

Performance and Genetic Variance among S_1 Lines and Testcrosses of Iowa Stiff Stalk Synthetic Maize

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ABSTRACT

Iowa Stiff Stalk Synthetic (BSSSC0) maize (*Zea mays* L.) population has been used in two long-term recurrent selection programs: reciprocal recurrent selection (R) and half-sib followed by S_2 -progeny (S) recurrent selection. Advanced populations after nine cycles of reciprocal recurrent selection [BSSS(R)C9] and seven cycles of half-sib and three cycles of S_2 progeny selection [BS13(S)C3] were evaluated. Objectives of this study were to compare performance and amount of genetic variation present among S_1 lines from BSSSC0, BSSS(R)C9, BS13(S)C3, and BSSS(R)C9 \times BS13(S)C3 ($C3 \times C9$) and, also, to compare performance and genetic variation among testcrosses of the S_1 lines by using two testers of different heterotic background, B73 and Mo17. The S_1 lines from BSSS(R)C9 and BS13(S)C3 showed significant increases in grain yield compared with S_1 lines from BSSSC0. The $C3 \times C9$ S_1 lines showed high-parent heterosis for grain yield. Genetic variance component estimates of S_1 lines were significant in all four populations, and $C3 \times C9$ reflected midparent estimates between the estimates for C3 and C9. Mean grain yield for Mo17 testcrosses was significantly greater than for B73 testcrosses within each of the four populations. Testcrosses involving C3 and a related inbred, B73, showed a nonsignificant grain yield variance estimate. The average yield for the testcrosses of S_1 lines from $C3 \times C9$ for both testers was intermediate between the testcrosses of S_1 lines from C3 and C9; thus, the high-parent heterosis observed for $C3 \times C9$ S_1 lines was not observed for the testcross means.

RECURRENT SELECTION, in the form of mass selection, has been used since maize was first domesticated (Hallauer et al., 1988). Recurrent selection can be described as a cyclical selection process because it involves the development of progenies, evaluation of progenies in replicated trials, and recombination of superior progenies for the next cycle of selection (Hallauer and Miranda, 1988). The source population used in this study was Iowa Stiff Stalk Synthetic (BSSSC0) (Sprague, 1946). Half-sib recurrent selection in BSSS with a double-cross tester, Iowa 13, was initiated in 1939. Seven cycles of half-sib selection were followed by three cycles of S_2 progeny selection to create BS13(S)C3. Reciprocal recurrent selection (RRS) was initiated in BSSSC0 in 1949, and nine cycles of selection were completed with BSCB1 to create BSSS(R)C9. Highly significant improvements for hybrid yields have been achieved in both recurrent selection programs. Smith (1983) evaluated BS13 populations per se and calculated the response to selection for the C0 to C4 (0.08 ± 0.02 Mg ha⁻¹ cycle⁻¹) and C4 to C7 (0.25 ± 0.04 Mg ha⁻¹ cycle⁻¹). Total gain from direct response in the BSSS(R)Cn \times BSCB1(R)Cn crosses ranged in separate evaluations

from 7.0% (Penny and Eberhart, 1971) to 36.9% (Stangland et al., 1983). Crosses of earlier cycles for BS13(S) and BSSS(R) had shown significant heterotic expression for grain yield (Russell and Eberhart, 1975; Stangland et al., 1983; Smith, 1983), but there have not been detailed evaluations of germplasm from such crosses. Objectives of this study were to (i) evaluate progress achieved in BSSS through cycles of recurrent selection for quantitative traits; (ii) compare estimates of genetic variation among S_1 lines from the original BSSSC0, BSSS(R)C9 and BS13(S)C3, and the population cross of BSSS(R)C9 and BS13(S)C3; and (iii) compare genetic variation among testcrosses of S_1 lines from these sources by testers of different heterotic background.

MATERIALS AND METHODS

The details of the RRS program, initiated by G.F. Sprague in 1949, were given by Penny and Eberhart (1971) and the details of half-sib selection in BS13 [BSSS(HT)] were given by Eberhart et al. (1973). The four populations used in this study were BSSSC0 (C0), BS13(S)C3 (C3), BSSS(R)C9 (C9), and BS13(S)C3 \times BSSS(R)C9 ($C3 \times C9$). The $C3 \times C9$ was random-mated one generation. The S_1 lines for Exp. 1 were produced in 1985 and increased by sib-mating each line in 1986. All S_1 lines were random, with the only constraint being that there be enough seed for line increases and for testcross seed production. One hundred S_1 lines from each source were planted on an ear-to-row basis in a breeding nursery and approximately five sib-matings (10 plants sampled) were made. A total of 200 unselected S_1 lines (50 from each source) were used as entries in Exp. 1 in an incomplete block design arranged as replicates in sets as described by Hallauer and Miranda (1988). There were two replicates within each of five sets; each set included 10 lines from each of C0, C3, C9, and $C3 \times C9$, for a total of 40 lines per set.

