CONCEPT OF GENERAL AND SPECIFIC COMBINING ABILITY IN RELATION TO DIALLEL CROSSING SYSTEMS

By B. Griffing*

Summary

A detailed examination of the concept of combining ability in relation to diallel crossing systems is made. Eight different analyses are presented. These result from a consideration of four different diallel crossing systems together with two alternative assumptions with regard to the sampling nature of the experimental material. A numerical example is given.

I. INTRODUCTION

The concept of combining ability is becoming increasingly important in plant and animal breeding. It is especially useful in connection with "testing" procedures, in which it is desired to study and compare the performances of lines in hybrid combination. In this paper we are concerned with the definitions of general and specific combining ability when the testing procedure utilizes a diallel crossing system. It was with such a system that the terms general and specific combining ability were originally defined by Sprague and Tatum (1942). They defined the terms as follows: "The term 'general combining ability' is used to designate the average performance of a line in hybrid combination. . . . The term 'specific combining ability' is used to designate those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved."

By a diallel crossing system is meant one in which a set of p inbred lines is chosen and crosses among these lines are made. This procedure gives rise to a maximum of p^2 combinations. Data from such combinations can be most conveniently set out in a $p \times p$ table in which x_{ii} represents the mean value for the ith inbred, x_{ij} the mean value for the F_1 resulting from crossing the ith and jth inbreds, and x_{ji} represents its reciprocal. Thus the p^2 combinations can be divided into three groups: (1) the p parental lines themselves, (2) one set of $\frac{1}{2}p(p-1)$ F_1's, and (3) the set of $\frac{1}{2}p(p-1)$ reciprocal F_1's.

Even though this discussion is restricted to diallel crosses, we must still consider possible variations in the diallel crossing system itself and in the assumptions concerning the sampling nature of the experimental material.

Diallel crossing techniques may vary depending upon whether or not the parental inbreds or the reciprocal F_1's are included or both. With this as a basis for classification there are four possible experimental methods: (1) parents, one set of F_1's and reciprocal F_1's are included (all p^2 combinations); (2) parents and one set of F_1's are included but reciprocal F_1's are not ($\frac{1}{2}p(p+1)$ combinations); (3) one set of F_1's and reciprocals are included but not the parents ($p(p-1)$ combinations); and (4) one set of F_1's but neither parents nor reciprocal F_1's is included ($\frac{1}{2}p(p-1)$ combinations). Each method necessitates a different form of analysis.

* Division of Plant Industry, C.S.I.R.O., Canberra, A.C.T.

With regard to the sampling assumptions it is necessary to distinguish between (1) the situations in which the parental lines simply or the experimental material as a whole are assumed to be a random sample from some population about which inferences are to be made, and (2) the situations in which the lines are deliberately chosen and cannot be regarded as a random sample from any population. This second assumption can be expressed somewhat differently by stating that the experimental material constitutes the entire population about which valid inferences can be made.

These two different assumptions give rise to different estimation problems and different tests of hypotheses regarding combining ability effects.

The purpose of this paper is to bring together the eight different analyses arising from the different assumptions and diallel methods, to indicate the situations in which each might be used, and finally, to give a detailed numerical example. It is hoped that this will contribute to the usefulness of the ever-increasing application of the concept of combining ability in conjunction with diallel crosses.

II. PRESENTATION OF ANALYSES
(a) *Introduction*

For each of the four experimental methods we shall consider separately the two analyses arising from the different assumptions regarding the sampling nature of the experimental material. However, we must first consider the experimental design which is employed in obtaining the experimental data.

We shall restrict our analyses to conform to only one design, namely the randomized-blocks design. We choose this design primarily because of its common usage and its applicability to this type of study. The combining ability analyses can easily be used with various other designs.

In the randomized-blocks design we assume that there are a varieties (i.e. the genotypes determined by the diallel crossing method), each of which is assigned at random to each of b blocks, and that there are c individuals in each of the ab plots. Thus the mathematical model for the $ijkl$th observation is assumed to be

$$x_{ijkl} = u + v_{ij} + b_k + (bv)_{ijk} + e_{ijkl},$$

where u is the population mean effect, v_{ij} is the effect for the ijth genotype, b_k is the kth block effect, $(bv)_{ijk}$ is the interaction between the ijth genotype and the kth block, and e_{ijkl} is the environmental effect peculiar to the $ijkl$th individual. A double subscript notation is used for the variety (i.e. genotypic) effect because it is desired to denote the genotypic means in the combining ability analyses as x_{ij}, where x_{ii} is the mean for the ith parent, and x_{ij} is the mean for the F_1 resulting from crossing the ith and jth parents. In the combining ability analyses, the variety effects are considered in terms of general and specific combining ability effects, such that

$$v_{ij} = g_i + g_j + s_{ij}$$

for those diallel crossing methods in which reciprocal F_1's are not included, and

$$v_{ij} = g_i + g_j + s_{ij} + r_{ij}$$

for methods in which reciprocal F_1's are included. In these equations g_i is the general combining ability (denoted as g.c.a.) effect of the ith parent, s_{ij} is the specific com-

bining ability (denoted as s.c.a.) effect for the cross between the ith and jth parents, and r_{ij} is the reciprocal effect involving the ith and jth parents.

In this study we wish to present analyses for the two assumptions in which the genotypes are assumed to be (1) a random sample from a population, and (2) a chosen or fixed set. In the first situation the genotypic effects are considered random variables and in the second they are considered constants. We must now consider how these assumptions are to be integrated with the more general set of assumptions which are made with regard to the elements in the mathematical model for the randomized-block design.

There are four sets of assumptions which can be considered with regard to the variety (genotypic) and block effects. These are (1) the variety and block effects are constants, (2) the variety effects are random variables and the block effects are constants, (3) the variety effects are constants, and the block effects are random variables, and (4) the variety and block effects are both random variables.

The first set of assumptions leads to a model in which all effects except the error are regarded as constants. The last set of assumptions leads to a model in which all effects except u are random variables. These two classes of models have been designated as models I and II respectively by Eisenhart (1947). The second and third sets of assumptions lead to mixed models which we designate as mixed A and mixed B respectively. Table 1 gives the analysis of variance for the randomized-block design together with the expectations of mean squares for each of the four sets of assumptions.

In the analyses to follow, we shall consider only those two sets of assumptions characterized by models I and II. However, the mixed models can be used in all cases, and their application will be briefly described later.

It is clear that the objectives of the analyses and the analyses themselves are different for the two basic assumptions regarding the experimental material.

In model I the experimental material is to be regarded as the population about which inferences are to be made. The objectives are to compare combining abilities of the parents when the parents themselves are used as testers, and to identify the higher yielding combinations. Thus we are particularly interested in estimating combining ability effects and computing appropriate standard errors for differences between effects. For testing procedures it is necessary to assume only that the e_{ijkl} are normally and independently distributed with mean zero and variance σ_e^2.

In model II the assumption is that we are dealing with random samples from some parent population, and the inferences are not to be made about the individual lines in the sample but about the parameters in the parent population. In particular, we are interested in estimating the genetic and environmental components of the complex population variance. To do this we assume that the effects in the model (except u) are normally and independently distributed with means zero and variances σ_θ^2, where $\theta = b, g, s,$ or r. The variance component estimates are then obtained for any given diallel crossing method by equating the observed to the expected mean squares in the appropriate analysis of variance. The standard errors for the variance component estimates are calculated from the variances of the appropriate mean squares. The procedure will be indicated for each experimental method.

TABLE 1

RANDOMIZED-BLOCKS ANALYSIS OF VARIANCE GIVING EXPECTATIONS OF MEAN SQUARES FOR THE ASSUMPTIONS OF MODELS I, II, MIXED A, AND MIXED B

Source	D.F.	Mean Square*	Expectations of Mean Squares			
			Model I	Model II	Mixed A	Mixed B
Varieties	$a-1$	M_v	$\sigma_e^2 + bc\phi(v)$	$\sigma_e^2 + c\sigma_{bv}^2 + bc\sigma_v^2$	$\sigma_e^2 + bc\sigma_v^2$	$\sigma_e^2 + c\phi_2(bv) + bc\phi(v)$
Blocks	$b-1$	M_b	$\sigma_e^2 + ac\phi(b)$	$\sigma_e^2 + c\sigma_{bv}^2 + ac\sigma_b^2$	$\sigma_e^2 + c\phi_3(bv) + ac\phi(b)$	$\sigma_e^2 + ac\sigma_b^2$
Varieties × blocks	$(a-1)(b-1)$	M_{bv}	$\sigma_e^2 + c\phi_1(bv)$	$\sigma_e^2 + c\sigma_{bv}^2$	$\sigma_e^2 + c\phi_3(bv)$	$\sigma_e^2 + c\phi_2(bv)$
Error	$ab(c-1)$	M_e	σ_e^2	σ_e^2	σ_e^2	σ_e^2

* Where

$$\phi(v) = \frac{1}{a-1}\sum_i v_i^2; \qquad \phi_1(bv) = \frac{1}{(a-1)(b-1)}\sum_{i<j}\sum_k \sum_k (bv)_{ijk}^2;$$

$$\phi(b) = \frac{1}{b-1}\sum_k b_k^2; \qquad \phi_2(bv) = \frac{1}{a-1}\sum_{i<j}\sum (bv)_{ijk}^2;$$

$$\phi_3(bv) = \frac{1}{b-1}\sum_k (bv)_{ijk}^2.$$

It should be emphasized that the proper interpretation of the combining ability effects and variance depends on the particular diallel method, the assumptions regarding the experimental material, and the conditions imposed on the combining ability effects. For example, when model I is used the equations for estimating the combining ability effects vary from one diallel method to another. These estimators yield unbiased estimates of the combining ability effects only when the specified constraints are imposed on the elements. These constraints vary from one method to another. Finally, valid inferences can be made only about the particular experimental material used. When model II is used, the kinds of inferences which can validly be made will depend on the particular diallel crossing method employed and on the nature of the population from which the lines were drawn.

