DOUBLED HAPLOIDS FOR STUDYING THE INHERITANCE
OF QUANTITATIVE CHARACTERS

T. M. CHOO

Research Station, Agriculture Canada, P. O. Box 1210, Charlottetown,
Prince Edward Island, Canada, C1A 7M8

Manuscript received August 20, 1980
Revised copy received August 25, 1981

ABSTRACT

By using a doubled-haploid population derived from $F_2$ plants, additive and
additive $\times$ additive genetic variances, as well as the number of segregating
genes, can be estimated. An $F_2$-derived doubled-haploid population may contain
almost 50% more of the best recombinant than an $F_1$-derived population. How-
ever, the best recombinant occurs in the same frequency in the two populations
when there is no linkage between genes. The difference in the frequency of the
best recombinant between $F_2$- and $F_1$-derived populations is small. This implies
that the doubled-haploid method using $F_2$ plants provides only slightly less op-
portunity for recombination than the conventional breeding methods of self-
pollinating crops. In the absence of additive epistasis, a weighted mean of re-
combination values can be estimated using an $F_2$-derived population and its
parental lines. When additive epistasis is present, it can be estimated from
doubled-haploid populations derived from two backcrosses. Studies on the link-
age of quantitative characters are needed for determining whether doubled
haploids should be produced from $F_2$ or from $F_1$ plants in a breeding program.

HAPLOIDS can be produced by means of various production techniques such
as anther culture, interspecific hybridization, and so on. They form doubled
haploids after their chromosomes are doubled by colchicine. Using doubled-
haploid techniques, truly homozygous lines can be obtained from the gametes of
$F_1$ hybrids; thereby, the time required to develop new varieties may be shortened
by 2 to 3 generations. The first doubled-haploid variety of barley, Mingo, was
developed by Ciba Geigy Seeds Ltd., Ontario, and was licensed for sale in Canada
in 1979, only five years after its parental lines were crossed (Ho and Jones 1980).

Doubled-haploid techniques also offer tremendous potential for the study of
quantitative inheritance. It has been shown that the number of segregating genes
in a single cross can be estimated from a doubled-haploid population produced
from $F_1$ plants (Choo and Reinbergs, unpublished), and that the nature of addi-
tive epistasis, if present, can be revealed by studying the skewness of a biparental
doubled-haploid population (Choo and Reinbergs, unpublished). If doubled hap-
loids are derived from a diallel set of crosses, estimates of both additive and additive $\times$ additive genetic variances can be obtained; in addition, the mean and

1 Contribution No. 457 from Agriculture Canada Research Station, Charlottetown, Prince Edward Island, Canada C1A 7M8.

variance of recombination values can also be estimated from the diallel (Choo 1981).

When diallel crosses are used for estimating genetic variances and parameters of recombination values, the numbers of parental lines used in diallel crosses and of doubled-haploid lines produced from each crosses could be limited by the availability of the experimenter’s resources. Both would introduce sampling errors that may seriously affect the accuracy of the estimates of genetic variances and parameters of recombination values. This is further complicated by the fact that genes in the parents may not be at equilibrium. The present paper reports an approach that is simpler and requires less labor than the diallel for studying the inheritance of quantitative characters. The optimum segregating generation for the production of doubled haploids from a cross of two parents is also discussed.

Estimation of genetic variances

Additive and additive × additive variances: Suppose that two diploid inbred parents differing in two genes, A–a and B–b, are crossed, nine different genotypic classes with one having two linkage phases can be obtained in the F₂ generation, as given in Table 1. Using a haploid-production technique (see KASHA 1974), haploids can be extracted from F₂ plants. These haploids are then used to produce doubled haploids by doubling the chromosomes. For simply inherited characters, JOHNS (1974) observed that doubled-haploid lines of barley represent random samples of gametes from F₂ plants. Based on the assumption of random gametes, it is thus possible to calculate the expected frequencies of different doubled-haploid families produced from each genotypic class in the F₂ generation (Table 1).

Let m be a constant depending on the action of genes not under consideration, $d_a$ and $d_b$ be half of the differences between AA–aa and BB–bb homozygotes, respectively, and $i$ be the homozygote × homozygote interaction. These four parameters are defined as:

\[
\begin{align*}
    m &= \frac{(AA BB + AA bb + aa BB + aa bb)}{4} \\
    d_a &= \frac{(AA BB + AA bb - aa BB - aa bb)}{4} \\
    d_b &= \frac{(AA BB - AA bb + aa BB - aa bb)}{4} \\
    i &= \frac{(AA BB - AA bb - aa BB + aa bb)}{4}.
\end{align*}
\]

They, in turn, are used to describe the genotypic values of the four kinds of doubled haploids; symbolically,

\[
\begin{align*}
    AA BB &= m + d_a + d_b + i \\
    AA bb &= m + d_a - d_b - i \\
    aa BB &= m - d_a + d_b - i \\
    aa bb &= m - d_a - d_b + i.
\end{align*}
\]

Given the expected frequencies and the genotypic values of doubled-haploid families from F₂ plants, the total variance of doubled-haploid progeny ($\sigma^2_{F₂, DH}$) can be obtained as

\[
\sigma^2_{F₂, DH} = d_a^2 + d_b^2 + i^2 \pm 2(1-r)(1-2r)d_ad_b - (1-r)^2(1-2r)^2i^2,
\]

where the upper sign of the “±” applies to a cross of two associated parents ($AA BB \pm aa bb$), the lower sign applies to a cross of two dispersed parents.
TABLE 1

Frequencies and phenotypic means of ten doubled-haploid (DH) families produced from F2 plants of a cross of two associated parents (AA BB x aa bb)

