ANALYSIS OF DIALLEL, TRIALLEL AND QUADRALLEL CROSSES USING A GENERAL GENETIC MODEL

by

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1. INTRODUCTION

The estimation of genetic variances is generally accomplished in the following way, Cockerham, 1963. Relatives are created in some mating design and tested in some environmental design. Expectations of the sums of squares of a quadratic analysis of the observations lead to estimates of design components of variance and covariance which can be interpreted genetically and environmentally. The quadratic analysis can be viewed as resulting from a sequential fitting of a progressively more complicated model, called herein the design model. The components of variance of the design model are translated into covariances of relatives. It is the covariances of relatives that are often interpretable in terms of components of genetic variance.

Kempthorne, 1957, formulated a general factorial model of genetic effects for genes at multiple loci in diploids. Cockerham, 1972, organized these effects into summary ones reflecting the ancestral sources of the genes in the mating design. A quadratic analysis can be developed by successively fitting effects of this model. In that way, design effects are genetic effects and the procedure of translating from design effects to genetic effects (by way of covariances of relatives) is replaced with direct attention on genetic effects. Eberhart, 1964, Eberhart and Gardner, 1966, and Gardner and Eberhart, 1966, have discussed a similar genetic model for fixed effects. The analyses of diallel, triallel, and quadrallel hybrids have been considered separately by several authors, Hayman, 1954a,b, 1958a,b; 1960; Griffing, 1950, 1956; Kempthorne, 1956, 1957; and

Rawlings and Cockerham, 1962a,b; to name but a few, but never before have all three types of hybrids been analyzed in conformity with the same general genetic model.

The purpose of this dissertation is to develop quadratic analyses for these three types of hybrids by successive fitting of genetic effects of a general genetic model. The resulting analyses can be viewed as either of fixed effects or random effects, depending upon the experimental material utilized.

2. GENERAL MODEL

2.1 Genetic Model

The factorial model of gene effects, Kempthorne, 1957, is presented for genes at two loci in diploids. Consider for an individual genotype, loci x and y as in Figure 1 with i, j, k, and ℓ indexing the alleles. Using a for additive effects and d

Figure 1 Diagram of two loci with indexing of positions

for dominance effects the model for the genotypic effect can be written as

Notation	Description
$G_{ijk\ell}$ =	Genotypic effect =
$(a_i + a_j + d_{ij})$	(additive, a, and dominance, d, effects for locus x)
$+ (a_k + a_\ell + d_{k\ell})$	+ (additive, a, and dominance, d, effects for locus y)
$+ \{(aa)_{ik} + (aa)_{i\ell} + (aa)_{jk}$	+ (additive x additive effects)
$+ (aa)_{j\ell}\}$	

$+ \{(ad)_{i(k\ell)} + (ad)_{j(k\ell)}$ + (additive x dominance effects)

$+ (ad)_{k(ij)} + (ad)_{\ell(ij)}\}$

$+ (dd_{ijk\ell})$ + (dominance x dominance effects)

These effects can be summed over an unknown number of loci for individuals or entries such as hybrids and indexed so that the index is descriptive of the parental source of the genes, Cockerham, 1972. For additive effects let A_i indicate the summation of the additive effects of genes from the $i^{\underline{th}}$ parental source, and $\alpha_i/2$ the proportion of the genes received from the $i^{\underline{th}}$ parent. Then for any entry under consideration $\Sigma\alpha_i = 2$. For dominance effects, $\Sigma\delta_{ij}D_{ij}$, let $\delta_{ij}(\delta_{ii})$ be the proportion of genotypes for loci in the entry with alleles from parents i and $j(i)$. D_{ij} is the sum of dominance effects for these genes from parental sources i and j. $\Sigma\delta_{ij} = 1$ and $\alpha_i = 2\delta_{ii} + \Sigma_{j\neq i}\delta_{ij}$. A general model for an entry as a deviation from the population mean can now be written as

$$G = \Sigma\alpha_i A_i + \Sigma\delta_{ij}D_{ij} + (\Sigma\alpha_i A_i)^2 + (\Sigma\alpha_i A_i)(\Sigma\delta_{ij}D_{ij})$$

$$+ (\Sigma\delta_{ij}D_{ij})^2 + (\Sigma\alpha_i A_i)^3 + (\Sigma\alpha_i A_i)^4 + \ldots .$$

Expansions of the epistatic terms are instructive; for example,

$$(\Sigma\alpha_i A_i)^2 = \Sigma_i \alpha_i^2 (AA)_{ii} + 2\Sigma_{i<j} \alpha_i\alpha_j (AA)_{ij} .$$

The first summation in the expansion is for additive x additive interaction between alleles from the same parent and the latter involves

alleles from different parents. Also note that $(AA)_{ij}$ is an average of two additive x additive interaction effects: x genes from parent i with y genes from parent j , and y genes from parent i with x genes from parent j .

Models for three types of entries, diallel, triallel, and quadrallel, are now presented. First consider the entries of a diallel experiment in which selfs and reciprocals are omitted: $\alpha_i = \alpha_j = \delta_{ij} = 1$

$$G_{ij} = A_i + A_j + D_{ij} + (AA)_{ii} + (AA)_{jj} + 2(AA)_{ij}$$

$$+ (AD)_{i(ij)} + (AD)_{j(ij)} + (DD)_{(ij)(ij)} + \cdots . \qquad (2.1)$$

Next consider progeny of a three-way cross i x (j x k) with distinct parents: $\alpha_i = 1$, $\alpha_j = \alpha_k = \delta_{ij} = \delta_{ik} = \frac{1}{2}$,

$$G_{i(jk)} = A_i + \tfrac{1}{2} A_j + \tfrac{1}{2} A_k + \tfrac{1}{2} D_{ij} + \tfrac{1}{2} D_{ik} + (AA)_{ii}$$

$$+ \tfrac{1}{4} (AA)_{jj} + \tfrac{1}{4} (AA)_{kk} + \tfrac{2}{2} (AA)_{ij} + \tfrac{2}{2} (AA)_{ik}$$

$$+ \tfrac{2}{4} (AA)_{jk} + \tfrac{1}{2} (AD)_{i(ij)} + \tfrac{1}{2} (AD)_{i(ik)}$$

$$+ \tfrac{1}{4} (AD)_{j(ij)} + \tfrac{1}{4} (AD)_{k(ik)} + \tfrac{1}{4} (AD)_{j(ik)}$$

$$+ \tfrac{1}{4} (AD)_{k(ij)} + (AAA)_{iii} + \tfrac{1}{8} (AAA)_{jjj}$$

$$+ \tfrac{1}{8} (AAA)_{kkk} + \tfrac{3}{2} (AAA)_{iij} + \tfrac{3}{2} (AAA)_{iik}$$

$$+ \frac{3}{4}(AAA)_{jji} + \frac{3}{8}(AAA)_{jjk} + \frac{3}{4}(AAA)_{kki}$$

$$+ \frac{3}{8}(AAA)_{kkj} + \frac{6}{4}(AAA)_{ijk} + \frac{1}{4}(DD)_{(ij)(ij)}$$

$$+ \frac{1}{4}(DD)_{(ik)(ik)} + \frac{2}{4}(DD)_{(ij)(ik)} + \cdots . \qquad (2.2)$$

Three locus, all-additive types of interactions are included in the model since they are to be utilized in the analysis.

Finally, consider the model for the progeny of a four-way cross from four distinct parents $(i \times j) \times (k \times \ell)$, $\alpha_i = \alpha_j = \alpha_k = \alpha_\ell = \frac{1}{2}$ and $\delta_{ik} = \delta_{i\ell} = \delta_{jk} = \delta_{j\ell} = \frac{1}{4}$:

$$G_{(ij)(k\ell)} = \frac{1}{2}(A_i + A_j + A_k + A_\ell) + \frac{1}{4}(D_{ik} + D_{i\ell} + D_{jk} + D_{j\ell})$$

$$+ \frac{1}{4}\{(AA)_{ii} + (AA)_{jj} + (AA)_{kk} + (AA)_{\ell\ell}\} + \frac{2}{4}\{(AA)_{ij}$$

$$+ (AA)_{ik} + (AA)_{i\ell} + (AA)_{jk} + (AA)_{j\ell} + (AA)_{k\ell}\}$$

$$+ \frac{1}{8}\{(AAA)_{iii} + (AAA)_{jjj} + (AAA)_{kkk} + (AAA)_{\ell\ell\ell}\}$$

$$+ \frac{3}{8}\{(AAA)_{iij} + (AAA)_{iik} + (AAA)_{ii\ell} + (AAA)_{jji}$$

$$+ (AAA)_{jjk} + (AAA)_{jj\ell} + (AAA)_{kki} + (AAA)_{kkj} + (AAA)_{kk\ell}$$

$$+ (AAA)_{\ell\ell i} + (AAA)_{\ell\ell j} + (AAA)_{\ell\ell k}\}$$

$$+ \frac{6}{8}\{(AAA)_{ijk} + (AAA)_{ij\ell} + (AAA)_{ik\ell} + (AAA)_{jk\ell}\}$$

