QUANTITATIVE GENETIC ANALYSIS OF CHARACTERS IN WHEAT USING CROSSES OF CHROMOSOME SUBSTITUTION LINES (THEORETICAL CONSIDERATIONS)¹

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COMPARED to studies based on ordinary homozygous varieties, the use of chromosome substitution lines obtained by means of aneuploid series in *Triticum aestivum* L. (SEARS 1944, 1953; UNRAU, PERSON and KUSPIRA 1956; PERSON 1956) permits a more complete, detailed and reliable analysis of the genetic structure of hexaploid wheats (KUSPIRA and UNRAU 1957; SEARS, LOEGERING and RODENHISER 1957; LOEGERING and SEARS 1966).

The present paper attempts to show the development of a quantitative genetic analysis of characters in common wheat using triparental groups consisting of three parents, of which one or two are disomic substitution lines, and of the corresponding crosses and some of the backcrosses. The analysis basically follows the scaling test pattern (MATHER 1949), the obtained genotypic values representing the interaction effects of sets of genes at the level of homologous and/or non-homologous chromosomes.

A preliminary section under the heading Definitions and Concepts is intended to provide the formulation of the simple theoretical foundations underlying the analyses. The symbols of set theory are used in this section, and partly in the subsequent sections (e.g. see KEMENY, SNELL and THOMPSON 1957; LIPSCHUTZ 1964; HALMOS 1965).

1. Definitions and Concepts

The genotype of an individual (a zygote) is the set of nuclear genes controlling the manifestation and the inheritance of its characters. The individual in the present case is a common wheat plant, and the character considered is one of its metrical, presumably polygenically controlled, characters.

Let \( G \) denote the set of nuclear genes constituting the genotype of the wheat plant in question, and \( C \) one of its subsets. If it is assumed that \( C \) contains all the genes constituting the homozygous loci of the genotype, then its relative complement with respect to \( G \), denoted as \( C_\complement \) in this case, must contain all the genes (if any) constituting its heterozygous loci. Note that \( G = C \cup C_\complement \) and, as such, represents a genotype in general.

In the case of a quantitative character, the set \( G \), as a whole, most likely in-

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volves all pairs of homologous chromosomes of the individual, whereas its subsets 
$C$ and $\bar{C}_o$, considered apart, may involve all, some or none of them. Therefore, 
given $G \neq \phi$, $C = \phi$ implies $\bar{C}_o \neq \phi$, and vice versa; and $C \neq \phi$ does not preclude 
$\bar{C}_o \neq \phi$, and vice versa.

Suppose that the wheat plant in question is homozygous at some but not all of 
the loci controlling the character considered, i.e., $C \neq \phi$ and $\bar{C}_o \neq \phi$. Since $C$
constitutes the homozygous portion of the genotype it may be left as it is, and
closer consideration given to its heterozygous portion $\bar{C}_o$. This portion may consist
of a single heterozygous locus, or it may represent the union of two or more
heterozygous loci involving one or more than one linkage group. Consequently,
$\bar{C}_o$ may be conceived as the union of linkage groups, each linkage group as the
union of heterozygous loci, and each such locus as the union of two differential
alleles, an allele being thus thought of as a unit set.

If a linkage group is denoted as $L_n$, a locus as $L_o$, and a gene (or allele) as $\{a\}$
we may write:

\[ \bar{C}_o = \bigcup_{u \in U} (L_n)_u \]  
\[ (L_n)_u = \bigcup_{m \in M_u} (L_o)_m \]  
\[ (L_o)_m = \bigcup_{k \in K_m} \{a\}_k \]  

Where $u$, $m$, and $k$ are indices, $U$, $M_u$ and $K_m$ the corresponding index sets, and
$(L_n)_u$, $(L_o)_m$ and $\{a\}_k$ the indexed sets. Since in a zygote there are two genes per
locus, $K_m = 2$; and since the number of pairs of chromosomes in common wheat
is 21, $U \leq 21$.

If the two alleles $\{a\}_{k=1}$ and $\{a\}_{k=2}$ are denoted simply as $\{r\}$ and $\{s\}$, respec-
tively, we may write $(L_o)_m = \{r,s\}_m$. Substituting first in (1.02) we obtain
$(L_n)_u = \bigcup_{m \in M_u} \{r,s\}_m$, and then substituting in (1.01) we obtain
$\bar{C}_o = \bigcup_{u \in U} \left( \bigcup_{m \in M_u} \{r,s\}_m \right)$. The generalized form of the genotype of the wheat plant in
question, i.e., $G = C \cup \bar{C}_o$, can be written now in a more detailed form as:

\[ G = C \cup \bigcup_{u \in U} \left( \bigcup_{m \in M_u} \{r,s\}_m \right) \]  

Note that, if $\bar{C}_o$ consists of a single segregating locus, i.e. if the wheat plant in
this case is a monohybrid, then $U = 1$ and $M_u = 1$, and the expression (1.04)
reduces to $G = C \cup \{r,s\}_u$. Further, $U = 1$ and $M_u > 1$ in (1.04) will denote
a polyhybrid with all the segregating loci united into one linkage group; $U > 1$
and $M_u > 1$, a polyhybrid involving more than one linkage group; $U > 1$ and
$M_u = 1$, a polyhybrid involving a number of independently transmitted differential
genes; and $U > 1$, with $M_u = 1$ for some $u \in U$, and $M_u > 1$ for others, a
polyhybrid involving both independent and linked genes.

If it is assumed that all genes $\{r\}_m \subset G$ were contributed by the parent $R$
and their alleles $\{s\}_m \subset G$ by the parent $D$, then the genetic make up of the
corresponding gametes must have been:
Provided that the two parents were homozygous for the character considered, the expressions (1.05) and (1.06) represent also their genotypes. Note that homozygosity results from the union of two isogenic gametes (i.e. from selfing in the present case). Such a union is equivalent to the union of two equal sets and, therefore, by idempotence, \( G(R) \cup G(R) = G(R) \) and similarly \( G(D) \cup G(D) = G(D) \).

Let \( I \) and \( J \) be two disjoint and exhaustive subsets of the index set \( U \). If \( uI \subset U \) is denoted as \( i \) and \( uJ \subset U \) as \( j \), and if it is assumed that \( I = 1 \) and \( J > 1 \), the genotypes of the presumably homozygous parents \( R \) and \( D \) can be written as:

\[
G(R) = C \cup \left( \bigcup_{u \in U} \left( \bigcup_{m \in M_i} \{r\}_m \right) \right) \cup \left( \bigcup_{m \in M_j} \{r\}_m \right)
\]

and

\[
G(D) = C \cup \left( \bigcup_{u \in U} \left( \bigcup_{m \in M_i} \{s\}_m \right) \right) \cup \left( \bigcup_{m \in M_j} \{s\}_m \right)
\]

where \( C = G(R) \cap G(D) \), i.e., the set of all loci at which the two parents are alike.