<table>
<thead>
<tr>
<th>F2 family</th>
<th>Frequency*</th>
<th>DH family</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>AA BB</td>
<td>( \frac{(1-r)^2}{4} ) AA BB</td>
<td>( d_a + d_b + i )</td>
<td></td>
</tr>
<tr>
<td>AA Bb</td>
<td>( \frac{r(1-r)}{2} \left( \frac{1}{2} AA BB + \frac{1}{2} AA bb \right) )</td>
<td>( d_a )</td>
<td></td>
</tr>
<tr>
<td>AA bb</td>
<td>( \frac{r^2}{4} ) AA bb</td>
<td>( d_a - d_b - i )</td>
<td></td>
</tr>
<tr>
<td>Aa BB</td>
<td>( \frac{r(1-r)}{2} \left( \frac{1}{2} AA BB + \frac{1}{2} aa BB \right) )</td>
<td>( d_b )</td>
<td></td>
</tr>
<tr>
<td>Aa Bb</td>
<td>( \frac{(1-r)^2}{2} \left( \frac{1-r}{2} AA BB + \frac{1}{2} aa BB + \frac{r}{2} AA bb + \frac{r}{2} aa BB \right) )</td>
<td>((1-2r)i)</td>
<td></td>
</tr>
<tr>
<td>Aa bb</td>
<td>( \frac{r^2}{2} \left( \frac{r}{2} AA BB + \frac{1}{2} r aa bb + \frac{1-r}{2} AA bb + \frac{1-r}{2} aa BB \right) )</td>
<td>((1-2r)i)</td>
<td></td>
</tr>
<tr>
<td>aa BB</td>
<td>( \frac{r^2}{4} ) aa BB</td>
<td>(-d_a + d_b - i)</td>
<td></td>
</tr>
<tr>
<td>aa Bb</td>
<td>( \frac{r(1-r)}{2} \left( \frac{1}{2} aa BB + \frac{1}{2} aa bb \right) )</td>
<td>(-d_a)</td>
<td></td>
</tr>
<tr>
<td>aa bb</td>
<td>( \frac{(1-r)^2}{4} ) aa bb</td>
<td>(-d_a - d_b + i)</td>
<td></td>
</tr>
</tbody>
</table>

* \( r \) is the recombination value. Mean of all DH progeny = \((1-3r+2r^2)i\).

\((AA bb \times aa BB)\) and \(r\) is the recombination value. (Hereafter, the double sign with the same application will be used).

This variance can be partitioned into two components; namely, variance among F2-derived doubled-haploid families (\(\sigma_{BF,DH}^2\)) and variance within F2-derived doubled-haploid families (\(\sigma_{WF,DH}^2\)). Mathematically, the two variance components can be expressed as:

\[
\sigma_{BF,DH}^2 = \frac{1}{2} d_a^2 + \frac{1}{2} d_b^2 \pm \left(1 - 2r\right) d_a d_b + r \left(2 - 5r + 4r^2\right) i^2
\]

\[
\sigma_{WF,DH}^2 = \frac{1}{2} d_a^2 + \frac{1}{2} d_b^2 \pm \left(1 - 2r\right)^2 d_a d_b + 4r \left(1 - r\right) \left(1 - r + r^2\right) i^2.
\]

In this paper, additive genetic variance (\(\sigma_A^2\)) is defined as the summation of variances due to additive effects, e.g., \(\sigma_A^2 = d_a^2 + d_b^2\), and additive \times\ additive genetic variance (\(\sigma_{AA}^2\)) as the summation of variances due to homozygote \times\ homozygote interaction, e.g., \(\sigma_{AA}^2 = i^2\), in a two-locus system. In the absence of linkage \((r = 0.5)\), the above three equations in a multiple-locus system can be written as
\[
\sigma^2_{\text{DF,DH}} = \sigma_A^2 + \sigma_{\text{AA}}^2
\]
\[
\sigma^2_{\text{BF,DH}} = \frac{1}{2} \sigma_A^2 + \frac{1}{4} \sigma_{\text{AA}}^2
\]
\[
\sigma^2_{\text{WP,DH}} = \frac{1}{2} \sigma_A^2 + \frac{3}{4} \sigma_{\text{AA}}^2
\]

Therefore, both \(\sigma_A^2\) and \(\sigma_{\text{AA}}^2\) can be estimated by simultaneously solving any two of the three equations.

Suppose \(v\) doubled haploids are produced from each of \(F_2\) plants and the total number, i.e., \(v\) times the number \((f)\) of \(F_2\) plants, of double haploids are evaluated in a completely randomized block layout with \(r_1\) replications. The analysis of variance and the expected mean squares for these doubled haploids are outlined in Table 2. It is clear that

\[
\hat{\sigma}^2_{\text{BP,DH}} = \frac{1}{r_1v} (\text{MS}_b - \text{MS}_e)
\]
\[
\hat{\sigma}^2_{\text{WP,DH}} = \frac{1}{r_1} (\text{MS}_w - \text{MS}_e)
\]

where the "hat" (\(\hat{\cdot}\)) denotes "estimate of." Hence,

\[
\hat{\sigma}^2_A = 3 \hat{\sigma}^2_{\text{BP,DH}} - \hat{\sigma}^2_{\text{WP,DH}} = \frac{3}{r_1v} (\text{MS}_b - \text{MS}_w) - \frac{1}{r_1} (\text{MS}_w - \text{MS}_e)
\]
\[
\hat{\sigma}^2_{\text{AA}} = 2 (\hat{\sigma}^2_{\text{WP,DH}} - \hat{\sigma}^2_{\text{BP,DH}}) = \frac{2}{r_1} (\text{MS}_w - \text{MS}_e) - \frac{2}{r_1v} (\text{MS}_b - \text{MS}_w)
\]

To obtain sampling variances of these estimates, it is necessary to make some assumptions about the distribution of doubled-haploid effects and environmental deviations. If they are normally distributed, then the sampling variance of any mean square can be shown to be \(2(\text{MS})^2/(\text{df} + 2)\), where \(\text{MS}\) is the average value of the mean square in question and \(\text{df}\) is the corresponding degrees of freedom. Therefore, the sampling variance of \(\hat{\sigma}_A\) or \(\hat{\sigma}_{\text{AA}}^2\) can be obtained by finding the variance of a linear function of the appropriate mean squares (Crump 1946).

