INBREEDING DEPRESSION AND GENE FREQUENCY CHANGES FOR AGRONOMIC TRAITS IN CORN SYNTHETIC SELECTED FOR RESISTANCE TO EUROPEAN CORN BORER

J. R. Klenke, W. A. Russell, W. D. Guthrie, and O. S. Smith

Abstract: A corn (Zea mays L.) synthetic, BS9, was evaluated to determine the effect that four cycles of S1 recurrent selection to improve resistance to European corn borer (ECB), Ostrinia nubilalis (Hubner), had on several other agronomic traits. The analysis used is a modification of linear regression analysis that is a more powerful technique than a means separation test to measure changes in agronomic traits during recurrent selection for ECB resistance. The model allows partition of the changes in agronomic traits into those caused by changes in allelic frequencies due to selection (implying linkage or pleiotropy), and changes caused by genetic drift, which results because of small population size. Recurrent selection for ECB resistance caused significant decreases in BS9 for grain yield (YLD), 300-kernel weight (KWT), ear diameter (EDI), ear length (ELH), ear height (EHT), and plant height (PHT). Changes in gene frequency (Δp) were significant for EDI, EHT, and PHT, and it was suggested that indirect selection for shorter internode length was the primary cause of these changes. Yield decreased from 6.07 Mg ha⁻¹ for BS9CO to 4.42 Mg ha⁻¹ for BS9(CB)C4, a 27.2% reduction. Change in gene frequency was estimated to cause an 8.4% reduction, and inbreeding depression was estimated to cause an 18.8% reduction, but only the latter was significant. The random fixation with loss of favorable alleles at some loci that were heterozygous in the CO (referred as drift) appears to have lowered the advanced cycle means. Selection to maintain maturity was effective by compensating for the weighted change in gene frequencies at heterozygous loci with an increase in the fixation of the favorable alleles. S2 recurrent selection, therefore, was recommended to include yield in the selection criteria to reduce the yield loss in advanced cycles from recurrent selection for resistance to the two generations of ECB.

Key Words: Maize, Zea mays, Ostrinia nubilalis.

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The primary objective of a recurrent selection program is to increase the frequency of the favorable alleles, while maintaining the genetic variability, for a quantitatively inherited trait such as yield or European corn borer (ECB), Ostrinia nubilalis (Hubner), resistance (Hallauer and Miranda 1981). Usually, it is preferred that other agronomic traits do not change in their phenotypic characteristics. Assessment of the progress from recurrent selection, therefore, involves evaluation of traits under selection and also indirect effects of selection on other traits.

Studies on the progress of many recurrent selection programs have been summarized by Hallauer and Miranda (1981). Usually, the analysis used to evaluate progress from selection regresses changes in means of populations on cycles of selection by using least-squares procedures (Eberhart 1964).

Realized gains from recurrent selection programs are often less than predicted gains because of inbreeding depression caused by small population size (Smith 1984).
Realized response in the change of the mean of the population is a function of the change in gene frequency and inbreeding depression (Smith 1979a). Smith (1979a,b, 1983) proposed a modification of the Hammond and Gardner model to separate changes in the mean caused by increase in frequencies of favorable alleles from changes in the mean due to inbreeding depression.

The Smith model has been applied to results of several recurrent selection programs to demonstrate the effects of drift on grain yield. Eberhart et al. (1973) reported that the means of two populations in a reciprocal recurrent selection (RRS) program for grain yield had not changed significantly. Smith (1979a), however, was able to detect from this study that RRS was effective in increasing the frequencies of favorable alleles. The estimate of drift effects accounted for the lack of significance in the change of the means of the populations. Similar results were obtained by Smith (1979b) in two populations in a recurrent selection program with an inbred tester reported by Russell et al. (1973). Effects of inbreeding depression due to small population size were evident in the means of the populations per se in three other studies by Smith (1979b, 1983, 1984).

BS9(CB)C4 was released to the seed industry in 1982 after four cycles of S1 recurrent selection for ECB resistance because of its potential value in breeding programs for resistance to the two generations of ECB normally found in Iowa (Russell and Guthrie 1982). The objectives of this study were to estimate gene frequency changes and inbreeding depression on agronomic traits of BS9 by using the model proposed by Smith.

MATERIALS AND METHODS

The original population, BS9CO, was developed by mating 10 corn inbred lines that were selected for their combining abilities and for their resistance to both ECB generations (Pesho et al. 1965). A more detailed description of the lines and development of BS9 is given by Russell and Guthrie (1982).