Suppose that \( \bigcup_{m \in M_i} \{s\}_m \subset G(D) \) is substituted for \( \bigcup_{m \in M_i} \{r\}_m \subset G(R) \) or, stated specifically, suppose that \( R \) and \( D \) are used, respectively, as the recipient and the donor varieties in producing a disomic substitution line \( L_i \). The genotype of this line, expressed in relation to those of \( R \) and \( D \), will be:

\[
G(L_i) = C \cup \left( \bigcup_{i \in I} \left( \bigcup_{m \in M_i} \{r\}_m \right) \right) \cup \left( \bigcup_{j \in J} \left( \bigcup_{m \in M_j} \{r\}_m \right) \right)
\]

On the assumption of \( I > 1 \) and \( J = 1 \), and by analogy, the genotype of a second disomic substitution line, line \( L_j \), may be denoted as:

\[
G(L_j) = C \cup \left( \bigcup_{i \in I} \left( \bigcup_{m \in M_i} \{r\}_m \right) \right) \cup \left( \bigcup_{m \in M_j} \{s\}_m \right)
\]

The loci by which the lines \( L_i \) and \( L_j \) differ from each other are those constituting the linkage groups indexed by \( m \in M_i \) and \( m \in M_j \), respectively. Consequently the corresponding genotypes, denoted with respect to each other, are:

\[
G(L_i) = C \cup \left( \bigcup_{m \in M_i} \{s\}_m \right) \cup \left( \bigcup_{m \in M_j} \{r\}_m \right)
\]

\[
G(L_j) = C \cup \left( \bigcup_{m \in M_i} \{r\}_m \right) \cup \left( \bigcup_{m \in M_j} \{s\}_m \right)
\]

The genotype of the recipient \( R \), in relation to those of \( L_i \) and \( L_j \) as given by (1.11) and (1.12), has to be written as:

\[
G(R) = C \cup \left( \bigcup_{m \in M_i} \{r\}_m \right) \cup \left( \bigcup_{m \in M_j} \{r\}_m \right)
\]

Consider now the triplets consisting of \( R, L_i \) and \( L_j \) with the genotypic notation as in (1.13), (1.11) and (1.12), and of \( R, L_i \) and \( D \) with the genotypic notation.
as in (1.07), (1.09) and (1.08). Note that the \( C \) term in the two triplets is not the same, unless \( L_j \) and \( D \) are genotypically the same, i.e., unless \( G(L_j) = G(D) \).

2. The Triparental Groups and Their Analysis

The crossings made within the triplets \( R, L_i, L_j \) and \( R, L_i, D \), assuming \( D \neq L_j \), will result in two triparental groups, triparental group 1 and triparental group 2, respectively, each consisting of corresponding selfs and crosses.

The analysis of the triparental groups, as given in the present paper, involves \( P, F_1, F_2 \) and some of the backcross generations and assumes (a) equivalence of the reciprocal crosses, i.e., no maternal effects, (b) normal meiosis, and (c) no differential fertility nor viability, so that 1:1 ratios of the allelomorphs of each gene will be preserved in the segregating generations.

2a. The analysis of the triparental group 1: The genotypes of the parents and of the first generation of their crosses in this group are collected in Table 1.

Let \( x_{rr}, x_{ii}, x_{jj}, x_{ri(P_1)}, x_{rij(P_1)} \) and \( x_{ij(P_1)} \) denote, respectively, the measurements of the parents and of the crosses shown in Table 1.

Using the customary notation (e.g., see Mather 1949; Aksel and Johnson 1961, 1964), the differences between the measurements of the two lines and the recipient are:

\[
x_{ii} - x_{rr} = 2(d)_i \quad (2.01)
\]
\[
x_{jj} - x_{rr} = 2(d)_j \quad (2.02)
\]

and the differences between the measurements of the \( F_1 \) generation of the crosses and the corresponding parental means are:

\[
x_{ri(P_1)} - 2^{-1}(x_{ii} + x_{rr}) = (h)_i \quad (2.03)
\]
\[
x_{ij(P_1)} - 2^{-1}(x_{jj} + x_{rr}) = (h)_j \quad (2.04)
\]
\[
x_{ij(P_1)} - 2^{-1}(x_{ii} + x_{jj}) = (h)_{ij} \quad (2.05)
\]

**TABLE 1**

*The genotypes of the \( P \) and \( F_1 \) generations in triparental group 1*

<table>
<thead>
<tr>
<th>Numerical order</th>
<th>Parents (selfs)</th>
<th>Genotypes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>( R )</td>
<td>( C \cup (\bigcup_{meM_i} {r}<em>m) \bigcup \bigcup</em>{meM_j} {r}_m) )</td>
</tr>
<tr>
<td>2</td>
<td>( L_i )</td>
<td>( C \cup (\bigcup_{meM_i} {s}<em>m) \bigcup \bigcup</em>{meM_j} {r}_m) )</td>
</tr>
<tr>
<td>3</td>
<td>( L_j )</td>
<td>( C \cup (\bigcup_{meM_i} {r}<em>m) \bigcup \bigcup</em>{meM_j} {s}_m) )</td>
</tr>
<tr>
<td></td>
<td>Crosses ((F_1))</td>
<td>( C \cup (\bigcup_{meM_i} {r,s}<em>m) \bigcup \bigcup</em>{meM_j} {r}_m) )</td>
</tr>
<tr>
<td>1</td>
<td>( R \times L_i )</td>
<td>( C \cup (\bigcup_{meM_i} {r,s}<em>m) \bigcup \bigcup</em>{meM_j} {r}_m) )</td>
</tr>
<tr>
<td>2</td>
<td>( R \times L_j )</td>
<td>( C \cup (\bigcup_{meM_i} {r}<em>m) \bigcup \bigcup</em>{meM_j} {r,s}_m) )</td>
</tr>
<tr>
<td>3</td>
<td>( L_i \times L_j )</td>
<td>( C \cup (\bigcup_{meM_i} {r,s}<em>m) \bigcup \bigcup</em>{meM_j} {r,s}_m) )</td>
</tr>
</tbody>
</table>
Since the disomic substitution lines \( L_i \) and \( L_j \) were obtained, respectively, by substituting \( U_{mEM_i} \{s\}_m \subset G(D) \) for \( \cup_{mEM_i} \{r\}_m \subset G(R) \) and \( \cup_{mEM_j} \{s\}_m \subset G(D) \) for \( \cup_{mEM_j} \{r\}_m \subset G(R) \), 2\((d)_i \) and 2\((d)_j \) represent the effects of these substitutions.

The character-metric differences between the F\(_1\) generation of the crosses and the corresponding parental means may be restated, respectively, as follows:

\[
2^{-1}((x_{ri(r)} - x_{ii}) + (x_{ri(r)} - x_{rr})) = (h)_i ,
\]
\[
2^{-1}((x_{rf(r)} - x_{if}) + (x_{rf(r)} - x_{rr})) = (h)_j ,
\]
\[
2^{-1}((x_{ij(r)} - x_{ij}) + (x_{ij(r)} - x_{ij})) = (h)_{ij} .
\]

If the character-metric differences within the parentheses in the above equations are compared with the corresponding genotypes shown in Table 1, it will be clear that \((h)_i\) and \((h)_j\) denote the mean effects of the change of zygosity at the \( i \)th and \( j \)th pairs of homologues separately; whereas, \((h)_{ij}\) represents the mean effect of such a change at both pairs jointly. Consequently, if the effect of the change of zygosity at the \( i \)th chromosome-pair is not affected by the simultaneous change of zygosity at the \( j \)th chromosome-pair, and vice-versa, it will be expected that \((h)_{ij} = (h)_i + (h)_j\). On the contrary, if the effect of the change of zygosity at the \( i \)th chromosome-pair is affected by the simultaneous change at the \( j \)th chromosome-pair, it will be expected that \((h)_{ij} \neq (h)_i + (h)_j\) or presented in equational form,

\[
(h)_{ij} = (h)_i + (h)_j + \tilde{\sigma}_{ij} \tag{2.06}
\]

