Evaluation of Theory for Identifying Populations for Genetic Improvement of Maize Hybrids

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Abstract
The ability to identify populations with the greatest chance for breeding success may increase the use of unadapted populations by concentration of resources on favorable germplasm. This study was conducted to evaluate the effectiveness of a method (estimates of $\theta$) for identifying maize ($Zea mays$ L.) populations with the greatest number of dominant alleles at loci that are homozygous recessive in a single cross. This study also evaluates the effectiveness of a relationship estimator for detecting similarities between a population and the inbreds of a single cross. Estimates of $\theta$ and the relationship estimator were calculated by using donor populations of known composition and relationship to the recipient single cross. Six recipient single crosses were formed from the diallel cross of maize inbreds B73, B79, B77, and Mo17. Donor populations were composed of various proportions of inbreds B79 and B77. Estimates of correctly identified the population expected to have the largest number of unique dominant alleles in three of five single crosses (60%) for grain yield. for ear height, correctly identified the population expected to have the largest number of unique dominant alleles in four or five single crosses (80%). Estimates of did not identify populations expected to contain dominant alleles for earlier silking, suggesting that additive gene action or epistasis were important for silking date. The relationship estimator for yield correctly identified the known relationship between the populations and the inbred parents of the single crosses. The successful application of to exotic populations is uncertain because of a low frequency of favorable dominant alleles contained by exotics for important economic traits.

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

Comments

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Evaluation of Theory for Identifying Populations for Genetic Improvement of Maize Hybrids

David G. Pfarr and Kendall R. Lamkey*

ABSTRACT

The ability to identify populations with the greatest chance for breeding success may increase the use of unadapted populations by concentrating resources on favorable germplasm. This study was conducted to evaluate the effectiveness of a method (estimates of $\theta_{\mu'\mu}$) for identifying maize (Zea mays L.) populations with the greatest number of dominant alleles at loci that are homozygous recessive in a single cross. This study also evaluates the effectiveness of a relationship estimator for detecting similarities between a population and the inbreds of a single cross. Estimates of $\theta_{\mu'\mu}$ and the relationship estimator were calculated by using donor populations of known composition and relationship to the recipient single cross. Six recipient single crosses were formed from the diallel cross of maize inbreds B73, B79, B77, and Mo17. Donor populations were composed of various proportions of inbreds B79 and B77. Estimates of $\theta_{\mu'\mu}$ correctly identified the population expected to have the largest number of unique dominant alleles in three of five single crosses (60%). For ear height, $\theta_{\mu'\mu}$ correctly identified the population expected to have the largest number of unique dominant alleles in four of five single crosses (80%). Estimates of $\theta_{\mu'\mu}$ did not identify populations expected to contain dominant alleles for earlier silking, suggesting that additive gene action or epistasis were important for silking date. The relationship estimator for yield correctly identified the known relationship between the populations and the inbred parents of the single crosses. The successful application of $\theta_{\mu'\mu}$ to exotic germplasm is uncertain because of a low frequency of favorable dominant alleles contained by exotics for important economic traits.

The degree of success attained by a breeding program is a function of the germplasm and breeding procedure. A poor choice of germplasm will limit the success of the breeding program regardless of the breeding procedure (Hallauer and Miranda, 1988). Exotic or unadapted populations may be excellent sources of favorable alleles not currently present in populations used for inbred development (Hallauer, 1978; Brown, 1983). Use of unadapted germplasm would also help increase the genetic diversity among widely grown elite commercial cultivars (Stuber, 1978; Anonymous, 1972; Geadelmann, 1984; Holley and Goodman, 1988). Goodman (1985) reviewed the status of exotic maize germplasm use and attributed the limited success to poor choices of exotic germplasm rather than to the breeding procedures used.