The sampling variances of \(\hat{\sigma}_A^2\) and \(\hat{\sigma}_{\text{AA}}^2\) are relatively large, and both are dependent upon variables \(f, v\) and \(r_1\). The effects of the three variables on the size of

TABLE 2

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Mean square</th>
<th>Expected mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replications</td>
<td>(r_1 - 1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Doubled haploids</td>
<td>(fv - 1)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between families</td>
<td>(f - 1)</td>
<td>(\text{MS}_b)</td>
<td>(r_1 v \sigma^2_{\text{BP,DH}} + r_1 \sigma^2_{\text{WP,DH}} + \sigma_e^2)</td>
</tr>
<tr>
<td>Within families</td>
<td>(f(v - 1))</td>
<td>(\text{MS}_w)</td>
<td>(r_1 \sigma^2_{\text{WP,DH}} + \sigma_e^2)</td>
</tr>
<tr>
<td>Error</td>
<td>((r_1 - 1) (fv - 1))</td>
<td>(\text{MS}_e)</td>
<td>(\sigma_e^2)</td>
</tr>
</tbody>
</table>
sampling variances are illustrated by using two hypothetical populations. Suppose that two doubled-haploid populations, one with $\sigma^2_A = 10$ and $\sigma^2_{AA} = 20$ and the other with $\sigma^2_A = 20$ and $\sigma^2_{AA} = 10$, are evaluated in a field plot with an environmental variance ($\sigma^2_e$) of 70. The sampling standard errors of $\hat{\sigma}^2_A$ and $\hat{\sigma}^2_{AA}$ for the two populations under various numbers of $f$, $v$ and $r$, can be easily calculated. In both populations, variables $f$ and $v$ have a greater effect than number of replications ($r_i$) in terms of reduction of the sampling standard errors. Increasing both $f$ and $v$ may result in a decrease of sampling errors. But for a fixed number of doubled haploids, sampling errors decrease with increasing $f$ and decreasing $v$, and the smallest sampling errors do not necessarily occur in the population in which $v = 2$, suggesting that there is an optimum combination of $f$ and $v$ for the smallest sampling errors in a fixed number of doubled haploids. With a sample size as large as 300 doubled haploids, only the larger variances, i.e., either $\sigma^2_A$ or $\sigma^2_{AA}$, is greater than twice its sampling error. Therefore, a large sample size is needed in order to detect additive and additive $\times$ additive genetic variances by the analysis of variance.

**Dominance variance:** Dominance variance can be estimated also if $F_2$ plants are included along with an $F_2$-derived doubled-haploid population in the test trial. Assuming that the recombination value ($r$) is equal to 0.5, MATHER and JINKS (1971) showed that variance of $F_2$ in a two-locus system is as follows:

$$\sigma^2_{F_2} = \frac{1}{2} \left( d_a + \frac{1}{2} j \right)^2 + \frac{1}{2} \left( d_b + \frac{1}{2} k \right)^2 + \frac{1}{4} \left( h_a + \frac{1}{2} l \right)^2 + \frac{1}{4} \left( h_b + \frac{1}{2} l \right)^2 + \frac{1}{4} \left( h_a \frac{1}{2} + l \right)^2 + \frac{1}{4} \left( h_b + \frac{1}{2} l \right)^2 + \frac{1}{4} \left( h_a + \frac{1}{2} l \right)^2 +$$

$$+ \frac{1}{4} i^2 + \frac{1}{8} (j^2 + k^2) + \frac{1}{16} P_2 ,$$

where $h_a$, $h_b$ are the effects of dominance at the two loci, $j$, $k$ are the homozygote $\times$ heterozygote interactions, respectively, and $l$ is the heterozygote $\times$ heterozygote interaction. By subtracting $\sigma^2_{F_2, DH}$ from $\sigma^2_{F_2}$, the remainder,

$$\frac{1}{4} \left( h_a + \frac{1}{2} l \right)^2 + \frac{1}{4} \left( h_b + \frac{1}{2} l \right)^2 + \frac{1}{4} (j^2 + k^2) + \frac{1}{16} P_2 + \frac{1}{2} (d_{aj} + d_{bk}) ,$$

is essentially the sum of dominance effects, homozygote $\times$ heterozygote and heterozygote $\times$ heterozygote interaction. We define dominance variance as the summation of variances due to dominance effects, e.g., $\sigma^2_d = h_a^2 + h_b^2$, and then the remainder becomes $\frac{1}{4} \sigma^2_d$ when $j = k = l = 0$.

$F_2$ diploid and $F_2$-derived doubled-haploid populations may be evaluated in a split-plot experiment with populations as main plot units and individual plants as subplot units. The presence of dominance effects is clearly indicated if the between-populations mean square is greater than the error $b$ mean square (Table 3). An estimate of dominance variance and its sampling variance can be obtained in the conventional manner (assuming that $j$, $k$ and $l$ are negligible).
TABLE 3

Analysis of variance for F<sub>1</sub> diploid and F<sub>1</sub>-derived doubled-haploid populations

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Mean square</th>
<th>Expected mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replications</td>
<td>r&lt;sub&gt;1&lt;/sub&gt;-1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between populations</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Error a</td>
<td>r&lt;sub&gt;1&lt;/sub&gt;-1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Diploid population</td>
<td>n-1</td>
<td>MS&lt;sub&gt;f&lt;/sub&gt;</td>
<td>r&lt;sub&gt;1&lt;/sub&gt; σ&lt;sub&gt;f&lt;/sub&gt;&lt;sup&gt;2&lt;/sup&gt; + σ&lt;sub&gt;e&lt;/sub&gt;&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td>DH population</td>
<td>fυ-1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between families</td>
<td>f-1</td>
<td>MS&lt;sub&gt;b&lt;/sub&gt;</td>
<td>r&lt;sub&gt;1&lt;/sub&gt; υ σ&lt;sub&gt;b&lt;/sub&gt;&lt;sup&gt;2&lt;/sup&gt; + r&lt;sub&gt;1&lt;/sub&gt; σ&lt;sub&gt;w&lt;/sub&gt;&lt;sup&gt;2&lt;/sup&gt; + σ&lt;sub&gt;e&lt;/sub&gt;&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td>Within families</td>
<td>f(ν-1)</td>
<td>MS&lt;sub&gt;ω&lt;/sub&gt;</td>
<td>r&lt;sub&gt;2&lt;/sub&gt; σ&lt;sub&gt;ω&lt;/sub&gt;&lt;sup&gt;2&lt;/sup&gt; + σ&lt;sub&gt;e&lt;/sub&gt;&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
<tr>
<td>Error b</td>
<td>(r&lt;sub&gt;2&lt;/sub&gt;-1)(n+υ-2)</td>
<td>MS&lt;sub&gt;e&lt;/sub&gt;</td>
<td>σ&lt;sub&gt;e&lt;/sub&gt;&lt;sup&gt;2&lt;/sup&gt;</td>
</tr>
</tbody>
</table>

Types of gene action

FISHER, IMMER and TEDIN (1932) showed that, for a one-locus system, the skewness of the frequency distribution of F<sub>2</sub> plants is equal to \(-\frac{3}{4} h d^2\). Assuming no epistasis and no linkage, the skewness of F<sub>2</sub> plants in a multiple-locus system is simply the sum of \(-\frac{3}{4} h d^2\) terms of each locus. Thus, one can determine whether the average \( h \) is positive or negative by studying the skewness of the frequency distribution of F<sub>2</sub> plants. Positive average \( h \) makes the frequency distribution skewed to the left, indicating that desirable alleles are dominant. On the other hand, negative average \( h \) produces rightward skewness with the undesirable alleles being dominant.