The value of \( \tilde{\sigma}_{ij} \) in terms of character-metrics, is:

\[
\tilde{\sigma}_{ij} = x_{ij(r)} - x_{ri(r)} - x_{rf(r)} + x_{rr} \tag{2.07}
\]

Note that \((h)_i\) and \((h)_j\) pertain to the \( \cup_{mEM_i} \{r,s\}_m \) and \( \cup_{mEM_j} \{r,s\}_m \) sets of loci (or linkage groups) separately and, as such, are the resultants of the allelic and/or nonallelic interaction effects at the level of homologous chromosomes; whereas, \( \tilde{\sigma}_{ij} \) pertains to both sets jointly and, consequently, is the resultant of the nonallelic interaction effects at the level of nonhomologous chromosomes.

Consider the linkage group \( \cup_{mEM_w} \{r,s\}_m; w = i,j \). Let \( M_w = n \geq 2 \) and suppose there is a certain amount of crossing over. Since the exchange of homologous segments of chromosomes may involve 0,1,2, \ldots, \( n \) pairs of differential alleles at a time, the output of gametic or haploid sets of genes by the linkage group in question may consist of \( 2^n \) different combinations, of which two are expected to be the original nonrecombinants \( \cup_{mEM_w} \{r\}_m = R_w \) and \( \cup_{mEM_w} \{s\}_m = D_w \), and \( 2(2^{n-1} - 1) \) recombinants.

If the \( t \)th recombinant is denoted as

\[
(Z_w)_t = (\cup_{mEM_w} \{a\}_m; \text{some} \{a\}_m = \{r\}_m, \text{some} \{a\}_m = \{s\}_m)_t
\]

and its frequency as \( f_t \) (\( t = 1,2, \ldots, 2(2^{n-1} - 1); f_t \geq 0 \)) then the collection (or
family) of all recombinants is \( \{(Z_w)_{it}\}_{itT} = R_w^* \) say, and their total frequency
\( \sum f_t = p \) say; \( T \leq 2^{(2^w - 1)} - 1 \). Taking the total of the frequencies of all \( 2^w \)
combinations as unity, the proportion of nonrecombinants \( R_w \) and \( D_w \) will be
\( 2^{-1}(1-p) \) and \( 2^{-1}(1-p) \) respectively.

Using the adopted notation and dispensing with the set of homozygous loci
which are the same in the cross and the corresponding parents, the genotypic
composition of the \( F_2 \) and the backcross populations of Crosses 1 and 2 may be
presented conventionally, in a generalized form, as given in Table 2.

Note that in Table 2 \( R_w R_w \) is the same as \( R_w \cup R_w = R_w = \cup \{r\}_{m} \); \( R_w D_w \)
is the same as \( R_w \cup D_w = \cup \{r,s\}_{m} \), and \( D_w D_w \) is the same as \( D_w \cup D_w = \cup \{s\}_{m} \). In other words, the first three genotypes are noncrossovers,
constitutionally and character-metrically the same as the two parents and the
corresponding \( F_1 \) hybrid. The rest of the genotypes constitute three different
collections of crossovers, i.e.,
\[
R_w R_w^* = \{R_w \cup (Z_w)_{it}\}_{itT}, \\
D_w R_w^* = \{D_w \cup (Z_w)_{it}\}_{itT} \quad \text{and} \\
R_w^* R_w^* = \{(Z_w)_{a} \cup (Z_w)_{b} : a,b = t, a = b \text{ or } a \neq b\}_{itT},
\]
with the corresponding weighted character-metric means \( x^*_w, x^*_d \) and \( x^{**} \).

From the entries in Table 2 the character-metric means of the \( F_2 \) generation
and that of the two backcrosses considered jointly, may be presented, respectively, as follows:
\[
x_{w(F_2)} = x - 2p(x-y) + p^2((x-y) + (x^{**}-y)) \quad (2.08)
\]
\[
2^{-1}(x_{B(R)} + x_{B(B_Iw)}) = x - p(x-y) \quad (2.09)
\]
where \( x = 2^{-2}(x_{rr} + 2x_{w(F_2)} + x_{wco}) \) and \( y = 2^{-1}(x^*_w + x^*_d) \).

By assumption, the ratio of homozygous to heterozygous loci is the same (1:1
in this case) within the noncrossover and the crossover subpopulations of both the
\( F_2 \) and the pooled backcross populations. Consequently, if the individual loci are
independent in their action, it will be expected that \( x = y = x^{**} \) and, implicitly,

\[\text{TABLE 2}\]

The genotypic composition of the \( F_2 \) and the backcross generations of
Crosses 1 and 2 (\( w = 1,i \))

<table>
<thead>
<tr>
<th>Genotypes</th>
<th>Character metrics</th>
<th>The frequency of the genotypes in:</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R_w R_w )</td>
<td>( x_{rr} )</td>
<td>( F_i = F_i \times F_i )</td>
</tr>
<tr>
<td>( R_w D_w )</td>
<td>( x_{w(F_2)} )</td>
<td>( B(R) = F_i \times R )</td>
</tr>
<tr>
<td>( D_w D_w )</td>
<td>( x_{wco} )</td>
<td>( B(L_w) = F_i \times L_w )</td>
</tr>
<tr>
<td>( R_w R_w^* )</td>
<td>( x_R )</td>
<td>( 2^{-2}(1-p)^2 )</td>
</tr>
<tr>
<td>( D_w R_w^* )</td>
<td>( x_R^* )</td>
<td>( 2^{-2}(1-p)^2 )</td>
</tr>
<tr>
<td>( R_w^* R_w^* )</td>
<td>( x^{**} )</td>
<td>( p(1-p) )</td>
</tr>
<tr>
<td>( p )</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
\( x - y = x^{**} - y = 0 \); and if they are not independent, \( x - y \neq 0 \) and \( x^{**} - y \neq 0 \), provided \( p > 0 \) and, implicitly, \( y \) and \( x^{**} \) exist.