$$+\frac{1}{8}\{(AD)_{i(ik)}+(AD)_{i(i\ell)}+(AD)_{j(jk)}+(AD)_{j(j\ell)}$$

$$+(AD)_{k(ik)}+(AD)_{k(jk)}+(AD)_{\ell(i\ell)}+(AD)_{\ell(j\ell)}\}$$

$$+\frac{1}{8}\{(AD)_{i(jk)}+(AD)_{i(j\ell)}+(AD)_{j(ik)}+(AD)_{j(i\ell)}$$

$$+(AD)_{k(i\ell)}+(AD)_{k(j\ell)}+(AD)_{\ell(ik)}+(AD)_{\ell(jk)}\}$$

$$+\frac{1}{16}\{(AAAA)_{iiii}+(AAAA)_{jjjj}+(AAAA)_{kkkk}$$

$$+(AAAA)_{\ell\ell\ell\ell}\}$$

$$+\frac{4}{16}\{(AAAA)_{iiij}+(AAAA)_{iiik}+(AAAA)_{iii\ell}+(AAAA)_{jjji}$$

$$+(AAAA)_{jjjk}+(AAAA)_{jjj\ell}+(AAAA)_{kkki}+(AAAA)_{kkkj}$$

$$+(AAAA)_{kkk\ell}+(AAAA)_{\ell\ell\ell i}+(AAAA)_{\ell\ell\ell j}+(AAAA)_{\ell\ell\ell k}\}$$

$$+\frac{6}{16}\{(AAAA)_{iijj}+(AAAA)_{iikk}+(AAAA)_{ii\ell\ell}+(AAAA)_{jjkk}$$

$$+(AAAA)_{jj\ell\ell}+(AAAA)_{kk\ell\ell}\}$$

$$+\frac{12}{16}\{(AAAA)_{iijk}+(AAAA)_{iij\ell}+(AAAA)_{iik\ell}+(AAAA)_{kkij}$$

$$+(AAAA)_{kki\ell}+(AAAA)_{kkj\ell}+(AAAA)_{jjik}+(AAAA)_{jji\ell}$$

$$+ (AAAA)_{jjk\ell} + (AAAA)_{\ell\ell ij} + (AAAA)_{\ell\ell ik} + (AAAA)_{\ell\ell jk}\}$$

$$+ \frac{24}{16} (AAAA)_{ijk\ell}$$

$$+ \frac{1}{16} \{(DD)_{(ik)(ik)} + (DD)_{(i\ell)(i\ell)} + (DD)_{(jk)(jk)}$$

$$+ (DD)_{(j\ell)(j\ell)}\}$$

$$+ \frac{2}{16} \{(DD)_{(ik)(i\ell)} + (DD)_{(ik)(jk)} + (DD)_{(i\ell)(j\ell)}$$

$$+ (DD)_{(jk)(j\ell)}\}$$

$$+ \frac{2}{16} \{(DD)_{(ik)(j\ell)} + (DD)_{(i\ell)(jk)}\} + \ldots . \qquad (2.3)$$

For four-way crosses, three and four-locus, all-additive types of interactions are included in the model since they are to be utilized in the analysis.

Note that when all the effects of a particular type are added for any model $G = 2A + D + 4AA + 2AD + DD + \ldots$. Numerators in the models indicate the number of distinct effects that are averaged.

When individuals are random members of a linkage equilibrium, randomly mating population, the genetic effects are uncorrelated, Cockerham, 1963, and the total variance can be expressed as a sum of the variances of the effects:

$$\text{Total } \sigma^2_G = 2\sigma^2_A + \sigma^2_D + 4\sigma^2_{AA} + 2\sigma^2_{AD} + \sigma^2_{DD} + \ldots .$$

Comparing this to the model of Cockerham, 1954, where variances of a kind are summed into one term,

$$\text{Total } \sigma^2_G = \sigma^2_{\alpha} + \sigma^2_{\delta} + \sigma^2_{\alpha\alpha} + \sigma^2_{\alpha\delta} + \sigma^2_{\delta\delta} + \cdots ,$$

and the translation from one representation to the other is obvious.

For single crosses, G_{ij} , and assuming uncorrelated effects, the variance among unrelated single cross means is the total variance.

$$\sigma^2_G = 2\sigma^2_A + \sigma^2_D + 2\sigma^2_{AA_1} + 2\sigma^2_{AA_2} + 2\sigma^2_{AD_2} + \sigma^2_{DD_2} + 2\sigma^2_{AAA_1} + 6\sigma^2_{AAA_2} + \cdots .$$

The numerical subscripts refer to the number of lines involved in a variance component. If we let the components within a class be the same, i.e., $E(AA)^2_{ii} = E(AA)^2_{ij}$, or $\sigma^2_{AA_1} = \sigma^2_{AA_2}$, then

$$\sigma^2_G = 2\sigma^2_A + \sigma^2_D + 4\sigma^2_{AA} + 2\sigma^2_{AD} + \sigma^2_{DD} + 8\sigma^2_{AAA} + \cdots .$$

The variance among three-way cross means, which is not the total variance, is

$$\sigma^2_{G_{i(jk)}} = \frac{3}{2}\sigma^2_A + \frac{1}{2}\sigma^2_D + \frac{9}{8}\sigma^2_{AA_1} + \frac{9}{8}\sigma^2_{AA_2} + \frac{5}{8}\sigma^2_{AD_2} + \frac{1}{8}\sigma^2_{AD_3} + \frac{1}{8}\sigma^2_{DD_2}$$

$$+ \frac{1}{8}\sigma^2_{DD_3} + \frac{33}{32}\sigma^2_{AAA_1} + \frac{33}{32}\sigma^2_{AAA_2} + \frac{3}{8}\sigma^2_{AAA_3} + \cdots .$$

The numerical subscripts distinguish among 1, 2, and 3 line effects. Again if the components are the same within a category

$$\sigma^2_{G_{i(jk)}} = \frac{3}{2}\sigma^2_A + \frac{1}{2}\sigma^2_D + \frac{9}{4}\sigma^2_{AA} + \frac{3}{4}\sigma^2_{AD} + \frac{1}{4}\sigma^2_{DD} + \frac{27}{8}\sigma^2_{AAA} + \cdots .$$

Finally, the variance among four-way crosses is

$$\sigma^2_{G_{(ij)(k\ell)}} = \sigma^2_A + \tfrac{1}{4}\sigma^2_D + \tfrac{1}{4}\sigma^2_{AA_1} + \tfrac{3}{4}\sigma^2_{AA_2} + \tfrac{1}{8}\sigma^2_{AD_2} + \tfrac{1}{8}\sigma^2_{AD_3} + \tfrac{1}{64}\sigma^2_{DD_2}$$
$$+ \tfrac{1}{32}\sigma^2_{DD_3} + \tfrac{1}{64}\sigma^2_{DD_4} + \tfrac{1}{16}\sigma^2_{AAA_1} + \tfrac{9}{16}\sigma^2_{AAA_2} + \tfrac{6}{16}\sigma^2_{AAA_3}$$
$$+ \tfrac{1}{64}\sigma^2_{AAAA_1} + \tfrac{21}{64}\sigma^2_{AAAA_2} + \tfrac{36}{64}\sigma^2_{AAAA_3} + \tfrac{6}{64}\sigma^2_{AAAA_4} + \cdots .$$

If the components within a category are the same, then

$$\sigma^2_{G_{(ij)(k\ell)}} = \sigma^2_A + \tfrac{1}{4}\sigma^2_D + \sigma^2_{AA} + \tfrac{1}{4}\sigma^2_{AD} + \tfrac{1}{16}\sigma^2_{DD} + \sigma^2_{AAA} + \sigma^2_{AAAA} + \cdots .$$

Note that when components in a category are equated, the entire variance, whether it be for total, single crosses, three-way crosses or double crosses can be generated from the coefficients of σ^2_A and σ^2_D. Organizing the variance components into categories reflecting the number of contributing lines affords a convenient way of summarizing the kinds of effects involved in quadratic forms even though the effects are viewed as fixed effects.

Linkage affects the coefficients of the epistatic components when there is control over the grandparents; for example, in a four-way cross $(i \times j) \times (k \times \ell)$, without some recombination of genes within a chromosome or reassortment of chromosomes there can be no $(DD)_{(ij)(k\ell)}$ component and all of the dominance x dominance interactions would be of the $(DD)_{(ik)(ik)}$ type. With recombination and/or reassortment, dominance x dominance interactions of the type $(DD)_{(ik)(i\ell)}$ and $(DD)_{(ik)(j\ell)}$ become possible. With free

recombination the coefficients for triallel and quadrallel crosses are those given in (2.1) and (2.2). Linkage does not affect the coefficients of additive and dominance effects.

2.2 Experimental Model

Each type of hybrid is to be analyzed separately with the same experimental model giving rise to three analyses of variance. The experimental model is

$$Y_{[\ ]m} = \mu + r_m + G_{[\ ]} + e_{[\ ]m}$$

where

$Y_{[\ ]m}$ is the value of the progeny of cross [] in rep m

μ is the overall mean

r_m is the effect of replicate m

$G_{[\ ]}$ is the genotypic effect of cross []

$e_{[\ ]m}$ is the random error associated with cross [] in replicate m.