Experimental plots for this study were planted in eight environments, four Iowa locations in 1983 and 1984, and the experiment consisted of five entries: BS9CO, BS9(CB)C4, BS9C × BS9(CB)C4, BS9CO selfed, and BS9(CB)C4 selfed. The experimental design was a split-plot, with random-mated and selfed populations being nested in separate, bordered subplots within replications.

Agronomic practices, including planting date, fertilization, and weed control, were followed in all environments to promote high productivity. The Ames and Ankeny locations were hand-planted in single-row plots, 0.76 m × 4.32 m. Seeds were planted two per hill in 17 hills spaced 25.4 cm, and plants were later thinned to one per hill for a final density of 51,666 plants per hectare. The Kanawha and Martinsburg locations were machine-planted in single-row plots, 0.76 m × 5.00 m. Thirty-four seeds were planted, and plants were later thinned to a uniform stand of 19, for a final density of 50,000 plants per hectare.

Anthesis (POL) and silking (SIL) dates were recorded at the Ames location when 50% of the plants in a row were shedding pollen and silking, respectively. After pollination had been completed, plant and ear heights were taken on five competitive plants in each plot at all locations. Plant height (PHT) was measured to the flag leaf at the base of the tassel, and ear (EHT) was measured to the top ear node.

Ten competitive plants per plot were hand-harvested and the ears were dried to a uniform moisture. Data were taken on the diameter of the primary ears (EDI)
and length of all ears (ELH) and recorded on a per-plant basis. The ears were then shelled, and the grain was weighed and recorded on a per-plot basis (YLD). A sample of the grain was saved of each plot to permit a determination of 300-kernel weights (KWT).

The statistical model used to analyze changes in the population means for agronomic traits is based on the model developed by Smith (1979). In this analysis, the population mean for the original cycle of selection (CO) is written as a function of the homozygous (A_o) and heterozygous (D_o) effects in the CO. The population means and crosses after n cycles of selection are expressed as changes in allelic frequencies association with selection (A_t + D_t), and changes in allelic frequencies caused by drift (D_q). The A_o, D_o, A_t, D_t, and D_q terms can be related to additive and dominance effects at a single locus and the allelic frequencies at those loci as follows (Smith 1979b) and Table 1:

- A_o — the weighted sum (where the weights are the allelic frequencies) of the contribution of homozygous effects (a) to the mean of the CO:
- D_o — the weighted sum of the contribution of heterozygous effects (d) to the mean of the CO:
- A_t — the linear function of the changes in allelic frequencies caused by selection (Δρ), weighted by additive effects;
- D_t — the linear function of Δρ due to selection, dominance effects; and
- D_q — the quadratic function of Δρ caused by selection drift, weighted by dominance effects.

The mathematical expectations of the parameters are presented in Table 1. The assumptions are that the base population (CO) is diploid and that there is no epistasis. Estimates of the parameters were derived in this study from the following equations (Smith 1979b):

\[
\begin{align*}
\text{CO} &= A_o + 2D_o \\
\text{C4} &= A_o + 2D_o + 2A_t(N) + 2D_t(N) + 2D_q(N^2) \\
\text{CO selfed} &= A_o + D_o \\
\text{C4 selfed} &= A_o + D_o + 2A_t(N) + D_t(N) + D_q(N^2) \\
\text{CO × C4} &= A_o + 2D_o + A_t(N) + D_t(N)
\end{align*}
\]

where N is the number of cycles of selection. A more thorough description of the parameters is given below in the order that they were estimated.

D_o can be estimated from the difference of the CO and CO selfed. One generation of selfing reduces the number of heterozygous loci by half. D_o, therefore, is an estimate of the amount of inbreeding depression observed after one generation of selfing. Doubling D_o (2D_o) estimates the total contributions of the heterozygous loci to the CO mean.

A_o is the remainder of the contribution to the CO mean, which is an estimate of the homozygous loci effects. A_o also is the estimate of the mean of a random sample of inbred lines (homozygous) developed from the base population.

\[A_t(N) + D_t(N)\] is the difference between the CO and the population cross (CO × Cn), which is \((A_t + D_t)(N)\). This is an estimate of the weighted change in allelic frequencies, independent of the effect of drift, because \(A_t + D_t = Δρa + Δρ(q-p)d = Δρa\), which is half the change in the mean of a random-mating population from
selection (Kempthorne 1973). The difference between CO and CO × Cn, therefore, is the linear function of the change in allelic frequencies due to selection, weighted by additive and dominance effects.