If \( 2^{-1}(x_{rr} + 2x_{rw(F_1)} + x_{ww}) \) and \( 2^{-1}(x_{R}^* + x_{D}^*) \) are substituted for \( x \) and \( y \), equation (2.09) becomes:

\[
2^{-1}(x_{B(R)} + x_{B(L_w)}) = 2^{-1}(x_{rr} + 2x_{rw(F_1)} + x_{ww}) - 2^{-1}p(2^{-1}(x_{rr} + 2x_{rw(F_1)} + x_{ww}) - x_{R}^* - x_{D}^*)
\]

Since \( x_{rr} \) and \( x_{R}^* \) pertain to \( B(R) \), \( x_{ww} \) and \( x_{D}^* \) to \( B(L_w) \) and \( x_{rw(F_1)} \) to both of them, the two right side terms of the last expression can be presented, respectively, as:

\[
2^{-1}(2^{-1}(x_{rr} + x_{rw(F_1)}) + 2^{-1}(x_{rw(F_1)} + x_{ww}))
\]

and

\[
2^{-1}p(2^{-1}(x_{rr} + x_{rw(F_1)}) - x_{R}^* + 2^{-1}(x_{rw(F_1)} + x_{ww}) - x_{D}^*)
\]

If the two differences within the outer parentheses of the second term are denoted, respectively, as \( AR \) and \( AD \), it becomes

\[
pA_R = 2^{-1}(x_{rr} + x_{rw(F_1)}) - x_{B(R)}
\]

\[
pA_D = 2^{-1}(x_{rw(F_1)} + x_{ww}) - x_{B(L_w)}
\]

By definition \( x = 2^{-1}(x_{rr} + 2x_{rw(F_1)} + x_{ww}) \), \( \Delta_R = 2^{-1}(x_{rr} + x_{rw(F_1)}) - x_{R}^* \) and \( \Delta_D = 2^{-1}(x_{rw(F_1)} + x_{ww}) - x_{D}^* \). Therefore, \( p(x-y) = 2^{-1}p(\Delta_R + \Delta_D) \), and since \( y = 2^{-1}(x_{R}^* + x_{D}^*) \); equation (2.08) can be written also as:

\[
x_{rw(F_2)} = x - p(\Delta_R + \Delta_D) + 2^{-2}p^2(\Delta_R + \Delta_D) + p^2(x^{**} - 2^{-1}(x_{R}^* + x_{D}^*))
\]

Since \( p \) is not known \( 2^{-1}p^2(\Delta_R + \Delta_D) \) and, implicitly, \( p^2(x^{**} - 2^{-1}(x_{R}^* + x_{D}^*)) \) cannot be evaluated separately. Therefore, denoting them jointly as \( \Delta \) we obtain:

\[
\Delta = x_{rw(F_2)} - x + p(\Delta_R + \Delta_D)
\]

or, in terms of the pertaining character-metrics,

\[
\Delta = x_{rw(F_2)} + 2^{-2}(x_{rr} + 2x_{rw(F_1)} + x_{ww}) - (x_{B(R)} + (x_{B(L_w)})
\]

Note that \( pA_R = pA_D = \Delta = 0 \) may denote the absence of recombination \( (p = 0) \), or the absence of nonallelic interaction \( (p > 0; x = y = x^{**}) \) or some sort of balanced effects with resultant zero.

If linkage is complete \( (p = 0) \), the homologous-chromosomal sets of differential genes will be inherited and will act as a single allelic pair with the obvious result that the phenotypic distribution in \( F_2 \) and the backcrosses will follow a monogenic pattern.

If linkage is incomplete \( (p > 0; x = y = x^{**} \) or \( x \neq y, x \neq x^{**}, y \neq x^{**} \) the phenotypic distribution in the populations in question will be of polygenic pattern.

The same \( i \)th and \( j \)th pairs of homologous chromosomes involved in Crosses 1 and 2 separately, are involved jointly in Cross 3. Therefore, the output of gametic sets of nuclear genes by the set \( \bigcup_{m \in M_i} \{r,s\}_m \cup \bigcup_{m \in M_j} \{r,s\}_m \) in the \( F_3 \) genotype of Cross 3 is expected to consist of \( 2^{n_1+n_2} \) types of combinations \( (n_1 \neq n_1 \) or \( n_1 = n_2) \), of which two will be the original nonrecombinants \( D,R \) and \( D,D \), and two the noncrossover recombinants \( R,R \) and \( D,D \). The remaining \( 2^2(2^{n_1+n_2} - 2 - 1) \) combinations will be crossover recombinants, each with its frequency \( f \geq 0 \) and, likely, its particular effect.
Let \( q \) be the proportion of the crossover genotypes and \( 1 - q \) that of the noncrossover genotypes in the \( F_2 \) population of Cross 3. If the weighted mean character-metric of the noncrossovers is denoted as \( x_{ij} \) and that of the crossovers as \( y_{ij} \), then the character-metric of the \( F_2 \) generation, as population mean, will be

\[
x_{ij(F_2)} = (1-q)x_{ij} + qy_{ij}, \operatorname{or}
\]

\[
x_{ij(F_2)} = x_{ij} - q(x_{ij} - y_{ij}).
\]

(2.13)

The inequality \( q(x_{ij} - y_{ij}) \neq 0 \) implies \( q > 0 \) and \( x_{ij} \neq y_{ij} \), i.e., the presence of both the recombination and the nonallelic interaction at the levels of homologous and/or nonhomologous chromosomes.

The genotypes constituting the noncrossover subpopulation of the \( F_2 \) population in question, their relative frequency within this subpopulation, and the corresponding character-metrics are given in Table 3. Note that in Table 3 only three out of nine genotypes are new, and the rest are those already given in Table 1.

If it is assumed that the homologous-chromosomal sets of genes \( R_ir_i, D_id_i, R_jr_j, D_jd_j, R_ir_j, \) and \( R_jd_i \), as entities, are independent in their action and, as such, their contributions to the character metrics are purely additive, it will be expected that:

\[
x_{ij(F_2 \text{ or } F_1)} = x_{ri(F_1)} + x_{rj(F_1)} - x_{rr}
\]

\[
y_{(RD)}_{ij(F_2)} = x_{ri(F_1)} + x_{jj} - x_{rr}
\]

\[
y_{(DD)}_{ij} = x_{ii} + x_{jj} - x_{rr}.
\]

By appropriate substitution in Table 3 the weighted mean of the noncrossovers is obtained as:

\[
x_{ij} = 2^{-1}(x_{ii} + x_{jj}) + 2^{-1}(h)_i + 2^{-1}(h)_j
\]

(2.14)

If the assumption of independence of action of the homologous-chromosomal sets of genes does not hold, then:

\[
x_{ij} \neq 2^{-1}(x_{ii} + x_{jj}) + 2^{-1}(h)_i + 2^{-1}(h)_j
\]

(2.15)

Since one fourth of the genotypes in Table 3 are of the original \( F_1 \) type, the difference between the two sides of the inequality (2.15) may be denoted as

\[
\text{TABLE 3}
\]

The noncrossover genotype in the \( F_2 \) population of Cross 3

<table>
<thead>
<tr>
<th>Genotypes</th>
<th>Character metrics</th>
<th>Relative frequency</th>
</tr>
</thead>
<tbody>
<tr>
<td>( R_iR_iR_jR_j )</td>
<td>( x_{rr} )</td>
<td>1/16</td>
</tr>
<tr>
<td>( D_iD_iR_jR_j )</td>
<td>( x_{ii} )</td>
<td>1/16</td>
</tr>
<tr>
<td>( R_iR_iD_jD_j )</td>
<td>( x_{jj} )</td>
<td>1/16</td>
</tr>
<tr>
<td>( R_iD_jR_jR_j )</td>
<td>( x_{ri(F_1)} )</td>
<td>2/16</td>
</tr>
<tr>
<td>( R_iR_iD_jD_j )</td>
<td>( x_{rj(F_1)} )</td>
<td>2/16</td>
</tr>
<tr>
<td>( R_iD_jD_jD_j )</td>
<td>( x_{ij(F_1)} )</td>
<td>4/16</td>
</tr>
<tr>
<td>( R_iD_iD_jD_j )</td>
<td>( y_{(RD)}_{ij(F_1)} )</td>
<td>2/16</td>
</tr>
<tr>
<td>( D_iD_iR_jD_j )</td>
<td>( y_{(DD)}_{ij} )</td>
<td>2/16</td>
</tr>
<tr>
<td>( D_iD_jD_jD_j )</td>
<td>( y_{(DD)}_{ij} )</td>
<td>1/16</td>
</tr>
</tbody>
</table>
\[ x_{ij} = 2^{-2}(x_{ii} + x_{ij} + (h)_i + (h)_j) + 2^{-2}\hat{d}_{ij} + \delta_{ij} \]