The ability to effectively screen populations to identify those most promising for breeding success may enhance the use of unadapted or exotic germplasm in U.S. maize production. Theory for identifying populations for use in crossing with inbreds of elite single crosses has been proposed by Dudley (1984, 1987b). Loci Classes $i$, $j$, $k$, and $\ell$ are divisions of the loci controlling the trait of interest and are determined by the single cross to be improved. Loci at Class $i$ are homozygous dominant in the single cross. Loci at Classes $j$ and $k$ are heterozygous, with the dominant allele from parent one designating Class $J$ and the dominant allele from parent two designating Class $K$. Class $\ell$ loci are homozygous recessive in the single cross. The most immediate improvement of the single cross is by introgression of dominant alleles into Class $\ell$ loci (Dudley, 1984). Dudley (1984) developed a statistic ($\theta_{p,\mu}$) that is a measure of the frequency of dominant alleles in a population at loci that are homozygous recessive in the single cross to be improved (Class $\ell$ loci). Assumptions used to derive $\theta_{p,\mu}$ include a constant genotypic value ($\mu$) for loci affecting the trait, complete dominance, and no epistasis. Gerloff and Smith (1988) compared $\theta_{p,\mu}$ with other population identification statistics by using computer simulation. In the derivation of $\theta_{p,\mu}$, Dudley (1984) assumed that the frequency of favorable alleles at Class $j$ ($\hat{p}_j$) and $k$ ($\hat{p}_k$) loci in the population was equal. Gerloff and Smith (1988) established that failure of this assumption would decrease the ability of $\theta_{p,\mu}$ to correctly identify populations with the greatest frequency of favorable alleles at Class $\ell$ loci. Dudley (1987b) proposed a modified method of population identification that removes the $\hat{p}_j = \hat{p}_k$ assumption. The modified method also provides a test for determining the relationship between the populations and the parents of the single cross.

Dudley (1987b) compared the modified estimator ($\theta_{p,\mu'}$) to $\theta_{p,\mu}$ and other statistics by using computer simulation data generated by Gerloff (1985). Estimates of $\theta_{p,\mu'}$ were closest in agreement to the actual superiority measures of the simulated populations. Dudley (1988) evaluated 19 populations for their ability to improve the single cross B73 × Mo17. The traits measured were grain yield, root lodging, stalk lodging, ear height, and days to pollen shed. For grain yield, 8 of the 19 populations had estimates of $\theta_{p,\mu'}$ greater than two times the standard error. Of these eight populations, only one was relatively unselected for combining ability with maize lines adapted to the U.S. Corn Belt. Hogan and Dudley (1991) critically evaluated the ability of $\theta_{p,\mu'}$ to rank donor populations for which the relative magnitude of $\theta_{p,\mu}$ was known. Linear regression of $\theta_{p,\mu'}$ on the proportion of donor germplasm accounted for 87 to 99% of the variation in $\theta_{p,\mu'}$ for four traits. They concluded that $\theta_{p,\mu'}$ precisely ranks populations or inbreds relative to frequencies of useful alleles to improve a single cross and that $\theta_{p,\mu'}$ should be useful in choosing parents to improve elite single crosses.

This paper presents an empirical evaluation of Dudley’s (1984, 1987b) theory by applying the methods.
The data for the individual environments in the inbred experiment were analyzed as a randomized complete-block design with five replications. The inbred experiment was grown in the same six environments as the population cross experiment. Currently acceptable management and cultural practices were used for all plots. Plant densities for the inbred experiment were identical to those of the population cross experiment. The experimental units and design. The experiment was grown at the Agronomy and Agricultural Engineering Research Center near Ames, the University of Iowa.

A balanced bulk of seeds from the second random-mating generation was obtained from chain-sibbed plants from each population. In the second random-mating generation, 240 to 360 ears were harvested from a balanced bulk of the chain-sibbed plants in the first random-mating generation. Six backcross populations and one hybrid for a total of 56 populations crossed with the two single crosses, the six single crosses B73 × Mo17 and B79 × B77. The minimum number of plants sampled in any population was backcrossed to both parental lines in 1983, producing (B79 × B77) F2 population were then random-mated in the testcross. Inbred B77 was derived from 10 lines with two-eared characteristics and good combining ability (Russell et al., 1971). Inbred B79 was selected from the Population BS10, previously designated as Iowa Two-Ear Synthetic and B77. The inbred B79 was selected from the Population BS11, previously designated as Pioneer No. 1 (Russell and Hallauer, 1976). BS10 was synthesized from the Population BS11, previously designated as Pioneer Two-Ear Composite (Russell and Hallauer, 1974). BS11 was selected from a backcrossing scheme involving maize inbreds B79 and B77 and adapted Corn Belt lines.