Experiment 2 included the same lines as for Exp. 1 in testcrosses with B73 and Mo17. Inbred line B73 was derived from BSSS(HT)C5 maize synthetic variety (Russell, 1972) and is a Reid Yellow Dent-type line. The populations used in this study are related to B73, with the closest relationship being with BS13(S)C3. Inbred Mo17 was selected via pedigree selection from the cross CI187-2 \times C103 (Zuber, 1973) and is a Lancaster Sure Crop-type line. Lines B73 and Mo17 represent two different heterotic groups in maize germplasm.

In 1986, 100 S_1 lines from each of the four sources were planted in separate isolation blocks for making testcross seed with B73 and Mo17. The S_1 lines were detasseled and, at harvest, ≈ 15 ears from each line were bulked to make testcross seed. Fifty lines from each of the eight source \times tester combinations were used as entries in Exp. 2. These 400 testcrosses were included in an incomplete block design arranged as replicates in sets. There were two replicates within each of 10 sets; each set included five crosses from C0 \times B73, C3 \times B73, C9 \times B73, ($C3 \times C9$) \times B73, C0 \times Mo17, C3 \times Mo17, C9 \times Mo17, and ($C3 \times C9$) \times Mo17, for a total of 40 testcross entries per set.

The experiments were conducted in six environments (Ames, Ankeny, and Martinsburg, IA, in 1987 and 1988). All plots were machine planted in two-row plots, 1.52 m wide by 5.09 m long. Plots were overplanted and thinned

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to 59 300 plant ha⁻¹. Data were collected for grain yield (Mg ha⁻¹) adjusted to 155 g kg⁻¹ of moisture, grain moisture, stalk lodging (percentage of plants broken below the ear), root lodging (percentage of plants inclined more than 30° from the vertical), and dropped ears (percentage of ears on the ground at harvest). All trials were machine harvested, with no gleaning of ears.

Environments and S₁ progenies within each population were considered as random effects in Exp. 1. In Exp. 2, environments and testcross lines within each source were considered random and sources and testers were considered fixed effects. In both experiments, population means were compared by using LSD ($P = 0.05$) calculated by using the genotype \times environment mean square. Estimates of genetic variance for each trait were calculated from the combined analysis of variance. Confidence intervals for variance components were calculated by using the method of Knapp et al. (1987). Heritabilities were estimated as the ratio of genetic variance within a population to the phenotypic variance on a progeny-mean basis. Confidence intervals for heritabilities were calculated using the method of Knapp et al. (1985). For estimates of both genetic variances and heritabilities, if confidence intervals of two estimates did not overlap, they were considered significantly different. The genetic variance among S₁ progenies is an estimate of $\sigma_A^2 + (1/4)\sigma_B^2$ (Hallauer and Miranda, 1988).

RESULTS

S₁ Lines

Analyses of variance (not shown) combined across six environments indicated significant differences among entries for all traits. Although the genotype \times environment interaction mean square was significant for all traits, the sums of squares were less than sums of squares for entries. The interaction was caused by large climatic differences in growing seasons between 1987 and 1988. The growing season of 1987 was good for high productivity except near Martinsburg, where rainfall was less than normal. The 1988 season was a low productivity year at all locations because of high temperatures during flowering and below average rainfall.

The S₁ lines from the improved populations (C3, C9, and C3 \times C9) showed significant improvement for grain yield compared with S₁ lines from BSSSC0 (Table 1). Average yields of S₁ lines from C3 and C9 were similar, and C3 \times C9 showed significant high-parent heterosis. The significant increase for grain yield of C3 \times C9 S₁ lines compared with S₁ lines from C3 and C9 indicates that the two recurrent selection programs have changed allelic frequencies at different sets of loci. Means of S₁ lines from C3 \times C9 were

Table 1. Means across 50 S₁ progenies for five traits for each of four Iowa Stiff Stalk Synthetic populations evaluated in six environments.