Consequently, the inequality (2.15) can be written in equational form as follows:

\[ x_{ij} = 2^{-1}(x_{ii} + x_{ij} + (h)_i + (h)_j) + 2^{-2}\hat{d}_{ij} + \Delta_{ij} \] (2.16)

where

\[ \Delta_{ij} = \delta_{ij} - q(x_{ij} - y_{ij}) \]

It may be easily found that the \( \Delta_{ij} \), expressed in terms of character-metrics, is:

\[ \Delta_{ij} = x_{ij}(\bar{r}_j) - 2^{-2}(x_{iij} + (h)_{ij} + (h)_{ij} + 2^{-2}\hat{d}_{ij} + \Delta_{ij}) \] (2.17)

Since \( \Delta_{ij} = \delta_{ij} - q(x_{ij} - y_{ij}) \), \( \Delta_{ij} \neq 0 \) denotes the presence of nonallelic interaction at the level of homologous and/or nonhomologous chromosomes, different from \( \hat{d}_{ij} \). Therefore, both \( \Delta_{ij} \neq 0 \) and \( \Delta_{ij} = 0 \) do not prove or disprove the presence or the absence of the crossing over.

Note that in the absence of crossing over the phenotypic distribution in the F2 generation of this cross is expected to follow a digenic pattern.

The backcrosses of Cross 3 are not considered.

2b. The analysis of the triparental group 2: The genotypes of the three parents and of the first generation of their crosses in this group are given in Table 4. Note that \( L_i, R \) and \( R \times L_i \) are the same as in triparental group 1 (see Table 1), with the difference that their genotypes are symbolized with respect to \( D \) instead of \( L_i \).

If the character-metrics of the parents \( L_i, R \) and \( D \) are denoted as \( x_{LL}, x_{RR} \) and \( x_{DD} \) respectively, and those of the corresponding crosses as \( x_{RL}(F_1), x_{DL}(F_1) \) and \( x_{RD}(F_1) \), the differences between the parental measurements can be written as:

\[ \text{TABLE 4} \]

The genotypes of the P and F1 generations in triparental group 2

<table>
<thead>
<tr>
<th>Numerical order</th>
<th>Parents (selfs)</th>
<th>Genotypes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>( L_i )</td>
<td>( C(U_{meM_i} {s}<em>m) \cup (U</em>{iJ}(U_{meM_j} {r}_m)) )</td>
</tr>
<tr>
<td>2</td>
<td>( R )</td>
<td>( C(U_{meM_i} {r}<em>m) \cup (U</em>{iJ}(U_{meM_j} {r}_m)) )</td>
</tr>
<tr>
<td>3</td>
<td>( D )</td>
<td>( C(U_{meM_i} {s}<em>m) \cup (U</em>{iJ}(U_{meM_j} {s}_m)) )</td>
</tr>
<tr>
<td>( R \times L_i)</td>
<td></td>
<td>( C(U_{meM_i} {r,s}<em>m) \cup (U</em>{iJ}(U_{meM_j} {r}_m)) )</td>
</tr>
<tr>
<td>( D \times L_i)</td>
<td></td>
<td>( C(U_{meM_i} {s}<em>m) \cup (U</em>{iJ}(U_{meM_j} {r,s}_m)) )</td>
</tr>
<tr>
<td>( R \times D )</td>
<td></td>
<td>( C(U_{meM_i} {r,s}<em>m) \cup (U</em>{iJ}(U_{meM_j} {r,s}_m)) )</td>
</tr>
</tbody>
</table>
and the differences between the measurements of the F₁ generation of the crosses and the respective parental means as:

$$x_{RL(F₁)} - 2^{-1}(x_{RR} + x_{LL}) = (h)_{i}$$  \hspace{1cm} (2.21)

$$x_{DL(F₁)} - 2^{-1}(x_{DD} + x_{LL}) = (h)_{k}$$  \hspace{1cm} (2.22)

$$x_{RD(F₁)} - 2^{-1}(x_{RR} + x_{DD}) = (h)_{ik}$$  \hspace{1cm} (2.23)

Note that

$$2(d)_{ik} = x_{DD} - x_{RR} = (x_{LL} - x_{RR}) + (x_{DD} - x_{LL}) = 2(d)_{i} + 2(d)_{k}$$

and that

$$(d)_{i}$$ and $$(h)_{i}$$ are the same as in triparental group 1.

The difference $2(d)_{k}$ may be interpreted as representing the metrical effect of the substitution of $$∪_{i≠j}(∪_{meM_j}\{r,s\}_m) ⊂ G(D)$$ for $$∪_{i≠j}(∪_{meM_j}\{r\}_m) ⊂ G(R)$$, given that $$∪_{meM_i}\{r\}_m) ⊂ G(D)$$ was substituted for $$∪_{meM_i}\{r\}_m) ⊂ G(R)$$. It is clear that the two substitutions would transform R into D and the effect of this transformation would be $2(d)_{i} + 2(d)_{k}$.

The difference $$(h)_{k}$$ pertains to the set $$∪_{i≠j}(∪_{meM_j}\{r,s\}_m) ⊂ G(D × L_i)$$; whereas the difference $$(h)_{ik}$$ pertains to both $$∪_{meM_i}\{r,s\}_m$$ and $$∪_{i≠j}(∪_{meM_j}\{r,s\}_m)$$ sets jointly.

If it is assumed that the homologous-chromosomal sets of differential genes (or linkage groups, as conceived in this case) are independent in their action, then it will be expected that $$(h)_{k} = ∑_{j≠i}(h)_{j}$$ and $$(h)_{ik} = (h)_{i} + ∑_{j≠i}(h)_{j}$$. On the contrary, if the above assumption does not hold, obviously, $$(h)_{k} ≠ ∑_{j≠i}(h)_{j}$$ and $$(h)_{ik} ≠ (h)_{i} + ∑_{j≠i}(h)_{j}$$. These inequalities may be written in equational form as:

$$(h)_{k} = ∑_{j≠i}(h)_{j} + \bar{\varepsilon}_{k}$$  \hspace{1cm} (2.24)

and

$$(h)_{ik} = (h)_{i} + ∑_{j≠i}(h)_{j} + \bar{\varepsilon}_{k} + \bar{\varepsilon}_{ik}$$  \hspace{1cm} (2.25)

for instance, where $$\bar{\varepsilon}_{k}$$ denotes the resultant effect of the interaction between the J subsets of the set $$∪_{i≠j}(∪_{meM_j}\{r,s\}_m)$$, and $$\bar{\varepsilon}_{ik}$$ the effect of the interaction between this set and the set $$∪_{meM_i}\{r,s\}_m$$. From (2.24) and (2.25) we obtain:

$$\bar{\varepsilon}_{ik} = (h)_{ik} - (h)_{i} - (h)_{k}$$  \hspace{1cm} (2.26)

or, in terms of character-metrics,

$$\bar{\varepsilon}_{ik} = x_{RD(F₁)} - x_{DL(F₁)} - x_{RL(F₁)} + x_{LL}$$  \hspace{1cm} (2.27)

There is no solution for $$\bar{\varepsilon}_{k}$$.

