EVALUATION OF DIALLEL ANALYSIS WITH RESPECT TO THE GENETICS AND BREEDING OF SELF-POLLINATED CROPS

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

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The expression of many economically important traits of self-pollinated crops is controlled by quantitative gene action. Diallel analysis procedures have been used to gain an understanding of the inheritance of these traits.

In the present study, the genetic information available from the results of diallel experiments was examined. The importance of the genetic assumptions required for interpretation of these results was also investigated. Data for diallel experiments were simulated for a series of genetic models. These data were then analyzed using Gardner and Eberhart's (1966) Analysis III. Results revealed that, if gene frequencies do not equal 0.5 and if epistasis is present, the general combining ability estimates of Analysis III are not estimates of purely additive gene effects.

The relationships among the diallel analysis methods proposed by Hayman (1954b), Griffing (1956b) and Gardner and Eberhart (1966) were investigated. Results of this investigation revealed that the methods are highly interrelated. None of the methods appear better than the others because all are estimating similar characteristics and expressing them in different terms.

Correlations between general combining ability and variety effects were examined under various genetic models. In most cases, variety effects served as good indicators of general combining ability.

The effects of gene frequency, distribution of genes in the parents and type of gene action on the relative amounts of general and specific combining ability were assessed. Results of this study showed that these three factors, alone or in combination, altered the amounts of each type of combining ability. It was also shown that when gene frequencies were 0.5 at all loci and when there was zero correlation between loci, the amount of general combining ability reflected the amount of variation due to additive and additive x additive epistatic gene action.

The genetic assumptions required for valid interpretation of diallel results were examined. The assumption that gene frequencies are equal to 0.5 appears to be most crucial with respect to the genetic content of diallel statistics.

The effect of epistasis on the response to selection was examined. It appears that, when developing inbred lines, parental performance rather than general combining ability can be used as the basis for selection. However, neither variety performance nor the diallel statistics provide an indication of the amount of genetic variation within crosses.

1. INTRODUCTION

Many economically important traits of self-pollinated crops exhibit continuous variation. Inheritance of these quantitative traits is difficult to study due to the fact that many genes are responsible for the continuous range of phenotypes. Since individual gene effects cannot be identified, information concerning the inheritance of these types of traits must be derived from the combined effects of many genes.

Effective improvement of quantitative characteristics requires knowledge of the types of gene action governing their expression. Powers (1941) stated that information concerning inheritance of quantitative traits allows a breeding program to "... be pursued with much less expense and much more certainty of success ...". Robinson et al. (1949), Cockerham (1956), and Brim and Cockerham (1961) agree that information about the type and magnitude of genetic variation is essential for making accurate decisions in breeding programs.

Diallel crosses have been used in attempts to obtain information concerning the inheritance of quantitative traits. The use of diallel crosses was first discussed by Schmidt (1919). The method involves crossing a set of inbred lines in all possible combinations.

Sprague and Tatum (1942) utilized a diallel cross to evaluate the performance of inbred lines of corn. They used the term "general combining ability" to designate the average performance of a line in hybrid combination. The term "specific combining ability" was used to

designate those cases in which certain combinations did relatively better or worse than would be expected on the basis of average performance of the lines involved. Estimates of general and specific combining ability have been used by plant breeders in making decisions concerning appropriate breeding methods and in choosing parents for breeding programs.

Genetic interpretation of the results of diallel experiments has received considerable attention. Jinks (1954), Hayman (1954c), Griffing (1956b) and Gardner and Eberhart (1966) have discussed the genetic interpretation of data from diallel crosses. This type of interpretation may be of value in plant breeding programs and may also contribute to the general knowledge of the inheritance of quantitative traits.

Genetic interpretation of diallel experiments requires that certain assumptions be fulfilled. Kempthorne (1956), Gilbert (1958), and Matzinger and Cockerham (1963) have examined the assumptions required for valid interpretation of diallel results. They found that certain assumptions are more critical than others. Gilbert (1958) and Sprague (1966) have questioned some of the required assumptions as to whether they are realistic in practical situations.