In the following analyses we are concerned with equal subclass numbers. However, in certain problems, particularly those dealing with animals, the investigator is forced to consider unequal subclass numbers. Henderson (1948, 1952) has provided solutions to problems of estimation and tests of hypotheses for method 3, model II, for this type of data.

In order to clarify the notation used for the four diallel methods, an illustration is given for the case of $p = 3$. Since in all of the analyses only genotypic means are involved we shall simplify the usual notation for the mean of the ijth genotype from $\bar{x}_{ij..}$ to x_{ij}. The 3×3 table of mean observations may be set out as follows:

$$
\begin{array}{ccc}
x_{11} & x_{12} & x_{13} \\
x_{21} & x_{22} & x_{23} \\
x_{31} & x_{32} & x_{33}
\end{array}
$$

(i) For method (1) the following summation notation is used:

$$X_{i.} = \mathop{\Sigma}_{j} x_{ij} = x_{i1} + x_{i2} + x_{i3},$$

$$X_{.j} = \mathop{\Sigma}_{i} x_{ij} = x_{1j} + x_{2j} + x_{3j},$$

$$X_{..} = \mathop{\Sigma}_{i}\mathop{\Sigma}_{j} x_{ij} = x_{11} + x_{12} + \ldots + x_{33} \text{ (all nine observations).}$$

(ii) For method (2) the following summation notation is used:

$$X_{i.} = \mathop{\Sigma}_{j} x_{ij} = x_{i1} + x_{i2} + x_{i3},$$

where $x_{ij} = x_{ji}$; $X_{.j}$ need not be considered.

$$X_{..} = \mathop{\Sigma}_{i \leqslant j} \Sigma x_{ij} = x_{11} + x_{12} + x_{13} + x_{22} + x_{23} + x_{33}.$$

(iii) For method (3) the following summation notation is used:

$$X_{i.} = \mathop{\Sigma}_{j \neq i} x_{ij}, \text{ e.g. } X_{2.} = x_{21} + x_{23}.$$

$$X_{.j} = \mathop{\Sigma}_{i \neq j} x_{ij}, \text{ e.g. } X_{.2} = x_{12} + x_{32}.$$

$$X_{..} = \mathop{\Sigma}_{i \neq j} \Sigma x_{ij} = x_{12} + x_{13} + x_{21} + x_{23} + x_{31} + x_{32}.$$

(iv) For method (4) the following summation notation is used:

$$X_{i.} = \mathop{\Sigma}_{j \neq i} x_{ij},$$

where $x_{ij} = x_{ji}$, e.g. $X_{2.} = x_{12} + x_{23}$.

$X_{.j}$ need not be considered.

$$X_{..} = \underset{i<j}{\Sigma \Sigma} x_{ij} = x_{12} + x_{13} + x_{23}.$$

(b) Statistical Analyses

Let us assume that one of the four diallel crossing systems has been employed to obtain the experimental material, and that this experimental material has been grown in a randomized-block design in which there are a varieties (genotypes), b blocks, and c observations for each of the ab plots.

The test for differences among genotypes is made by either of the following F tests. For model I, use

$$F_{[(a-1),\, m]} = M_v/M_e,$$

where $(a-1)$ and m are the degrees of freedom associated with the numerator and denominator of the F ratio, and M_v and M_e are the variety and error mean squares respectively in the randomized-block analysis.

For model II, use

$$F_{[(a-1),\, (a-1)(b-1)]} = M_v/M_{bv},$$

where M_{bv} is the variety $\times$ block interaction mean square.

If significant F ratios occur we reject the null hypothesis and assume that there are genotypic differences, which may be investigated further with the appropriate combining ability analysis.

(i) *Experimental Method* 1 (*parents, one set of F_1's and reciprocal F_1's are included*).—This diallel crossing system gives rise to p^2 genotypes. Therefore in the randomized-block analysis $a = p^2$.

The combining ability analysis of variance is given in Table 2 (see also Hayman (1954)). To give the estimation and testing procedures we must consider the analyses based on models I and II separately.

Model I

The mathematical model for the combining ability analysis is assumed to be

$$x_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{bc}\underset{k\ l}{\Sigma\Sigma}e_{ijkl} \qquad \begin{cases} i, j = 1, \ldots, p, \\ k = 1, \ldots, b, \\ l = 1, \ldots, c, \end{cases}$$

where u is the population mean, $g_i(g_j)$ is the g.c.a. effect for the ith (jth) parents, s_{ij} is the s.c.a. effect for the cross between the ith and jth parents such that $s_{ij} = s_{ji}, r_{ij}$ is the reciprocal effect involving the reciprocal crosses between the ith and jth parents such that $r_{ij} = -r_{ji}$, and e_{ijkl} is the environmental effect associated with the $ijkl$th individual observation. The following restrictions are imposed on the combining ability elements: $\underset{i}{\Sigma}g_i = 0$ and $\underset{i}{\Sigma}s_{ij} = 0$ (for each j).

The expectations of mean squares are given in Table 2 in the column designated model I. It should be noticed that in this analysis

$$M_e' = M_e/bc,$$

where M_e is the error mean square for the randomized-block design and the expectation of M_e' is denoted as

$$E(M_e') = \sigma_e^2/bc = \sigma^2.$$

TABLE 2

ANALYSIS OF VARIANCE FOR METHOD 1 GIVING EXPECTATIONS OF MEAN SQUARES FOR THE ASSUMPTIONS OF MODELS I AND II

Source	D.F.	Sum of Squares*	Mean Squares	Expectation of Mean Squares	
				Model I	Model II
General combining ability	$p-1$	S_g	M_g	$\sigma^2+2p\left(\dfrac{1}{p-1}\right)\Sigma g_i^2$	$\sigma^2+\dfrac{2(p-1)}{p}\sigma_s^2+2p\sigma_g^2$
Specific combining ability	$p(p-1)/2$	S_s	M_s	$\sigma^2+\dfrac{2}{p(p-1)}\underset{i}{\Sigma}\underset{j}{\Sigma}s_{ij}^2$	$\sigma^2+\dfrac{2(p^2-p+1)}{p^2}\sigma_s^2$
Reciprocal effects	$p(p-1)/2$	S_r	M_r	$\sigma^2+2\left(\dfrac{2}{p(p-1)}\right)\underset{i<j}{\Sigma\,\Sigma}r_{ij}^2$	$\sigma^2+2\sigma_r^2$
Error	m	S_e	M_e'	σ^2	σ^2

* Where

$$S_g = \frac{1}{2p}\underset{i}{\Sigma}(X_{i.}+X_{.i})^2 - \frac{2}{p^2}X_{..}^2,$$

$$S_s = \frac{1}{2}\underset{i}{\Sigma}\underset{j}{\Sigma}x_{ij}(x_{ij}+x_{ji}) - \frac{1}{2p}\underset{i}{\Sigma}(X_{.i}+X_{i.})^2 + \frac{1}{p^2}X_{..}^2,$$

$$S_k = \frac{1}{2}\underset{i<j}{\Sigma\,\Sigma}(x_{ij}-x_{ji})^2.$$

Testing for overall differences among the various classes of effects can be accomplished as follows:

(1) To test g.c.a. effects use

$$F_{[(p-1),\,m]} = M_g/M_e'.$$

(2) To test s.c.a. effects use

$$F_{[p(p-1)/2,\,m]} = M_s/M_e'.$$

(3) To test for reciprocal effects use

$$F_{[p(p-1)/2,\,m]} = M_r/M_e'.$$

The various effects may be estimated as follows:

$$\hat{u} = \frac{1}{p^2}X_{..},$$

$$\hat{g}_i = \frac{1}{2p}(X_{i.}+X_{.i}) - \frac{1}{p^2}X_{..},$$

$$\hat{s}_{ij} = \frac{1}{2}(x_{ij}+x_{ji}) - \frac{1}{2p}(X_{i.}+X_{.i}+X_{j.}+X_{.j}) + \frac{1}{p^2}X_{..},$$

and,

$$\hat{r}_{ij} = \frac{1}{2}(x_{ij} - x_{ji}).$$

The variance of any parent or F_1 mean value is

$$\text{var}(x_{ij}) = \hat{\sigma}^2 = M_e',$$

and the variance of the difference between any two mean values is

$$\text{var}(x_{ij} - x_{kl}) = 2\hat{\sigma}^2.$$

Variances of effects and of differences between effects may be estimated as follows:

$$\text{var}(\hat{u}) = \frac{1}{p^2}\hat{\sigma}^2,$$

$$\text{var}(\hat{g}_i) = \frac{p-1}{2p^2}\hat{\sigma}^2,$$

$$\text{var}(\hat{s}_{ii}) = \frac{(p-1)^2}{p^2}\hat{\sigma}^2,$$

$$\text{var}(\hat{s}_{ij}) = \frac{1}{2p^2}(p^2 - 2p + 2)\hat{\sigma}^2 \qquad (i \neq j),$$

$$\text{var}(\hat{r}_{ij}) = \frac{1}{2}\hat{\sigma}^2 \qquad (i \neq j),$$

$$\text{var}(\hat{g}_i - \hat{g}_j) = \frac{1}{p}\hat{\sigma}^2 \qquad (i \neq j),$$

$$\text{var}(\hat{s}_{ii} - \hat{s}_{jj}) = \frac{2(p-2)}{p}\hat{\sigma}^2 \qquad (i \neq j),$$

$$\text{var}(\hat{s}_{ii} - \hat{s}_{ij}) = \frac{1}{2p}(3p - 2)\hat{\sigma}^2 \qquad (i \neq j),$$

$$\text{var}(\hat{s}_{ii} - \hat{s}_{jk}) = \frac{3}{2p}(p-2)\hat{\sigma}^2 \qquad (i \neq j, k;\ j \neq k),$$

$$\text{var}(\hat{s}_{ij} - \hat{s}_{ik}) = \frac{p-1}{p}\hat{\sigma}^2 \qquad (i \neq j, k;\ j \neq k),$$

$$\text{var}(\hat{s}_{ij} - \hat{s}_{kl}) = \frac{p-2}{p}\hat{\sigma}^2 \qquad (i \neq j, k, l;\ j \neq k, l;\ k \neq l),$$

$$\text{var}(\hat{r}_{ij} - \hat{r}_{kl}) = \hat{\sigma}^2 \qquad (i \neq j;\ k \neq l).$$

Model II

The mathematical model for the combining ability analysis is

$$x_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{b}\Sigma_k b_k + \frac{1}{b}\Sigma(bv)_{ijk} + \frac{1}{bc}\Sigma_k \Sigma_l e_{ijkl},$$

where all effects except u are considered to be random variables.