The skewness of the frequency distribution of a doubled-haploid population derived from F<sub>2</sub> plants in a two-locus system can be shown as

\[
K_{SP,DH} = 6 id_a d_b - 6q^2 id_a d_b + 2q(1-q^2) i^2 = 6 id_a d_b \text{ if } r = 0.5 ,
\]

where \( q = (1 - 3r + 2r^2) \).

When there is no additive epistasis, \( K_{SP,DH} \) is equal to zero, but is greater than or smaller than zero in the presence of complementary or duplicate interaction, respectively.

Degree of gene action

COMSTOCK and ROBINSON (1948) presented a method for estimating the degree of dominance. Their method may be modified for use in the doubled haploid materials. Assuming that all \( j, k \) and \( l \) are negligible, an estimate of the degree of dominance ("\( h \)") may be obtained by

\[
\left[ 4(\hat{\sigma}_p^2 - \hat{\sigma}_v^2) \right]^{1/2} \left[ 3 \hat{\sigma}_p^2 - \hat{\sigma}_v^2 \right]^{1/4} = \left[ \hat{\sigma}_p^2 \right]^{1/2} \left[ \hat{\sigma}_v^2 \right] = "h".
\]

If the estimate of "\( h \)" is significantly greater than unity, then there is over-dominance of genes at one or more loci. If it is significantly smaller than unity,
there is partial dominance of genes at one or more loci. When \( h \) is unity, complete dominance of genes are present. A significance test for the deviation of \( h \) from any hypothetical value is not available at the present time.

An estimate of the degree of additive epistasis (\( \hat{e} \)) can be obtained by the following relation:

\[
\left[ \frac{2(\hat{\sigma}_w^2 - \hat{\sigma}_b^2)}{3 \hat{\sigma}_b^2 - \hat{\sigma}_w^2} \right]^{1/2} = \left[ \frac{\hat{\sigma}_{AA}^2}{\hat{\sigma}_A^2} \right]^{1/2} = \hat{e}
\]

The estimate, \( \hat{e} \) is equal to unity when there is complete additive \( \times \) additive gene interaction, but in the presence of super- or partial interactions, it is greater or smaller than unity, respectively. The procedure suggested by W. G. Cochran and outlined in Comstock and Robinson (1948) may be used for tests of significance for the deviation of \( \hat{e} \) from any hypothetical value. We use the analysis of variance in Table 2 for illustration. The expected value of \( MS_w' \) assuming a specific value of \( e \), can be calculated by using the following equation:

\[
MS_w' = \frac{\left( \frac{3e^2 + 2}{e^2 + 2} \right)}{\frac{3e^2 + 2}{e^2 + 2} + \nu} \cdot \frac{\nu}{\left( \frac{3e^2 + 2}{e^2 + 2} + \nu \right)} \cdot MS_e
\]

\[
= C_1 MS_b + C_2 MS_e
\]

The degrees of freedom for \( MS_w' \) are

\[
= \frac{(C_1 MS_b + C_2 MS_e)^2}{C_1^2 MS_b^2 + C_2^2 MS_e^2} \cdot \frac{(f-1)}{(r_1-1)(fv-1)}
\]

(see Comstock and Robinson 1948).

An approximate \( F \) test can be used to compare \( MS_w' \) with the \( MS_w \) obtained from the analysis of variance table.

**Detection of linkage**

Two doubled-haploid populations from plants in different generations are needed in order to detect linkage. One way to detect linkage is to produce doubled haploids from both \( F_1 \) and \( F_2 \) plants and then to compare the mean, variance and skewness of the two populations. The mean (\( U_{F_1, DH} \)), variance (\( \sigma_{F_1, DH}^2 \)) and skewness (\( K_{F_1, DH} \)) of an \( F_1 \)-derived doubled-haploid population in a two-locus system are

\[
U_{F_1, DH} = m \pm \rho i
\]

\[
\sigma_{F_1, DH}^2 = d_a^2 + d_b^2 + i^2 \pm 2\rho d_a d_b - \rho^2 i^2
\]

\[
K_{F_1, DH} = 6 id_a d_b - 6\rho^2 id_a d_b + 2\rho (1-\rho^2) i^3,
\]

where \( \rho = 1 - 2r \)
In comparison, the mean \((U_{F,DH})\), variance and skewness of an \(F_2\)-derived population are

\[
U_{F,DH} = m \pm qi^2
\]

\[
\sigma^2_{F,DH} = d_a^2 + d_b^2 + i^2 \pm 2qd_a d_b - q^2 i^2
\]

\[
K_{3F,DH} = 6 i d_a d_b - 6q^2 i d_a d_b \pm 2q (1-q^2) i^2
\]

where \(q = (1-r)(1-2r)\).

Therefore, if linkage is present, \(U_{F,DH} \neq U_{F,DH}\) unless \(i = 0\), \(\sigma^2_{F,DH} \neq \sigma^2_{F,DH}\) for any value of \(i\) and \(K_{3F,DH} \neq K_{3F,DH}\) unless \(i = 0\). In contrast, at \(r = 0.5\) or \(r = 0.0\), \(U_{F,DH} = U_{F,DH}\), \(\sigma^2_{F,DH} = \sigma^2_{F,DH}\), and \(K_{3F,DH} = K_{3F,DH}\) even in the presence of additive epistasis.