From this preliminary examination it is apparent that several methods exist for analyzing the data of a diallel experiment. Also, interpretation of the analysis requires certain assumptions, of which some appear to be more critical than others. Finally, these assumptions, although required, may be unrealistic to impose in a practical breeding program. With these points in mind, this study was initiated to examine three questions. First, what type of information is provided by each

type of diallel analysis? Second, what are the consequences to the interpretation of this information when certain assumptions are not fulfilled? Third, what genetic information is required by breeders of self-pollinating species and does diallel analysis supply this information? To answer the first question, a mathematical comparison was made of several methods available for analyzing data from diallel crosses. Computer simulation of various genetic models was used to investigate the importance of various genetic assumptions and to determine the types of genetic information that can be derived from diallel analysis.

2. LITERATURE REVIEW

2.1. Statistical Analysis of Diallel Experiments

Various statistical techniques have been proposed for analyzing diallel experiments. Of the methods developed, Hayman (1954b) was the first to apply a diallel analysis procedure to a self-pollinated crop. The analysis presented by Hayman was designed to detect the presence of additive genetic variation and variation due to dominance deviations in a complete diallel cross. Using Hayman's analysis, m estimates the overall mean of the parents and the progeny, l measures the difference between the progeny and the parents, j_i measures the effect of gametes produced by the i^{th} parent, l_i measures the difference in performance of gametes of the i^{th} parent in combination with themselves and with gametes of other parents, and l_{ij} measures the specific interaction of gametes from the i^{th} and j^{th} parents.

This analysis, as proposed by Hayman (1954b), can be used only when all possible mating combinations have been made. Frequently, reciprocal differences can be assumed to be absent. In this case, only one set of F_1 progeny need be produced. Jones (1965) modified Hayman's analysis to apply to the half diallel (i.e. parents plus one set of F_1 progeny). Eliminating reciprocal crosses reduces the number of crosses necessary for a diallel experiment and allows a larger number of parents to be evaluated.

In 1956, Griffing (1956b) presented four different diallel crossing

schemes along with their respective analyses. The differences among these methods arise due to the presence or absence of the parents, the F_1 reciprocal progeny, or both. Method 1 includes the parents, the F_1 progeny and the F_1 reciprocal progeny in the analysis. Method 2 utilizes only the parents and the F_1 progeny. The F_1 progeny and the F_1 reciprocal progeny are analyzed in Method 3 while only the F_1 progeny are considered in Method 4. Griffing (1956a) has commented that the term "diallel" refers to those crossing schemes that include the parents whereas those methods in which the parents are not included have been called "modified diallels". Based on this distinction, Methods 1 and 2 should be referred to as "diallels" while Methods 3 and 4 should be referred to as "modified diallels". It should also be noted that Methods 2 and 4 are similar in that, in both methods, reciprocal differences are assumed to be absent, and reciprocal crosses are, therefore, not included in the analysis.

Griffing's (1956b) presentation also included a discussion of the sampling procedure used to derive the parental material. The parents of a diallel may constitute the entire population with which a researcher is interested. Or they may represent a random sample from a much larger population of interest. If the parents comprise the entire population, then a set of parameters descriptive of the specific group of parents can be obtained. The parameters include a mean (m), a general combining ability effect (g_i) due to a particular parent and a specific combining ability effect (s_{ij}) due to the interaction of two parents. On the other hand, if parents represent a random sample, one estimates components of variance due to general and specific combining ability.

In 1966, Gardner and Eberhart presented three methods of analysis for diallel experiments. Their methods apply when the parents constitute the entire population of interest. The first method (Analysis I) can only be used if the parents are not inbred. In this analysis the parents, the F_1 progeny and the F_1 reciprocal progeny are utilized. If parents are inbred, then either Analysis II or III can be used. Analysis II was developed for use when only the parents and F_1 progeny are grown while Analysis III considers only the F_1 progeny in the analysis.

