_0 and S_1 composites, significant changes relative to BSSSC0 were observed in one or more improved populations for all traits. Maturity traits became earlier, pollen–silk interval decreased, plant and ear heights decreased, ear length increased, and 300-kernel weight decreased. The C3 × C9 S_0 yielded significantly more than the other S_0 populations; however, neither C3 nor C9 yielded more than C0, probably a result of inbreeding depression in the advanced cycles because a small number of superior lines were recombined to form the first eight successive cycles. The C3, C9, and C3 × C9 S_1 composites yielded significantly more than C0 S_1 composites, and C3 × C9 S_1 composite yielded significantly more than either C3 or C9 S_1 composite. Ear length seems to have been the primary yield component to account for the increased yields of the improved populations. Among S_0 entries and S_1 composites, C3 × C9 showed high-parent heterosis for grain yield.

The data suggest that inbred lines developed from any of the improved populations should be higher yielding than lines from C0, and lines from C3 × C9 may be higher yielding than lines from either C3 or C9. Also, inbred lines from the improved populations may be expected to be earlier than lines from C0 and to have less delay for silk emergence. The improvements for these traits are important for the hybrid seed producer.

Inbreeding depression, as the difference between S_0 and S_1 means and as a percentage, is shown in Table 2. For flowering traits, there were increases from S_0 to S_1 (i.e., flowering became later), but only (C3 × C9)-S_0 vs. (C3 × C9)-S_1 had significant values. Significant decreases (S_0 to S_1) were observed in all populations for plant and ear heights, ear length, ear diameter, and grain yield. Kernel depth, number of kernel rows, ears per plant, and 300-kernel weight had significant decreases for one or more populations. The trend observed for most traits was a decrease in the amount of inbreeding depression for the improved populations compared with BSSSC0, which is confirmed by the percentage values.

Theoretically, as a population is improved by recurrent selection, the frequency of favorable alleles increases with a corresponding decrease in the frequency of deleterious alleles. As a result, when an improved cycle is self-pollinated, fewer deleterious alleles are expressed for a given quantitative trait. Thus, inbreeding depression has less of an effect for improved cycles of selection as compared with the original population if the original population had average allelic frequencies ≥0.50, two alleles per locus, and directional dominance (Hallauer and Miranda, 1988). Inbreeding depression (S_0 to S_1) observed for grain yield in BSSSC0, BS13(S)C4, and BSSS(R)C9 was 1.65, 0.85, and 1.12 Mg ha^{-1}, respectively, as reported by Lamkey and Smith (1987). Rodriguez and Hallauer (1988) calculated inbreeding depression (S_0 to S_1) for grain yield in BSSS populations. They found that BSSSC0, BS13(S)C4, and BSSS(R)C9 showed inbreeding depressions of 1.76, 0.79, and 1.31 Mg ha^{-1}, respectively. The inbreeding values reported by Lamkey and Smith (1987) and Rodriguez and Hallauer (1988) agree with those reported in this study. Inbreeding depression tended to be greatest for BSSSC0 compared with the improved populations for most traits, although the differences were significant in relatively few instances. The inbreeding depression for yield was significantly greater for C0 than for C3, but not greater than for C9 and C3 × C9. RRS, which was used to develop C9, was proposed by Comstock et al. (1949) as a breeding method to use all types of gene action (i.e., additive and all nonadditive types). If overdominance is relatively unimportant, then three cycles of S_2 progeny selection that were used to develop C3 following seven cycles of half-sib selection can be expected to have accelerated the increase of homozygous loci with favorable alleles. The data seem to support that C3 has a greater frequency of homozygous loci than does C9. Horner et al. (1989) noted a similar difference for inbreeding depression between populations developed from RRS and S_2 recurrent selection.

They attributed this difference to a higher level of dominance, including overdominance, in the population developed by selection based on testcross performance using inbred testers compared with the population developed by selection among S_2 progenies.

The percentage of inbreeding depression (S_0 to S_1) for the C3 × C9 population was between parental values for most traits. None of the differences was great enough to be significant. The loci had different allelic frequencies in C3 and C9 for yield because C3 × C9 yielded significantly more than either C3 or C9. Some loci may have become fixed in C3 but not in C9; however, some of these fixed loci became heterozygous again when C3 × C9 was made, thus increasing the number of heterozygotes in C3 × C9, but the effects were not great enough to cause significant differences for inbreeding depression. Part of the change in the mean for C3 × C9 (F_1) to C3 × C9 (S_0) was caused by a change in genotypic equilibrium in the population with random mating the F_1 and therefore should not be considered inbreeding depression. The yield decrease for F_1 to S_1 was similar to the inbreeding depression for BSSSC0.

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