Note that both $$(h)_{k}$$ and $$(h)_{ik}$$ pertain to unions of homologous-chromosomal sets of differential genes and, as such, are the resultants of the allelic and/or nonallelic interaction effects at the level of homologous and/or nonhomologous chromosomes.

The analysis of the F₂ and the backcross generations of Cross 1 was given in 2a.

The expected proportions of the F₁ genotypes within the noncrossover sub-
populations of the F$_2$ population of Cross 2 and 3 are 2$^{-J}$ and 2$^{-1(J+1)}$ respectively. Consequently we may write:

\[ x_{DL(F_2)} = 2^{-1} x_{DL(F_1)} - 2^{-2} (x_{DD} + x_{LL}) = 2^{-J} \hat{\delta}_k + \delta_k \]  
(2.28)

\[ x_{RD(F_2)} = 2^{-1} x_{RD(F_1)} - 2^{-2} (x_{DD} + x_{DD}) = 2^{-U} \hat{\delta}_u + \delta_u \]  
(2.29)

where \( U = J + 1 \), and \( \hat{\delta}_u \) contains both \( \hat{\delta}_k \) and \( \hat{\delta}_{ik} \). Since \( J \) is unknown and the value of \( \hat{\delta}_k \) can not be evaluated, 2$^{-J} \hat{\delta}_k + \delta_k$ and 2$^{-U} \hat{\delta}_u + \delta_u$ will be considered as they are, and denoted, for the sake of simplicity, as \( \Delta_k \) and \( \Delta_u \) respectively. The corresponding working formulas will be, of course,

\[ \Delta_k = x_{DL(F_2)} - 2^{-2} (x_{DD} + 2x_{DL(F_1)} + x_{LL}) \]  
(2.30)

and

\[ \Delta_u = x_{RD(F_2)} - 2^{-2} (x_{RR} + 2x_{RD(F_1)} + x_{DD}) \]  
(2.31)

With repeated observations, as they usually are, the standard errors of the parameters \((d)_i, (d)_j, (h)_i, (h)_j, \hat{\delta}_{ij}, \hat{\delta}_{ik}, \hat{\delta}_{jk}, \hat{\delta}_{ik}, \hat{\delta}_{jk}, \Delta_k, \Delta_u, \) and \( \Delta_{ij} \) (formulas: 2.01, 2.02, 2.03, 2.04, 2.07, 2.10, 2.12, 2.17, 2.19, 2.22, 2.27, 2.30 and 2.31 respectively) may be found by means of the following formula (Cochran and Cox 1957):

\[ s_p = \pm s \left( r_1^{-1} l_1^2 + r_2^{-1} l_2^2 + \ldots + r_n^{-1} l_n^2 \right)^{1/2} \]

where \( s \) is the square root of the pooled error variance of the involved nonsegregating generations, \( r \) the number of observations (or replications) and \( l \) the coefficient of a character metric in a formula. The error variances of the F$_2$ and backcross generations are presumed to be the same as the pooled error variance of the corresponding P and F$_1$ generations.

**GENERAL DISCUSSION**

The difficulties inherent in quantitative-genetic analyses are aggravated in the case of common wheat by its polyploid nature, which tends to increase the number of genes controlling the expression of a character and to complicate the resultant effect of gene action and interaction. By reducing the character-metric difference to single-chromosomal sets of genes, in other words to individual linkage groups, and considering them in appropriate combinations, a fairly detailed analysis of quantitative-genetic structure of common wheat can be achieved.

It is obvious that a character-metric difference between a disomic substitution line \( L_i \) and the respective recipient variety \( R \) represents the effect of the substitution of the \( i \)th chromosome-pair \( (i = 1, 2, \ldots, 21) \) of a donor variety \( D \) for its counterpart in the recipient \( R \), and reveals thus the presence or, possibly, the absence of differential genes in these chromosomes. When all 21 disomic lines of the same donor \( D \) and recipient \( R \) are available, the character-metric difference

\[ 21x_D - \sum_{i=1}^{21} (x_L)_i \]  

may be used to detect interaction between the homozygous sets of differential genes. Although \( 21x_D - \sum_{i=1}^{21} (x_L)_i \neq 0 \) shows that interaction is present, \( 21x_D - \sum_{i=1}^{21} (x_L)_i = 0 \) does not necessarily mean its absence, because the possibility of balanced effects can not be precluded.
The behaviour of genes in heterozygous stage at loci at which the donor and the recipient varieties differ can be studied by means of appropriate crosses. The analysis of triparental groups as given in this paper, dealing with sets of genes in both homozygous and heterozygous stages, makes possible the detection of the nonallelic interaction on both nonhomologous and homologous-chromosomal levels, the manifestation of the latter necessitating the presence of gene recombination. When the character-metrics can be recorded on a single-plant basis, or as progeny means of individual $F_2$ plants (provided the number of $F_2$ lines and the number of plants within these lines are sufficiently high) the members of the triparental group 1 may be subjected to further analysis.

The differential genes involved in Crosses 1 and 2 of this group belong to single linkage groups and, therefore, the phenotypic distribution in the segregating generations is expected to be, basically, of the monogenic pattern. The degree of deviation from this pattern (ignoring the effects of the environmental agencies) will be in function of the recombination fraction $(p)$. Repeated backcrossing to $R$ and $L_i$ in Cross 1, and to $R$ and $L_j$ in Cross 2, with subsequent selfing (e.g., see WEHRHAHN and ALLARD 1965), will result in monogenic lines reflecting the genetic structure of the $i$th and the $j$th chromosomes of the recipient and the donor varieties as related to each other.

Since the differential genes in Cross 3 involved two pairs of homologues, the same as those involved in Crosses 1 and 2 separately, the segregation is expected to be of digenic pattern if there is complete linkage, or if the involved pairs of homologues each differ at one locus. The genic effects and the grouping of the segregants will depend on the presence or absence of nonallelic interaction at the level of nonhomologous chromosomes. The digression from the digenic pattern of segregation will depend upon the presence and the intensity of recombination in the two pairs of differential homologues.

The recipient $R$ and the disomic line $L_i$ were considered to be the same in triparental groups 1 and 2. This, however, does not constitute a necessary condition, since the two groups can be, and actually were, analysed individually, the loss of information being negligible.

The author wishes to thank Dr. C. Person of the Department of Botany, University of British Columbia, and Drs. W. E. Smith and L. P. V. Johnson from the Department of Genetics, University of Alberta, for their assistance in the preparation of this manuscript.