Table 1. Two-allele and multiple-allele notations for expectations of parameters used in the model to estimate change in gene frequency in BS9.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>One-locus two-alleles (Smith 1979)*</th>
<th>More than one locus, multiple-alleles (Smith 1979)</th>
</tr>
</thead>
<tbody>
<tr>
<td>A₀</td>
<td>( \mu + (p-q)a )</td>
<td>( \sum_{k=1}^{n} \left( \mu_k + 2 \sum_{i=1}^{l} \rho_{ik} a_{ik} \right) )</td>
</tr>
<tr>
<td>D₀</td>
<td>( 2pqd )</td>
<td>( \sum_{i \neq i'} \sum_{k=1}^{l} \rho_{ik} \rho_{i'k} d_{i'k} )</td>
</tr>
<tr>
<td>Aᵣ</td>
<td>( \Delta \rho a )</td>
<td>( \sum_{i=1}^{n} \sum_{k=1}^{l} \Delta \rho_{ik} a_{ik} )</td>
</tr>
<tr>
<td>Dᵣ</td>
<td>( \Delta \rho(q-p)d )</td>
<td>( \sum_{i \neq i'} \sum_{k=1}^{l} \Delta \rho_{ik} \rho_{i'k} d_{i'k} )</td>
</tr>
<tr>
<td>Dᵣ</td>
<td>( \Delta \rho^2d )</td>
<td>( \sum_{i \neq i'} \sum_{k=1}^{l} \Delta \rho_{ik} \Delta \rho_{i'k} d_{i'k} )</td>
</tr>
</tbody>
</table>

* \( p \) = frequency of favorable allele, \( q = 1-p \), \( a \) = homozygous effect of favorable allele, \( d \) = heterozygous effect, and \( \Delta \rho \) = change in allelic frequency after selection.

The differences between CO × Cn and Cn is \( (A_r + D_r)(N) + 2D_q (N^2) \). The Cn contains twice the effect of the weighted change in gene frequency due to selection \((A_r + D_r)\) compared with CO × Cn, and removing this effect provides an estimate of \( D_q \). Quadratic changes in allelic frequencies from a small number of cycles of selection are usually small relative to the effects of drift (Smith 1979b). The \( D_q \) term, therefore, is primarily the effect of drift or loss of heterozygotes in the Cn population causing inbreeding depression after the effects of selection have been removed. \( D_q \) also is a measure of the loss in amount of predicted gain due to finite population size.

For a quantitative trait controlled by many loci, the expected change in allelic frequency due to drift (sampling) is zero (i.e., \( \Sigma A \Delta \rho = 0 \)). Drift, therefore, should have little effect on the estimates of \( A_r \) and \( D_r \). The sum of the change in allelic frequencies squared, however, is always positive and can be large relative to \( A \) due to selection, depending on the number of lines recombined. From the equation \( D_q = \Delta \rho^2d \), drift is the square of the change in allelic frequencies, weighted by the dominance effects. This, by definition, is the estimate of mid-parent heterosis (Falconer 1981). The \( D_q \) term, therefore, can also be considered an estimate of heterosis in the CO × Cn cross (Smith 1983).
A₀ and D₀ in Δρα can be separated because of the loss of half the heterozygous loci in the selfed population affects D₁ but not A₁. The D₁ term can be estimated from a linear function of the population per se, per se selfed, and the cross of the CO to the Cn. The A₁ term is finally estimated from the remainder.

The standard errors for the parameter estimates were calculated as described by Draper and Smith (1966).

RESULTS AND DISCUSSION

Least-square estimates of genetic parameters and means for various agronomic traits are presented in Table 2. Means decreased significantly in the C₄ population relative to CO for YLD, KWT, ED₁, ELH, EHT, and PHT and increased significantly for SIL. The means for CO × C₄ were significantly lower than the CO population per se for EHT, PHT, and ED₁, which is also indicated by the significant Δρα.

The A₁ and D₁ terms were not significant for ED₁, but the sum of the two (Δρα) was significant, indicating that a change in allelic frequencies caused by selection, weighted by additive and dominance effects, significantly decreased ED₁. For EHT and PHT, the D₁ term was significant, indicating that selection caused a change in gene frequency detected by a decrease in the contribution of the heterozygous loci to the mean. A A₁ term, however, was not significant for EHT and PHT, indicating no detectable change in the contribution of the homozygous loci.