Population	Lodging		Dropped ears	Grain moisture	Grain yield
	Root	Stalk			
	%			g kg ⁻¹	Mg ha ⁻¹
BSSSC0	6.8	11.2	0.3	197	2.92
BS13(S)C3	5.5*	12.3*	0.1*	184*	3.92*
BSSS(R)C9	4.9*	6.7*	0.5*	189*	3.91*
C3 \times C9	7.1*	7.5*	0.2*	185*	4.19*
LSD (0.05)	1.3	1.1	0.1	3.0	0.12

* Significantly different from BSSSC0 at the 0.05 probability level.

similar to the midparent values for the other traits except for percentage of root lodging, where C3 \times C9 was significantly greater than the midparent means. Means of S₁ lines decreased significantly from the C0 to the C9 for root and stalk lodging. The C3 showed significantly less root lodging, but greater stalk lodging than BSSSC0. All improved populations except C9 showed decreases for percentage of dropped ears. Grain moisture decreased significantly from C0 in the three improved populations.

The distributions of S₁ lines from each population for grain yield are shown in Fig. 1. The distributions show the significantly higher yield of the improved populations, compared with the C0, and the high-parent heterosis for C3 \times C9. The distribution for C3 does not show some classes as high yielding as C9 and C3 \times C9, probably because some S₁ lines were susceptible to *Helminthosporium* leaf spot [incited by Race I *Helminthosporium carbonum* (Ullstrup) = *Bipolaris zeicola* (G.L. Stout) Shoemaker].

Genetic variation among S₁ lines for the improved populations decreased compared with BSSSC0 for all traits except stalk lodging, where C3 showed an increase (Table 2). Not all these decreases were significant, as shown by the 90% confidence intervals. Data for dropped ears are not shown because no $\hat{\sigma}_e^2$ or h^2 values were significant. Decreases in genetic variability were expected, as some loci became fixed for favorable alleles and others increased in frequency with effective selection. The S₁ lines from C3 \times C9 showed no general trend for genetic variation relative to the variation of the S₁ lines of the parental populations. Genetic variance component estimates among S₁ lines were significantly greater than zero in all populations for grain yield. Estimates of genetic variation for grain yield of the C3 and C3 \times C9 populations were similar, while the estimate of genetic variation from C9 was larger than the estimates observed from C3 or C3 \times C9. Because estimates of genetic variance for yield in C3, C9, and C3 \times C9 were significant, it seems that

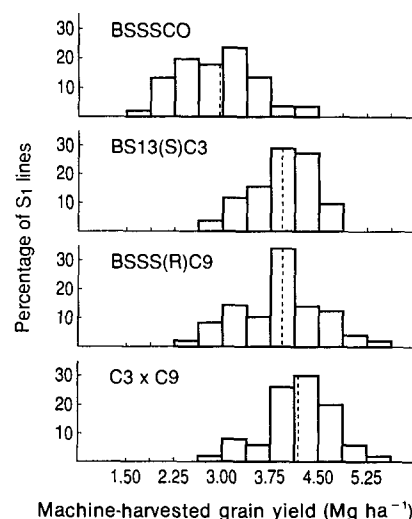


Fig. 1. Frequency distributions of 50 S₁ lines averaged across six environments for yield for each of four Iowa Stiff Stalk Synthetic populations (class interval = standard deviation, dashed vertical line = mean value).

response to selection can be expected in subsequent cycles. Also, the heritability (h^2) estimates for most traits exceeded 0.50, except for dropped ears, indicating that further selection would be effective. For most traits, the h^2 estimates for S_1 line means for the improved populations were smaller than for BSSSC0. No trend was observed for h^2 estimates from $C3 \times C9$ relative to parental population estimates.

Testcrosses

Significant differences were observed among entries within sets for all traits in the combined analyses of variance (not shown) for Exp. 2. The entries source of variation was subdivided into eight source \times tester components from which testcross genetic variance components were calculated. Two improved-population \times B73 testcross means, C9 and $C3 \times C9$, had significantly less stalk lodging than did $C0 \times B73$, and two improved-population \times Mo17 testcross means, C3 and $C3 \times C9$, had significantly less stalk lodging than did $C0 \times Mo17$ (Table 3). No differences were

Table 2. Estimates of genetic variance (σ_g^2) among 50 S_1 progenies and heritability estimates (h^2) on a S_1 progeny-mean basis for four traits from each of four Iowa Stiff Stalk Synthetic populations evaluated in six environments.