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Material and methods

Genetic materials

No. 1 (Russell and Hallauer, 1976). BS10 was synthesized from the Population BS11, previously designated as Pioneer Two-Ear Synthetic and B77. The inbred B79 was selected from the Population BS10, previously designated as Iowa Two-Ear Synthetic. B79 and B77. The inbred B79 was selected from the Population BS11, previously designated as Pioneer Two-Ear Composite (Russell and Hallauer, 1974). BS11 was selected from a backcrossing scheme involving maize inbreds B79 and B77 and adapted Corn Belt lines.

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of the inability to determine the proper case in all than the performance per se of both inbred parents. Because the single-cross performance must be either greater or less than the performance of both inbreds, it is important to determine the appropriate case for obtaining the appropriate case and thus was used to estimate the relationship of the populations to be significantly different when the difference between estimates of effects within a single cross were considered to exceed two times the standard error of the estimate. Estimates of effects were calculated for yield, ear height, and plant height. The variance of effects may be underestimated owing to errors involved in choosing the appropriate case of means. The variance of effects of the relationship estimates were calculated as the square root of the variance of the linear combination of errors of the relationship estimates were calculated as the variance of a linear function of means used to calculate the estimate.

Environmental conditions were poor for maize production in the experiment. The testcrosses of the populations to B73, the single-cross hybrids B73 × Mo17 and B79 × B73 produced the greatest grain yields. Per se performance of both parents of the single cross for grain yield. Standard error of the difference is equal to the number of favorable dominant alleles for inbreds to have the smallest estimate of effects. For B73 with the populations, we expect the population with the greatest percentage of the common alleles for grain yield to contribute to B73 × Mo17. The single crosses B73 × B77, B79 × Mo17, B73 × B79, and B77 × Mo17 share one common parent population (P1), which is predominantly B79, with the populations. Therefore, we expect the population to B77. These results agree with those of Pfarr and Lamkey (1992), who found that B79 has greater ear height, and plant height. The grain yield of P7 was significantly greater than P6, by 1.29 Mg ha⁻¹. The ear height of B79 in per se performance, but ear height of B77 was significantly lower than the ear height of P6, by 1.29 Mg ha⁻¹. The ear height of B77 was significantly lower than the ear height of B73 × Mo17 (Table 3).
within B73, MolT, and B77. For B79 × Mo17 and was the single cross to be improved. These data sug-

Population expected to have the largest estimate of ~

Estimates for B79 and B77 are estimates of *

Estimate significantly different from zero at

no epistasis are appropriate for yield.

of complete dominance, constant genotpic value, and expectation that the estimates of ~'ffeX' will not be

simulations. These results generally agree with the

grain yield, and the estimate of £zffe~' for

populations. There was generally a failure of

differences were detected among the estimates. This

differences were detected between P7 and the other

populations. There was generally a failure of

differences were detected among the estimates. This

ent from zero for B73 × B79, although few significant

two estimates of ~'ffeP-' were significantly different

B77 when B79 was a parent of the single cross. Only

may be because B77 has few unique dominant alleles

differences were detected among the estimates. This

may be because B77 has few unique dominant alleles

smaller than for P1, except for

estimates of effpelx' for P4 through P7 were significantly

for yield to contribute to the single crosses, or because

may be because B77 has few unique dominant alleles

difference among the populations for estimates of

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two estimates of ~'ffeP-' were significantly different

B77 when B79 was a parent of the single cross. Only

may be because B77 has few unique dominant alleles

difference among the populations for estimates of

Table 3. Estimates of ~ett' for the seven populations

<table>
<thead>
<tr>
<th>Population</th>
<th>~ett' of single crosses to be improved</th>
<th>~ett' of single crosses to be improved</th>
<th>~ett' of single crosses to be improved</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>87.5 0.79</td>
<td>0.96* 1.12&quot;</td>
<td>0.54* -- 0.44* 0.94*</td>
</tr>
<tr>
<td>P2</td>
<td>75.0 0.63*</td>
<td>0.60* 0.03</td>
<td>0.21</td>
</tr>
<tr>
<td>P3</td>
<td>62.5 0.52*</td>
<td>0.74* 0.36*</td>
<td>0.42*</td>
</tr>
<tr>
<td>P4</td>
<td>50.0 0.56*</td>
<td>0.21§ 0.17</td>
<td>0.32*</td>
</tr>
<tr>
<td>P5</td>
<td>25.0 0.34*§</td>
<td>0.79* 0.27</td>
<td>0.75*</td>
</tr>
<tr>
<td>P6</td>
<td>37.5 0.68*</td>
<td>0.38*§ 0.46*</td>
<td>0.58*</td>
</tr>
<tr>
<td>P7</td>
<td>12.5 0.28§</td>
<td>0.35* § 0.19</td>
<td>0.51*</td>
</tr>
</tbody>
</table>
Table 4. Estimates of $t_{el}^*$ for the maize donor populations with six recipient single crosses for ear height.