In the case of diallel, triallel, and quadrallel, [] becomes ij, $i(jk)$ and $(ij)(k\ell)$, repsectively. All line indexes, $i, j, k, \ell = 1, 2, 3, \ldots, n$, have the same range, where n is the total number of lines, except that they must be distinct for each hybrid. For replicates, $m = 1, 2, 3, \ldots, r$.

It is convenient at this point to lay out the notations to be used. A dot notation is used to indicate a summation, e.g., $Y_{(ij)(k\ell)}.$ is the summation over all reps of hybrid $(ij)(k\ell)$. $Y_{(ij)(..)}.$ is the summation of all quadrallel crosses with grandparental cross $i \times j$ over all reps. When parentheses are omitted, the summation is over all hybrids with the given parental identification regardless of how the hybrids are put together, e.g., $Y_{ijk..}$ is the summation of all four-way crosses involving grandparents i, j, and k regardless of how the grandparents were mated, summed over all reps; $Y_{ij..}$ is the summation of all three-way crosses involving lines i and j summed over all reps. The summations with parentheses removed can be calculated as simple sums of the sums with parentheses, but they are convenient for succinctly expressing sums of squares used in the analyses of variance. The notation n_i is used to denote $n-i$, and C_K^n to denote the number of combinations of n things taken K at a time.

The total number of hybrids is $C_2^n = nn_1/2$ for single crosses, $3.C_3^n = nn_1n_2/2$ for three-way crosses, and $3.C_4^n = nn_1n_2n_3/8$ for four-way crosses, where reciprocals are omitted. The factor of three for three-way and four-way crosses comes from the three ways that the same set of three or four lines can enter a cross.

3. ANALYSES OF VARIANCE

In each analysis the sums of squares for replications, treatments (hybrids), and error are the usual least squares partitions for a replicated experiment and are orthogonal by construction. The partitioning of the hybrid sum of squares follows from fitting effects in the general model in the order A, D, AA_1, AA_2, AD_2, AAA_1, AAA_2, AAA_3, AD_3, $AAAA_1$, $AAAA_2$, $AAAA_3$, $AAAA_4$, DD_2, DD_3, and DD_4, with A indicating additive effects; D , dominance effects; repetitions of letters, interactions; and the subscript, the number of lines involved in an interaction. Each sum of squares in the partitioning of the hybrid sum of squares is the additional accounted for by adding the effect to the model. The process of adding effects to the model was stopped when the entire hybrid sums of squares had been partitioned. Of course, it is not possible to obtain a sum of squares for each type of effect in the model for all analyses; for example, four-line interactions are not possible when only two-line crosses are made. Also some of the effects are completely confounded with previously fitted effects.

The analysis of variance for diallel crosses is given in Table 1. The hybrid sum of squares is broken into two parts, additive and dominance. The analysis of variance for triallel crosses is given in Table 2. The hybrid sum of squares is broken into seven additive parts, TA, TD, TAA_1, TAA_2, TAD_2, $TAAA_3$, and TAD_3 . The analysis of variance for quadrallel crosses is given in Table 3. The hybrid sum of squares is broken down into seven additive parts, QA, QD, QAA_2, $QAAA_3$, QAD_3, $QAAAA_4$, and QDD_4 .

Table 1 Analysis of variance for progeny of a diallel cross, selfs and reciprocals excluded

Source	df	Sums of Squares
Replicates	$r-1$	$\frac{2}{nn_1}\sum_m Y^2_{\cdot\cdot m} - \frac{2Y^2_{\cdots}}{rnn_1}$
Crosses	$\frac{nn_1}{2} - 1)$	$\frac{1}{r}\sum_{i<j}\sum Y^2_{ij\cdot} - \frac{2}{rnn_2} Y^2_{\cdots}$
Additive	n_1	$DA = \frac{1}{rn_2}\sum Y^2_{i\cdot\cdot} - \frac{4}{rnn_2} Y^2_{\cdots}$
Dominance	$\frac{nn_3}{2}$	$DD = \frac{1}{r}\sum_{i<j}\sum Y^2_{ij\cdot} - \frac{1}{rn_2}\sum_i Y^2_{i\cdot\cdot} + \frac{2}{rn_1n_2} Y^2_{\cdots}$
Error (Crosses x Replicates)	$(r-1)(\frac{nn_1}{2} - 1)$	DE by difference
Total	$\frac{rnn_1}{2} - 1$	$\sum_{i<j}\sum_m Y^2_{ijm} - \frac{2Y^2_{\cdots}}{rn_1n_2}$

Table 2 Analysis of variance of three-way crosses

Source	df	Sum of Squares
Correction factor	1	$C = \frac{2Y^2_{....}}{rnn_1n_2}$
Replications	(r-1)	$R = \frac{2\Sigma Y^2_{...m}}{nn_1n_2} - C$
Crosses	$(3C_3^n-1)$	$H = \frac{\Sigma\Sigma\Sigma_{i\ j<k\ j,k\neq i} Y^2_{i(jk)\cdot}}{r} - C$
Additive	n_1	$TA = \frac{1}{rn_2(3n-8)} \sum_i [2Y_{i(..)\cdot} + Y_{\cdot(i.)\cdot}]^2 - \frac{16}{rnn_2(3n-8)} Y^2_{....}$
Dominance	$\frac{nn_3}{2}$	$TD = \frac{1}{2rn_3} \sum_{i<j} [Y_{i(j.)\cdot} + Y_{j(i.)\cdot}]^2 - \frac{1}{2rn_2n_3} \sum_i [2Y_{i...} + Y_{\cdot(i.)\cdot}]^2 + \frac{4}{rn_1n_2n_3} Y^2_{....}$
Add. by Add. One-line	n_1	$TAA_1 = \frac{2}{rnn_2n_3(3n-8)} \sum_i [n_4Y_{i(..)\cdot} - n_2Y_{\cdot(i.)\cdot}]^2 - \frac{2}{rn_2n_3(3n-8)} Y^2_{....}$

Table 2 (Continued)

Add by Add Two-line	$\frac{nn_3}{2}$	$TAA_2 = \frac{1}{rn_1n_3n_4} \sum_{i<j} \sum [n_3Y_{.(ij).} + Y_{i(j.).} + Y_{j(i.).}]^2$	
		$- \frac{1}{rn_1n_2n_3n_4} \sum_{i} [2Y_{i(..).} + n_2Y_{.(i.).}]^2 + \frac{2}{rn_2n_3n_4} Y^2_{....}$	
Add by Dom Two-line	$\frac{n_1n_2}{2}$	$TAD_2 = \frac{1}{2rn_3} \sum_{i<j} \sum [Y_{i(j.).} - Y_{j(i.).}]^2 - \frac{1}{2rn_3} \sum_{i} [2Y_{i(..).} - Y_{.(i.).}]^2$	
Add by Add by Add Three-line	$\frac{nn_1n_5}{6}$	$TAAA_3 = \frac{1}{3r} \sum_{i<j<k} \sum \sum \sum Y^2_{ijk.} - \frac{1}{3rn_4} \sum_{i<j} \sum Y^2_{ij..} + \frac{2}{3rn_3n_4} \sum_{i} Y^2_{i...} - \frac{2}{rn_2n_3n_4} Y^2_{....}$	
Add by Dom Three-line	$\frac{nn_2n_4}{3}$	$TAD = \frac{1}{r} \sum_{i} \sum_{\substack{j<k \\ j,k \neq i}} \sum Y^2_{i(jk).} - TA - TD - TAA_1 - TAA_2 - TAD_2 - TAAA_3$	
Error	$(r-1)(3\ C^n_3-1)$	TE = By difference	
Total	$(3r\ C^n_3-1)$	$T = \sum_{i} \sum_{\substack{j<k \\ j,k \neq i}} \sum_{m} \sum \sum Y^2_{i(jk)m} - C$	

Table 3 Analysis of variance of four-way crosses

Source	df	Sum of Squares
Correction Factor	1	$C = \frac{8Y^2.....}{rnn_1n_2n_3}$
Replications	(r-1)	$R = \frac{8\sum Y^2....m}{nn_1n_2n_3} - C$
Crosses	$3C_4^n-1$	$H = \frac{1}{r}\sum_{\substack{i,j\neq k,\ell \\ i<k}}\sum_{i<j}\sum_{k<\ell}\sum Y^2_{(ij)(kl)\cdot} - C$
Additive	n_i	$QA = \frac{2}{rn_2n_3n_4}[\sum_i Y^2_{i....} - \frac{16}{n} Y^2.....]$
Dominance	$\frac{nn_3}{2}$	$QD = \frac{1}{r(n^2-7n+14)}[\sum_{i<j}\sum Y^2_{(i.)(j.).} - \frac{4}{n_2}\sum_i Y^2_{i....} + \frac{32}{n_1n_2} Y^2....]$
Add. by Add. Two-line	$\frac{nn_3}{2}$	$QAA_2 = \frac{2}{rn_4n_5(n^2-7n+14)}[\frac{1}{n_1n_2}\sum_{i<j}\sum \{(n^2-7n+14)Y_{(ij)(..).} + 2n_3Y_{(i.)(j.).}\}^2 - n_1\sum_i Y^2_{i....} + 8Y^2.....]$
Add. by Add. by Add. Three-line	$\frac{nn_1n_5}{6}$	$QAAA_3 = \frac{1}{3rn_6}\sum_{i<j<k}\sum\sum Y^2_{ijk..} - \frac{4}{3rn_4n_6}\sum_{i<j}\sum Y^2_{ij...} + \frac{6}{rn_3n_4n_6}\sum_i Y^2_{i....} - \frac{32\ Y^2....}{rn_2n_3n_4n_6}$