As is the case with other analyses, certain parameters can be estimated depending upon the Analysis used. These parameters will be descriptive of the specific set of parents used in the diallel. When Analysis I is used, the contributions of the homozygous loci (a_i) and the heterozygous loci (d_i) can be estimated for a particular parent. The authors have also provided a term that varies due to differences in gene frequencies and due to dominance in the parents. This term they have called a heterosis parameter (h_{ij}). This heterosis parameter can be subdivided into mean heterosis (h), mean heterosis of the i^{th} and j^{th} parent (h_i and h_j, respectively), and specific heterosis (s_{ij}) due to the interaction of two parents. An overall mean (m) is also estimated. Analysis II considers only the parents and one set of F_1 progeny. When parents are inbred and the complete diallel cross is not made, the contributions of the homozygous (a_i) and the heterozygous (d_i) loci are confounded and cannot be estimated separately. The variety effect (v_i) is used to estimate the joint effect of these two parameters. In addition, a variety mean (m_v) can be estimated. All other parameters

that can be estimated in the complete analysis (Analysis I) can be estimated in Analysis II. Analysis III considers only the F_1 progeny in the analysis, hence, the only parameters that can be estimated are the general (g_i) and specific (s_{ij}) combining ability effects and a progeny mean (m_c). If the parents are grown with the crosses, a variety mean (m_v) and variety effects (v_i) can also be obtained.

Some similarities do exist between the diallel methods discussed. Gardner and Eberhart (1966) compared the analyses of Hayman (1954b) and of Griffing (1956b) with their own. Their conclusion was that both Hayman and Griffing (Method 2, Model I) provide analyses that are identical to their Analysis II. They state, however, that Griffing does not subdivide his heterosis term which he calls specific combining ability. Although Hayman does subdivide heterosis, he does so in terms of deviations about the experiment mean. Gardner and Eberhart (1966) further state that, when the parents are inbred lines, their genetic model is identical to Hayman's. Gardner and Eberhart (1966) have also stated that, for their Analysis III, the sums of squares for crosses and its subdivision into general and specific combining ability is identical to Griffing's (1956b) Method 4, Model I.

When conducting a diallel experiment, certain statistical assumptions must be considered. One of these assumptions refers to the method used to select parental material for the diallel cross. According to Griffing (1956b), selection of the parents can occur in one of two ways. The first method involves selecting parents based on their individual desirability. Material chosen in this fashion can be considered to form the entire population to be analyzed. Any inferences

from the results are thereby limited to this specific set of parents. The second method requires that parents be a random sample from a larger parent population. When parents are chosen in this manner, any inferences apply to the larger population and not to the specific set of parents used.

Eisenhart (1947) was responsible for naming the two methods of sampling just described. The sampling technique in which the parents form the entire population to be analyzed has been termed a fixed effects model (or Model I). When the parents are chosen in a random manner, the term random effects model (or Model II) has been applied. Although the initial statistical analysis is similar for these two models, there are very important differences in the final parameters that are estimated and in the interpretation of results.

Under the fixed effects model, specific effects are estimated. When the random effects model applies, estimates of variance components are derived from the mean squares. Tests of significance and estimates of confidence intervals for the fixed effects model are exact because the probability distribution is known. However, the probability distributions of variance components are unknown. Hence, "... many of the tests and confidence intervals used involve either approximations or additional assumptions." (Dunn and Clark, 1974). Little is known about how well these approximations work in practice.

Of the diallel methods discussed, the procedures described by Hayman (1954b) and later modified by Jones (1965), and those described by Gardner and Eberhart (1966) fall into the class of fixed effects models. Griffing (1956b) developed his group of analyses to be used

when either a fixed or random effects model applies. Eberhart and Gardner (1966) have suggested that the bulk of the breeding material of interest to the plant geneticist has been highly selected in favor of economically important traits. For diallel analysis, such material cannot be regarded as a random sample from a larger reference population. If so, estimation of variance components (i.e. the use of Model II) does not provide useful information.

2.2. Genetic Interpretation

Evaluation of a diallel cross involves two stages. In the first stage, sums of squares are partitioned and various parameters are estimated. Because this stage consists only of statistical manipulations, no genetic assumptions are required. Stage two of the evaluation centers around interpretation of the estimated parameters. Because this second stage involves deriving genetic meaning from statistical values, various authors (Griffing, 1956b; Gamble, 1962; Matzinger, 1963; and Sprague, 1966) agree that certain genetic assumptions are required to simplify the interpretive process.

The first of these assumptions relates to the regularity of meiosis in the parents. Hayman (1954b, c), Griffing (1956a), Kempthorne (1956) and Gardner and Eberhart (1966) have all agreed that segregation must follow a normal diploid pattern. Cockerham (1963) has stated that the need for this assumption has arisen due to the fact that most of our knowledge concerning gene action is with reference to diploid species.