Trait	Population	σ_g^2	Confidence limits†		h^2	Confidence limits†	
			Lower	Upper		Lower	Upper
Root lodging, %	BSSSC0	35.82	27.85	45.01	0.73	0.59	0.81
	BS13(S)C3	24.72	18.06	32.02	0.66	0.48	0.76
	BSSS(R)C9	6.38	3.22	9.36	0.47	0.19	0.63
	$C3 \times C9$	30.27	22.95	38.53	0.70	0.54	0.79
Stalk lodging, %	BSSSC0	19.21	14.41	24.57	0.68	0.52	0.78
	BS13(S)C3	25.32	19.19	32.24	0.70	0.53	0.79
	BSSS(R)C9	10.06	7.86	12.63	0.73	0.60	0.81
	$C3 \times C9$	11.04	8.36	14.07	0.69	0.53	0.79
Moisture, g kg ⁻¹	BSSSC0	347	198	418	0.87	0.80	0.91
	BS13(S)C3	189	156	230	0.83	0.75	0.88
	BSSS(R)C9	260	216	314	0.86	0.79	0.90
	$C3 \times C9$	248	207	299	0.87	0.81	0.91
Grain yield, Mg ha ⁻¹	BSSSC0	0.29	0.24	0.36	0.83	0.74	0.89
	BS13(S)C3	0.18	0.14	0.23	0.68	0.51	0.78
	BSSS(R)C9	0.23	0.19	0.29	0.77	0.64	0.84
	$C3 \times C9$	0.17	0.12	0.22	0.66	0.47	0.77

† Confidence interval ($1 - \alpha = 0.90$) for variance component estimates and heritability estimates.

Table 3. Means across 50 testcrosses for five traits for each of four Iowa Stiff Stalk Synthetic populations crossed to two testers evaluated in six environments.

Population	Lodging		Dropped ears	Grain moisture	Grain yield
	Root	Stalk			
	%				
BSSSC0 × B73	4.9	17.2	0.4	196	5.99
BS13(S)C3 × B73	4.7	16.2	0.2*	197	6.42*
BSSS(R)C9 × B73	4.8	14.0*	0.5	194*	7.24*
(C3 × C9) × B73	5.4	14.1*	0.3	196	6.69*
BSSSC0 × Mo17	3.0	14.1	0.9	192	6.18
BS13(S)C3 × Mo17	2.1*	12.9	0.5*	190*	6.92*
BSSS(R)C9 × Mo17	1.5*	9.1*	1.1*	201*	7.46*
(C3 × C9) × Mo17	2.3	10.2*	0.8	192	7.02*
LSD (0.05)	0.8	1.4	0.2	2.0	0.11

* Significantly different from the respective BSSSC0 \times inbred line testcrosses at the 0.05 probability level.

observed among means of B73 testcrosses for root lodging, and only $C3 \times Mo17$ and $C9 \times Mo17$ showed significant decreases from $C0 \times Mo17$. $C3 \times B73$ testcrosses showed a significant decrease from $C0 \times B73$ for dropped ears. Similarly, $C3 \times Mo17$ had fewer dropped ears than $C0 \times Mo17$, and $C9 \times Mo17$ had significantly more dropped ears. $(C3 \times C9) \times B73$ and $Mo17$ testcrosses were intermediate between parental population testcrosses for dropped ears. Grain moisture decreased significantly for $C9 \times B73$ compared with $C0 \times B73$, but the other B73 testcrosses were not significantly different. The testcross $C3 \times Mo17$ showed a significant decrease, while $C9 \times Mo17$ showed a significant increase in grain mois-

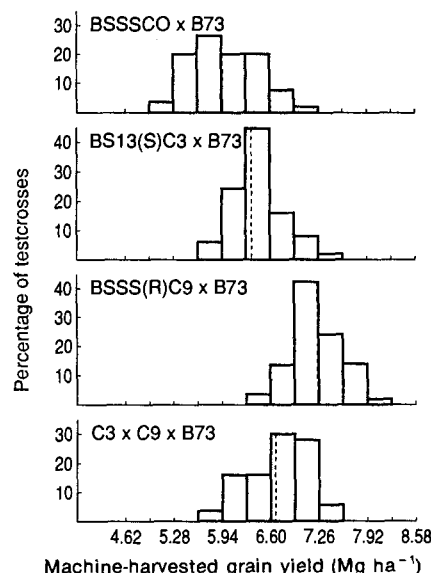


Fig. 2. Frequency distributions of 50 B73 testcrosses of S_1 lines from each of four Iowa Stiff Stalk Synthetic populations for yield averaged across six environments (class interval = standard deviation, dashed vertical line = mean value).