Table 3 (Continued)

Add. by Dom. Three-line	$\frac{nn_2n_4}{3}$	$QAD_3 = \frac{1}{rn_3} \sum_{\substack{i<j \\ i,j\neq k}} \sum_{k} Y^2_{(ij)(k.).} - \frac{1}{3rn_3} \sum_{i<j<k} \Sigma Y^2_{ijk..} - \frac{4}{rn_1n_3} \sum_{i<j} Y^2_{(ij)(..)} - \frac{2}{rn_1n_3} \sum_{i<j} Y^2_{(i.)(j.).} + \frac{4}{3rn_1n_3} \sum_{i<j} Y^2_{ij...}$
Add. by Add. by Add. by Add. Four-line	$\frac{nn_1n_2n_7}{24}$	$QAAAA_4 = \frac{1}{3r} \sum_{i<j<k<\ell} \Sigma Y^2_{ijk\ell.} - \frac{1}{3rn_6} \sum_{i<j<k} \Sigma Y^2_{ijk..} + \frac{2n_4}{3rn_4n_5n_6} \sum_{i<j} \Sigma Y^2_{ij...} - \frac{2}{rn_4n_5n_6} \sum_{i} Y^2_{i....} + \frac{2}{rn_3n_4n_5n_6} Y^2_{.....}$
Dom. by Dom. Four-line	$\frac{nn_1n_4n_5}{12}$	$QDD_4 = \frac{1}{r} \sum_{\substack{i<j \; k<\ell \\ i,j\neq k,\ell \\ i<k}} \sum \sum Y^2_{(ij)(k\ell).} - QA - QD - QAA_2 - QAAA_3 - QAD_3 - QAAAA_4$
Error	$(r-1)(3\,C^n_4-1)$	QE = by difference
Total	$3r\,C^n_4-1$	$T = \sum_{\substack{i<j \; k<\ell \; m \\ i,j\neq k,\ell \\ i<k}} \sum \sum \sum Y^2_{(ij)(k\ell)m} - C$

4. EXPECTED MEAN SQUARES

Three methods were used in obtaining the expected mean squares for the three analyses. Those for the diallel, Table 4, were obtained by substituting the model of effects into the mean squares and taking expectations assuming uncorrelated effects.

Table 4 Expectations of the mean squares of diallel analysis in terms of the variance components of the general model truncated to dominance by dominance effects

Source	E(MS)
Additive	$\sigma_e^2 + r(\sigma_D^2 + 2\sigma_{AA_2}^2 + 2\sigma_{AD_2}^2 + \sigma_{DD_2}^2) + rn_2(\sigma_A^2 + \sigma_{AA_1}^2)$
Dominance	$\sigma_e^2 + r(\sigma_D^2 + 2\sigma_{AA_2}^2 + 2\sigma_{AD_2}^2 + \sigma_{DD_2}^2)$
Error	σ_e^2

This method was used to check some of the results for the triallel and quadrallel analyses, but was found to be extremely tedious. The following method was used to obtain the expected mean squares for the triallel and quadrallel analyses. First, the covariances of genetic effects of three-way, Table 5, and four-way, Table 6, hybrid relatives were defined and their expectations obtained in terms of components of genetic variance. Next the expectations of the uncorrected products and squares of sums were obtained in terms of μ^2, σ_r^2, σ_e^2 and the covariances of relatives. These are given in Table 7 for the triallel analysis and Table 8 for the quadrallel analysis. Finally the results of Tables 5 and 7 were substituted into Table 2 and the

Table 5 Covariances of the genotypic effects of three-way hybrid relatives and their expectations in terms of components of genetic variance

Covariance*	Number of lines common	Coefficients of Variance Component										
		σ^2_A	σ^2_D	$\sigma^2_{AA_1}$	$\sigma^2_{AA_2}$	$\sigma^2_{AD_2}$	$\sigma^2_{AD_3}$	$\sigma^2_{AAA_1}$	$\sigma^2_{AAA_2}$	$\sigma^2_{AAA_3}$	$\sigma^2_{DD_2}$	$\sigma^2_{DD_3}$
$Cov_1 = E[G_{i(jk)}G_{i(jk)}]$	3	3/2	1/2	9/8	9/8	5/8	1/8	66/64	63/32	3/8	1/8	1/8
$Cov_2 = E[G_{i(jk)}G_{j(ik)}]$	3	5/4	1/4	9/16	1	1/4	1/16	17/64	42/32	3/8	1/16	0
$Cov_3 = E[G_{i(j-)}G_{i(j-)}]$	2	5/4	1/4	17/16	1/2	5/16	0	65/64	30/32	0	1/16	0
$Cov_4 = E[G_{i(j-)}G_{j(i-)}]$	2	1	1/4	1/2	1/2	1/4	0	16/64	24/32	0	1/16	0
$Cov_5 = E[G_{i(j-)}G_{-(ij)}]$	2	3/4	0	5/16	1/4	0	0	9/64	9/32	0	0	0
$Cov_6 = E[G_{-(ij)}G_{-(ij)}]$	2	1/2	0	1/8	1/8	0	0	2/64	3/32	0	0	0
$Cov_7 = E[G_{i(--)}G_{i(--)}]$	1	1	0	1	0	0	0	64/64	0	0	0	0
$Cov_8 = E[G_{i(--)}G_{-(i-)}]$	1	1/2	0	1/4	0	0	0	8/64	0	0	0	0
$Cov_9 = E[G_{-(i-)}G_{-(i-)}]$	1	1/4	0	1/16	0	0	0	1/64	0	0	0	0

*Dashes indicate any lines not common in the two relatives.

Table 6 Covariances of the genotypic effects of four-way hybrid relatives and their expectations in terms of components of genetic variance

Covariance*	Number of lines common	Coefficients of variance component															
		σ^2_A	σ^2_D	$\sigma^2_{AA_1}$	$\sigma^2_{AA_2}$	$\sigma^2_{AD_2}$	$\sigma^2_{AD_3}$	$\sigma^2_{AAA_1}$	$\sigma^2_{AAA_2}$	$\sigma^2_{AAA_3}$	$\sigma^2_{AAAA_1}$	$\sigma^2_{AAAA_2}$	$\sigma^2_{AAAA_3}$	$\sigma^2_{AAAA_4}$	$\sigma^2_{DD_2}$	$\sigma^2_{DD_3}$	$\sigma^2_{DD_4}$
$Cov_1 = E\, G_{(ij)(kl)}G_{(ij)(kl)}$	4	1	1/4	1/4	3/4	1/8	1/8	1/16	9/16	3/8	1/64	21/64	9/16	3/32	1/64	1/32	1/64
$Cov_2 = E\, G_{(ij)(kl)}G_{(ij)(kl)}$	4	1	1/8	1/4	3/4	1/16	1/16	1/16	9/16	3/8	1/64	21/64	9/16	3/32	1/128	0	1/128
$Cov_3 = E\, G_{(ij)(k-)}G_{(ij)(k-)}$	3	3/4	1/8	3/16	3/8	1/16	1/32	3/64	9/32	3/32	3/256	21/128	9/64	0	1/128	1/128	0
$Cov_4 = E\, G_{(ij)(k-)}G_{(ik)(j-)}$	3	3/4	1/16	3/16	3/8	1/32	1/64	3/64	9/32	3/32	3/256	21/128	9/64	0	1/256	0	0
$Cov_5 = E\, G_{(i-)(j-)}G_{(i-)(j-)}$	2	1/2	1/16	1/8	1/8	1/32	0	1/32	3/32	0	1/128	7/128	0	0	1/256	0	0
$Cov_6 = E\, G_{(ij)(--)}G_{(ij)(--)}$	2	1/2	0	1/8	1/8	0	0	1/32	3/32	0	1/128	7/128	0	0	0	0	0
$Cov_7 = E\, G_{(ij)(--)}G_{(i-)(j-)}$	2	1/2	0	1/8	1/8	0	0	1/32	3/32	0	1/128	7/128	0	0	0	0	0
$Cov_8 = E\, G_{(i-)(--)}G_{(i-)(--)}$	1	1/4	0	1/16	0	0	0	1/64	0	0	1/256	0	0	0	0	0	0

*Dashes indicate any lines not common in the two relatives.