The cause for the indirect selection on ED₁, EHT, and PHT was not obvious. Russell et al. (1979) reported a change in gene frequency for these traits in three synthetics after three cycles of recurrent selection for first-generation resistance. They stated that a change in gene frequency may have been caused by pleiotropism, linkage, and independent selection. In the present study, no selection was imposed on EHT or PHT because no measurements were taken. Additionally, first-generation ECB damage ratings tend to favor more vigorous plants because they can “grow-out” of the larval feeding sites more quickly and thus reduce the size of the lesions. Chromosome linkage and pleiotropism are unlikely causes because taller and later lines tend to be the most resistant.

Selection for second-generation ECB resistance (SGR) in BS9 was primarily based on resistance to stalk tunneling by the fifth-instar larvae (borers), which was determined by cavity counts (CVC) (one cavity ca. 2.5 cm), with secondary emphasis on resistance to sheath-collar feeding in the last two cycles of selection (W. A. Russell, W. D. Guthrie, and P. R. White, unpublished, Maize Breeding Research Project Annual Reports, 1972, 1975, 1978, 1980, Dep. of Agronomy, Iowa State Univ., Ames). Selection for a low number of cavities based on total plant counts may have been a possible cause for reduction of EHT and PHT, but the amount of tunneling in the S₁ lines of BS9 populations was too low for plant size to be a contributing factor. Although a high correlation exists between SGR and CVC (Guthrie et al. 1978), progress in SGR was slower than CVC in BS9. This may suggest that resistance to sheath-collar feeding was caused by some kind of antibiosis, but that resistance to tunneling was caused by hardness of the stalk (W. A. Russell, W. D. Guthrie, and P. R. White, unpublished, Maize Breeding Research Project Annual Report, 1980, Dep. of Agronomy, Iowa State Univ., Ames). Martin and Russell (1984) reported that internode length was significantly correlated with hardness of stalk, measured as rind strength, and ear diameter (r = -0.62** and r = 0.74**, respectively). Selection for reduced CVC, therefore, could indirectly influence internode length, which caused the decrease in ED₁, EHT, and PHT.
Table 2. Least-square estimates of genetic parameters and means for yield, yield components, and other agronomic traits of BS9 populations evaluated in six environments.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>POL</th>
<th>SIL</th>
<th>YLD</th>
<th>KWT</th>
<th>EDI</th>
<th>ELH</th>
<th>EHT</th>
<th>PHT</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A_0$</td>
<td>29.3 ± 0.6</td>
<td>34.2 ± 1.3</td>
<td>1.49 ± 0.41</td>
<td>60.1 ± 3.4</td>
<td>3.58 ± 0.09</td>
<td>10.6 ± 1.0</td>
<td>77.1 ± 3.5</td>
<td>155.7 ± 5.4</td>
</tr>
<tr>
<td>$D_0$</td>
<td>-3.5 ± 0.4</td>
<td>-4.5 ± 0.8</td>
<td>2.29 ± 0.26</td>
<td>5.3 ± 2.2</td>
<td>0.32 ± 0.06</td>
<td>3.2 ± 0.6</td>
<td>12.0 ± 2.2</td>
<td>27.5 ± 3.3</td>
</tr>
<tr>
<td>$A_1$</td>
<td>-0.4 ± 0.1</td>
<td>-0.3 ± 0.2</td>
<td>0.02 ± 0.07</td>
<td>0.5 ± 0.6</td>
<td>-0.01 ± 0.02</td>
<td>0.1 ± 0.2</td>
<td>-0.5 ± 0.6</td>
<td>0.4 ± 1.0</td>
</tr>
<tr>
<td>$D_1$</td>
<td>0.3 ± 0.1</td>
<td>0.2 ± 0.3</td>
<td>-0.09 ± 0.11</td>
<td>-0.1 ± 0.9</td>
<td>-0.02 ± 0.02</td>
<td>-0.1 ± 0.3</td>
<td>-2.2 ± 0.8</td>
<td>-3.6 ± 1.2</td>
</tr>
<tr>
<td>$\Delta p\alpha$</td>
<td>-0.1 ± 0.1</td>
<td>-0.0 ± 0.2</td>
<td>-0.06 ± 0.06</td>
<td>-0.5 ± 0.5</td>
<td>-0.03 ± 0.01</td>
<td>0.1 ± 0.2</td>
<td>-2.7 ± 0.3</td>
<td>-3.2 ± 0.4</td>
</tr>
<tr>
<td>$D_\alpha$</td>
<td>0.0 ± 0.1</td>
<td>0.1 ± 0.1</td>
<td>-0.04 ± 0.01</td>
<td>-0.1 ± 0.1</td>
<td>0.00 ± 0.01</td>
<td>-0.1 ± 0.1</td>
<td>0.1 ± 0.1</td>
<td>0.1 ± 0.2</td>
</tr>
</tbody>
</table>