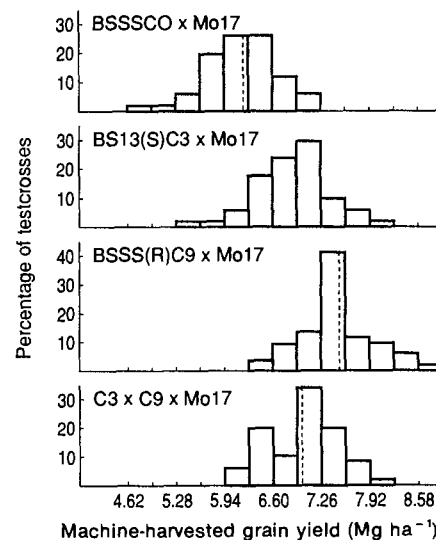


Fig. 3. Frequency distributions of 50 Mo17 testcrosses of S_1 lines from each of four Iowa Stiff Stalk Synthetic populations for yield averaged across six environments (class interval = standard deviation, dashed vertical line = mean value).

ture from C0 × Mo17. The C3 × C9 testcrosses were similar to C3 testcrosses for grain moisture in both B73 and Mo17 testcrosses. For grain yield, significant increases were observed for all improved-population testcrosses compared with C0 testcrosses; C9 testcrosses showed the greatest average yield when crossed to either tester. The C3 × C9 testcrosses with both testers were between parental testcross mean values for most traits, including grain yield.

Frequency distributions are shown for B73 testcrosses in Fig. 2 and for Mo17 testcrosses in Fig. 3. In both instances, the significantly higher mean yields are evident for the improved populations compared with C0 and for C9 compared with C3 and C3 × C9. Higher mean yields were obtained for the improved populations because of fewer low-yielding testcrosses and more high-yielding testcrosses. In general, more classes and greater yields were observed for Mo17 testcrosses compared with B73 testcrosses, probably because Mo17 is an unrelated heterotic group tester.

Table 4. Estimates of genetic variance ($\hat{\sigma}_g^2$) and heritability estimates (\hat{h}^2) on a testcross line-mean basis among 50 testcrosses for four traits for each of four Iowa Stiff Stalk Synthetic populations crossed to two testers evaluated in six environments.

Trait	Population	$\hat{\sigma}_g^2$	Confidence limits†		\hat{h}^2	Confidence limits†	
			Lower	Upper		Lower	Upper
Root lodging, %	C0 × B73	2.28	1.60	3.04	0.65	0.45	0.76
	C3 × B73	2.08	1.33	2.87	0.59	0.35	0.71
	C9 × B73	2.09	1.27	2.94	0.56	0.31	0.69
	(C3 × C9) × B73	3.03	2.13	4.03	0.65	0.45	0.76
	C0 × Mo17	1.08	0.66	1.52	0.56	0.31	0.69
	C3 × Mo17	0.09	-0.07	0.21	0.20	0.00	0.45
	C9 × Mo17	0.12	0.04	0.19	0.42	0.09	0.60
	(C3 × C9) × Mo17	0.45	0.24	0.66	0.50	0.21	0.65
Stalk lodging, %	C0 × B73	4.61	3.14	6.20	0.63	0.41	0.74
	C3 × B73	2.17	1.19	3.14	0.52	0.24	0.67
	C9 × B73	0.42	-0.60	1.21	0.16	0.00	0.42
	(C3 × C9) × B73	2.60	1.60	3.64	0.56	0.32	0.70
	C0 × Mo17	4.60	2.94	6.34	0.59	0.35	0.71
	C3 × Mo17	1.47	0.39	2.42	0.38	0.04	0.57
	C9 × Mo17	0.55	-0.18	1.14	0.25	0.00	0.49
	(C3 × C9) × Mo17	1.90	1.24	2.59	0.60	0.37	0.72
Moisture, g kg ⁻¹	C0 × B73	23	18	29	0.80	0.69	0.86
	C3 × B73	6	1	10	0.72	0.56	0.81
	C9 × B73	17	13	22	0.68	0.51	0.78
	(C3 × C9) × B73	32	26	39	0.85	0.77	0.90
	C0 × Mo17	23	19	29	0.80	0.68	0.86
	C3 × Mo17	14	11	18	0.73	0.59	0.82
	C9 × Mo17	17	13	22	0.71	0.55	0.80
	(C3 × C9) × Mo17	26	21	32	0.82	0.72	0.88
Grain yield, Mg ha ⁻¹	C0 × B73	0.38	0.27	0.50	0.66	0.47	0.77
	C3 × B73	0.07	0.01	0.14	0.34	0.00	0.54
	C9 × B73	0.17	0.08	0.25	0.47	0.17	0.64
	(C3 × C9) × B73	0.24	0.16	0.33	0.59	0.36	0.72
	C0 × Mo17	0.38	0.27	0.51	0.66	0.47	0.77
	C3 × Mo17	0.58	0.45	0.73	0.78	0.65	0.85
	C9 × Mo17	0.27	0.17	0.37	0.59	0.35	0.71
	(C3 × C9) × Mo17	0.35	0.24	0.47	0.64	0.44	0.75