The expectations of combining ability mean squares are given in Table 2 in the column designated model II. In this analysis the expectation of M_e' is

$$E(M_e') = \frac{1}{bc}(\sigma_e{}^2 + c\sigma_{bv}{}^2) = \sigma^2.$$

Thus σ^2 is estimated by M_{bv}/bc, where M_{bv} is the block $\times$ variety interaction mean square in the randomized-block analysis.

For testing hypotheses pertaining to the variance components, F ratios may again be employed:

(1) To test $\sigma_g{}^2 = 0$ it is necessary to synthesize a new mean square, M^* say, defined by

$$M^* = (1-A)M_e' + AM_s,$$

where

$$A = \frac{p(p-1)}{p^2-p+1}.$$

Then the approximate F test

$$F_{[(p-1),\, f]} = M_g/M^*,$$

may be used. f denotes the degrees of freedom associated with M^*, and is obtained from

$$f = \frac{mp^3(p-1)[p+2(p-1)K]^2}{p^5(p-1)(1-A)^2 + 2mA^2[p^2+2cK]^2},$$

where

$$K = \frac{p^2}{2c}\left(\frac{M_s - M_e'}{M_e'}\right),$$

and

$$c = p^2 - p + 1.$$

(2) To test $\sigma_s{}^2 = 0$ use

$$F_{[p(p-1)/2,\, m]} = M_s/M_e'.$$

(3) To test $\sigma_r{}^2 = 0$ use

$$F_{[p(p-1)/2,\, m]} = M_r/M_e'.$$

Variance components are estimated by equating the observed and expected mean squares in Table 2. The estimates are computed as follows:

$$\hat{\sigma}_g{}^2 = \frac{1}{2p}\left[M_g - \frac{M_e' + p(p-1)M_s}{c}\right],$$

$$\hat{\sigma}_s{}^2 = \frac{p^2}{2c}[M_s - M_e'],$$

and

$$\hat{\sigma}_r{}^2 = \tfrac{1}{2}[M_r - M_e'],$$

where

$$c = p^2 - p + 1.$$

Approximate estimates of the variances for the variance components may be obtained from the following formulae:

$$\mathrm{var}(\hat{\sigma}_g{}^2) \cong \frac{1}{2p^2(p-1)}M_g{}^2 + \frac{p-1}{pc^2}M_s{}^2 + \frac{1}{2p^2c^2m}(M_e{}')^2,$$

$$\mathrm{var}(\hat{\sigma}_s{}^2) \cong \frac{p^3}{(p-1)c^2}M_s{}^2 + \frac{p^4}{2c^2m}(M_e{}')^2,$$

$$\mathrm{var}(\hat{\sigma}_r{}^2) \cong \frac{1}{p(p-1)}M_r{}^2 + \frac{1}{2m}(M_e{}')^2,$$

and

$$\mathrm{var}(\hat{\sigma}^2) \cong \frac{2}{m}(M_e{}')^2,$$

where　　　　　　　$c = p^2 - p + 1.$

(ii) *Experimental Method 2 (parents and one set of F_1's are included but not reciprocal F_1's).*—This diallel crossing system gives rise to $p(p+1)/2$ different genotypes. Therefore, in the randomized-block analysis $a = p(p+1)/2$. Table 3 presents an orthogonal partitioning of the variety sum of squares.

TABLE 3

ANALYSIS OF VARIANCE FOR METHOD 2 GIVING EXPECTATIONS OF MEAN SQUARES FOR THE ASSUMPTIONS OF MODELS I AND II

Source	D.F.	Sum of Squares*	Mean Squares	Expectation of Mean Squares	
				Model I	Model II
General combining ability	$p-1$	S_g	M_g	$\sigma^2 + (p+2)\left(\frac{1}{p-1}\right)\Sigma g_i{}^2$	$\sigma^2 + \sigma_s{}^2 + (p+2)\sigma_g{}^2$
Specific combining ability	$p(p-1)/2$	S_s	M_s	$\sigma^2 + \frac{2}{p(p-1)}\Sigma_i \Sigma_j s_{ij}{}^2$	$\sigma^2 + \sigma_s{}^2$
Error	m	S_e	$M_e{}'$	σ^2	σ^2

* Where

$$S_g = \frac{1}{p+2}\left\{ \Sigma_i (X_i. + x_{ii})^2 - \frac{4}{p}X..^2 \right\},$$

$$S_s = \Sigma_{i \leqslant j} \Sigma x_{ij}{}^2 - \frac{1}{p+2}\Sigma_i (X_i. + x_{ii})^2 + \frac{2}{(p+1)(p+2)}X..^2.$$

Model I

The mathematical model for the combining ability analysis is assumed to be

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{bc}\Sigma\Sigma_{k\,l} e_{ijkl} \qquad \begin{cases} i, j = 1, \ldots, p, \\ k = 1, \ldots, b, \\ l = 1, \ldots, c, \end{cases}$$

where u is the population mean, $g_i(g_j)$ is the g.c.a. effect, s_{ij} is the s.c.a. effect such that $s_{ij} = s_{ji}$, and e_{ijkl} is the effect peculiar to the $ijkl$th observation. The restrictions

$$\sum_i g_i = 0,$$

and

$$\sum_j s_{ij} + s_{ii} = 0 \text{ (for each } i\text{)},$$

are imposed. As in method 1, model I, $M_e' = M_e/bc$.

The following F ratios may be used to test for g.c.a. and s.c.a. effects. To test for differences among g.c.a. effects use

$$F_{[(p-1),\, m]} = M_g/M_e',$$

and to test for differences among s.c.a. effects use

$$F_{[p(p-1)/2,\, m]} = M_s/M_e'.$$

The effects may be estimated as follows:

$$\hat{u} = \frac{2}{p(p+1)} X_{..},$$

$$\hat{g}_i = \frac{1}{p+2}[X_{i.} + x_{ii} - \frac{2}{p} X_{..}],$$

and

$$\hat{s}_{ij} = x_{ij} - \frac{1}{p+2}[X_{i.} + x_{ii} + X_{j.} + x_{jj}] + \frac{2}{(p+1)(p+2)} X_{..}$$

The variance of any parent or F_1 mean value is

$$\mathrm{var}(x_{ij}) = \hat{\sigma}^2 = M_e',$$

and the variance of the difference between any two mean values is

$$\mathrm{var}(x_{ij} - x_{kl}) = 2\hat{\sigma}^2.$$

Variances of effects and of differences between effects may be estimated as follows:

$$\mathrm{var}(\hat{u}) = \frac{2}{p(p+1)}\hat{\sigma}^2,$$

$$\mathrm{var}(\hat{g}_i) = \frac{p-1}{p(p+2)}\hat{\sigma}^2,$$

$$\mathrm{var}(\hat{s}_{ii}) = \frac{p(p-1)}{(p+1)(p+2)}\hat{\sigma}^2,$$

$$\mathrm{var}(\hat{s}_{ij}) = \frac{p^2+p+2}{(p+1)(p+2)}\hat{\sigma}^2 \qquad (i \neq j),$$

$$\mathrm{var}(\hat{g}_i - \hat{g}_j) = \frac{2}{p+2}\hat{\sigma}^2 \qquad (i \neq j),$$

$$\mathrm{var}(\hat{s}_{ii} - \hat{s}_{jj}) = \frac{2(p-2)}{p+2}\hat{\sigma}^2 \qquad (i \neq j),$$

$$\mathrm{var}(\hat{s}_{ij} - \hat{s}_{ik}) = \frac{2(p+1)}{p+2}\hat{\sigma}^2 \qquad (i \neq j,\, k;\; j \neq k),$$

$$\mathrm{var}(\hat{s}_{ij} - \hat{s}_{kl}) = \frac{2p}{p+2}\hat{\sigma}^2 \qquad (i \neq j,\, k,\, l;\; j \neq k,\, l;\; k \neq l).$$

Model II

The mathematical model for the combining ability analysis is

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{b}\Sigma_k b_k + \frac{1}{b}\Sigma_k (bv)_{ijk} + \frac{1}{bc}\Sigma_k\Sigma_l e_{ijkl},$$

where all effects except u are random variables.

The expectations of combining ability mean squares are given in Table 3 in the column designated as model II. In this analysis

$$E(M_e') = \frac{1}{bc}(\sigma_e{}^2 + c\sigma_{bv}{}^2) = \sigma^2.$$

The following F ratios are used for testing hypotheses pertaining to the different variance components. To test $\sigma_g{}^2 = 0$ use

$$F_{[(p-1),\ p(p-1)/2]} = M_g/M_s,$$

and to test $\sigma_s{}^2 = 0$ use

$$F_{[p(p-1)/2,\ m]} = M_s/M_e'.$$

The variance components may be estimated as follows:

$$\hat{\sigma}_g{}^2 = \frac{1}{p+2}[M_g - M_s],$$

and

$$\hat{\sigma}_s{}^2 = M_s - M_e'.$$

Approximate estimates of the variances for the variance components may be obtained from the following formulae:

$$\mathrm{var}(\hat{\sigma}_g{}^2) \cong \frac{2}{(p-1)(p+2)^2}M_g{}^2 + \frac{4}{p(p-1)(p+2)^2}M_s{}^2,$$

$$\mathrm{var}(\hat{\sigma}_s{}^2) \cong \frac{4}{p(p-1)}M_s{}^2 + \frac{2}{m}(M_e')^2,$$

and

$$\mathrm{var}(\hat{\sigma}^2) \cong \frac{2}{m}(M_e')^2.$$

(iii) *Experimental Method 3 (one set of F_1's and reciprocals are included but not the parents).*—This diallel crossing system gives rise to $a = p(p-1)$ different genotypes which fill all of the cells of a p^2 table except those occurring on the main diagonal.

