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

Comments

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

ABSTRACT

Iowa Stiff Stalk Synthetic (BSSS(C0) maize (Zea mays L.) population has been used in two long-term recurrent selection programs: reciprocal recurrent selection (R) and half-sib followed by S1 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 S1 progeny selection [BS13(S)C3] were evaluated. Objectives of this study were to compare performance and amount of genetic variation present among S1 lines from BSSS(C0), BSSS(R)C9, BS13(S)C3, and BSSS(R)C9 × BS13(S)C3 (C3 × C9) and, also, to compare performance and genetic variation among testcrosses of the S1 lines by using two testers of different heterotic background, B73 and Mo17. The S1 lines from BSSS(R)C9 and BS13(S)C3 showed significant increases in grain yield compared with S1 lines from BSSS(C0). The C3 × C9 S1 lines showed high-parent heterosis for grain yield. Genetic variance component estimates of S1 lines were significant in all four populations, and C3 × 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 S1 lines from C3 × C9 for both testers was intermediate between the testcrosses of S1 lines from C3 and C9; thus, the high-parent heterosis observed for C3 × C9 S1 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 (BSSS(C0) (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 S1 progeny selection to create BS13(S)C3. Reciprocal recurrent selection (RRS) was initiated in BSSS(C0) 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 × 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 S1 lines from the original BSSS(C0), 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 S1 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 BSSS(C0), BS13(S)C3 (C3), BSSS(R)C9 (C9), and BS13(S)C3 × BSSS(R)C9 (C3 × C9). The C3 × C9 was random-mated one generation. The S1 lines for Exp. 1 were produced in 1985 and increased by sib-mating each line in 1986. All S1 lines were random, with the only constraint being that there be enough seed for line increases and for testcross seed production. One hundred S1 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 S1 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 × 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 C1187-2 × 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 S1 lines from each of the four sources were planted in separate isolation blocks for making testcross seed with B73 and Mo17. The S1 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 × 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 B73 × B73, C3 × B73, C9 × B73, (C3 × C9) × B73, C0 × Mo17, C3 × Mo17, C9 × Mo17, and (C3 × C9) × 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
ance on a progeny-mean basis. Confidence intervals for variance for each trait were calculated from the combined genotype X environment mean square. Estimates of genetic compared by using LSD (P = 0.05) calculated by using the environments and testcross lines within each source were considered as random effects in Exp. 1. In Exp. 2, en-

...ance (percentage of ears on the ground at harvest). All trials were machine harvested, with the vertical), and dropped ears (percentage of ears on the lodging (percentage of plants inclined more than 30 ° from lodging (percentage of plants broken below the ear), root

...to 59 300 plant ha -1. Data were collected for grain yield (Mg ha-1). The S~ lines from the improved populations (C3, C9, and C3 × C9) showed significant improvement for grain yield compared with S~ lines from BSSSC0 and C9, and C3 × C9) showed significant improvement for grain yield compared with S~ lines from BSSSC0.

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...analyses of variance (not shown) combined across six environments indicated significant differences for all traits, the sums of squares were less than sums of squares for entries. The interaction was caused by overlap, they were considered significantly different. The genetic variation among S~ lines for the improved populations decreased compared with BSSSC0 for all five traits except for percentage of dropped ears. The distributions of S~ lines from each population showed decreases for percentage of dropped ears. The S~ lines from the improved populations (C3, C9, and C3 × C9) showed significant improvement for dropped ears. The C3 × C9 S~ lines compared with S~ lines from BSSSC0. All improved populations except C9 showed greater than BSSSC0. All improved populations except C9 was significantly greater than the midparent means. The C3 showed similar to the midparent values for the other traits except for percentage of root lodging, where C3 × C9 was significantly greater than the midparent means.

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response to selection can be expected in subsequent cycles. Also, the heritability ($h^2$) estimates for most traits exceeded 0.50, 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 X 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 variation was subdivided into eight source X tester components from which testcross genetic variance components were calculated. Two improved-population × B73 testcross means, C9 and C3 × C9, had significantly less stalk lodging than did CO × B73, and two improved-population X Mo17 testcross means, C3 and C3 × C9, had significantly less stalk lodging than did CO X M017 (Table 3). No differences were observed among means of B73 testcrosses for root lodging, and only C3 × Mo17 and C9 × Mo17 showed significant decreases from CO × Mo17. C3 × B73 testcrosses showed a significant decrease from CO × B73 for dropped ears. Similarly, C3 X Mo17 had fewer dropped ears than CO × Mo17, and C9 X Mo17 had significantly more dropped ears. (C3 × C9) × B73 and Mo17 testcrosses were intermediate between parental population testcrosses for dropped ears. Grain moisture decreased significantly for C9 × B73 compared with CO X B73, but the other B73 testcrosses were not significantly different. The testcross C3 X M017 showed a significant decrease, while C9 × Mo17 showed a significant increase in grain moisture.