Suppose that an \(F_1\)-derived doubled-haploid population with a sample size of \(n_1\) and an \(F_2\)-derived population with a sample size of \(n_2\) are evaluated in a split-plot experiment. The appropriate analysis of variance for this experiment is given in Table 4. If the between-populations mean square is significantly greater than the error \(b\) mean square, as evidenced by an F test, then the \(F_1\) population mean differs from the \(F_2\) population mean. Similarly, if the \(F_1\) population mean square is not equal to the \(F_2\) population mean square as shown by an F test, then the two mean squares are not homogeneous. The inequalities suggest that linkage is present between genes. It should be noted that tests on variances, such as the F test, are very sensitive to departures from normality and that doubled-haploid effects are not normally distributed except where additive epistasis is absent and the number of genes controlling the quantitative character under study exceeds 100 (Choo and Reinbergs, unpublished). In view of this, it may be desirable to transform the data into normally distributed variates first and then proceed with the analysis of variance. Tests robust to nonnormality (Games, Keselman and Clinch 1979) should perhaps be used to compare the two variances.

The frequency distribution of the two populations may also be compared by means of nonparametric tests, for example, the Mann-Whitney \(U\) test, Kolmogorov-Smirnov two-sample test and Wald-Wolfowitz runs test (Siegel 1956). These nonparametric tests are sensitive to any kind of difference in the distributions, such as difference in mean, in variance, in skewness, etc. In the ab-

---

**TABLE 4**

Analysis of variance for \(F_1\)- and \(F_2\)-derived doubled-haploid populations

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Mean square</th>
</tr>
</thead>
<tbody>
<tr>
<td>Replications</td>
<td>(r_1-1)</td>
<td>(MS_1)</td>
</tr>
<tr>
<td>Between populations</td>
<td>(1)</td>
<td>(MS_2)</td>
</tr>
<tr>
<td>Error (a)</td>
<td>(r_3-1)</td>
<td>(MS_3)</td>
</tr>
<tr>
<td>(F_1) population</td>
<td>(n'_1-1)</td>
<td>(MS_4)</td>
</tr>
<tr>
<td>(F_2) population</td>
<td>(n'_2-1)</td>
<td>(MS_5)</td>
</tr>
<tr>
<td>Error (b)</td>
<td>((r_1-1)(n'_1+n'_2-2))</td>
<td>(MS_6)</td>
</tr>
</tbody>
</table>
sence of linkage, the frequency distribution of the two populations are expected to be similar.

*Estimation of average recombination value*

*Without additive epistasis:* As mentioned earlier, the presence or absence of additive epistasis can be determined by studying the skewness \( (K_{sp, DH}) \) of the frequency distribution of doubled haploids. The finding based on the analysis of skewness may be further substantiated by studying the kurtosis of the frequency distribution of doubled haploids; the distribution of doubled haploids is leptokurtic only in the presence of additive epistasis, and it is always platykurtic or mesokurtic when additive epistasis is absent (Choo and Reinbergs, unpublished). If additive epistasis is found to be absent according to the analysis of skewness and kurtosis, then the variances among and within \( F_2 \)-derived doubled-haploid families become

\[
\sigma_{BF, DH}^2 = \frac{1}{2} d_a^2 + \frac{1}{2} d_b^2 \pm (1-2r) d_a d_b \\
\sigma_{WF, DH}^2 = \frac{1}{2} d_a^2 + \frac{1}{2} d_b^2 \pm (1-2r)^2 d_a d_b .
\]

Thus, \( \sigma_{BF, DH}^2 \) is greater than \( \sigma_{WF, DH}^2 \) in the doubled-haploid population derived from a cross of two associated parents. The relationship reverses for the doubled-haploid population derived from a cross of two dispersed parents. The two variances are equal at \( r = 0.5 \) or \( r = 0.0 \). As a result, a comparison of the two variances provides indications of the parental configuration and the presence or absence of linkage. The estimates of the two variances can be obtained from the analysis of variance table (Table 2). When the two parents are also included in the evaluation trial, then data from the trial provide another statistic: namely, the variance of the parents

\[
\sigma_p^2 = d_a^2 + d_b^2 \pm 2d_a d_b .
\]

Thus,

\[
\sigma_{BF, DH}^2 - \frac{1}{2} \sigma_p^2 = \mp 2r d_a d_b \\
\sigma_{WF, DH}^2 - \frac{1}{2} \sigma_p^2 = \mp 4r d_a d_b \pm 4r^2 d_a d_b .
\]

Again \( \sigma_{BF, DH}^2, \sigma_{WF, DH}^2 \) and \( \sigma_p^2 \) are estimated from the analysis of variance.

If \( \sigma_{BF, DH}^2 - \frac{1}{2} \sigma_p^2 \) or \( \sigma_{WF, DH}^2 - \frac{1}{2} \sigma_p^2 \) are significantly greater than their respective sampling errors, then linkage is present between loci. In such a case, a weighted mean of recombination values \( \langle \tilde{r} \rangle \) may be obtained in the following manner:

\[
\frac{\sigma_{WF, DH}^2 - 2 \sigma_{BF, DH}^2 + \frac{1}{2} \sigma_p^2}{2 \sigma_{BF, DH}^2 - \sigma_p^2} = \frac{r^2 d_a d_b}{r d_a d_b} = \tilde{r}
\]
With additive epistasis: In the presence of additive epistasis, a weighted mean of recombination values may be estimated by generating doubled haploids from two backcrosses. Again, a two-locus system is used to illustrate the backcross approach for estimating means of recombination values. In backcrossing the F₁ to the AA BB parent, four genotypic classes: AA BB, Aa Bb, AA Bb and Aa BB can be found in the backcross generation (B₁). The other backcross (B₂) produces four other genotypic classes: Aa Bb, aa bb, Aa bb and aa Bb. Doubled haploids are derived from plants of the two backcrosses (Table 5).