<table>
<thead>
<tr>
<th>Population</th>
<th>B79</th>
<th>B73 × Mo17</th>
<th>B73 × B77</th>
<th>B79 × Mo17</th>
<th>B73 × B79</th>
<th>B77 × Mo17</th>
<th>B79 × B77</th>
</tr>
</thead>
<tbody>
<tr>
<td>PI</td>
<td>100.0</td>
<td>11.68*</td>
<td>10.83*</td>
<td>--</td>
<td>14.50*</td>
<td>--</td>
<td>--</td>
</tr>
<tr>
<td>P2</td>
<td>87.5</td>
<td>12.08*</td>
<td>11.23*</td>
<td>4.35*§</td>
<td>4.97*</td>
<td>13.20*</td>
<td>3.07*</td>
</tr>
<tr>
<td>P3</td>
<td>75.0</td>
<td>9.38*</td>
<td>8.52*§</td>
<td>4.68*§</td>
<td>3.50*</td>
<td>13.18*</td>
<td>2.43*</td>
</tr>
<tr>
<td>P4</td>
<td>62.5</td>
<td>7.68*§</td>
<td>6.83*§</td>
<td>5.98*</td>
<td>5.40*</td>
<td>10.85*</td>
<td>5.52*</td>
</tr>
<tr>
<td>P5</td>
<td>50.0</td>
<td>9.23*</td>
<td>7.23*§</td>
<td>4.58*§</td>
<td>5.27*</td>
<td>8.43*§</td>
<td>3.67*</td>
</tr>
<tr>
<td>P6</td>
<td>37.5</td>
<td>9.13*</td>
<td>7.23*§</td>
<td>5.62*</td>
<td>3.40*</td>
<td>8.50*§</td>
<td>5.62*</td>
</tr>
<tr>
<td>P7</td>
<td>25.0</td>
<td>5.68*§</td>
<td>4.83*§</td>
<td>5.62*</td>
<td>3.40*</td>
<td>8.50*§</td>
<td>5.62*</td>
</tr>
<tr>
<td>B77</td>
<td>12.5</td>
<td>7.83*§</td>
<td>6.98*§</td>
<td>7.82*</td>
<td>5.55*</td>
<td>9.15*§</td>
<td>--</td>
</tr>
</tbody>
</table>

* Estimate significantly different from zero at $P < 0.05$.

Table 5. Estimates of $t_{el}^*$ for the maize donor populations with six recipient single crosses for silk date.

<table>
<thead>
<tr>
<th>Population</th>
<th>B79</th>
<th>B73 × Mo17</th>
<th>B73 × B77</th>
<th>B79 × Mo17</th>
<th>B73 × B79</th>
<th>B77 × Mo17</th>
<th>B79 × B77</th>
</tr>
</thead>
<tbody>
<tr>
<td>PI</td>
<td>87.5</td>
<td>1.33*</td>
<td>1.40*§</td>
<td>0.10§</td>
<td>0.05§</td>
<td>1.97*</td>
<td>0.12</td>
</tr>
<tr>
<td>P2</td>
<td>75.0</td>
<td>1.37*</td>
<td>1.85*</td>
<td>0.12§</td>
<td>0.60*§</td>
<td>1.57*</td>
<td>0.15</td>
</tr>
<tr>
<td>P3</td>
<td>62.5</td>
<td>1.85*</td>
<td>2.20*</td>
<td>1.20*</td>
<td>1.42*</td>
<td>2.35*</td>
<td>1.37*</td>
</tr>
<tr>
<td>P4</td>
<td>50.0</td>
<td>1.27*</td>
<td>1.12*</td>
<td>0.57</td>
<td>0.97*</td>
<td>0.92*§</td>
<td>0.30</td>
</tr>
<tr>
<td>P5</td>
<td>37.5</td>
<td>1.17*</td>
<td>1.25*</td>
<td>0.65*</td>
<td>1.05*</td>
<td>1.05*§</td>
<td>0.60</td>
</tr>
<tr>
<td>P6</td>
<td>25.0</td>
<td>2.00*</td>
<td>3.25*§</td>
<td>1.65*</td>
<td>2.85*§</td>
<td>2.25*</td>
<td>3.10*</td>
</tr>
<tr>
<td>P7</td>
<td>12.5</td>
<td>1.58*</td>
<td>1.70*</td>
<td>1.25*</td>
<td>1.67*</td>
<td>1.47*</td>
<td>1.22*</td>
</tr>
</tbody>
</table>

B77 | 0.0 | 1.03* | -- | 0.95* | 0.97* | -- | -- |

* Estimate significantly different from zero at $P < 0.05$.

