Selection response and efficiency of doubled-haploid recurrent selection in a cross-fertilized species*

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Summary. Computer simulation was used to compare the simulated response to doubled-haploid (DH) mass selection with the response predicted by mathematical formulae. The efficiency of DH versus diploid mass selection in a cross-fertilized species was also studied by means of theoretical consideration and computer simulation. Simulated gain was in agreement with the predicted gain in the DH population under both additive and complete dominance models. The simulated variance of response to DH mass selection was close to the predicted variance at both the 5% and 25% selection regimes under additive and complete dominance models. The efficiency of DH over diploid mass selection was shown to be dependent upon the allelic frequency, the degree of dominance, and the amount of environmental variance. In theory the efficiency can range from zero to infinity, but in reality it should be greater than one. The efficiency ranges from \( \sqrt{2} \) to 2 in the absence of dominance; it can be greater than two only in the presence of dominance and a small environmental variance. The variance of response to DH mass selection can be smaller than or up to twice as large as the variance of response to diploid mass selection. Computer simulation results agreed with the predicted efficiency of DH mass selection and with the predicted variance-of-response ratio of DH mass selection to diploid mass selection.

Key words: Computer simulation – Doubled haploids – Response to selection – Mass selection

Introduction

Haploids can be obtained by anther culture in many cross-fertilized species including maize and Brassica (Vasil 1980). Chase (1952) suggested that doubled haploids may prove useful as an adjunct to recurrent selection in maize. Griffing (1975) showed that if cycle lengths are equal, doubled haploid (DH) could be up to six times more effective than diploid selection procedures. Choo and Kannenberg (1978), using computer simulation, showed that DH mass selection was about 1.4 times faster than diploid mass selection and equal to Sl selection in terms of gain per year.

Mathematical formulae for predicting mean and variance of response to selection have been developed (Baker 1971; Empig et al. 1972; Hill 1974). In a computer simulation study on a diploid cross-fertilized species, Choo and Kannenberg (1981) found that predicted gain for diploid mass selection was in agreement with simulated gain under an additive model but not under a complete dominance model, and that the predicted variance of response to mass selection appeared to be in agreement with the simulated variance under both genetic models. However, the accuracy of the mathematical formulae for predicting mean and variance of response to DH mass selection in a cross-fertilized species is not known.

The objectives of this study were: (1) to compare the predicted response to DH mass selection with the simulated response in a diploid, cross-fertilized species, and (2) to compare the mean and variance of response to DH mass selection with the mean and variance of response to diploid mass selection.

Theory

Consider that doubled haploids are extracted from plants of a random-mating population of a diploid,
cross-fertilized species. M doubled-haploids are tested with one replication in the field and N doubled-haploid plants are selected on the basis of their phenotypic value. Open-pollinated progeny of selected plants are used to produce doubled haploids for the next selection cycle. Thus, selection is applied only to female parents. In each subsequent cycle, M doubled-haploids are produced and N plants are selected. The predicted mean response to selection for this DH population (ΔG) can be expressed as follows:

\[ ΔG = K \frac{σ^2_G}{σ_1} \]

where \( σ^2_G \) is the additive genetic variance, \( σ_1 \) is the phenotypic standard deviation of the DH population, and \( K \) is the standardized selection differential (see Empig et al. 1972 and Griffing 1975 for rationale). The predicted variance of response to selection for the DH population (\( σ^2_{2G} \)) can be expressed as follows:

\[ σ^2_{2G} = \frac{2 σ^2_a^2 + 2 σ^2_i}{M} + \frac{σ^2}{N} \left[ 1 - \left(1 - k_p\right) h^2 \right] \]

where \( k_p \) is a value associated with variances of order statistics (\( k_p = 0.30 \) for 5% selection intensity and \( k_p = 0.51 \) for 25% selection intensity), \( h^2 \) is the narrow-sense heritability in the DH population, and \( σ^2 \) is the phenotypic variance of the DH offspring population (see Baker 1971 and Hill 1974 for rationale).