Variance among (\(\sigma_{BB, DH}^2\)) and within (\(\sigma_{WB, DH}^2\)) doubled-haploid families for B₁ backcross can be shown to be

\[
\sigma_{BB, DH}^2 = \frac{1}{4} \left[ d_a \pm 2r(1-r)i \right]^2 + \frac{1}{4} \left[ d_b + 2r(1-r)i \right]^2 \\
\pm \frac{1}{2} (1-2r) d_a d_b + r(1-r)(1-3r + 3r^2) i^2
\]

and

\[
\sigma_{WB, DH}^2 = \frac{1}{2} (d_a \pm ri)^2 + \frac{1}{2} (d_b + ri)^2 \pm (1-r)(1-2r) d_a d_b \\
+ r(3-5r + 2r^2) i^2.
\]

**Table 5**

<table>
<thead>
<tr>
<th>Backcross family</th>
<th>Frequency*</th>
<th>DH family</th>
<th>Mean</th>
</tr>
</thead>
<tbody>
<tr>
<td>B₁: (AA BB × aa bb) × AA BB</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AA BB</td>
<td>((1-r)/2)</td>
<td>AA BB</td>
<td>(d_a + d_b + i)</td>
</tr>
<tr>
<td>Aa Bb</td>
<td>((1-r)/2)</td>
<td>(\frac{1-r}{2} AA BB \pm \frac{1-r}{2} aa bb + \frac{r}{2} AA bb + \frac{r}{2} aa BB)</td>
<td>((1-2r)i)</td>
</tr>
<tr>
<td>AA Bb</td>
<td>(r/2)</td>
<td>(\frac{1}{2} AA BB + \frac{1}{2} AA BB)</td>
<td>(d_a)</td>
</tr>
<tr>
<td>Aa BB</td>
<td>(r/2)</td>
<td>(\frac{1}{2} AA BB + \frac{1}{2} aa BB)</td>
<td>(d_b)</td>
</tr>
<tr>
<td>B₂: (AA BB × aa bb) × aa bb</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Aa Bb</td>
<td>((1-r)/2)</td>
<td>aa bb</td>
<td>(-d_a - d_b + i)</td>
</tr>
<tr>
<td>aa bb</td>
<td>((1-r)/2)</td>
<td>aa bb</td>
<td>(-d_b)</td>
</tr>
<tr>
<td>Aa bb</td>
<td>(r/2)</td>
<td>(\frac{1}{2} AA bb + \frac{1}{2} aa bb)</td>
<td>(-d_a)</td>
</tr>
<tr>
<td>aa Bb</td>
<td>(r/2)</td>
<td>(\frac{1}{2} aa BB + \frac{1}{2} aa bb)</td>
<td>(-d_a)</td>
</tr>
</tbody>
</table>

* \(r\) is the recombination value. Mean of B₁ = \(\frac{1}{2} d_a + \frac{1}{2} d_b + (1-r)^2 i\). Mean of B₂ = \(-\frac{1}{2} d_a - \frac{1}{2} d_b + (1-r)^2 i\).
DOUBLED HAPLOIDS

The corresponding variances for \( B_2 \) backcross are

\[
\sigma^2_{BB, DH} = \frac{1}{4} \left[ (d_a - 2r(1-r)i)^2 + (d_b - 2r(1-r)i)^2 \right] + \frac{1}{2} \left[ (1-2r)d_a d_b + r(1-r)(1-3r + 3r^2)i^2 \right]
\]

\[
\sigma^2_{WB, DH} = \frac{1}{2} (d_a + ri)^2 + \frac{1}{2} (d_b - ri)^2 + (1-r)(1-2r)d_a d_b + r(3-5r + 2r^2)i^2.
\]

Then

\[
\sigma^2_{BB, DH} - \sigma^2_{BB, DH} = \pm 2r(1-r)id_a + 2r(1-r)id_b
\]

\[
\sigma^2_{WB, DH} - \sigma^2_{WB, DH} = \pm 2rid_a + 2rid_b.
\]

Subsequently,

\[
1 - \frac{\sigma^2_{BB, DH} - \sigma^2_{BB, DH}}{\sigma^2_{WB, DH} - \sigma^2_{WB, DH}} = \frac{2r^2 (\pm id_a + id_b)}{2r (\pm id_a + id_b)} = r.
\]

Extending this to a multiple-locus system,

\[
\Sigma r^2_{ij} (\pm i_{ij} d_i + i_{ij} d_j)
\]

\[
r = \frac{\Sigma r^2_{ij} (\pm i_{ij} d_i + i_{ij} d_j)}{\Sigma r^2_{ij} (\pm i_{ij} d_i + i_{ij} d_j)}.
\]

It should be noted that the weighted mean of recombination values can be so obtained only when additive epistasis is present and it includes the recombination values of interacting genes, but not those of noninteracting genes.

When doubled haploids are evaluated in a split-plot experiment with backcrosses as main plot units and doubled haploids within each backcross as subplot units (Table 6), the estimates of \( \hat{\sigma}^2_{BB, DH} \) and \( \hat{\sigma}^2_{WB, DH} \) can be obtained as

\[
\hat{\sigma}^2_{BB, DH} = \frac{1}{r_1 v_1} (MS_{b1} - MS_{w1})
\]

\[
\hat{\sigma}^2_{WB, DH} = \frac{1}{r_1} (MS_{w1} - MS_{e}).
\]

<table>
<thead>
<tr>
<th>Table 6</th>
<th>Analysis of variance for doubled-haploid populations derived from two backcrosses</th>
</tr>
</thead>
<tbody>
<tr>
<td>Source</td>
<td>df</td>
</tr>
<tr>
<td>Replications</td>
<td>( r_1 - 1 )</td>
</tr>
<tr>
<td>Between populations</td>
<td>1</td>
</tr>
<tr>
<td>Error a</td>
<td>( r_1 - 1 )</td>
</tr>
<tr>
<td>( B_1 ) population ( b_1 v_1 - 1 )</td>
<td></td>
</tr>
<tr>
<td>Between families</td>
<td>( b_1 - 1 )</td>
</tr>
<tr>
<td>Within families</td>
<td>( b_1 (v_1 - 1) )</td>
</tr>
<tr>
<td>( B_2 ) population ( b_2 v_2 - 1 )</td>
<td></td>
</tr>
<tr>
<td>Between families</td>
<td>( b_2 - 1 )</td>
</tr>
<tr>
<td>Within families</td>
<td>( b_2 (v_2 - 1) )</td>
</tr>
<tr>
<td>Error b</td>
<td>( (r_1 - 1) (b_1 v_1 + b_2 v_2 - 2) )</td>
</tr>
</tbody>
</table>
Likewise, the estimates of $\sigma_{\text{BB,PH}}^2$ and $\sigma_{\text{WB,PH}}^2$ can be obtained as

$$\hat{\sigma}_{\text{BB,PH}}^2 = \frac{1}{r_1 V_1} (\text{MS}_{b_2} - \text{MS}_{e_2})$$

$$\hat{\sigma}_{\text{WB,PH}}^2 = \frac{1}{r_1} (\text{MS}_{e_2} - \text{MS}_e) .$$

The presence of linkage is confirmed if $\hat{\sigma}_{\text{BB,PH}}^2 - \hat{\sigma}_{\text{WB,PH}}^2$ or $\hat{\sigma}_{\text{WB,PH}}^2 - \hat{\sigma}_{\text{WB,PH}}^2$ is significantly greater than their respective sampling errors.