Table 7 The expectations of products and squares of sums in terms of μ^2, σ_r^2, σ_e^2 and the covariances of three-way cross relatives

Sum Squared or Product	Coefficients of Covariance										
	$(r\mu^2+\sigma_r^2)$	σ_e^2	Cov_1	Cov_2	Cov_3	Cov_4	Cov_5	Cov_6	Cov_7	Cov_8	Cov_9
$\frac{1}{rnn_1n_2} Y^2_{....}$	$\frac{nn_1n_2}{4}$	$\frac{1}{2}$	$\frac{r}{2}$	r	rn_3	rn_3	$2rn_3$	$\frac{rn_3}{2}$	$\frac{rn_3n_4}{4}$	rn_3n_4	rn_3n_4
$\frac{2}{rn_1n_2} Y^2_{i(..).}$	$\frac{n_1n_2}{2}$	1	r	0	$2rn_3$	0	0	0	$\frac{rn_3n_4}{2}$	0	0
$\frac{1}{rn_1n_2} Y^2_{.(i.).}$	n_1n_2	1	r	r	rn_3	0	$2rn_3$	rn_3	0	0	rn_3n_4
$\frac{1}{rn_1n_2} Y_{i(..).}Y_{.(i.).}$	$\frac{n_1n_2}{2}$	0	0	r	0	rn_3	rn_3	0	0	rn_3n_4	0
$\frac{1}{rn_2} Y^2_{i(j.).}$	n_2	1	r	0	rn_3	0	0	0	0	0	0
$\frac{1}{rn_2} Y^2_{.(ij).}$	n_2	1	r	0	0	0	0	rn_3	0	0	0
$\frac{1}{rn_2} Y_{i(j.).}Y_{.(ij).}$	n_2	0	0	r	0	rn_3	0	0	0	0	0
$\frac{1}{r} Y^2_{i(jk).}$	1	1	r	0	0	0	0	0	0	0	0
$\frac{2}{3rn_1n_2} Y^2_{i...}$	$\frac{3n_1n_2}{2}$	1	r	2r	$\frac{4rn_3}{3}$	$\frac{4rn_3}{3}$	$\frac{8rn_3}{3}$	$\frac{2rn_3}{3}$	$\frac{rn_3n_4}{6}$	$\frac{2rn_3n_4}{3}$	$\frac{2rn_3n_4}{3}$
$\frac{1}{3rn_2} Y^2_{ij..}$	$3n_2$	1	r	2r	$\frac{2rn_3}{3}$	$\frac{2rn_3}{3}$	$\frac{4rn_3}{3}$	$\frac{rn_3}{3}$	0	0	0
$\frac{1}{3r} Y^2_{ijk.}$	3	1	r	2r	0	0	0	0	0	0	0

Table 8 The expectations of products and squares of sums in terms of μ^2, μ_r^2, σ_e^2 and the covariances of four-way cross relatives

Sum Squared or Product	Coefficients of Covariance									
	$(r\mu^2+\sigma_r^2)$	σ_e^2	Cov_1	Cov_2	Cov_3	Cov_4	Cov_5	Cov_6	Cov_7	Cov_8
$\frac{64}{rnn_1n_2n_3} Y^2....$	$nn_1n_2n_3$	8	8r	16r	$32rn_4$	$64rn_4$	$32rn_4n_5$	$8rn_4n_5$	$32rn_4n_5$	$164n_4n_5n_6$
$\frac{4}{rn_1n_2n_3} Y^2_{i...}$	$n_1n_2n_3$	2	2r	4r	$6rn_4$	$12rn_4$	$4rn_4n_5$	rn_4n_5	$4rn_4n_5$	$rn_4n_5n_6$
$\frac{4}{rn_2n_3} Y^2_{ij...}$	$9n_2n_3$	6	6r	12r	$12rn_4$	$24rn_4$	$4rn_4n_5$	rn_4n_5	$4rn_4n_5$	0
$\frac{1}{3rn_3} Y^2_{ijk..}$	$3n_3$	1	r	2r	rn_4	$2rn_4$	0	0	0	0
$\frac{1}{rn_2n_3} Y^2_{(i.)(j.).}$	n_2n_3	1	r	r	$2rn_4$	$2rn_4$	rn_4n_5	0	0	0
$\frac{2}{rn_2n_3} Y_{(ij)(..)}.Y_{(i.)(j.).}$	n_2n_3	0	0	2r	0	$4rn_4$	0	0	rn_4n_5	0
$\frac{4}{rn_2n_3} Y^2_{(ij)(..).}$	n_2n_3	2	2r	0	$4rn_4$	0	0	rn_4n_5	0	0
$\frac{1}{rn_3} Y^2_{(ij)(k.).}$	n_3	1	r	0	rn_4	0	0	0	0	0
$\frac{1}{r} Y^2_{(ij)(kl).}$	1	1	r	0	0	0	0	0	0	0

results of Tables 6 and 8 into Table 3 to give expected sums of squares for the triallel and quadrallel analyses respectively. Dividing by the degrees of freedom gave the expected mean squares for the triallel analysis, Table 9, and quadrallel analysis, Table 10.

The intermediate results, the expected mean squares in terms of covariances of relatives, are given in Appendices I and II. These types of results are instructive in the case of the diallel, Kempthorne, 1957, but do not appear to be here.

A third method of calculating expected mean squares, Gaylor, Lucas, and Anderson, 1970, using the forward solution of the abbreviated Doolittle method was used to check the expected mean squares of the triallel analysis. This method would be useful for a particular experiment where the number of lines is fixed, but it is difficult to apply to a general analysis. This method is of limited utility if the number of lines is large, as an excessively large matrix must be swept out by the abbreviated Doolittle method.

Table 9 Expectations of the mean squares of three-way crosses in terms of components of genetic variance

	Components of Variance										
Mean Square	σ^2_e	$\frac{\sigma^2_{DD_3}}{8}$	$\sigma^2_{AD_3}$	$\sigma^2_{AAA_3}$	$\sigma^2_{AD_2}$	$\sigma^2_{AAA_2}$	$\sigma^2_{AA_2}$	$\sigma^2_{AAA_1}$	$\sigma^2_{AA_1}$	$\{\sigma^2_D+\frac{1}{2}\sigma^2_{DD_2}\}$	σ^2_A
	Coefficients of Components of Variance										
TA*	1	r	$\frac{r(11n-32)}{16(3n-8)}$	$\frac{3rn_3}{(3n-8)}$	$\frac{r(41n^2-217n+288)}{16(3n-8)}$	$\frac{3r(101n^2-562n+784)}{32(3n-8)}$	$\frac{r(7n-20)^2}{8(3n-8)}$	$\frac{rn_2(9n-20)^2}{64(3n-8)}$	$\frac{rn_2(5n-12)^2}{16(3n-8)}$	$\frac{r(3n-8)}{4}$	$\frac{rn_2(3n-8)}{4}$
TD*	1	r	$\frac{r(3n-11)}{16n_3}$	$\frac{3rn_4}{4n_3}$	$\frac{9rn_3}{16}$	$\frac{3r(3n-10)^2}{16n_3}$	$\frac{r(2n-7)^2}{4n_3}$	0	0	$\frac{rn_3}{4}$	
TAA_1^*	1	r	$\frac{rn_2}{4(3n-8)}$	$\frac{3rn}{8(3n-8)}$	$\frac{rn_2n_3}{r(3n-8)}$	$\frac{3rn_3(5n-8)}{16(3n-8)}$	$\frac{rnn_3}{4(3n-8)}$	$\frac{9rnn_2n_3}{32(3n-8)}$	$\frac{rnn_2n_3}{8(3n-8)}$		
TAA_2^*	1	r	$\frac{rn_2}{8n_3}$	$\frac{3rn}{8n_3}$	0	$\frac{3rn_1n_4}{32n_3}$	$\frac{rn_1n_4}{8n_3}$				
TAD_2^*	1	r	$\frac{r}{16}$	0	$\frac{rn_3}{16}$	$\frac{3rn_3}{16}$					
$TAAA_3^*$	1	r	$\frac{r}{4}$	$\frac{9r}{8}$							
TAD_3^*	1	r	$\frac{r}{16}$								
TE*	1										

* Sum of squares divided by its degrees of freedom.