**Means**

<table>
<thead>
<tr>
<th>Trait</th>
<th>CO</th>
<th>C4</th>
<th>CO selfed</th>
<th>C4 selfed</th>
<th>CO × C4</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>POL</td>
<td>22.3</td>
<td>22.3</td>
<td>25.8**</td>
<td>24.2**</td>
<td>22.0</td>
<td>23.3</td>
</tr>
<tr>
<td>SIL</td>
<td>25.2</td>
<td>26.5**</td>
<td>29.7**</td>
<td>29.3**</td>
<td>25.0</td>
<td>27.1</td>
</tr>
<tr>
<td>YLD</td>
<td>6.07</td>
<td>4.42**</td>
<td>3.78**</td>
<td>3.04**</td>
<td>5.81</td>
<td>4.62</td>
</tr>
<tr>
<td>KWT</td>
<td>70.7</td>
<td>61.4**</td>
<td>65.4*</td>
<td>62.6**</td>
<td>68.5</td>
<td>65.7</td>
</tr>
<tr>
<td>EDI</td>
<td>4.21</td>
<td>3.84**</td>
<td>3.85**</td>
<td>3.66**</td>
<td>4.08*</td>
<td>3.94</td>
</tr>
<tr>
<td>ELH</td>
<td>17.0</td>
<td>15.7*</td>
<td>13.8**</td>
<td>13.6**</td>
<td>17.2</td>
<td>15.5</td>
</tr>
<tr>
<td>EHT</td>
<td>102.0</td>
<td>80.6**</td>
<td>89.3**</td>
<td>76.7**</td>
<td>89.8**</td>
<td>87.7</td>
</tr>
<tr>
<td>PHT</td>
<td>211.1</td>
<td>185.2**</td>
<td>183.2**</td>
<td>171.7**</td>
<td>196.9**</td>
<td>189.6</td>
</tr>
</tbody>
</table>

* **Significantly different from CO at the 0.05 and 0.01 probability level, respectively.
† Abbreviations for traits: POL = date of anthesis, SIL = date of silking, YLD = grain yield, KWT = 300-kernel weight, EDI = ear diameter, ELH = ear length, EHT = ear height, and PHT = plant height.
‡ Parameters are defined in Smith (1983).
§ $\alpha$ = average effect of an allelic substitution, $\alpha = a + (q - p)d$. 

**Note:** The table includes least-square estimates of genetic parameters and means for yield, yield components, and other agronomic traits of BS9 populations evaluated in six environments. The parameters are defined as follows: $A_0$ and $D_0$ are additive and dominance effects, respectively, and $A_1$, $D_1$, and $\Delta p\alpha$ are associated with an allelic substitution. The means are given for different treatments, including CO (Check), C4, CO selfed, C4 selfed, and CO × C4. The abbreviations for traits are as follows: POL = date of anthesis, SIL = date of silking, YLD = grain yield, KWT = 300-kernel weight, EDI = ear diameter, ELH = ear length, EHT = ear height, and PHT = plant height. The significant differences are indicated by asterisks (*) and double asterisks (**) at the 0.05 and 0.01 probability levels, respectively. The parameters are defined in Smith (1983), and $\alpha$ represents the average effect of an allelic substitution, $\alpha = a + (q - p)d$. 

**References:**
- Smith (1983).
The $D_q$ term was significant only for YLD. Substitution of the estimates for the parameters in the equation for the C4 population, \( \Delta \rho_0[2A(N) + 2D(N)] \) and \( D_q[N(N-1)] \), caused reductions of 0.51 and 1.14 Mg ha\(^{-1}\), respectively, from the CO mean for YLD. Changes in gene frequency (\( \Delta \rho a \)) and inbreeding depression (\( D_q \)), thus, were estimated to account for 8.4 and 18.8%, respectively, of the reduction in yield in BS9(CB)C4. The $D_q$ term, however, was the only estimate that was significant. If the $\Delta \rho^2$ term in $D_q$ was caused primarily by drift (Smith 1979b), then the greatest decrease in the C4 yield was caused by inbreeding depression due to a small population size.