In the absence of additive epistasis,

$$2 \sigma_{\text{BB,PH}}^2 - \sigma_{\text{WB,PH}}^2 = 2 \sigma_{\text{BB,PH}}^2 - \sigma_{\text{WB,PH}}^2 = \pm r (1 - 2r) d_a d_b .$$

Thus, in the absence of gene interaction, the above relationship can provide us indications of the parental configuration and of the presence or absence of linkage. Further, a weighted mean of recombination values can be estimated from the equations of $\sigma_{\text{BB,PH}}^2$, $\sigma_{\text{BB,PH}}^2$, and $\sigma_{\text{WB,PH}}^2$, or of $\sigma_{\text{WB,PH}}^2$, $\sigma_{\text{BB,PH}}^2$, and $\sigma_{\text{WB,PH}}^2$.

When linkage is absent, additive and additive x additive variances may be estimated from either of the two backcrosses. If $\sigma_{A(i)}^2$ is the summation of effects of $(d \pm \frac{1}{2} i)$, then in a multiple-locus system,

$$\sigma_{\text{BB,PH}}^2 = \frac{1}{4} \sigma_{A(i)}^2 + \frac{1}{16} \sigma_{AA}^2$$

$$\sigma_{\text{WB,PH}}^2 = \frac{1}{2} \sigma_{A(i)}^2 + \frac{1}{2} \sigma_{AA}^2 .$$

Thus,

$$\sigma_{A(i)}^2 = \frac{16}{3} \sigma_{\text{BB,PH}}^2 - \frac{2}{3} \sigma_{\text{WB,PH}}^2$$

$$\sigma_{AA}^2 = \frac{8}{3} \sigma_{\text{WB,PH}}^2 - \frac{16}{3} \sigma_{\text{BB,PH}}^2$$

and

$$\hat{\sigma}_{A(i)}^2 = \frac{16}{3 r_1} (\text{MS}_{m_2} - \text{MS}_e) - \frac{2}{3 r_1 V_1} (\text{MS}_{b_1} - \text{MS}_{m_1})$$

$$\hat{\sigma}_{AA}^2 = \frac{8}{3 r_1 V_1} (\text{MS}_{b_1} - \text{MS}_{e_1}) - \frac{16}{3 r_1} (\text{MS}_{e_1} - \text{MS}_e)$$

$$V(\hat{\sigma}_{A(i)}^2) = \frac{256}{9} V(\hat{\sigma}_{\text{BB,PH}}^2) + \frac{4}{9} V(\hat{\sigma}_{\text{WB,PH}}^2)$$

$$V(\hat{\sigma}_{AA}^2) = \frac{64}{9} V(\hat{\sigma}_{\text{WB,PH}}^2) + \frac{256}{9} V(\hat{\sigma}_{\text{BB,PH}}^2) .$$

As defined earlier, $\sigma_{A(i)}^2$ is composed of variances due to additive effects and variances due to gene interaction. The truly additive genetic variance, however, can be estimated if doubled haploids are derived from the two backcrosses. It can be shown that
\[ \sigma_{BB, DH}^2 + \sigma_{BB, DH}^2 = \frac{1}{2} \sigma_A^2 + \frac{3}{8} \sigma_{AA}^2 \]

\[ \sigma_{WB, DH}^2 + \sigma_{WB, DH}^2 = \sigma_A^2 + \frac{3}{2} \sigma_{AA}^2 \]

and

\[ \sigma_A^2 = 4(\sigma_{BB, DH}^2 + \sigma_{BB, DH}^2) - (\sigma_{WB, DH}^2 + \sigma_{WB, DH}^2) \]

Thus,

\[ \hat{\sigma}_A^2 = 4 \left[ \frac{1}{r_1 \nu_1} (MS_{b1} - MS_{a1}) + \frac{1}{r_2 \nu_2} (MS_{b2} - MS_{a2}) \right] - \]

\[ \left[ \frac{1}{r_1} (MS_{w1} - MS_e) + \frac{1}{r_2} (MS_{w2} - MS_e) \right] \]

\[ V(\hat{\sigma}_A^2) = 16V(\hat{\sigma}_{BB, DH}^2) + 16V(\hat{\sigma}_{BB, DH}^2) + V(\hat{\sigma}_{WB, DH}^2) + V(\hat{\sigma}_{WB, DH}^2) \]

Apparently, the sampling variances of \( \hat{\sigma}_A^2 \) and \( \hat{\sigma}_{AA}^2 \) are larger in the backcross approach than in the \( F_2 \) approach. Therefore, it is recommended that if estimation of genetic variances is the main objective of the experiment, then doubled haploids produced from \( F_2 \) plants instead from the backcrosses should be used.

It is not possible to obtain estimates of additive and additive \( \times \) additive genetic variances that are free from linkage effects by the backcross approach when linkage is present. However, they can be obtained using diallel crosses provided that genes in the parents are at linkage and Hardy-Weinberg equilibria and either of the following two conditions is true: (1) gene frequencies of one-half at each locus and no homozygote \( \times \) heterozygote interactions for all pairs of loci, and (2) no dominance at each locus and no homozygote \( \times \) heterozygote interactions and no heterozygote \( \times \) heterozygote interactions for all pairs of loci (Choo 1981).

**Estimation of the number of segregating genes**

Assuming equal genic effects, Choo and Reinbergs (unpublished) showed that the number of segregating genes pertinent to a quantitative character can be estimated by dividing the square of the deviation of the most extreme doubled haploid from the population mean by the genotypic variance of doubled haploids. They also determined that, with an \( F_1 \)-derived doubled-haploid population, the estimated number of genes obtained in such a way is biased in the presence of additive epistasis. Further, they found that, with linkage, the number is underestimated if doubled haploids are produced from a cross of two preponderantly associated parents, and it is overestimated if doubled haploids are produced from a cross of two preponderantly dispersed parents.