Table 4 presents the combining ability analysis of variance. The construction of this analysis is given by Yates (1947), and a detailed derivation of the expectations of mean squares, when the effects are considered as random variables, is given by Kempthorne (1952). The appropriate analyses for non-orthogonal data when the effects are random variables is given by Henderson (1948, 1952).

Model I

We assume the model for the combining ability analysis to be

$$x_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{bc}\Sigma_k\Sigma_l e_{ijkl} \qquad \begin{cases} i, j = 1, \ \ldots, \ p, \\ k = 1, \ \ldots, \ b, \\ l = 1, \ \ldots, \ c, \end{cases}$$

where u is the population mean, g_i and g_j are the g.c.a. effects, s_{ij} is the s.c.a. effect such that $s_{ij} = s_{ji}$, r_{ij} is the reciprocal genotypic effect such that $r_{ij} = -r_{ji}$, and e_{ijkl} is the error effect peculiar to the $ijkl$th observation. The restrictions

$$\sum_i g_i = 0$$

and

$$\sum_{i \neq j} s_{ij} = 0 \text{ (for each } j\text{)},$$

are imposed on the combining ability effects.

TABLE 4

ANALYSIS OF VARIANCE FOR METHOD 3 GIVING EXPECTATIONS OF MEAN SQUARES FOR THE ASSUMPTIONS OF MODELS I AND II

Source	D.F.	Sum of Squares*	Mean Squares	Expectation of Mean Squares	
				Model I	Model II
General combining ability	$p-1$	S_g	M_g	$\sigma^2 + 2(p-2)\left(\dfrac{1}{p-1}\right)\Sigma g_i^2$	$\sigma^2 + 2\sigma_s^2 + 2(p-2)\sigma_g^2$
Specific combining ability	$p(p-3)/2$	S_s	M_s	$\sigma^2 + 2\left(\dfrac{2}{p(p-3)}\right)\underset{i<j}{\Sigma \Sigma} s_{ij}^2$	$\sigma^2 + 2\sigma_s^2$
Reciprocal effects	$p(p-1)/2$	S_r	M_r	$\sigma^2 + 2\left(\dfrac{2}{p(p-1)}\right)\underset{i<j}{\Sigma \Sigma} r_{ij}^2$	$\sigma^2 + 2\sigma_r^2$
Error	m	S_e	M_e'	σ^2	σ^2

* Where

$$S_g = \frac{1}{2(p-2)}\Sigma(X_{i.} + X_{.i})^2 - \frac{2}{p(p-2)}X_{..}^2,$$

$$S_s = \frac{1}{2}\underset{i<j}{\Sigma \Sigma}(x_{ij} + x_{ji})^2 - \frac{1}{2(p-2)}\Sigma(X_{i.} + X_{.i})^2 + \frac{1}{(p-1)(p-2)}X_{..}^2,$$

$$S_r = \frac{1}{2}\underset{i<j}{\Sigma \Sigma}(x_{ij} - x_{ji})^2.$$

The expectations of mean squares are given in the column designated model I of Table 4. As in method 1, model I, $M_e' = M_e/bc$.

Differences within classes of effects are tested by F ratios:

(1) To test g.c.a. effects use

$$F_{[(p-1),\, m]} = M_g/M_e'.$$

(2) To test s.c.a. effects use

$$F_{[p(p-3)/2,\, m]} = M_s/M_e'.$$

(3) To test reciprocal effects use

$$F_{[p(p-1)/2,\, m]} = M_r/M_e'.$$

The effects may be estimated as follows:

$$\hat{u} = \frac{1}{p(p-1)} X_{..},$$

$$\hat{g}_i = \frac{1}{2p(p-2)} [p(X_{i.}+X_{.i})-2X_{..}],$$

$$\hat{s}_{ij} = \tfrac{1}{2}(x_{ij}+x_{ji}) - \frac{1}{2(p-2)}(X_{i.}+X_{.i}+X_{j.}+X_{.j}) + \frac{1}{(p-1)(p-2)} X_{..},$$

and

$$\hat{r}_{ij} = \tfrac{1}{2}(x_{ij}-x_{ji}).$$

The variance of any parent or F_1 mean value is

$$\mathrm{var}(x_{ij}) = \hat{\sigma}^2 = M_e',$$

and the variance of the difference between any two mean values is

$$\mathrm{var}(x_{ij}-x_{kl}) = 2\hat{\sigma}^2.$$

Variances of effects and of differences between effects may be estimated as follows:

$$\mathrm{var}(\hat{u}) = \frac{1}{p(p-1)} \hat{\sigma}^2,$$

$$\mathrm{var}(\hat{g}_i) = \frac{p-1}{2p(p-2)} \hat{\sigma}^2,$$

$$\mathrm{var}(\hat{s}_{ij}) = \frac{p-3}{2(p-1)} \hat{\sigma}^2 \qquad (i \neq j),$$

$$\mathrm{var}(\hat{r}_{ij}) = \tfrac{1}{2}\hat{\sigma}^2 \qquad (i \neq j),$$

$$\mathrm{var}(\hat{g}_i-\hat{g}_j) = \frac{1}{p-2} \hat{\sigma}^2 \qquad (i \neq j),$$

$$\mathrm{var}(\hat{s}_{ij}-\hat{s}_{ik}) = \frac{p-3}{p-2} \hat{\sigma}^2 \qquad (i \neq j,\ k;\ j \neq k),$$

$$\mathrm{var}(\hat{s}_{ij}-\hat{s}_{kl}) = \frac{p-4}{p-2} \hat{\sigma}^2 \qquad (i \neq j,\ k,\ l;\ j \neq k,\ l;\ k \neq l).$$

Model II

The mathematical model for the combining ability analysis is

$$x_{ij} = u+g_i+g_j+s_{ij}+r_{ij}+\frac{1}{b}\Sigma_k b_k+\frac{1}{b}\Sigma_k (bv)_{ijk}+\frac{1}{bc}\Sigma_k \Sigma_l e_{ijkl},$$

where all effects except u are random variables.

The expectations of mean squares are given in Table 4 in the column designated model II. In this analysis

$$E(M_e') = \frac{1}{bc}(\sigma_e^2+c\sigma_{bv}^2) = \sigma^2.$$

F ratios may be used for testing hypotheses pertaining to the different variance components:

(1) To test $\sigma_g{}^2 = 0$ use

$$F_{[(p-1),\ p(p-3)/2]} = M_g/M_s.$$

(2) To test $\sigma_s{}^2 = 0$, use

$$F_{[p(p-3)/2,\ m]} = M_s/M_e'.$$

(3) To test $\sigma_r{}^2 = 0$ use

$$F_{[p(p-1)/2,\ m]} = M_r/M_e'.$$

The variance components are estimated as follows:

$$\hat{\sigma}_g{}^2 = \frac{1}{2(p-2)}[M_g - M_s],$$

$$\hat{\sigma}_s{}^2 = \tfrac{1}{2}[M_s - M_e'],$$

and

$$\hat{\sigma}_r{}^2 = \tfrac{1}{2}[M_r - M_e'].$$

Approximate estimates of the variances for the variance components may be obtained from the following formulae:

$$\mathrm{var}(\hat{\sigma}_g{}^2) \cong \frac{1}{2(p-1)(p-2)^2}M_g{}^2 + \frac{1}{p(p-2)^2(p-3)}M_s{}^2,$$

$$\mathrm{var}(\hat{\sigma}_s{}^2) \cong \frac{1}{p(p-3)}M_s{}^2 + \frac{1}{2m}(M_e')^2,$$

$$\mathrm{var}(\hat{\sigma}_r{}^2) \cong \frac{1}{p(p-1)}M_r{}^2 + \frac{1}{2m}(M_e')^2,$$

and

$$\mathrm{var}(\hat{\sigma}^2) \cong \frac{2}{m}(M_e')^2.$$

(iv) *Experimental Method* 4 (*one set of* F_1's *but neither parents nor reciprocal* F_1's *is included*).—In this, the most common of the diallel crossing systems, there are $a = p(p-1)/2$ different F_1 mean values.

The combining ability analysis of variance is given in Table 5. The analysis was originally presented by Sprague and Tatum (1942).

Model I

The model for the combining ability analysis is

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{bc}\Sigma\Sigma_{k\ l} e_{ijkl} \qquad \left\{\begin{aligned} i, j &= 1,\ \ldots,\ p, \\ k &= 1,\ \ldots,\ b, \\ l &= 1,\ \ldots,\ c, \end{aligned}\right.$$

where u is the population mean, g_i and g_j are the g.c.a. effects, s_{ij} is the s.c.a. effect such that $s_{ij} = s_{ji}$, and e_{ijkl} is the error effect peculiar to the $ijkl$th observation.

The restrictions

$$\sum_i g_i = 0,$$

and

$$\sum_{i \neq j} s_{ij} = 0 \text{ (for each } j),$$

are imposed on the combining ability effects.