Table 6. Expected and estimated values of $t_j$ and $t_k$ for the maize donor populations with the recipient single cross B79 × B77.

<table>
<thead>
<tr>
<th>Locus</th>
<th>Trait class</th>
<th>Pl</th>
<th>P2</th>
<th>P4</th>
<th>P5</th>
<th>P6</th>
<th>P7</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Expected $t_j$</td>
<td>0.875</td>
<td>0.750</td>
<td>0.625</td>
<td>0.500</td>
<td>0.375</td>
<td>0.250</td>
</tr>
<tr>
<td></td>
<td>Expected $t_k$</td>
<td>0.125</td>
<td>0.250</td>
<td>0.375</td>
<td>0.500</td>
<td>0.625</td>
<td>0.750</td>
</tr>
</tbody>
</table>

$_{-} q_k (0.75)$ (0.50) (0.25) (0.00) (--0.25) (--0.50) (--0.75)

Yield $t_j$ 0.76 0.57 0.57 0.42 0.38 0.50 0.40

$q_k x 0.19 0.35 0.35 0.66 0.69 0.51 0.68$

$_{X-k} (0.57) (0.22) (0.22) (-0.24) (-0.31) (-0.01) (-0.28)$

Ear $t_j$ 0.65 0.63 0.50 0.50 0.48 0.50

$X-q_k (0.38) (0.29) (0.22) (-0.24) (-0.31) (0.08)$

Silk $t_j$ 0.79 0.67 0.59 0.43 0.44 0.50

$X-q_k (0.18) (0.29) (0.36) (0.63) (0.61) (0.54) (0.66)$

$X-q_k (0.61) (0.38) (0.23) (-0.20) (-0.17) (-0.04) (-0.27)$
Table 7. Estimates of relationship for the populations for B73 × B77, B79 × Mo17, B73 × B79, and B77 × Mo17 were calculated for each of the single crosses. The relationship estimator data for grain yield in-
and plant height, and flowering dates. Of the nine traits measured, only grain yield, ear height, and plant height produced meaningful estimates of $\epsilon^e$. Our study differs from Hogan and Dudley's (1991) study primarily in the genetic structure of the donor populations. Hogan and Dudley (1991) created donor arrays by crossing a line or population with the recipient single cross (FRB73 x FRMolV) in ways that produced populations that ranged from 0% donor population (the recipient single cross) to 100% donor germplasm (the donor line or population) in 25% increments. With this crossing scheme, they expected a linear relationship between $\epsilon^e$ and the proportion of donor germplasm, because $p_e$ (the frequency of favorable alleles at Class $e$ loci) changed proportionately across the donor array. They reported that linear regression accounted for 87 to 99% of the variation in $\epsilon^e$ for four traits. They concluded that $\epsilon^e$ precisely ranks lines relative to the frequency of alleles at Class $e$ loci and should be useful in selecting parents to improve single crosses.

We expected a linear relationship between $\epsilon^e$ and the percentage of B79 in the donor populations only for the four recipient single-crosses that shared a common parent with the donor populations and B73 x Mo 17, assuming the donor populations had favorable alleles to contribute to these single crosses. We evaluated the effectiveness of $\epsilon^e$, however, on the basis of whether the estimates were significantly different from zero and whether estimates for specific donor populations were significantly different from the donor expected to have the largest estimate of $\epsilon^e$. We chose this approach because, when the method is applied to donor populations of unknown merit, the best donor will be chosen on the basis of whether the estimate of $\epsilon^e$ is significant and significantly different from the other donor populations. Therefore, our conclusions about the effectiveness of $\epsilon^e$ in ranking and identifying populations, particularly when the frequency of dominant alleles at Class $e$ is low, differ from the conclusions of Hogan and Dudley (1991).