Table 10 Expectations of the mean squares of four-way crosses in terms of components of genetic variance

Mean Square	Components of Variance							
	σ^2_e	$\sigma^2_{DD_4}$	$\sigma^2_{AAAA_4}$	$\sigma^2_{AD_3}$	$\{\sigma^2_{AAA_3}+\frac{3}{2}\sigma^2_{AAAA_3}\}$	$\{\sigma^2_{AA_2}+\frac{3}{4}\sigma^2_{AAA_2}+\frac{7}{16}\sigma^2_{AAAA_2}\}$	$\{\sigma^2_D+\frac{1}{2}\sigma^2_{AD_2}+\frac{1}{16}\sigma^2_{DD_2}\}$	$\{\sigma^2_A+\frac{1}{4}\sigma^2_{AA_1}+\frac{1}{16}\sigma^2_{AAA_1}+\frac{1}{64}\sigma^2_{AAAA_1}\}$
QA*	1	$\frac{r}{32}$	$\frac{9r}{32}$	$\frac{3rn_4}{16}$	$\frac{27rn_4}{32}$	$\frac{9rn_2n_3}{32}$	$\frac{rn_3n_4}{8}$	$\frac{rn_2n_3n_4}{8}$
QD*	1	$\frac{r(3n^2-25n+54)}{128(n^2-7n+14)}$	$\frac{3rn_4n_5}{16(n^2-7n+14)}$	$\frac{r(3n^3-39n^2+17n-268)}{32(n^2-7n+14)}$	$\frac{3rn_4n_5^2}{8(n^2-7n+14)}$	$\frac{rn_4n_5^2}{16(n^2-7n+14)}$	$\frac{r(n^2-7n+14)}{16}$	
QAA^*_2	1	$\frac{r(n^2-5n+8)}{64(n^2-7n+14)}$	$\frac{3rn_1n_2}{32(n^2-7n+14)}$	$\frac{rn_2^2n_5}{16(n^2-7n+14)}$	$\frac{3rn_1n_2n_5}{16(n^2-7n+14)}$	$\frac{rn_1n_2n_4n_5}{32(n^2-7n+14)}$		
$QAAA^*_3$	1	$\frac{r}{32}$	$\frac{9r}{32}$	$\frac{rn_6}{16}$	$\frac{9rn_6}{32}$			
QAD^*_3	1	$\frac{r}{128}$	0	$\frac{rn_3}{64}$				
$QAAAA^*_4$	1	$\frac{r}{32}$	$\frac{9r}{32}$					
QDD^*_4	1	$\frac{r}{128}$	0					
QE*	1							

5. TESTS OF HYPOTHESES FOR FIXED EFFECTS

Certain tests of hypotheses are available without making any assumptions about the genetic effects. The mean square expectations in Tables 4, 9, and 10 in this case serve only as guides to the types of effects that can contribute to the mean squares; the mean squares actually involve quadratic functions of these types of effects. The error mean square can be used as the denominator in an F ratio testing sequentially up each table. Table 11 gives lowest order types of effects that are tested in each mean square for each analysis; higher order effects are also tested for in each. As we proceed to test up the table lower order genetic effects become involved. The method of obtaining each analysis of variance guarantees that quadratic forms of previously fitted effects do not appear in subsequent mean squares, although similar interaction type effects, e.g., AA_2 after the fitting of AA_1, and AD_3 after the fitting of AD_2, may appear in subsequent mean squares. Also there are two things which complicate the interpretation of the non-significance of a particular mean square. First, the genetic model effects are a summation of allelic effects and may sum to zero when allelic effects are present. Also, the quadratic functions of a particular type of genetic effect differ from mean square to mean square so the conclusion that certain quadratic functions are zero in one mean square does not guarantee that the same is true in another mean square.

Table 11 Lowest order type of effects tested for in the diallel, triallel and quadrallel analyses for the various mean squares. A -- indicates there is no corresponding mean square for that analysis

Mean Square	DIALLEL	TRIALLEL	QUADRALLEL
A	A_i	A_i	A_i
D	D_{ij}	D_{ij}	D_{ij}
AA_1	--	AA_{ii}	--
AA_2	--	AA_{ij}	AA_{ij}
AD_2	--	$AD_{i(ij)}$	--
AAA_3	--	AAA_{ijk}	AAA_{ijk}
AD_3	--	$AD_{i(jk)}$	$AD_{i(jk)}$
$AAAA_4$	--	--	$AAAA_{ijk\ell}$
DD_4	--	--	$DD_{(ij)(k\ell)}$

6. VARIANCE COMPONENTS AND TESTS OF HYPOTHESES

By assuming the effects of the genetic model are random, and uncorrelated, and that there are common variances within certain categories, genetic variance components can be estimated. These assumptions were made in arriving at the expectations of the mean squares. When the general model is truncated for each analysis to those terms given in Table 11, the comparable variance components can be estimated by equating mean squares to expected mean squares and solving the resulting equations. In the diallel it is possible to estimate σ^2_A and σ^2_D; in the triallel, σ^2_A, σ^2_D, $\sigma^2_{AA_1}$, $\sigma^2_{AA_2}$, $\sigma^2_{AD_2}$, $\sigma^2_{AAA_3}$, and $\sigma^2_{AD_3}$; and in the quadrallel, σ^2_A, σ^2_D, $\sigma^2_{AA_2}$, $\sigma^2_{AAA_3}$, $\sigma^2_{AD_3}$, $\sigma^2_{AAAA_4}$, and $\sigma^2_{DD_4}$. Other variance components defined and given in the tables of expected mean squares are confounded with these estimators although not always in a simple manner.

The diallel analysis gives a good example of simple patterns of confounding; all one-line variance components are completely confounded and estimated as one package, $\sigma^2_A + \sigma^2_{AA_1}$, and all two-line variance components are estimated together, $\sigma^2_D + 2\sigma^2_{AA_2} + 2\sigma^2_{AD_2} + \sigma^2_{DD_2}$. An example of a more difficult confounding pattern can be seen in the triallel analysis for $\sigma^2_{AD_3}$ and $\sigma^2_{DD_3}$ in the following manner. Two types of additive by dominance, three-line variance components are distinguished, depending on how the effects come together in taking expectations. Let $E\{AD^2_{\underline{i}(j\underline{k})}\} = E\{AD^2_{\underline{i}(\underline{j}k)}\} = \sigma^2_{1AD_3}$ and $E\{AD_{\underline{i}(\underline{j}k)} \cdot AD_{\underline{i}(j\underline{k})}\} = \sigma^2_{2AD_3}$, the underscore indicating whether the grandparental source of alleles is the same, $\sigma^2_{1AD_3}$, or

different, $\sigma^2_{2AD_3}$. In $\sigma^2_{1AD_3}$ the underscore emphasizes that $E\{AD^2_{\underline{i}(jk)}\} = E\{AD_{\underline{i}(jk)} \cdot AD_{\underline{i}(jk)}\}$ and that i x j was the grandparental cross referenced by i and j. In $\sigma^2_{2AD_3}$ the effects, $AD_{\underline{i}(jk)}$ and $AD_{\underline{i}(j\underline{k})}$, come from different grandparental sources, i x j and i x k. With this distinction made, $\sigma^2_{DD_3}$ is completely confounded with $\sigma^2_{1AD_3}$. The distinction, other than to show that $\sigma^2_{DD_3}$ and $\sigma^2_{AD_3}$ are confounded, does not appear useful so $\sigma^2_{1AD_3}$ is assumed equal to $\sigma^2_{2AD_3}$ and both are termed $\sigma^2_{AD_3}$.

Any variance component or sum of variance components that can be estimated can be tested, subject to the condition that the effects in the model are distributed normally. The error mean square can be used as the denominator in an F-test to test certain exact and composite hypotheses. With each analysis restricted to terms in Table 11, DD*/DE*, TAD^*_3/TE^*, and QDD^*_4/QE^* provide exact tests for $\sigma^2_D = 0$, $\sigma^2_{AD_3} = 0$ and $\sigma^2_{DD_4} = 0$. Composite hypotheses, testing each mean square versus error, are possible for the linear functions of variance components given in the tables of expected mean squares, e.g., in the triallel TAD^*_2/TE^* tests the hypothesis that

$$\frac{r}{16}\sigma^2_{AD_3} + \frac{rn_3}{16}\sigma^2_{AD_2} + \frac{3rn_3}{16}\sigma^2_{AAA_2} = 0 .$$

Exact tests are not generally available for testing other variance components; however, approximate F-tests are.

Satterthwaite, 1946, suggested that a linear function of mean squares, $(\Sigma a_i MS_i)$ is approximately distributed as $\chi^2\sigma^2/f'$ with f' degrees of freedom where

$$f' = (\Sigma a_i MS_i)^2/\Sigma(a_i^2 MS_i^2/f_i) \qquad (6.1)$$

and f_i denotes the degrees of freedom for mean squares MS_i. Using Satterthwaite's approximation, error terms can be constructed to test each of the components of variance. For example, in the triallel analysis

$$4TAD_3^* - 3TE^*$$

has expectation $\sigma_e^2 + \frac{r}{4}\sigma_{AD_3}^2$, the correct expectation of an error term for testing the significance of $\sigma_{AAA_3}^2$ in $TAAA_3^*$ and can be used to form an approximate F-test

$$\frac{TAAA_3^*}{4TAD_3^* - 3TE^*}$$

with degrees of freedom $nn_1n_5/6$ and f' where f' can be obtained from (6.1).

7. DISCUSSION OF RESULTS

7.1 Diallel

Since truncation of the general model to additive and dominance effects corresponds exactly to the usual model for general and specific combining ability, the partitioning of the sums of squares is identical. Several things become apparent from examination of the expected mean squares. There are two types of effects, and consequently variance components, single-line and two-line. The single-line types are confounded with each other and must be estimated jointly. The two-line types are also completely confounded and must be estimated in a single package. It is the splitting of the epistatic variance into two parts, within line and between lines, that makes the estimation of single-line and two-line packages possible. All single-line effects are removed with additive effects. As one would expect from the expression of the total genetic variance for two-line crosses, only one-line and two-line variance components appear in the analysis.

7.2 Triallel

Examination of the expected mean squares indicates that whereas the genetic model is simple in concept and interpretation the expected mean squares are complex. It can be seen that the order of fitting of dominance and additive by additive, single-line effects is immaterial. This is also true for additive by additive, two-line effects and additive by dominance, two-line effects.