TABLE 5

ANALYSIS OF VARIANCE FOR METHOD 4 GIVING EXPECTATIONS OF MEAN SQUARES FOR THE ASSUMPTIONS OF MODELS I AND II

Source	D.F.	Sum of Squares*	Mean Squares	Expectation of Mean Squares	
				Model I	Model II
General combining ability	$p-1$	S_g	M_g	$\sigma^2 + (p-2)\left(\dfrac{1}{p-1}\right)\sum_i g_i^2$	$\sigma^2 + \sigma_s^2 + (p-2)\sigma_g^2$
Specific combining ability	$p(p-3)/2$	S_s	M_s	$\sigma^2 + \left(\dfrac{2}{p(p-3)}\right)\sum_{i<j}\sum s_{ij}^2$	$\sigma^2 + \sigma_s^2$
Error	m	S_e	M_e'	σ^2	σ^2

* Where

$$S_g = \frac{1}{p-2}\sum_i X_{i.}^2 - \frac{4}{p(p-2)}X_{..}^2,$$

$$S_s = \sum_{i<j}\sum x_{ij}^2 - \frac{1}{p-2}\sum X_{i.}^2 + \frac{2}{(p-1)(p-2)}X_{..}^2.$$

The expectations of mean squares are given in the column designated model I of Table 5. In this analysis

$$M_e' = M_e/bc.$$

Differences within classes of effects are tested by F ratios.

(1) To test g.c.a. effects use

$$F_{[(p-1),\ m]} = M_g/M_e'.$$

(2) To test s.c.a. effects use

$$F_{[p(p-3)/2,\ m]} = M_s/M_e'.$$

The effects may be estimated as follows:

$$\hat{u} = \frac{2}{p(p-1)}X_{..},$$

$$\hat{g}_i = \frac{1}{p(p-2)}[pX_{i.} - 2X_{..}],$$

and

$$\hat{s}_{ij} = x_{ij} - \frac{1}{p-2}(X_{i.} + X_{j.}) + \frac{2}{(p-1)(p-2)}X_{..}$$

The variance of any F_1 mean value is

$$\text{var}(x_{ij}) = \hat{\sigma}^2 = M_e',$$

and the variance of a difference between any two mean values is

$$\text{var}(x_{ij} - x_{kl}) = 2\hat{\sigma}^2.$$

Variances of effects and of differences between effects may be estimated as follows:

$$\text{var}(\hat{u}) = \frac{2}{p(p-1)}\hat{\sigma}^2,$$

$$\text{var}(\hat{g}_i) = \frac{p-1}{p(p-2)}\hat{\sigma}^2,$$

$$\text{var}(\hat{s}_{ij}) = \frac{p-3}{p-1}\hat{\sigma}^2 \qquad (i \neq j),$$

$$\text{var}(\hat{g}_i - \hat{g}_j) = \frac{2}{p-2}\hat{\sigma}^2 \qquad (i \neq j),$$

$$\text{var}(\hat{s}_{ij} - \hat{s}_{ik}) = \frac{2(p-3)}{p-2}\hat{\sigma}^2 \qquad (i \neq j, k; \; j \neq k),$$

$$\text{var}(\hat{s}_{ij} - \hat{s}_{kl}) = \frac{2(p-4)}{p-2}\hat{\sigma}^2 \qquad (i \neq j, k, l; \; j \neq k, l; \; k \neq l).$$

Model II

The model for the combining ability analysis is

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{b}\sum_k b_k + \frac{1}{b}\sum_k (bv)_{ijk} + \frac{1}{bc}\sum_k \sum_l e_{ijkl},$$

where all effects except u are random variables.

The expectations of mean squares are given in Table 5 in the column designated model II. As with other model II analyses

$$E(M_e') = \frac{1}{bc}(\sigma_e^2 + c\sigma_{bv}^2) = \sigma^2.$$

F ratios may be used to test hypotheses pertaining to the variance components:

(1) To test $\sigma_g^2 = 0$ use

$$F_{[(p-1), \, p(p-3)/2]} = M_g/M_s.$$

(2) To test $\sigma_s^2 = 0$ use

$$F_{[p(p-3)/2, \, m]} = M_s/M_e'.$$

The variance components are estimated as follows:

$$\hat{\sigma}_g^2 = \frac{1}{p-2}[M_g - M_s],$$

and

$$\hat{\sigma}_s^2 = M_s - M_e'.$$

Approximate estimates of the variances for the variance components may be obtained as follows:

$$\text{var}(\hat{\sigma}_g{}^2) \cong \frac{2}{(p-1)(p-2)^2}M_g{}^2 + \frac{4}{p(p-2)^2(p-3)}M_s{}^2,$$

$$\text{var}(\hat{\sigma}_s{}^2) \cong \frac{4}{p(p-3)}M_s{}^2 + \frac{2}{m}(M_e')^2,$$

and

$$\text{var}(\hat{\sigma}^2) \cong \frac{2}{m}(M_e')^2.$$

(c) Use of Mixed Models

Mixed model A can be used for all four diallel crossing systems. In those diallel crossing systems in which reciprocal F_1's are not included the mathematical model for the combining ability analysis is

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{bc}\underset{k}{\Sigma}\underset{l}{\Sigma}e_{ijkl},$$

and for those diallel systems in which the reciprocal F_1's are included the model is

$$x_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{bc}\underset{k}{\Sigma}\underset{l}{\Sigma}e_{ijkl}.$$

In both models all elements except u are random variables.

The combining ability analyses are the same as those involving model II except that $M_e' = \hat{\sigma}^2 = M_e/bc$ is used as the error mean square.

Use of mixed model B introduces the "mixed" elements $(bv)_{ijk}$ into the combining ability analyses. Thus, for the diallel crossing systems which do not include reciprocal F_1's the model is

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{b}\underset{k}{\Sigma}b_k + \frac{1}{b}\underset{k}{\Sigma}(bv)_{ijk} + \frac{1}{bc}\underset{k}{\Sigma}\underset{l}{\Sigma}e_{ijkl}.$$

When the reciprocal F_1's are included the model is

$$x_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{b}\underset{k}{\Sigma}b_k + \frac{1}{b}\underset{k}{\Sigma}(bv)_{ijk} + \frac{1}{bc}\underset{k}{\Sigma}\underset{l}{\Sigma}e_{ijkl}.$$

In both models the restrictions

$$\underset{i}{\Sigma}g_i = 0,$$

$$\underset{i}{\Sigma}s_{ij} = 0 \text{ (for each } j\text{)},$$

and

$$\underset{i<j}{\Sigma}\ \Sigma(bv)_{ijk} = 0$$

are imposed.

The introduction of the mixed elements into the combining ability analyses causes difficulty. When mixed model B is used, somewhat arbitrary and inconsistent assumptions must be made with regard to the mixed elements in order to obtain manageable expectations of mean squares and variances. However, if mixed model B

is used, the combining ability analyses are essentially the same as model I analyses, except that $M_e' = M_{bv}/bc$.

(d) Extension to more than One Variable

No difficulty arises in the simultaneous analysis of two or more variables. In fact in those combining ability analyses employing model II it is possible to use variance and covariance components to estimate the population regression and correlation coefficients for any type of effect in the model. Thus the regression of the ith variable on the jth variable for the θ effect is estimated as

$$b_{\theta_{ij}} = \hat{\sigma}_{\theta_{ij}}{}^2 / \hat{\sigma}_{\theta_j}{}^2.$$

The correlation coefficient between the ith and jth variables for the θ effect is estimated as

$$r_{\theta_{ij}} = \hat{\sigma}_{\theta_{ij}}{}^2 / \sqrt{\{(\hat{\sigma}_{\theta_i}{}^2)(\hat{\sigma}_{\theta_j}{}^2)\}},$$

where $\hat{\sigma}_{\theta_{ij}}{}^2$ = covariance component for the θ effect involving the ith and jth variables,

$\hat{\sigma}_{\theta_i}{}^2$ = variance component for the θ effect for the ith variable,

and

θ = phenotypic, genotypic, g.c.a., s.c.a., reciprocal, or error effects.

This procedure is particularly useful in plant and animal breeding and is a direct consequence of the earlier notions of the partitioning of the genotypic variance and of discriminant functions, both developed by Fisher (1918, 1936). (The direct application of discriminant functions to plant selection was first made by Smith (1936).) Hazel, Baker, and Reinmiller (1943) made an early application of the use of variance components to estimate correlation coefficients in an animal breeding problem, and an application of the technique in an analysis of tomato yield was made by the author (1948, 1953).

The distribution of such statistics computed from variance and covariance components is not known, and therefore their standard errors cannot be calculated.

III. Numerical Example

Space does not permit a detailed example to be given for each of the eight possible analyses. Therefore, attention shall be concentrated on experimental method 4 and a numerical example will be given to illustrate the two analyses arising from models I and II.

Method 4 is chosen for the following reasons:

(1) It represents the most commonly used diallel crossing system.

(2) When the necessary assumptions concerning the sampling nature of the set of inbreds can be validly made, it is possible to give an exact genetic interpretation to the general and specific combining ability variances.

(3) Reciprocal genotypic effects are generally non-existent in plant data of the sort we wish to consider in the illustrative example and therefore it is not necessary to introduce the additional complication of reciprocal F_1's.

For convenience we shall use the same set of data to illustrate the two analyses associated with models I and II. This is done to focus attention more clearly on the differences in analysis and interpretation which result from the two sets of assumptions. In reality the set of lines used in the example were deliberately chosen and, therefore, the analysis based on model I is appropriate. However, for illustrative purposes we shall also present the analysis based on model II.

TABLE 6

F_1 MEAN VALUES FOR X_1 = TOTAL YIELD, X_2 = COB WEIGHT, AND X_3 = SHELLED CORN WEIGHT

Parent Number	Variable	Parent Number							
		2	3	4	5	6	7	8	9
1	X_1	240·0	260·0	230·4	257·0	241·5	266·9	240·1	300·4
	X_2	31·8	34·7	32·3	45·0	39·0	35·1	35·7	40·1
	X_3	208·2	225·3	198·1	212·0	202·5	231·8	204·4	260·3
2	X_1		209·0	217·3	233·1	229·5	266·9	216·3	214·2
	X_2		27·9	30·8	39·6	33·1	30·9	30·9	28·5
	X_3		181·1	186·5	193·5	196·4	236·0	185·4	185·7
3	X_1			183·7	253·7	250·1	268·8	222·3	252·1
	X_2			25·2	41·4	35·5	34·9	32·1	32·4
	X_3			158·5	212·3	214·6	233·9	190·2	219·7
4	X_1				233·8	213·7	255·7	197·4	281·0
	X_2				42·6	35·7	35·6	32·7	41·3
	X_3				191·2	178·0	220·1	164·7	239·7
5	X_1					206·8	272·2	242·9	260·8
	X_2					40·1	43·6	41·8	44·2
	X_3					166·7	228·6	201·1	216·6
6	X_1						261·8	270·3	283·9
	X_2						39·1	43·5	41·5
	X_3						222·7	226·8	242·4
7	X_1							273·2	302·2
	X_2							38·3	41·1
	X_3							234·9	261·1
8	X_1								259·8
	X_2								35·2
	X_3								224·6

For the example, maize yield data previously reported by Griffing and Lindstrom (1954) will be used. From this study we shall select data from the 36 F_1's resulting from diallel crossing among nine inbred lines. The variables to be considered are X_1 = total yield, X_2 = cob weight, and X_3 = shelled corn weight.