DETAILED SUMMARY

The quantitative genetic analysis is based on homologous-chromosomal sets of genes (or linkage groups) belonging to and acting within, a system of nuclear genes controlling the same metrical character in three specifically related parents. The three parents and their crosses, considered jointly, are referred to as a triparental group. Two such groups are considered. The parental set in the triparental group 1 consists of two disomic substitution lines $L_i$ and $L_j$ ($i \neq j$) and the corresponding recipient variety $R$, and that in the triparental group 2 of a disomic substitution line $L_i$ and the corresponding recipient and donor varieties...
As related to each other within a group the genotypes of the parents, in terms of the corresponding sets of nuclear genes, are:

**Triparental Group 1**

\[
\begin{align*}
G(R) &= C \cup (\bigcup_{m \in M_i} \{r\}_m) \cup (\bigcup_{m \in M_j} \{r\}_m) \\
G(L_i) &= C \cup (\bigcup_{m \in M_i} \{s\}_m) \cup (\bigcup_{m \in M_j} \{r\}_m) \\
G(L_j) &= C \cup (\bigcup_{m \in M_j} \{r\}_m) \cup (\bigcup_{m \in M_j} \{s\}_m)
\end{align*}
\]

**Triparental Group 2**

\[
\begin{align*}
G(L_i) &= C \cup (\bigcup_{m \in M_i} \{s\}_m) \cup (\bigcup_{m \in M_j} \{r\}_m) \\
G(R) &= C \cup (\bigcup_{m \in M_i} \{r\}_m) \cup (\bigcup_{m \in M_j} \{r\}_m) \\
G(D) &= C \cup (\bigcup_{m \in M_i} \{s\}_m) \cup (\bigcup_{m \in M_j} \{s\}_m)
\end{align*}
\]

where \(C\) stands for the set of all loci which are the same in all three, presumably homozygous, parents within a group and, implicitly, in the progeny of their crosses. In both groups \(\bigcup_{m \in M_i} \{s\}_m\) and \(\bigcup_{m \in M_j} \{r\}_m\) are the sets of alleles at which the \(i\)th chromosomes of \(D\) and \(R\) differ respecting the character considered. The sets \(\bigcup_{m \in M_i} \{s\}_m\) and \(\bigcup_{m \in M_j} \{r\}_m\) have the same meaning with regard to \(j\)th chromosomes of \(D\) and \(R\). The unions of sets of genes \(\bigcup_{m \in M_i} \{s\}_m\) and \(\bigcup_{m \in M_j} \{r\}_m\) imply all the differential loci at which all \(jeJ\) (\(j \neq i, J \leq 20\)) chromosomes of \(D\) and \(R\), and implicitly of \(L_i\), differ for the character in question.

Since in general \(S \cup S = S\) (\(S = G(R), G(L_i), G(L_j), G(D)\)), the genotypic notation of the parents represents both the zygotic and the gametic stages, so that the union of two of them belonging to the same triparental group, gives the genotype of the corresponding F1 hybrid.

The analysis of the triparental groups considered yields the values of the pertinent parameters. These parameters and the corresponding formulas, expressed in terms of appropriate character-metrics \((x)\), are collected in Table 5.

The standard errors of the parameters \((s_p)\) may be found by the following formula (Cochran and Cox 1957):

\[
s_p = s \left( r^{-1} p_1^2 + r^{-1} p_2^2 + \cdots + r^{-1} p_n^2 \right)^{1/2}
\]

where \(s\) is the square root of the pooled error variance of the involved nonsegregating generations, \(r\) the number of observations (replications) and \(l\) the coefficient of a character-metric \((x)\) in a given formula. The error variances of the F2 and backcross generations are presumed to be the same as the pooled error variance of the corresponding P and F1 generations.

The parameter \((d)_{w}\) \((w = i,j)\) measures the deviation of the character-metrics of the recipient \(R\) and the disomic substitution line \(L_w\) from their mean measurement and, as such, refers to the homozygous allelomorphic sets of genes \(\bigcup_{m \in M_w} \{r\}_m\) and \(\bigcup_{m \in M_w} \{s\}_m\) contained in the \(u\)th homologues of \(R\) and \(L_w\), the only homologues at which they differ genotypically.
The parameters and the corresponding formulas

<table>
<thead>
<tr>
<th>Triparental groups involved</th>
<th>Parameters</th>
<th>The corresponding formulas*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 and 2</td>
<td>(d)</td>
<td>( \frac{1}{2} (x_{i} - x_{rr}) )</td>
</tr>
<tr>
<td>1 and 2</td>
<td>(h)</td>
<td>( x_{ri}(P_{1}) - \frac{1}{2} (x_{i} + x_{rr}) )</td>
</tr>
<tr>
<td>1</td>
<td>( \theta_{ij} )</td>
<td>( x_{ij}(P_{1}) - x_{ri}(P_{1}) - \frac{1}{2} (x_{ii} + x_{jj}) + x_{rr} )</td>
</tr>
<tr>
<td>1</td>
<td>(d)</td>
<td>( \frac{1}{2} (x_{ij} - x_{rr}) )</td>
</tr>
<tr>
<td>1</td>
<td>(h)</td>
<td>( x_{rj}(P_{1}) - \frac{1}{2} (x_{ij} + x_{rr}) )</td>
</tr>
<tr>
<td>1</td>
<td>( p\Delta_{R} )</td>
<td>( \frac{1}{2} (x_{rr} + x_{rw}(P_{1})) - x_{E(R)} )</td>
</tr>
<tr>
<td>1</td>
<td>( p\Delta_{D} )</td>
<td>( \frac{1}{2} (x_{rw}(P_{1}) + x_{wo}) - x_{E(D)} )</td>
</tr>
<tr>
<td>1</td>
<td>( \Delta )</td>
<td>( x_{rw}(P_{1}) + \frac{1}{2} (x_{ir} + 2x_{rw}(P_{1}) + x_{wo}) - x_{E(R)} - x_{E(D)} )</td>
</tr>
<tr>
<td>1</td>
<td>( \Delta_{ij} )</td>
<td>( x_{ij}(P_{2}) - \frac{1}{4} (x_{ij}(P_{1}) + x_{ri}(P_{1}) + x_{rj}(P_{1}) + x_{ii} + x_{jj} - x_{rr}) )</td>
</tr>
<tr>
<td>2</td>
<td>( (d) )</td>
<td>( \frac{1}{2} (x_{DD} - x_{LL}) )</td>
</tr>
<tr>
<td>2</td>
<td>( (h) )</td>
<td>( x_{BD}(P_{1}) - \frac{1}{2} (x_{RR} + x_{DD}) )</td>
</tr>
<tr>
<td>2</td>
<td>( \theta_{ik} )</td>
<td>( x_{BD}(P_{1}) - 2x_{RL}(P_{1}) + x_{LL} )</td>
</tr>
<tr>
<td>2</td>
<td>( \Delta_{k} )</td>
<td>( x_{DL}(P_{2}) - \frac{1}{4} (x_{DD} + 2x_{DL}(P_{1}) + x_{LL}) )</td>
</tr>
<tr>
<td>2</td>
<td>( \Delta_{u} )</td>
<td>( x_{RD}(P_{2}) - \frac{1}{4} (x_{RR} + 2x_{RD}(P_{1}) + x_{DD}) )</td>
</tr>
</tbody>
</table>

* In the formulas, \( x_{i}, x_{ij}, x_{rr} \), and \( x_{wo} \) are the mean measurements of the substitution lines \( L_{i} \) and \( L_{j} \) and of the recipient and the donor varieties \( R \) and \( D \) respectively; \( x_{wo} \), \( x_{rw} \), and \( x_{RD} \) those of the respective hybrids; \( F_{1} \) and \( B \) in the subscripts refer to the corresponding population means and \( (r) \) and \( (L) \) denote backcrossing to \( R \) and \( L \) respectively. Note that \( w = i,j \) refers to the chromosome substituted.