A second assumption required by Jinks and Hayman (1953), Hayman (1954b, c), Griffing (1956a) and Gardner and Eberhart (1966)

concerns the state of inbreeding in the parents of the diallel cross. The assumption requires the parents to be homozygous. Griffing (1950) has provided two reasons for the use of homozygous as opposed to heterozygous parental material. First, progeny of heterozygous parents will be segregating and linkage will have to be reckoned with when interpreting results. Second, a much larger population of individuals is required to adequately estimate the various parameters of a group of heterozygous parents. The larger population size is required to obtain estimates with the same degree of accuracy as those obtained with homozygous parents (Cockerham, 1956).

A third assumption required for the analyses of Jinks and Hayman (1953), Hayman (1954b, c) and Gardner and Eberhart (1966) is that epistasis must be absent. When epistasis is present, estimates of additive and dominance variance components are not unique but also contain variation due to epistasis (Jinks and Stevens, 1959).

A fourth assumption, specified by Gardner and Eberhart (1966) refers to the presence of linkage. These authors point out that linkage is only a problem when epistasis is present. Diallel analysis involves the analysis of parent and progeny means. In the absence of epistasis, generation means are not affected by linkage (Jinks and Stevens, 1959). Hayman (1954b, c) and Kempthorne (1956) have both agreed that valid interpretation of diallel results is possible only if genes are distributed independently in the parents. For this assumption to hold true, either linkage must be absent in the parent population or the parents of the diallel must be derived from a random mating population.

A final assumption that has been specified by Hayman and

Mather (1955) and Gardner and Eberhart (1966) is that gene frequencies must be 0.5 at all loci. According to Matzinger and Cockerham (1963), gene frequencies of 0.5 are required only if dominance is included in the genetic model of the crosses. Hayman and Mather (1955) have commented that unequal gene frequencies cause the additive and dominance variation to be statistically confounded. Sprague (1966) has reported in his review of papers on the detection of epistasis, that studies that provide positive evidence for the presence of epistasis have all been carried out with populations in which the initial gene frequency was 0.5. In those studies showing no significant epistasis present, initial gene frequencies were unknown. This failure to detect varietal epistasis in the second group of studies could have been due to an averaging effect for gene frequencies near 1.0 or zero (Sprague, 1966).

Matzinger and Cockerham (1963) believe that some of the genetic assumptions required are more important than others. Kempthorne (1956) has supported this view and has further stated that independent distribution of the genes between the parents is one of the more critical assumptions, without which the analysis is pointless.

If the assumptions required for Griffing's (1956b) analysis are fulfilled, Griffing has stated that the components of variance due to general and specific combining ability can be interpreted genetically. The interpretation is such that the general vs. specific combining ability variance is equivalent to additive vs. non-additive genetic variance. As Sampson (1971) has stated, it is generally felt that additive genetic variance is the result of mainly additive gene action while non-additive genetic variance is composed of dominance and

epistatic variance. In addition to this interpretation, it must be realized that dominance variation decreases by one-half for each generation of selfing and thus is not fixable in self-pollinated crops. On the other hand, epistatic variation also decreases with selfing but some is fixable in self-pollinated crops (Sampson, 1971). However, due to the lack of understanding of epistasis, Cockerham (1956) has stated that any distinction between the various types of epistasis would be of little value when selecting a breeding procedure. The presence of epistasis can cause the measurement of the fundamental properties of a population to be confounded (Kempthorne, 1956) or contribute to estimates of additive and dominance effects (Gardner and Eberhart, 1966).

Some authors have examined the assumptions required for valid interpretation. Both Gilbert (1958) and Sprague (1966) are of the opinion that information derived from a diallel experiment may be of little value in a genetic sense. The reason for this statement lies in the fact that some of the genetic assumptions are so unrealistic that it is doubtful that they could all be fulfilled in a practical case.