These variables are related: $X_1 = X_2 + X_3$. The mean F_1 values for these three variables are given in Table 6.

The experimental design consisted of six randomized blocks. In each block each F_1 plot contained 13 plants. After thinning, the plants were spaced singly and approximately 1 ft apart. The ears were bagged soon after silking to minimize loss.

The first stage in the analysis is to test the null hypotheses that there are no genotypic differences among the F_1 genotypes. These tests involve the randomized-block analyses of variance and covariance. For these analyses we note that $a = 36$,

TABLE 7

OBSERVED MEAN SQUARES FROM RANDOMIZED-BLOCKS ANALYSES OF VARIANCE FOR VARIABLES X_1 = TOTAL YIELD, X_2 = COB WEIGHT, AND X_3 = SHELLED CORN WEIGHT, AND MEAN CROSS-PRODUCTS FOR VARIABLES X_2 AND X_3

| Source | D.F. | Mean Squares | | | Mean Cross-products $X_2 X_3$ |
		X_1	X_2	X_3	
Varieties	35	61,889·36	2,039·31	50,422·97	4,713·54
Blocks	5	257,943·53	2,596·49	210,901·86	22,222·59
Varieties × blocks	175	11,803·61	235·82	9,056·45	1,255·67
Error	2558	1,642·48	46·61	1,247·39	174·24

$b = 6$, and $c = 13$. The observed mean squares for X_1, X_2, and X_3 and mean cross-products for X_2, X_3 are given in Table 7. For model I we use $F_{[35, 2558]} = M_v / M_e$, and for model II we use $F_{[35, 175]} = M_v / M_{bv}$. Since highly significant F ratios are obtained for all variables we reject the null hypotheses and assume that genotypic differences exist. We are now prepared to continue with the combining ability analyses.

Model I

The mathematical model for the combining ability analysis is

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{78} \Sigma \Sigma e_{ijkl} \qquad \begin{cases} i, j = 1, \dots, 9, \\ k = 1, \dots, 6, \\ l = 1, \dots, 13, \end{cases}$$

where the definitions of the elements and the restrictions imposed on them are given in method 4, model I.

The combining ability analyses of variance and covariance are given in Table 8. Highly significant F ratios occur in all variables for both general and specific combining ability effects. Therefore, we assume that true differences among these effects do occur. It may be noted that in these analyses the mean squares and mean cross-products (involving X_2, X_3) are related as follows:

$$_1M_i = {}_2M_i + {}_3M_i + 2({}_{23}CP_i),$$

where $_1M_i$ is the mean square for the ith source of variation involving variable X_1,

etc., and $_{23}CP_i$ is the mean cross-product for the ith source of variation involving variables X_2 and X_3.

MEAN SQUARES AND CROSS-PRODUCTS FROM COMBINING ABILITY ANALYSES, BASED ON MODEL I, FOR VARIABLES X_1 = TOTAL YIELD, X_2 = COB WEIGHT, AND X_3 = SHELLED CORN WEIGHT

Source	D.F.	Mean Squares			Mean Cross-products $X_2 X_3$
		X_1	X_2	X_3	
General combining ability	8	2325·74**	90·98**	1948·66**	143·05**
Specific combining ability	27	339·44**	6·99**	260·49**	35·98**
Error	2558	21·05	0·60	15·99	2·23

Components	X_1	X_2	X_3	$X_2 X_3$
$\frac{1}{8}\widehat{\Sigma g_i{}^2}$	329·24	12·91	276·09	20·12
$\frac{1}{27}\widehat{\underset{i<j}{\Sigma\,\Sigma}\,s_{ij}{}^2}$	318·39	6·39	244·50	33·75
$\hat{\sigma}^2$	21·05	0·60	15·99	2·23

**$P < 0·01$.

ESTIMATES OF GENERAL COMBINING ABILITY EFFECTS ($_1\hat{g}_i$, $_2\hat{g}_i$, AND $_3\hat{g}_i$) FOR VARIABLES X_1 = TOTAL YIELD, X_2 = COB WEIGHT, AND X_3 = SHELLED CORN WEIGHT

Parent	General Combining Ability Effects		
	$_1\hat{g}_i$	$_2\hat{g}_i$	$_3\hat{g}_i$
1 (standard)	9·35	0·27	9·08
2	−20·65	−5·48	−15·17
3	−10·16	−3·96	−6·20
4	−22·55	−2·23	−20·32
5	−1·51	6·64	−8·15
6	−1·89	2·24	−4·13
7	28·12	0·97	27·15
8	−6·93	−0·23	−6·70
9	26·22	1·78	24·44
S.E. $(\hat{g}_i - \hat{g}_j)$	2·45	0·41	2·14

The next step is the estimation of effects. This can be done for each variable using the formulae given in method 4, model I, by letting $p = 9$. The g.c.a. estimates

TABLE 10

ESTIMATES OF SPECIFIC COMBINING ABILITY CONSTANTS $(\hat{s}_{ij})$ FOR VARIABLES X_1 = TOTAL YIELD, X_2 = COB WEIGHT, AND X_3 = SHELLED CORN WEIGHT

Parent Number	Trait	Parent Number							
		2	3	4	5	6	7	8	9
1	X_1	4·94	14·46	−2·76	2·80	−12·31	−16·93	−8·67	18·47
	X_2	0·53	1·91	−2·21	1·61	0·01	−2·61	−0·81	1·57
	X_3	4·41	12·55	−0·55	1·19	−12·32	−14·32	−7·86	16·90
2	X_1		−6·54	14·14	8·90	5·68	13·07	−2·47	−37·73
	X_2		0·86	2·03	1·96	−0·14	−1·07	0·13	−4·29
	X_3		−7·40	12·11	6·94	5·82	14·14	−2·60	−33·44
3	X_1			−29·94	19·01	15·80	4·48	−6·96	−10·31
	X_2			−5·09	2·25	0·74	1·41	−0·19	−1·89
	X_3			−24·85	16·76	15·06	3·07	−6·77	−8·42
4	X_1				11·50	−8·21	3·77	−19·47	30·97
	X_2				1·71	−0·79	0·39	−1·31	5·27
	X_3				9·79	−7·42	3·38	−18·16	25·70
5	X_1					−36·16	−0·77	4·99	−10·27
	X_2					−5·25	−0·49	−1·09	−0·70
	X_3					−30·91	−0·28	6·08	−9·57
6	X_1						−10·78	32·77	13·22
	X_2						−0·59	5·01	1·00
	X_3						−10·19	27·76	12·22
7	X_1							5·66	1·50
	X_2							1·09	1·87
	X_3							4·57	−0·37
8	X_1								−5·85
	X_2								−2·83
	X_3								−3·02

Standard Error	X_1	X_2	X_3	Limitations
S.E.$(\hat{s}_{ij}-\hat{s}_{ik})$	6·01	1·01	5·24	$i \neq j, k; j \neq k$
S.E.$(\hat{s}_{ij}-\hat{s}_{kl})$	5·48	0·93	4·78	$i \neq j, k, l; j \neq k, l; k \neq l$

are given in Table 9 and the s.c.a. estimates are given in Table 10. For any one variable each F_1 mean value can be represented by a linear function of these effects, i.e.

$$x_{ij} = \hat{u} + \hat{g}_i + \hat{g}_j + \hat{s}_{ij}.$$

TABLE 11

ESTIMATES OF GENERAL AND SPECIFIC COMBINING ABILITY VARIANCES ASSOCIATED WITH EACH
PARENT, AND ESTIMATES OF THE ENVIRONMENTAL VARIANCES ON INDIVIDUAL AND MEAN BASES

Parent	Variable	$\hat{\sigma}_{g_i}^2$ *	$\hat{\sigma}_{s_i}^2$ *	Individual Basis $(\hat{\sigma}_e^2)$	Mean Basis $(\hat{\sigma}^2)$
1	X_1	84·75	139·60	1642·48	21·05
	X_2	0	2·54	46·61	0·60
	X_3	80·41	112·42	1247·39	15·99
	$X_2 X_3$	2·17	12·32	174·24	2·23
2	X_1	423·75	264·69	1642·48	21·05
	X_2	29·95	3·57	46·61	0·60
	X_3	228·10	218·84	1247·39	15·99
	$X_2 X_3$	82·85	21·14	1 74·24	2·23
3	X_1	100·55	258·26	1642·48	21·05
	X_2	15·60	5·42	46·61	0·60
	X_3	36·41	195·38	1247·39	15·99
	$X_2 X_3$	24·27	28·73	174·24	2·23
4	X_1	505·83	361·40	1642·48	21·05
	X_2	4·90	9·22	46·61	0·60
	X_3	410·87	260·16	1247·39	15·99
	$X_2 X_3$	45·03	46·01	174·24	2·23
5	X_1	−0·40	270·42	1642·48	21·05
	X_2	44·01	5·76	46·61	0·60
	X_3	64·39	202·06	1247·39	15·99
	$X_2 X_3$	−54·40	31·30	174·24	2·23
6	X_1	0·90	435·28	1642·48	21·05
	X_2	4·94	7·38	46·61	0·60
	X_3	15·02	335·82	1247·39	15·99
	$X_2 X_3$	−9·53	46·04	174·24	2·23
7	X_1	788·06	73·80	1642·48	21·05
	X_2	0·87	1·69	46·61	0·60
	X_3	735·09	64·97	1247·39	15·99
	$X_2 X_3$	26·05	3·57	174·24	2·23
8	X_1	45·36	221·08	1642·48	21·05
	X_2	−0·02	4·91	46·61	0·60
	X_3	42·86	169·39	1247·39	15·99
	$X_2 X_3$	1·26	23·39	174·24	2·23
9	X_1	684·81	431·51	1642·48	21·05
	X_2	3·09	8·81	46·61	0·60
	X_3	595·28	327·06	1247·39	15·99
	$X_2 X_3$	43·22	47·82	174·24	2·23

* Where $\sigma_{g_i}^2 = (\hat{g}_i)^2 - \frac{8}{63}\hat{\sigma}^2$, $\hat{\sigma}_{s_i}^2 = \frac{1}{7}\sum_j \hat{s}_{ij}^2 - \frac{6}{7}\hat{\sigma}^2$.