The parameter \( (h)_{w} \) (\( w = i,j \)) measures the deviation of the \( (R \times L_{w})F_{1} \) from the corresponding parental mean and represents the resultant effect of the allelic and/or the nonallelic interaction within the heterozygous set \( U_{m \in M_{w}} \{r,s\}_{m} \) involving the \( w \)th pair of homologues contributed by the parents \( R \) and \( L_{w} \).

The parameter \( \theta_{ij} \) refers to the simultaneous change from homozygous to heterozygous stage at the \( i \)th and the \( j \)th chromosomes in the \( (L_{i} \times L_{j})F_{1} \) and, as such, denotes the effect of the interaction between the sets \( U_{m \in M_{i}} \{r,s\}_{m} \) and \( U_{m \in M_{j}} \{r,s\}_{m} \). In other words, \( \theta_{ij} \) is a measure of the interaction between the \( i \)th and \( j \)th chromosomes when both are in heterozygous stage within the same organism.

The parameters \( p\Delta_{R} \) and \( p\Delta_{D} \), when significantly different from zero, reveal the presence of recombination \( (p > 0) \) and nonallelic interaction at the level of homologous chromosomes in the \( (R \times L_{w})F_{1} \times R \), \((R \times L_{w})F_{1} \times L_{w} \) and \((R \times L_{w})F_{2} \) populations \( (w = i,j) \).

The parameter \( \Delta \) is a compound quantity consisting of \( \frac{1}{2} p(p\Delta_{R} + p\Delta_{D}) \) and \( p^2 \) times the difference between the weighted mean of the recombinant \( \times \) recombinant genotypes and the mean of weighted means of the two kinds of nonrecombinant genotypes in the \( (R \times L_{w})F_{2} \) population \( (w = i,j) \). Like \( p\Delta_{R} \) and \( p\Delta_{D} \), when different from zero, \( \Delta \) proves that the differential loci \( \{r,s\}_{m} \) in \( U_{m \in M_{w}} \{r,s\}_{m} \) are
not independent in their action; in other words, that the effect of $\cup_{meM_w}\{r,s\}_m$ is different from $\sum_{meM_w}$ effect $\{r,s\}_m$.

By definition the parameter $\Delta_{ij}$ is equal to $\delta_{ij} - q(x_{ij} - y_{ij})$. The first term of this difference, i.e., $\delta_{ij}$, stands for the resultant of the nonallelic interaction effects at the level of nonhomologous chromosomes within the noncrossover subpopulation of the $(L_i \times L_i)F_2$ population other than $\delta_{ij}$ and, as such, pertains to the last three genotypes in Table 3. The second term, $q(x_{ij} - y_{ij})$, refers to both the presence of a crossover subpopulation in $(L_i \times L_i)F_2$ ($q > 0$) and the nonallelic interaction at the level of homologous and/or nonhomologous chromosomes within this subpopulation. Note that $q > 0$ implies crossing over and $x_{ij} - y_{ij} \neq 0$ implies nonallelic interaction. Since $\delta_{ij}$ and $q(x_{ij} - y_{ij})$ cannot be evaluated separately $\Delta_{ij} = \delta_{ij} - q(x_{ij} - y_{ij}) \neq 0$ shows that within the $(L_i \times L_i)F_2$ population there are nonallelic interactions other than $\delta_{ij}$, interactions involving both the chromosome and gene recombinations.

The parameter $(d)_k$ measures the deviation of the character-metrics of the donor $D$ and the disomic substitution line $L_i$ from their mean measurement and refers, therefore, to the homozygous allelomorphic sets $\cup_{i \neq j}(\cup_{meM_j}\{s\}_m)$ and $\cup_{i \neq j}(\cup_{meM_j}\{r\})$ contained in some or all $(J \leq 20)$ homologues of $D$ and $L_i$, except the $i$th homologue which is genotypically the same in both of them.

The parameter $(h)_k$ measures the deviation of the $(D \times L_i)F_1$ metric from the respective parental mean and represents the resultant effect of the interaction between all the sets $\cup_{meM_w}\{r,s\}_m \subset \cup_{i \neq j}(\cup_{meM_j}\{r,s\}_m)$ and of the allelic and/or nonallelic interaction within them. In other words, a significant $(h)_k$ value implies the presence of allelic interaction and/or nonallelic interaction at the level of homologous and/or nonhomologous chromosomes in heterozygous stage.

The parameter $(h)_{ik}$ measures the deviation of the $(D \times R)F_1$ metric from the respective parental mean. Since this cross is assumed to involve $U$ linkage groups and each linkage group to consist of $M_u$ differential loci $(M_u \geq 1)$ the implications of a significant $(h)_{ik}$ value are similar to those of $(h)_k$.

By definition $U = I \cup J : I \cap J = \phi$ and, by assumption $I = 1$, $J \geq 2$. Therefore, $\cup_{u \in U}(\cup_{meM_n}\{r,s\}_m) = \cup_{meM_i}\{r,s\}_m \cup (\cup_{i \neq j}(\cup_{meM_j}\{r,s\}_m))$. The resultant effect of the allelic and/or nonallelic interactions within the set $\cup_{meM_i}\{r,s\}_m$ is $(h)_i$, and that within the set $\cup_{i \neq j}(\cup_{meM_j}\{r,s\}_m)$ is $(h)_k$, as already noted. Consequently if these sets, as components of $\cup_{u \in U}(\cup_{meM_n}\{r,s\}_m)$, are independent in their action then $(h)_{ik} = (h)_i + (h)_k$, and if not $(h)_{ik} = (h)_i - (h)_k = \delta_{ik}$; $\delta_{ik} \neq 0$. Concisely: the parameter $\delta_{ik}$ indicates the presence of interaction between the $i$th pair and the set of $J$ pairs of homologues in the $(D \times R)F_1$ where they all are in heterozygous stage. The parameter $\delta_{ik}$, like $\delta_{ij}$, when different from zero reveals the presence of nonallelic interaction at the level of nonhomologous chromosomes.

The parameters $\Delta_k$ and $\Delta_u$ when different from zero both reveal the presence
of nonallelic interaction. Since both are compound quantities it is not possible to state how much of this interaction is of homologous-chromosomal and how much of nonhomologous chromosomal nature.

SUMMARY ABSTRACT

The quantitative-genetic analysis presented in this study is based on homologous-chromosomal sets of genes belonging to and acting within a system of nuclear genes controlling a metrical character in three specifically related parents. The three parents and their crosses, considered jointly, are referred to as a triparental group. Two types of such a group are considered: Type 1 and Type 2.

—The parental set constituting the basis of a group of Type 1 consists of a recipient variety and two of its disomic substitution lines; and that constituting the basis of a group of Type 2 consists of a recipient variety, a donor variety and one of the respective disomic substitution lines. —Set theory notation is used in deriving the nature of the parameters involved. If the recipient and donor varieties involved in the two group types are the same, their joint analysis provides 15 numerically computable parameters; and if at least one of them is different, then 17 such parameters are obtained. These parameters refer to gene action and interaction at the levels of homologous and nonhomologous chromosomes and/or groups of chromosomes.

LITERATURE CITED