2.3. Utilization of Results of Diallel Experiments

How can estimates of the types of gene action best be used? According to Townsend (1975), estimates of additive and non-additive genetic variance are of value to a plant breeder. He feels that these estimates provide a measure of the expected effectiveness of selection. Pederson (1969) has shown that in the absence of linkage and epistasis, response to selection in self-pollinated crops depends only on additive effects. Matzinger (1963) has stated that estimates of genetic

and environmental parameters are of value when making decisions about breeding programs. These decisions may increase the efficiency of the program. Genetic information can still be of value even if it does not suggest any new breeding procedure. For example, where additive x additive epistatic effects make up a large portion of the genotypic variance, breeding methods would require little change from those when variance includes only additive effects. Homozygous genotypes are still desired. Matzinger (1963) suggested that selection must not be too severe in the early stages of a breeding program. This would allow desirable epistatic combinations to be formulated.

Various types of selection programs have been developed to exploit particular types of gene action. Recurrent selection for general combining ability (Jenkins, 1940) was designed to utilize additive gene effects. On the other hand, recurrent selection for specific combining ability was recommended by Hull (1945) as a method of exploiting dominance and epistasis (non-additive effects). Comstock et al. (1949) developed reciprocal recurrent selection for use when both additive and non-additive gene effects are to be utilized.

In self-pollinated crops non-additive genetic variance can be exploited only if hybrid seed production is commercially feasible (Singh et al., 1970). Morley (1963) states that although non-additive genetic effects must be present for heterosis to exist, the presence of heterosis by itself is not sufficient cause for favoring development of hybrids rather than inbreds.

3. RELATIONSHIPS AMONG FIVE METHODS OF ANALYZING DIALLEL EXPERIMENTS

Statistical models for the analysis of diallel crosses have been presented by various authors. For the present study the method proposed by Hayman (1954b), two of those proposed by Griffing (1956b) and two of those proposed by Gardner and Eberhart (1966) were examined. Because reciprocal differences are not common in self-pollinated crops, only those methods that do not include reciprocal crosses were considered. The method of analysis proposed by Hayman (1954b) is applicable to the full diallel cross (i.e. all possible crosses). However, Jones (1965) provided a modification of Hayman's analysis which allows it to be applied to the half diallel cross (i.e. only parents and one set of F_1 progeny). The statistical model that applies to Hayman's (1954b) diallel analysis is

$$\begin{aligned} Y_{ii} &= m + 2j_i - \frac{p-1}{2} l - (p - 2) l_i \\ Y_{ij} &= m + j_i + j_j + l + l_i + l_j + l_{ij} \end{aligned} \qquad \ldots\ (1)$$

where Y_{ii} is the average performance of the i^{th} parent ($i = 1, p$) and Y_{ij} is the average performance of the F_1 hybrid derived by crossing parent i with parent j ($i < j$). In this model, m is the mean of the parents and progeny, l measures the difference between the progeny and parents, j_i measures the effect of gametes produced by the i^{th} parent (both in inbred and hybrid combination), l_i measures the difference in performance of gametes of the i^{th} parent in combination with themselves and with gametes from other parents, and l_{ij} measures the specific

interaction between gametes from the i^{th} and j^{th} parents.

Griffing (1956b) provided two methods of analysis (Methods 2 and 4) that do not include reciprocal progeny in the analysis. The model for Method 2 (parents plus one set of F_1 progeny) is

$$\begin{aligned} Y_{ii} &= m + 2\, g_i + s_{ii} \\ Y_{ij} &= m + g_i + g_j + s_{ij} \end{aligned} \qquad \ldots\ (2)$$

where m is the mean of the parents plus progeny, g_i and g_j are the general combining ability of gametes from the i^{th} and j^{th} parents, s_{ii} is the specific combining ability of gametes mated with themselves and s_{ij} is the specific combining ability of gametes from the i^{th} and j^{th} parents. For Method 4 (one set of F_1 progeny only) the parents are not considered in the analysis. The model for the progeny is

$$Y_{ij} = m_c + g_i + g_j + s_{ij} \qquad \ldots\ (3)$$

where m_c is the mean performance of the F_1 progeny and g_i, g_j and s_{ij} have the same meaning as in Method 2.