Suppose that mass selection is also conducted in a diploid population in an identical manner and under identical conditions. The only difference between DH and diploid mass selections is that the former involves testing and selection of doubled haploids, the latter testing and selection of diploids. The mathematical formulae for predicting mean and variance of response to mass selection in a diploid population were given by Choo and Kannenberg (1981). The efficiency of DH mass selection relative to diploid mass selection (E), or ratio of genetic gains, can be shown to be twice the ratio of diploid phenotypic standard deviation (\( σ_{1d} \)) to DH phenotypic standard deviation if dominance is absent or if, in the presence of dominance, allelic frequencies are equal to one-half, i.e.,

\[ E = 2 \frac{σ_{1d}}{σ_1} = 2 \sqrt{\frac{σ^2_a^2 + σ^2_i}{2} + \frac{σ^2}{2}} \]

where \( σ^2_a \) and \( σ^2_i \) are the dominance variance and the environmental variance, respectively. With no dominance, the efficiency is equal to \( \frac{1}{2} \) if the environmental variance is zero (i.e. heritability = 1), while it approaches two as the environmental variance approaches infinity (i.e. heritability = 0). The efficiency can be larger than two only in the presence of dominance and a small environmental variance. In theory, the efficiency can range from zero to infinity if allelic frequencies are not equal to one-half and dominance is present. Let \( p \) be the frequency of the dominant allele, \( q \) be the frequency of the recessive allele, \( 2a \) be the difference between two homozygotes, and \( d \) be the deviation of the heterozygote from the mid-parent. If the environmental variance is equal to zero and the population is in equilibrium, the efficiency formula for a one-locus system can be rewritten as follows:

\[ E = \frac{\sqrt{p q a^2} \sqrt{2 p q [a + d (q - p)]^2 + (2 p q d)^2}}{2 p q [a + d (q - p)]^2} \]

The efficiency can be studied by assigning different values of \( p, a \) and \( d \) (Table 1). DH mass selection is more efficient than diploid mass selection if the frequency of dominant desirable alleles exceeds 0.5 (Choo and Kannenberg 1978, Fig. 3) or if the frequency of recessive desirable alleles is less than 0.5. This observation differs from the one by Griffing (1975), who reported that the efficiency of DH mass selection is increased when the frequency of dominant desirable allele is less than 0.5, or when the frequency of recessive desirable allele is greater than 0.5. This theoretical consideration illustrates that the efficiency of DH over diploid mass selection is dependent upon the allelic frequency, the degree of dominance, and the amount of environmental variance. In reality, the expression of most quantitative traits in different species is affected by environment. Many quantitative traits have a low heritability in actual selection programs. Therefore, DH mass selection is most likely more efficient (i.e., \( E > 1 \)) than diploid mass selection.

Assume that the genetic variance of the offspring population is the same as that of the parental population, and that the environmental variance is constant from cycle to cycle. Then, the variance-of-response ratio of DH mass selection to diploid mass selection (VR) can be described as follows:

\[ VR = \frac{4 N (4 σ^2_a^2 + σ^2_i) + 2 σ^2_i [N + M [1 - (1 - k_p) h^2]]}{4 N (2 σ^2_a^2 + σ^2_i) + σ^2_i [N + M [1 - (1 - k_p) h^2]]} \]

Table 1. Effects of allelic frequency and degree of dominance on the efficiency of DH mass selection over diploid mass selection, assuming \( σ^2_a = 0 \) and \( a = 1 \)

<table>
<thead>
<tr>
<th>Allelic frequency</th>
<th>Efficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>d = 1</td>
<td>d = 2</td>
</tr>
<tr>
<td>p = 0.01, q = 0.99</td>
<td>0.06</td>
</tr>
<tr>
<td>p = 0.10, q = 0.90</td>
<td>0.63</td>
</tr>
<tr>
<td>p = 0.50, q = 0.50</td>
<td>1.73</td>
</tr>
<tr>
<td>p = 0.90, q = 0.10</td>
<td>16.58</td>
</tr>
<tr>
<td>p = 0.99, q = 0.01</td>
<td>507.47</td>
</tr>
</tbody>
</table>