The inbreeding coefficient of the C4, where $N_v \equiv N$ (Robertson 1961), was calculated to be 6.9% (Klenke 1985), but the $D_q$ term was 18.8%. The difference between these two estimates may be accounted for by using the product for the effects of drift on the components of yield. Although none was significant, the reductions due to $D_q$ for KWT, EDI, and ELH were 6.9, 2.8, and 10.3% of the BS9CO mean, respectively. Subtraction of these three terms from unity gives the values of C4 for the three traits, expressed as a percentage of the CO caused by drift, of 93.1, 97.2, and 89.7%, respectively. The product of the components is 81.2%, which is an 18.8% reduction and equal to the 18.8% reduction in yield. Similarly, the product of the three components based on $\Delta F = 6.9\%$ is $(0.931)^3 = 80.7\%$, which is a 19.3% reduction. In this study, the reduction in yield due to drift, therefore, seems to be related to the inbreeding depression of the three components of yield.

Another explanation, indicated by the Smith model, for the decrease in yield of the C4 could be a large amount of random fixation at heterozygous loci (drift). Estimates for the contributions to yield of the BS9CO from the homozygous loci ($A_0$) and heterzygous loci ($2D_0$) were 1.49 and 4.58 Mg ha\(^{-1}\), or 24.5 and 75.5%, respectively.

The $A_1$ term is not significant but positive, indicating that there was no loss in the frequency of the favorable alleles; thus, repulsion-phase linkage was not a contributing factor. Linkage to alleles for other traits under direct and indirect selection (FGR, SGR, CVC, and POL, and EDI, EHT, and PHT, respectively) could contribute to inbreeding depression because populations in linkage equilibrium would fix alleles not influenced by selection at random. The greatest decrease in subsequent cycles of BS9, therefore, seemed to be the result of random fixation of alleles contributing to yield, perhaps increased by linkages to other traits affected by selection, rather than by a change in gene frequencies due to selection.

The $A_1$ term was significant for only POL, which was the only trait influenced by direct selection in BS9. Selection was imposed on POL in BS9 so that the relative maturity of the selected $S_1$ lines was no later than the mean of the $S_1$ population. The means of the CO, C4, and CO $\times$ C4 were not significantly different; thus $D_q$ and $\Delta \rho_0$ were not significant. The $A_1$ and $D_1$ terms, however, were significant but of opposite sign. Because dominance of POL was for earliness and earliness is the most desirable direction of selection, the $A_1$ and $D_1$ terms are more easily understood if they are expressed as days before a certain date. To keep the mean of the CO and C4 populations approximately the same, the POL data were converted to the number of days before August 14, which will make dominance and gain, in the desired direction, positive. The only parameter in the Smith model that is changed by this transformation is $A_0$, which will not affect the interpretations.
The estimates of the parameters become:

\[
\begin{align*}
A_0 & = 15.8 \pm 0.6 \\
D_0 & = 3.5 \pm 0.4 \\
A_1 & = 0.4 \pm 0.1 \\
D_1 & = -0.3 \pm 0.1 \\
\Delta p_{\alpha} & = -0.1 \pm 0.1 \\
D_q & = 0.0 \pm 0.1
\end{align*}
\]

The \(A_1\) and \(D_1\) terms are of approximately equal magnitude, which sum to produce a \(\Delta p_{\alpha}\) term that is not significant. The weighted change in gene frequencies at heterozygous loci (\(D_1\)), or heterozygous effects, therefore, was compensated by the fixing of the favorable alleles or homozygous effects. Fixation of the favorable allele rather than random fixation was caused by selection.

The effects of selection on POL may also perform similarly with other traits such as yield. Selection may not reduce drift or may increase \(D_q\) if \(\Delta p_{\alpha k}\) and \(\Delta p_{\pi k}\) (Table 1) are increased. The effect of selection to reduce unfavorable changes in the mean would be to ensure that fixation is primarily of the favorable allele. Because of limited resources for replication yield trials and the importance of population size to reduce drift, a \(S_2\) recurrent selection program as described by Hallauer and Miranda (1981) would be the most desirable method to implement. Although this would require an extra year in temperate zones, selection can be conducted in two seasons. The \(S_1\) lines could be evaluated for FGR, POL, PHT, and SGR in one or two replications to eliminate the most undesirable lines. These traits could then be evaluated again in a small population of \(S_2\) lines, in addition to evaluations for yield in replicated trials. The main emphasis of selection should be on SGR and YLD, with lesser emphasis on FGR, while attempting to maintain the means for POL and PHT.

ACKNOWLEDGMENTS


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