Since the variables are related $(X_1 = X_2 + X_3)$ we can break down the effects for X_1 into contributions due to X_2 and X_3, i.e.

$$_1\hat{g}_i = {}_2\hat{g}_i + {}_3\hat{g}_i,$$

and

$$_1\hat{s}_{ij} = {}_2\hat{s}_{ij} + {}_3\hat{s}_{ij},$$

where the subscript in front of the effect indicates the variable; for example, $_2\hat{s}_{ij}$ is the s.c.a. effect involving variable X_2 for the hybrid of the ith and jth parents. In this way each observed value of X_1 can be represented in terms of estimated effects of X_2 and X_3 as follows:

$$_1x_{ij} = {}_2\hat{u} + {}_3\hat{u} + {}_2\hat{g}_i + {}_3\hat{g}_i + {}_2\hat{g}_j + {}_3\hat{g}_j + {}_2\hat{s}_{ij} + {}_3\hat{s}_{ij}.$$

Standard errors for effects and for differences between effects may be computed by the formulae given in method 4, model I.

Comparisons of the performances of the individual lines is of considerable interest. Clearly the g.c.a. of the lines may be compared directly from Table 9. The next question is, how can the average s.c.a. of the series of crosses involving one line be compared with the average s.c.a. of the series of crosses involving a different line? This may be done by computing

$$\hat{\sigma}_{s_i}^2 = \frac{1}{p-2}\widehat{\sum_j s_{ij}^2}$$

for each line. The s.c.a. effects may be used to calculate $\hat{\sigma}_{s_i}^2$ as follows:

$$\hat{\sigma}_{s_i}^2 = \frac{1}{p-2}\sum_{j \neq i} \hat{s}_{ij}^2 - \frac{p-3}{p-2}\hat{\sigma}^2.$$

Values of $\hat{\sigma}_{s_i}^2$ are given in Table 11.

In addition to comparing values of $\hat{\sigma}_{s_i}^2$ for different lines it is also informative to compare the relative magnitudes of g.c.a., s.c.a., and error variances. Appropriate statistics for these comparisons are given in Table 11. The combining ability variance associated with the ith line is denoted as

$$\hat{\sigma}_{g_i}^2 = \widehat{(g_i^2)},$$

and may be computed from the g.c.a. estimate g_i as follows:

$$\hat{\sigma}_{g_i}^2 = (\hat{g}_i)^2 - \frac{p-1}{p(p-2)}\hat{\sigma}^2.$$

A brief summary of results indicate these facts. (1) From Table 9 we note that lines 7 and 9 have significantly greater combining ability than line 1 which is taken as the standard. (2) Differences in g.c.a. for total yield (X_1) are largely due to differences in shelled corn weight (X_3). (3) Although lines 7 and 9 are similar in that they both exhibit high g.c.a., they attain their high average performance by entirely different means. The relatively low s.c.a. variance associated with line 7 (i.e. $\hat{\sigma}_{s_7}^2$, Table 11) indicates that line 7 uniformly transmits its high yielding ability to all of its F$_1$'s, whereas the high s.c.a. variance associated with line 9 indicates that there are specific combinations of line 9 with certain inbreds which yield considerably more than would

be expected and other combinations which yield much less than expected. For this reason line 7 is probably superior to line 9 for inclusion in the production of a synthetic variety, and line 9 is probably superior to line 7 if specific high yielding combinations are desired. Both lines 7 and 9 should be tested more thoroughly in order that maximum use of their superior combining ability can be made. (4) In comparing the relative magnitudes of $\hat{\sigma}_{g_i}^2$, $\hat{\sigma}_{s_i}^2$, and error variances it may be noted that the relatively enormous values of the error variances on an individual basis are brought into manageable magnitudes by the inclusion of a fairly large number (78) of individual observations for each genotype. Thus for X_1 the error variance on an individual basis, $\hat{\sigma}_e^2 = 1642 \cdot 48$, is reduced to $\hat{\sigma}_e^2/78 = 21 \cdot 05$ on a mean basis. In this way the precision of the estimates of the genotypic effects and variances is enhanced. Even greater precision can be obtained by increasing the number of observations for each genotypic mean.

For a more detailed examination of the results of this experiment the reader is referred to the original paper from which the data were obtained.

Model II

As stated before, in reality the experimental material cannot be regarded as a random sample from some parent population. However, for illustrative purposes we

TABLE 12

MEAN SQUARES AND CROSS-PRODUCTS FROM COMBINING ABILITY ANALYSES, BASED ON MODEL II, FOR VARIABLES X_1 = TOTAL YIELD, X_2 = COB WEIGHT, AND X_3 = SHELLED CORN WEIGHT

Source	D.F.	Mean Squares			Mean Cross-products $X_2 X_3$
		X_1	X_2	X_3	
General combining ability	8	2325·75**	90·98**	1948·66**	143·05**
Specific combining ability	27	339·44**	6·99**	260·49**	35·98**
Error	175	151·33	3·02	116·11	16·10

**$P < 0 \cdot 01$.

shall assume that they do, and in fact we shall go even farther and pretend that the experimental material constitutes a random sample from a random mating population. By making this assumption we can estimate the additive and non-additive genetic variances of the parent population.

The mathematical model for the combining ability analysis is

$$x_{ij} = u + g_i + g_j + s_{ij} + \frac{1}{6}\sum_k b_k + \frac{1}{6}\sum_k (bv)_{ijk} + \frac{1}{78}\sum_k \sum_l e_{ijkl} \qquad \begin{cases} i, j = 1, \ldots, 9, \\ k = 1, \ldots, 6, \\ l = 1, \ldots, 13, \end{cases}$$

where the definitions of the elements are given in method 4, model I.

Using the formulae in Table 5 we can compute the combining ability analyses of variance for variables X_1, X_2, and X_3 and the analysis of covariance for X_2 and X_3. These are given in Table 12. When applying the appropriate F tests we find that there are highly significant differences among g.c.a. and among s.c.a. effects.

From these analyses we may estimate the variance and covariance components by equating the expected to the observed mean squares. These components, or functions of them, are given in Table 13. It may be noted that: (1) the following relation holds for any effect, $\hat{\sigma}_1^2 = \hat{\sigma}_2^2 + \hat{\sigma}_3^2 + 2\hat{\sigma}_{23}^2$ (where $\hat{\sigma}_1^2$, $\hat{\sigma}_2^2$, and $\hat{\sigma}_3^2$ are the estimated components of variance for X_1, X_2 and X_3, respectively, and $\hat{\sigma}_{23}^2$ is the estimated covariance component for X_2, X_3), and (2) estimates of covariances for X_1, X_2, and X_1, X_3 may be obtained by use of the equations $\hat{\sigma}_{12}^2 = \hat{\sigma}_2^2 + \hat{\sigma}_{23}^2$ and $\hat{\sigma}_{13}^2 = \hat{\sigma}_3^2 + \hat{\sigma}_{23}^2$.

TABLE 13

ESTIMATED VARIANCE AND COVARIANCE COMPONENTS FOR VARIABLES X_1 = TOTAL YIELD, X_2 = COB WEIGHT, AND X_3 = SHELLED CORN WEIGHT

Variable	Component	Variable		
		X_1	X_2	X_3
X_1	$\hat{\sigma}_P^2$	$2398\cdot11 \pm 342\cdot22$	$299\cdot30$	$2098\cdot81$
	$\hat{\sigma}_G^2$	$755\cdot63 \pm 339\cdot13$	$78\cdot45$	$677\cdot18$
	$2\hat{\sigma}_g^2$	$567\cdot52 \pm 333\cdot30$	$54\cdot60$	$512\cdot92$
	$\hat{\sigma}_s^2$	$188\cdot11 \pm 93\cdot79$	$23\cdot85$	$164\cdot26$
	$\hat{\sigma}_e^2$	$1642\cdot48 \pm 45\cdot93$	$220\cdot85$	$1421\cdot63$
X_2	$\hat{\sigma}_P^2$		$74\cdot58 \pm 13\cdot14$	$224\cdot72$
	$\hat{\sigma}_G^2$		$27\cdot97 \pm 13\cdot07$	$50\cdot48$
	$2\hat{\sigma}_g^2$		$24\cdot00 \pm 13\cdot01$	$30\cdot60$
	$\hat{\sigma}_s^2$		$3\cdot97 \pm 1\cdot93$	$19\cdot88$
	$\hat{\sigma}_e^2$		$46\cdot61 \pm 1\cdot30$	$174\cdot24$
X_3	$\hat{\sigma}_P^2$			$1874\cdot09 \pm 285\cdot36$
	$\hat{\sigma}_G^2$			$626\cdot70 \pm 283\cdot22$
	$2\hat{\sigma}_g^2$			$482\cdot32 \pm 279\cdot12$
	$\hat{\sigma}_s^2$			$144\cdot38 \pm 71\cdot98$
	$\hat{\sigma}_e^2$			$1247\cdot39 \pm 34\cdot88$

The population additive genetic and non-additive genetic variances can be estimated from the combining ability components by $\hat{\sigma}_a^2 = 2\hat{\sigma}_g^2$ and $\hat{\sigma}_{na}^2 = \hat{\sigma}_s^2$. (These estimates are unbiased only in the absence of epistatic effects.) The population genotypic and phenotypic variances may be estimated as $\hat{\sigma}_G^2 = 2\hat{\sigma}_g^2 + \hat{\sigma}_s^2$ and $\hat{\sigma}_P^2 = \hat{\sigma}_G^2 + \hat{\sigma}_e^2$. By estimating $\hat{\sigma}_P^2$ in this way we have disregarded the replication and replication $\times$ variety interaction effects and have included as the environmental variation the error variance associated with the individual plant observations.