† Confidence interval (1 - α = 0.90) for variance component estimates and heritability estimates.

Variance component estimates among testcrosses were significant for most traits, except for dropped ears, for which most testcross estimates were not significantly different from zero (Table 4). Data for dropped ears are not shown because only one $\hat{\sigma}_g^2$ value was significant. Generally, the variance component estimates for improved populations were smaller than those for C0 for both B73 and Mo17 testcrosses, particularly for grain yield. Genetic variance component estimates for C3 × C9 testcrosses were generally larger than estimates for the parental testcrosses; however, not all were significantly greater. The estimates of genetic variance for (C3 × C9) × B73 testcrosses were similar to the estimate for C9 × B73 testcrosses for grain yield and the estimates of genetic variance for (C3 × C9) × Mo17 testcrosses were similar to the estimates for the C0 and C9 × Mo17 testcrosses. The estimates of genetic variance for C3 and C9 × B73 testcrosses were significantly different from each other, as were the estimates of genetic variance for C3 and C9 × Mo17 testcrosses for grain yield. The C3 × Mo17 testcrosses had $\hat{\sigma}_g^2$ and h^2 values for yield that were significantly greater than those for the other group of testcrosses, whereas C3 × B73 testcrosses had $\hat{\sigma}_g^2$ and h^2 values significantly lower than for the other group of testcrosses.

DISCUSSION

The C3 × C9 S_1 lines had an average yield that gave significant high-parent heterosis of 7.0% (Table 1). These results indicate that the two recurrent selection programs have increased the frequencies of different dominant favorable alleles in BSSS. Heterosis in $F_1 = \Sigma dy^2$, where d is the level of dominance and y is the difference in allelic frequency between the parents (Falconer, 1981). It seems possible, also, that favorable interactions between loci in C3 × C9 may be present such that favorable types of epistasis contributed to the yield increase. When testcrosses of S_1 lines with B73 and Mo17 were made, genetic recombination in the parental S_1 lines could disperse favorable epistatic effects such that they would not function in the testcross progenies (Table 3). Consequently, the average testcross performance of S_1 lines from C3 × C9 would be expected to be similar to midparent values for testcrosses of S_1 lines from C3 and C9 insofar as epistasis is concerned. It can also be shown that certain assumed gene frequencies and levels of dominance will give significant heterosis in C3 × C9 vs. C3 and C9 S_1 lines, but it will not be expressed in testcrosses (O.S. Smith, 1989, personal communication).

As a source of inbred lines, C3 showed poor resistance to stalk lodging (Exp. 1) and some susceptibility to helminthosporium leaf spot. Improvement of these traits should permit C3 to become a source of good inbred lines. No new lines have been released from this program since B84 from BSSS(HT)C3 was released (Russell, 1979) because of continued problems with lodging and hybrid yield performance no better than B84. The $\hat{\sigma}_g^2$ for C3 × Mo17 testcrosses was significantly greater than for C0 × Mo17 for yield, which indicates that predicted gains should be greater for C3 than for C0 in testcrosses with Mo17. S_1 lines from C9 showed little lodging and had excellent yields. In

testcrosses, C9 consistently produced higher yields than did other populations when crossed to B73 or Mo17. Consequently, successful inbred lines should not be difficult to obtain from this population. The population cross may also be a good source of inbred lines. The S_1 lines per se from $C3 \times C9$ showed the greatest average grain yield in Exp. 1, which indicates that this should be the best source for high yielding inbred lines per se; however, these lines showed only average yield performance in testcross and had above average root lodging. Some additional cycles of selection in $C3 \times C9$ may be necessary to increase yields and resistance to root lodging.

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