As shown earlier, additive variance can be estimated using doubled haploids derived from \( F_1 \) instead of \( F_2 \) plants. Thus, the number of segregating genes, which is obtained by dividing the square of the deviation of the most extreme doubled haploid by the additive variance, is less affected by additive epistasis under the no linkage condition. In the absence of additive epistasis, an indication of the parental configuration and linkage can be obtained, and this in turn can determine if the estimate is overestimated or underestimated because of linkage. Furthermore, the frequency of recombination is higher in an \( F_2 \)-derived population, illustrated later, and this increases the probability of obtaining the most
T. M. CHOO

extreme doubled haploid and thus increases the accuracy of the deviation. Therefore, to obtain a better estimate of the number of segregating genes, one should produce doubled haploids from $F_2$ rather than from $F_1$ plants.

DISCUSSION

When diploid materials are used for quantitative genetic studies, it is common to assume that linkage and epistasis are absent in the materials in order to interpret the experimental results of the studies. These unrealistic assumptions are no longer required when doubled haploids are used for studying quantitative inheritance. Furthermore, not only can epistasis and linkage be detected, but also the types and the amount of additive epistasis, as well as a weighted mean of recombination values, can be estimated. Knowledge of additive epistasis and linkage are of value in improving the efficiency of the conventional breeding methods. If additive epistasis is important, selection should not be too intensive in early stages of a breeding program in order to allow desirable epistatic combinations to come together; a large population size is needed when genes are tightly linked. Such knowledge is particularly useful for the doubled-haploid breeding method, since there is only one chance for recombination. In case of tight linkage and high additive epistasis, a large number of doubled haploids should be produced from $F_1$ plants for the sake of obtaining the best recombinant. The probability of obtaining the best recombinant can also be enhanced by producing doubled haploids from plants in later generations. The former approach requires more effort and facilities, but the latter requires longer time for producing doubled haploids. Therefore, the choice between the two approaches depends upon the availability of resources and the urgency of needs of the plant breeder.

For the latter approach, one would certainly wish to know the optimum stage at which doubled haploids are produced from a single cross. In practice, a plant breeder hybridizes two parental lines in the hope of obtaining an inbred line that combines most of the desirable alleles from the two parents. Therefore, genes of the parents are usually dispersed. Suppose that two parents, $AA bb$ and $aa BB$, are crossed, then the respective frequencies of the best recombinant ($AA BB$) in the $F_{1r}$, $F_{2r}$, and $F_3$-derived doubled-haploid populations can be shown to be $\frac{r}{2} \frac{1}{4}$ $(3r-2r^2)$ and $\frac{1}{8} (7r-8r^2 + 4r^3)$, respectively. Differences in the frequency of $AA BB$ in the three populations under various recombination values are illustrated in Figure 1. At $r = 0$ and $r = 0.5$, the three populations have the same frequency of $AA BB$. Thus, there is absolutely no need to delay the production of doubled haploids to the later generations. Both $F_{2r}$- and $F_3$-derived populations have a markedly higher frequency of $AA BB$ than the $F_{1r}$-derived population when recombination value is between 0 and 0.5. The $F_3$-derived population has only a slightly higher frequency of $AA BB$ than the $F_{2r}$-derived population, indicating that a delay from $F_2$ to $F_3$ for producing doubled haploids is not worthwhile. This implies that the doubled-haploid method using $F_2$ plants provides only slightly
less opportunity for recombination than the conventional breeding methods for self-pollinating crops.

The relative efficiency between F1-derived and F2-derived doubled-haploid populations can be measured in this way. Let \( n'_1 \) and \( n'_2 \) be the sizes of the former and latter populations, respectively. In order to obtain at least the same number of AA BB individuals as in the F2-derived population, \( n'_1 \) must be equal to \( \frac{3}{2} - r \) \( n'_2 \). For instance, at \( r = 0.04 \), a size of 100 (= \( n'_2 \)) is required to obtain 2.92 AA BB individuals in an F2-derived population produced from a cross of two dispersed parents. For an F1-derived population, 146 doubled haploids should be produced if one expects to obtain 2.92 AA BB individuals. An increase in the number of doubled haploids from F1 plants demands more input of manpower and facilities and, furthermore, increases the costs of seed and field tests. It is thus less desirable than using doubled haploids from F2 plants under the tight linkage conditions.

Few studies, if any, have been conducted to detect the linkage between quantitative characters. Until now, there has been no biometrical method proposed for estimating average recombination value. No information is thus available in the literature on average recombination value for quantitative traits. Information on the linkage of quantitative characters is useful for increasing the efficiency of doubled-haploid and other breeding methods. The methods given in this paper
for detecting linkage and for estimating average recombination value are un-
doubtedly of value for such studies.

The $F_2$-derived doubled-haploid population has a higher frequency of the best
recombinant than does the $F_1$-derived one when linkage is present. It is possible to
estimate additive and additive $\times$ additive genetic variances and provide a good
estimate of the number of segregating genes using $F_2$-derived doubled haploids.
This assists the breeder in developing effective breeding strategies and procedures.
Furthermore, selection efficiency can be increased by using index selection in an
$F_2$-derived doubled-haploid population. The selection index can be constructed
on the basis of the performance of both family and individual line.

The backcross approach for estimating average recombination value is simpler
and requires less labor than the diallel approach (Choo 1981). More importantly,
no major assumptions are needed as with the diallel approach. However, with the
backcross approach, the variation of recombination values cannot be measured.

The author is grateful to G. C. C. Tai, Research Station, Agriculture Canada, Fredericton,
New Brunswick, and the reviewers for their valuable suggestions and critical review on this
manuscript.

LITERATURE CITED


COMSTOCK, R. E. and H. F. ROBINSON, 1948 The components of genetic variance in populations
of biparental progenies and their use in estimating the average degrees of dominance.
Biometrics 4: 254-266.

Bull. 2: 7-11.

FISHER, R. A., F. R. IMMER and OLOF TEDIN, 1932 The genetical interpretation of statistics of
the third degree in the study of quantitative inheritance. Genetics 17: 107-124.

GAMES, P. A., H. J. KESELMAN and J. J. CLINCH, 1979 Tests for homogeneity of variance in


JOHNS, W. A., 1974 A preliminary evaluation of haploidy as a breeding technique in barley

KASHA, K. J. (ed.), 1974 Haploids in Higher Plants. The office of Continuing Education, Uni-
versity of Guelph, Guelph, Ontario.


N.Y.

Corresponding editor: B. S. WEIR