The formulae for the calculation of approximate estimates of the variances of the variance components $\hat{\sigma}_e^2$ and $\hat{\sigma}_s^2$ were previously given. The corresponding

formulae for $2\hat{\sigma}_g{}^2$, $\hat{\sigma}_G{}^2$, and $\hat{\sigma}_P{}^2$ are as follows:

$$\operatorname{var}(2\hat{\sigma}_g{}^2) \cong \frac{8}{(p-1)(p-2)^2}M_g{}^2 + \frac{16}{p(p-2)^2(p-3)}M_s{}^2 = 4[\operatorname{var}(\hat{\sigma}_g{}^2)],$$

$$\operatorname{var}(\hat{\sigma}_G{}^2) \cong \frac{8}{(p-1)(p-2)^2}M_g{}^2 + \frac{4(p-4)^2}{p(p-2)^2(p-3)}M_s{}^2 + \frac{2}{m}M_e{}^2,$$

and

$$\operatorname{var}(\hat{\sigma}_P{}^2) \cong \frac{8}{(p-1)(p-2)^2}M_g{}^2 + \frac{4(p-4)^2}{p(p-2)^2(p-3)}M_s{}^2.$$

The standard errors attached to the estimated variance components in Table 13 are simply the square root of these approximate variances.

As outlined previously it is possible to examine the joint response of two variables for any effect in the model. The estimated correlation coefficients are given in Table 14. These correlation coefficients estimate the joint responses as they occur in the parent random mating population. The genotypic joint responses depend primarily on pleiotropic effects of genes and not on linkage.

TABLE 14

CORRELATION COEFFICIENTS CALCULATED FROM VARIANCE AND COVARIANCE COMPONENTS FOR VARIABLES X_1 = TOTAL YIELD, X_2 = COB WEIGHT, AND X_3 = SHELLED CORN WEIGHT

Variable	Kind of Correlation		X_2		X_3	
X_1	r_P		0·71		0·99	
	r_G		0·54		0·98	
		r_g		0·47		0·98
		r_s		0·87		1·00
	r_e		0·80		0·99	
X_2	r_P				0·60	
	r_G				0·38	
		r_g				0·28
		r_s				0·83
	r_e				0·72	

The following illustrates the type of interpretation which may be made concerning these correlated responses, assuming that the experimental material is in fact a random sample from a random mating population.

The genotypic correlation coefficient for variables X_2, X_3, $r_G = 0·38$, indicates a slight positive genetic association. On the average a gene causing increased cob weight also causes increased shelled corn weight. This is logical in that, other factors being constant, a gene causing increased cob surface area would make possible a greater number of kernels. However, the fact that the correlation coefficient is not large indicates that there are genetic factors operating in one variable which act independently of the other variable. For example, there may be genes causing variation in size and density of kernels which do not induce variability in cob weight.

On breaking down the genotypic joint response for variables X_2 and X_3 it is of interest to find that the additive and non-additive correlation coefficients, although both positive, differ considerably in magnitude. The additive effects show little association, $r_g = 0\cdot28$, and the non-additive effects show a close association, $r_s = 0\cdot83$. The small additive genetic correlation coefficient indicates that in the population selection could act on the two variables almost independently.

The large positive environmental correlation coefficient, $r_e = 0\cdot72$, may be interpreted to mean that for a given genotype increased nutrients tend to produce an increased cob size which in turn permits a greater shelled corn weight.

When, as above, interpretations of correlation coefficients computed from variance and covariance components are given, it should be pointed out that (1) the joint responses of pairs of variables are assumed linear, and (2) the reliability of the estimates is not known. Since the distribution of such statistics is not known their variances cannot be calculated.

IV. DISCUSSION

The appropriateness of the various kinds of diallel crossing methods depends on the experimental material and the objectives of the experiment.

When information on general and specific combining ability for a specific set of lines is desired in connection with a plant or animal breeding problem, experimental methods 3 or 4 are most applicable. In plant material, if it can be assumed that there will be no genotypic reciprocal effects (this is usually the case) method 4 is most suitable. If there is any doubt about whether or not reciprocal genotypic effects will occur, then both sets of F_1's should be included and diallel crossing method 3 used. In animal experiments, reciprocal crosses should be a fairly standard procedure. The reciprocal effects can be usefully employed to detect variation due to sex-linked genes and maternal effects. Thus method 3 would be most useful.

In most combining ability analyses in which a chosen set of lines is used, interest centres on the performance of F_1's. Therefore, the parental lines need not be included. However, in certain instances it might be advisable to include the parents. For example, if the combining ability analysis is employed to determine suitable lines to combine into a synthetic variety, and if considerable inbreeding occurs in the species, then it is advisable to include the parents and use methods 1 or 2.

In plant and animal breeding problems when a random set of lines is used, diallel crossing methods 3 or 4 are again most applicable. If it is desired to measure reciprocal effects method 3 must be used.

If it can be assumed that the experimental material constitutes a random sample from a population, then it is possible to use the genotypic components of variance and covariance to compute a discriminant function selection index which will aid in the simultaneous selection of several variables. If the further assumption can be made that the experimental material represents a random sample from a random mating population, the additive genetic variance and covariance components may be substituted for the genotypic components.

When a set of inbred lines is used in a diallel crossing system a genetic interpretation in terms of quantitative inheritance is made possible by the fact that the

analysis is really a "gamete" combining ability analysis. Thus the genetic properties of a diploid individual may be regarded as the combination of the genetic properties of the two gametes which united to form the individual. Therefore in the statistical analysis we may regard the genotypic effect of an individual as the summation of effects contributed by each gamete (i.e. set of genes in the gamete) and the interaction of gametes (i.e. the interaction of the genes in one gamete with those in the other).

If the experimental material can be assumed to be a random sample from a random mating population, the genetic interpretation can be pushed back to the gene rather than the gamete level, and an exact genetic interpretation may be given to the combining ability statistics (Griffing 1956). For this to be true we must assume that the set of inbred lines used in the diallel crosses is a random set of lines from a hypothetical population of inbred lines, which can be obtained from the parent random mating population by the imposition of an inbreeding system acting in the absence of forces which change gene frequencies. If this chain of assumptions can be validly made, then we can estimate the additive and non-additive genetic variances of the parent population. It should be pointed out that to obtain unbiased estimates, diallel crossing methods 3 or 4 must be used (i.e. the parents must not be included in the *combining ability analysis*). It is advisable, however, to include the parents in the experimental material grown in the experiment so that comparisons of hybrids with their parents can be made in other types of analyses.

In conclusion we see that diallel crossing systems may be used in at least two broad and related fields, namely, those of plant and animal breeding, and quantitative inheritance. The diallel crossing systems in which the parents are not included are generally the most useful in both fields. However, other systems may be used in special situations.

V. Acknowledgments

VI. References

EISENHART, C. (1947).—The assumptions underlying the analysis of variance. *Biometrics* **3**: 1–21.

FISHER, R. A. (1918).—The correlation between relatives on the supposition of Mendelian inheritance. *Trans. Roy. Soc. Edin.* **52**: 399–433.

FISHER, R. A. (1936).—The use of multiple measurements in taxonomic problems. *Ann. Eugen., Camb.* **7**: 179–88.

GRIFFING, B. (1948).—Statistical analysis of gene action in components of tomato yield. Unpublished Ph.D. Dissertation. (Iowa State College Library, Ames, Iowa.)

GRIFFING, B. (1953).—An analysis of tomato yield components in terms of genotypic and environmental effects. Bull. Ia. Agric. Exp. Sta. No. 397.

GRIFFING, B. (1956).—A generalized treatment of diallel crosses in quantitative inheritance. *Heredity* **10**: 31–50.

GRIFFING, B., and LINDSTROM, E. W. (1954).—A study of the combining abilities of corn inbreds having varying proportions of corn belt and non-corn belt germ plasm. *Agron. J.* **46**: 545–52.

HAYMAN, B. I. (1954).—The analysis of variance of diallel tables. *Biometrics* **10**: 235–44.

HAZEL, L. N., BAKER, M. L., and REINMILLER, C. F. (1943).—Genetic and environmental correlations between the growth rates of pigs at different ages. *J. Anim. Sci.* **2**: 118–28.

HENDERSON, C. R. (1948).—Estimation of general, specific, and maternal combining abilities in crosses among inbred lines of swine. Unpublished Ph.D. Dissertation. (Iowa State College Library, Ames, Iowa.)

HENDERSON, C. R. (1952).—Specific and general combining ability. In "Heterosis." (Ed. J. W. Gowen.) (Iowa State College Press: Ames.)

KEMPTHORNE, O. (1952).—"Design and Analysis of Experiments." (John Wiley & Sons, Inc.: New York.)

SMITH, H. F. (1936).—A discriminant function for plant selection. *Ann. Eugen., Camb.* **7**: 240–50.

SPRAGUE, G. F., and TATUM, L. A. (1942).—General versus specific combining ability in single crosses of corn. *J. Amer. Soc. Agron.* **34**: 923–32.

YATES, F. (1947).—The analysis of data from all possible reciprocal crosses between a set of parental lines. *Heredity* **1**: 287–301.