In considering a fixed effects model, it is possible to combine the mean squares in the analysis presented into single-line ($TA + TAA_1$), two-line ($TD + TAA_2 + TAD_2$) and three-line ($TAAA_3 + TAD_3$) partitions to give a new analysis. In testing against error sequentially up the resulting analysis, three-line, two-line, and single-line effects successively come into play.

In the estimation of genetic variances mean squares of the analysis may be combined to correspond to assumptions about the variance components. If it is assumed that $\sigma^2_{AA_1}$ and $\sigma^2_{AA_2}$ are identical, the corresponding mean squares in the analysis can be combined to estimate σ^2_{AA}. Likewise if it is assumed that $\sigma^2_{AD_2}$ and $\sigma^2_{AD_3}$ are identical, the corresponding mean squares can be combined to estimate σ^2_{AD}. When these mean squares are combined, weighting by the degrees of freedom, the coefficients of the variance components in the resulting expected mean squares remain complex. If it is assumed that $\sigma^2_{AD_3} = \sigma^2_{AD_2} = \sigma^2_{AD}$ and $\sigma^2_{AAA_2} = 0$, it then becomes possible to estimate $\sigma^2_{DD_3}$ by manipulation of the mean squares.

$$\hat{\sigma}^2_{DD_3} = \frac{8}{r}\left\{\frac{n_2}{n_3} TAD^*_3 - \frac{1}{n_3} TAD^*_2 - TE^*\right\} .$$

The point is that by assuming genetic variance components within a category to be equal, other higher order variance components become estimable.

This analysis can be compared to that of Rawlings and Cockerham, 1962a. There is a simple relation between the sums of squares in the two analyses, Table 12.

Table 12 Relation of sums of squares of Rawlings and Cockerham, 1962a, to those of the general model for triallel crosses

Description	Sums of Squares Rawlings and Cockerham 1962a		Sums of Squares General Model
1-line	$G + O_1$	=	$TA + TAA_1$
2-line 2-alleles	$S_2 + O_{2_a}$	=	$TD + TAA_2$
2-line 3-alleles	O_{2_b}	=	TAD_2
3-line 3-alleles	S_3	=	$TAAA_3$
	O_3	=	TAD_3

The two analyses differ in the genetic variance components that are estimable. In the analysis of Rawlings and Cockerham, 1962a, the design components of variance were expressed in terms of covariances of relatives, and these in turn in terms of genetic variance components. The estimation of genetic variance components was then accomplished by equating the estimated design components of variance to their expected values in terms of genetic components of variance, and solving the resulting equations after suitably restricting the genetic variance components. When the genetic variance components were restricted to the seven lowest order ones, it was found that there was a linear dependency in the seven resulting equations so that only six genetic variance components, σ^2_{α}, σ^2_{δ}, $\sigma^2_{\alpha\alpha}$, $\sigma^2_{\alpha\delta}$, $\sigma^2_{\delta\delta}$, and $\sigma^2_{\alpha\alpha\alpha}$, could be estimated. In the design presented here, seven

genetic variance components can be estimated, σ^2_A, σ^2_D, $\sigma^2_{AA_1}$, $\sigma^2_{AA_2}$, $\sigma^2_{AD_2}$, $\sigma^2_{AAA_3}$, and $\sigma^2_{AD_3}$, but only five distinct kinds of variance components. Again, if $\sigma^2_{AD_2}$ is assumed equal to $\sigma^2_{AD_3}$ then one can estimate $\sigma^2_{DD_3}$.

7.3 Quadrallel

The coefficients of the genetic components of variance in the expected mean squares are complex functions of the numbers of grandparents. The order of fitting of D and AA_2 affects the corresponding mean squares. The fitting of first D then AA_2 was adopted as most reasonable. This analysis does not offer the possibility of combining of mean squares for the estimation of variance components as was possible for the triallel analysis because mean squares in the analysis are not available for the two types of additive by additive or additive by dominance effects. It is reasonable, however, when analyzing fixed effects, to combine the mean squares for dominance and additive by additive, two-line effects to give a mean square corresponding to two-line effects. Combining $QAAA_3$ and QAD_3 gives a mean square for three-line effects; $QAAAA_4$ and QDD_4, a mean square for four-line effects. The analysis then separates one-line, two-line effects corrected for one-line effects; three-line effects corrected for one-line and two-line effects; and four-line effects corrected for one, two, and three-line effects.

With two exceptions there is an exact correspondence between the sums of squares for this analysis and those of Rawlings and Cockerham, 1962b, Table 13. Reversing the order of fitting of D and AA_2

effects gives the identical sums of squares of Rawlings and Cockerham, 1962b, $S_2 = QAA'_2$, $T_2 = QD'$, the prime indicating that the order of fitting effects is AA_2 , D .

Table 13 Relation of sums of squares of Rawlings and Cockerham, 1962b, to those of the general model for quadrallel crosses

Description	Sum of Squares Rawlings and Cockerham 1962b		Sum of Squares General Model
1-line	G	=	QA
2-line 2-alleles	$S_2 + T_2$	=	$QD + QAA_2$
	S_2	=	QAA'_2
	T_2	=	QD'
3-line 3-alleles	S_3	=	$QAAA_3$
	T_3	=	QAD_3
4-line 4-alleles	S_4	=	$QAAAA_4$
	T_4	=	QDD_4

With a restricted genetic model, Rawlings and Cockerham were able to estimate six genetic variance components, σ^2_α , σ^2_δ , $\sigma^2_{\alpha\alpha}$, $\sigma^2_{\alpha\delta}$, $\sigma^2_{\delta\delta}$, and $\sigma^2_{\alpha\alpha\alpha}$. A corresponding variance component is estimable for each of these in the analysis presented here. In the analysis

presented here we are able to estimate a seventh variance component, $\sigma^2_{AAAA_4}$. However, Rawlings and Cockerham could have estimated a corresponding variance component, $\sigma^2_{\alpha\alpha\alpha\alpha}$, had they not restricted their genetic model.

7.4 General Discussion

The primary purpose of developing the analyses of variance for diallel, triallel, and quadrallel crosses was to demonstrate how the hybrid sum of squares would be partitioned if a uniform genetic model was used in all three analyses. This use of a general genetic model for the development of the partitioning of the various hybrid sums of squares is in contrast to previous use of design models for each of the analyses. The sums of squares were developed by successively fitting a more complex genetic model so that each line in the resulting analysis of variance is corrected for previously fitted effects. The partitioning developed can be used in three ways. With no assumptions concerning population structure, the sums of squares can be used to test for fixed effects. This use would be helpful in analyzing crosses of elite lines where assumptions of random mating and of no selection are seldom tenable. With the assumptions given by Cockerham, 1954, 1961, covariances of relatives can be related to genetic variance components and the analyses presented here can be used to estimate and test these genetic variance components. Finally, a new set of genetic variance components can be defined in terms of the general genetic model used in developing the partitioning of the hybrid sum of squares and these can be estimated, tested, and related to previously used genetic variance components.

The variance components defined and used in these analyses are directly related to previously used variance components for additive and dominance effects. It is in the epistatic variance components that the two analyses differ; the previously defined epistatic variance components are partitioned into variance components that reflect the number of lines contributing effects. For example, the additive by additive genetic variance component, $\sigma^2_{\alpha\alpha}$, of the standard analysis is divided into an additive by additive, one-line component $\sigma^2_{AA_1}$ and an additive by additive, two-line component $\sigma^2_{AA_2}$. The one-line component arises from interactions of alleles between loci, but between the genes contributed by one line. The two-line component arises from interactions of alleles between loci and between genes of two lines. It could be argued that adapted lines have adapted AA_1 effects, giving some reason for separating AA_1 effects from AA_2 effects. The other epistatic components are partitioned similarly.

The correlations between the additive deviations, α, and between the dominance deviations, δ, of Rawlings and Cockerham, 1962a and 1962b, are directly related to the coefficients of the genetic variance components used in expressing the expectations of covariances of relatives. If lines used in constructing hybrids are completely inbred, summing coefficients of components of genetic variance within a category gives the corresponding correlation of Rawlings and Cockerham when their α is multiplied by two.

In the analysis of diallel crosses the hybrid sum of squares is partitioned into two parts, there are two covariances among relatives,

and with suitable restrictions there are two genetic variance components, σ^2_A , σ^2_D , that can be estimated. In the analysis of triallel crosses the hybrid sum of squares is partitioned into seven parts; there are nine covariances among relatives, and there are seven genetic variance components, σ^2_A , σ^2_D , $\sigma^2_{AA_1}$, $\sigma^2_{AA_2}$, $\sigma^2_{AD_2}$, $\sigma^2_{AAA_3}$, $\sigma^2_{AD_3}$; that can be estimated with suitable restrictions. If variance components within a category are assumed identical, then by pooling lines in the analysis of variance there are five variance components, σ^2_A , σ^2_D , σ^2_{AA} , σ^2_{AAA} , σ^2_{AD} , that can be estimated. In the analysis of quadrallel cross hybrids the hybrid sum of squares is partitioned into seven parts; there are eight covariances among relatives, and there are seven genetic variance components, σ^2_A , σ^2_D , $\sigma^2_{AA_2}$, $\sigma^2_{AAA_3}$, $\sigma^2_{AD_3}$, $\sigma^2_{AAAA_4}$, $\sigma^2_{DD_4}$, that can be estimated with suitable restrictions. In this analysis it is not possible to combine variance components within a category as only one variance component within a category is estimable.