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

<table>
<thead>
<tr>
<th>Trait</th>
<th>Population</th>
<th>Confidence limits</th>
<th>Confidence limits</th>
<th>$\hat{h}^2$ Lower</th>
<th>$\hat{h}^2$ Upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Root lodging, %</td>
<td>BSSSC0</td>
<td>35.82 27.85 45.01</td>
<td>0.73 0.59 0.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BSI3(S)C3</td>
<td>24.72 18.06 32.02</td>
<td>0.66 0.48 0.76</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BSSS(R)C9</td>
<td>6.38 3.22 9.36</td>
<td>0.47 0.19 0.63</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>C3 × C9</td>
<td>30.27 22.95 38.53</td>
<td>0.70 0.54 0.79</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BSSSC0</td>
<td>19.21 14.41 24.57</td>
<td>0.68 0.52 0.78</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BSI3(S)C3</td>
<td>25.32 19.19 32.24</td>
<td>0.70 0.53 0.79</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>BSSS(R)C9</td>
<td>10.06 7.86 12.63</td>
<td>0.73 0.60 0.81</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>C3 × C9</td>
<td>11.04 8.36 14.07</td>
<td>0.69 0.53 0.79</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th>Lodging</th>
<th>Dropped</th>
<th>Grain</th>
<th>Moisture</th>
<th>Grain yield</th>
</tr>
</thead>
<tbody>
<tr>
<td>Population</td>
<td>Root</td>
<td>Stalk</td>
<td>ears</td>
<td>g kg$^{-1}$</td>
</tr>
<tr>
<td>BSSSC0 × B73</td>
<td>4.9</td>
<td>17.2</td>
<td>0.4</td>
<td>196</td>
</tr>
<tr>
<td>BSI3(S)C3 × B73</td>
<td>4.7</td>
<td>16.2</td>
<td>0.2*</td>
<td>197</td>
</tr>
<tr>
<td>BSSS(R)C9 × B73</td>
<td>4.8</td>
<td>14.0*</td>
<td>0.5</td>
<td>194*</td>
</tr>
<tr>
<td>(C3 × C9) × B73</td>
<td>5.4</td>
<td>14.1*</td>
<td>0.3</td>
<td>196</td>
</tr>
<tr>
<td>BSSSC0 × Mo17</td>
<td>3.0</td>
<td>14.1</td>
<td>0.9</td>
<td>192</td>
</tr>
<tr>
<td>BSI3(S)C3 × Mo17</td>
<td>2.1*</td>
<td>12.9</td>
<td>0.5*</td>
<td>190*</td>
</tr>
<tr>
<td>BSSS(R)C9 × Mo17</td>
<td>1.5*</td>
<td>9.1*</td>
<td>1.1*</td>
<td>201*</td>
</tr>
<tr>
<td>(C3 × C9) × Mo17</td>
<td>2.3</td>
<td>10.2*</td>
<td>0.8</td>
<td>192</td>
</tr>
</tbody>
</table>

LSD (0.05) 0.8 1.4 0.2 2.0 0.11

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

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).
both testers were between parental testcross mean values for most traits, including grain yield. Testcrosses compared with CO testcrosses; C9 testcrosses increased for all improved-population classes and greater yields were observed for Mo17 testcrosses. For grain yield, significant increases were observed for all improved-population classes and greater yields were observed for Mo17 testcrosses. In both instances, the significantly higher mean yields for the improved populations compared with CO × Mo17. The C3 × C9 testcrosses were similar to C3 testcrosses for grain moisture in both populations because of fewer low-yielding testcrosses and more high-yielding testcrosses. In general, more heritability was the difference in allelic frequency between the parental populations.

Heritability estimates are the percentage of the total variance due to genetic differences among individuals. Heritability estimates are calculated as:

\[ h^2 = \frac{\sigma_g^2}{\sigma_t^2} \]

where \( \sigma_g^2 \) is the genetic variance and \( \sigma_t^2 \) is the total variance. The variance component estimates (Table 4) for improved populations were smaller than estimates for the parental testcrosses; however, this program since B84 from BSSS(HT)C3 was released will give significant heterosis in C3 × C9 vs. C3 and C9 would be expected to be similar to midparent values for testcrosses of 1 lines from C3 and C9 insofar as epistasis is concerned. It can also be shown that certain dominant favorable alleles in BSSS. Heterosis and selection have increased the frequencies of different dominant favorable alleles in BSSS. Heterosis and selection programs have increased the frequencies of different dominant favorable alleles in BSSS. Heterosis and selection programs have increased the frequencies of different dominant favorable alleles in BSSS. Heterosis and selection programs have increased the frequencies of different dominant favorable alleles in BSSS. Heterosis and selection programs have increased the frequencies of different dominant favorable alleles in BSSS. Heterosis and selection programs have increased the frequencies of different dominant favorable alleles in BSSS. Heterosis and selection programs have increased the frequencies of different dominant favorable alleles in BSSS.

The estimates of genetic variance for (C3 × C9) × Mo17 testcrosses were similar to the estimate for C9 × B73 testcrosses for grain yield and the estimates of genetic variance for (C3 × C9) × B73 testcrosses were significantly greater than those for the other group of testcrosses, whereas C3 × B73 testcrosses were significantly greater than those for the other group of testcrosses.
testcrosses, C9 consistently produced higher yields than did other populations when crossed to B73 or Mo 17. 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, lines per se from C3 X 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 X C9 may be necessary to increase yields and resistance to root lodging.