The minimum number of lines necessary for a complete analysis for each of the analyses is the minimum number of lines necessary to construct at least one pair of unrelated hybrids. For example, with four lines A, B, C, D, it is possible to construct unrelated single crosses A x B and C x D so that a complete diallel analysis is possible; for the triallel, six lines are needed; and for the quadrallel, eight lines are needed. The minimum number of hybrids are 6, 60, and 210 for diallel, triallel, and quadrallel designs, respectively. Additions to the numbers of parental lines sampled increase the number of hybrids dramatically. For example, adding

only one additional line to the three designs increases the numbers of hybrids to 10, 105 and 378. It is possible that some systematic subsampling of hybrids (partial designs) in the case of the triallel and quadrallel would be beneficial by allowing a greater sampling of parental lines without the concomitant increase in total hybrids required by the complete designs.

One point exemplified by these analyses is the confounding of genotypic effects with line effects. In the diallel analysis there are only one and two-line type effects. All one-line effects are completely confounded with additive effects. Two-line epistatic effects are combined with dominance effects. In the triallel analysis there are one, two, and three-line effects and these show up in the different mean squares of the analysis of variance, splitting mean squares that would correspond to the usual epistatic variance components. In the quadrallel analysis there are one, two, three, and four-line effects and within a category, say dominance by dominance, the lower-line variance components, $\sigma^2_{DD_2}$, $\sigma^2_{DD_3}$, are confounded with previously fitted categories.

8. SUMMARY

A quadratic analysis of diallel, triallel, and quadrallel hybrids is provided using a general genetic model. Sums of squares are developed by fitting successively additive, dominance, additive by additive, etc. effects. In the fitting process, the standard epistatic variance components are split into categories indexed by the number of lines contributing alleles to the effect. For example, the standard additive by additive variance component, $\sigma^2_{\alpha\alpha}$, is split into two components, $\sigma^2_{AA_1}$ and $\sigma^2_{AA_2}$, with numerical subscripts indexing the number of lines contributing to the effect. Also $\sigma^2_{\alpha\alpha} = 2\sigma^2_{AA_1} + 2\sigma^2_{AA_2}$; assuming $\sigma^2_{AA_1} = \sigma^2_{AA_2} = \sigma^2_{AA}$, then $\sigma^2_{\alpha\alpha} = 4\sigma^2_{AA}$.

For the diallel analysis, the results are essentially identical to those of the standard analysis (e.g., Kempthorne, 1957). There are two covariances of relatives, two hybrid sums of squares, and two variance components (if the model is suitably restricted) that can be estimated. For the triallel anaysis, the results are somewhat different from those of the analysis of Rawlings and Cockerham, 1962a. Both analyses have nine covariances of relatives and seven hybrid sums of squares. With the restrictions on the genetic model used by Rawlings and Cockerham, 1962a, six genetic variance components can be estimated. With the analysis presented here, seven genetic variance components can be estimated; however, some pairs of these components correspond to the same category of effects in the standard model, e.g., $\sigma^2_{AA_1}$, $\sigma^2_{AA_2}$ correspond to $\sigma^2_{\alpha\alpha}$. For the quadrallel analysis, the results are similar to the analysis of Rawlings and Cockerham, 1962b. Both

analyses have eight covariances of relatives and seven hybrid sums of squares. With the restrictions of Rawlings and Cockerham on their genetic model, there are six genetic variance components that can be estimated. Without their restrictions, seven variance components can be estimated, which correspond to the seven variance components estimated in the present analysis, σ^2_A, σ^2_D, $\sigma^2_{AA_2}$, $\sigma^2_{AAA_3}$, $\sigma^2_{AD_3}$, $\sigma^2_{AAAA_4}$, and $\sigma^2_{DD_4}$. Genetic variance components can be tested, although the tests usually involve linear combinations of mean squares. Tables of expected mean squares are given and are useful in determining confounding patterns of the genetic effects.

If the genetic effects are considered fixed, it is possible to make certain tests of hypotheses without making any assumptions about the genetic effects. These tests are discussed.

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Appendix I Expectations of the mean squares for the triallel analysis in terms of the covariances of relatives

Mean Square	Cov_1	Cov_2	Cov_3	Cov_4	Cov_5
TA*	r	$\frac{r(5n-16)}{3n-8}$	$\frac{rn_3(5n-16)}{3n-8}$	$\frac{4rn_3n_4}{3n-8}$	$\frac{2rn_3(3n-16)}{3n-8}$
TD*	r	$\frac{rn_5}{n_3}$	rn_5	$\frac{r(n^2-7n+14)}{n_3}$	$-\frac{2r(3n-11)}{n_3}$
TAA_1^*	r	$-\frac{2rn_4}{3n-8}$	$\frac{2rn_4(2n-5)}{3n-8}$	$-\frac{2r(2n^2-11n+16)}{(3n-8)}$	$\frac{4rn_4}{3n-8}$
TAA_2^*	r	$\frac{2r}{n_3}$	$-2r$	$-\frac{2r}{n_3}$	$-\frac{4r}{n_3}$
TAD_2^*	r	$-r$	rn_5	$-rn_4$	$2r$
$TAAA_3^*$	r	$2r$	$-2r$	$-2r$	$-4r$
TAD_3^*	r	$-r$	$-2r$	r	$2r$

Mean Square	Cov_6	Cov_7	Cov_8	Cov_9
TA*	$\frac{rn_3n_8}{3n-8}$	$\frac{rn_3n_4n_4}{3n-8}$	$\frac{2rn_3n_4n_8}{3n-8}$	$\frac{rn_3n_4(n-16)}{3n-8}$
TD*	$-\frac{rn_5}{n_3}$	$-rn_4$	$-\frac{2rn_4n_5}{n_3}$	$-\frac{rn_4n_9}{n_3}$
TAA_1^*	$\frac{r(2n^2-9n+8)}{(3n-8)}$	$\frac{rn_4(n^2-9n+16)}{2(3n-8)}$	$-\frac{2rn_4(n^2-5n+8)}{3n-8}$	$\frac{2rn_1n_4n_4}{3n-8}$
TAA_2^*	$\frac{r(n^2-6n+7)}{n_3}$	r	$\frac{4r}{n_3}$	$-\frac{2r(n^2-6n+6)}{n_3}$
TAD_2^*	$-r$	$-rn_4$	$2rn_4$	$-rn_4$
$TAAA_3^*$	$-r$	r	$4r$	$4r$
TAD_3^*	$-r$	r	$-2r$	r

Appendix II Expectations of the mean squares for the quadrallel analysis in terms of the covariances of relatives

Mean Square	Cov_1	Cov_2	Cov_3	Cov_4
QA*	r	2r	r(3n-16)	2r(3n-16)
QD*	r	$\frac{r(n^2-11n+26)}{(n^2-7n+14)}$	$\frac{2rn_4(n^2-9n+24)}{(n^2-7n+14)}$	$\frac{2rn_4(n^2-15n+46)}{(n^2-7n+14)}$
QAA^*_2	r	$\frac{4rn_3}{(n^2-7n+14)}$	$\frac{2r(n^3-12n^2+45n-58)}{(n^2-7n+14)}$	$\frac{4r(n^2-11n+22)}{(n^2-7n+14)}$
$QAAA^*_3$	r	2r	rn_{10}	$2rn_{10}$
QAD^*_3	r	-r	rn_7	$-rn_5$
$QAAAA^*_4$	r	2r	-4r	-8r
QDD^*_4	r	-r	-4r	4r

Mean Square	Cov_5	Cov_6	Cov_7	Cov_8
QA*	$2rn_5n_8$	$\frac{rn_5n_8}{2}$	$2rn_5n_8$	$\frac{rn_5n_6n_{16}}{2}$
QD*	$\frac{rn_4n_5(n^2-11n+42)}{(n^2-7n+14)}$	$-\frac{2rn_4n_5^2}{(n^2-7n+14)}$	$-\frac{8rn_4n_5^2}{(n^2-7n+14)}$	$-\frac{2rn_4n_5n_6n_9}{(n^2-7n+14)}$
QAA^*_2	$-\frac{4r(n^3-10n^2+29n-28)}{(n^2-7n+14)}$	$\frac{r(n^4-16n^3+93n^2-230n+216)}{2(n^2-7n+14)}$	$-\frac{8r(n^2-9n+16)}{(n^2-7n+14)}$	$-\frac{rn_1n_2n_6n_9}{(n^2-7n+14)}$
$QAAA^*_3$	$-4rn_3$	$-rn_8$	$-4rn_8$	3r(3n-22)
QAD^*_3	$-rn_5$	$-rn_5$	$2rn_5$	0
$QAAAA^*_4$	8r	2r	8r	-12r
QDD^*_4	2r	2r	-4r	0