Gardner and Eberhart (1966) have also provided two methods of diallel analysis, Analyses II and III, that do not include reciprocal progeny in the analysis. The statistical model for Analysis II (parents plus one set of F_1 progeny) is

$$\begin{aligned} Y_{ii} &= m_v + v_i \\ Y_{ij} &= m_v + 1/2\ (v_i + v_j) + h + h_i + h_j + s_{ij} \end{aligned} \qquad \ldots\ (4)$$

where m_v is the mean performance of the parents, v_i is the variety effect, h is the difference between the mean of the progeny and the mean of the parents, h_i measures the difference in performance of gametes of the i^{th} parent in combination with themselves and with gametes from other parents, and s_{ij} is the specific combining ability of gametes from the

i^{th} and j^{th} parents. Analysis III (one set of F_1 progeny only) normally does not consider the parents in the analysis. However, if parents are grown along with the progeny, the analysis can be performed according to the model

$$\begin{aligned} Y_{ii} &= m_v + v_i \\ Y_{ij} &= m_c + g_i + g_j + s_{ij} \end{aligned} \qquad \ldots\ (5)$$

where m_v, v_i and s_{ij} have the same meaning as in Analysis II, m_c is the mean performance of the F_1 progeny and g_i and g_j are the general combining abilities of gametes from the i^{th} and j^{th} parents.

Examination of these methods of diallel analysis suggested that close relationships exist among the same elements of the models. To clarify the nature of these relationships, it was decided to express the parameters (in each model) in terms of the Y_{ij}'s. Once all parameters had been expressed in these common terms, it was then possible to express the elements of each model in terms of the elements of one method of analysis. Gardner and Eberhart's (1966) Analysis III appeared to provide the simplest point of reference for relating the five methods of analysis. Table 3.1 provides a summary of the relationships of the four other analyses to Analysis III of Gardner and Eberhart (1966). The table gives the coefficient which, when multiplied by an estimate of the appropriate parameter of Analysis III, will translate estimates of Analysis III parameters into estimates of parameters of the other methods. From Table 3.1, the g_i parameter of Griffing's (1956b) Method 2 is composed of $2/(p+2)$ times the variety effect (v_i) of Analysis III plus $(p-2)/(p+2)$ times the general combining ability effect (g_i) of Analysis III.

TABLE 3.1. Coefficients required to translate parameters of Gardner and Eberhart Analysis III into parameters of four other models. #

Parameters of	Parameters of Gardner and Eberhart Analysis III				
	m_c	m_v	v_i	g_i	s_{ij}
Griffing Method 2					
m	$\frac{p-1}{p+1}$	$\frac{2}{p+1}$			
g_i			$\frac{2}{p+2}$	$\frac{p-2}{p+2}$	
s_{ii}	$\frac{1-p}{p+1}$	$\frac{p-1}{p+1}$	$\frac{p-2}{p+2}$	$\frac{4-2p}{p+2}$	
s_{ij}	$\frac{2}{p+1}$	$\frac{-2}{p+1}$	$\frac{-2}{p+1}$ ##	$\frac{4}{p+1}$ ###	1
Griffing Method 4					
m_c	1				
g_i				1	
s_{ij}					1
Hayman					
m	$\frac{p-1}{p+1}$	$\frac{2}{p+1}$			
j_i			$\frac{1}{p}$	$\frac{p-2}{p}$	
l	$\frac{2}{p+1}$	$\frac{-2}{p+1}$			
l_i			$\frac{-1}{p}$	$\frac{2}{p}$	
l_{ij}					1
Gardner and Eberhart analysis II					
m_v		1			
v_i			1		
h	1	-1			
h_i			-1/2	1	
s_{ij}					1

See text for definitions of parameters estimated by each model of diallel analysis. p = number of parents in the diallel cross.

To estimate s_{ij} of Griffing method 2, multiply $(v_i + v_j)$ by this coefficient.

To estimate s_{ij} of Griffing method 2, multiply $(g_i + g_j)$ by this coefficient.

From Table 3.1, it is clear that the relationships between m, m_v and m_c are such that the overall mean of the parents and progeny (m) is a weighted average of the mean of the progeny (m_c) and the mean of the parents (m_v). Both analyses of Gardner and Eberhart include estimates of variety effects (v_i). The general combining ability effects (g_i) of Griffing's (1956b) Method 4 are identical to the general combining ability effects estimated in Analysis III. The general combining ability effects (g_i) of Griffing's Method 2 and the j_i effects of Hayman (1954b) are similar in that both are weighted averages of the variety (v_i) and general combining ability (g_i) effects of Analysis III. Differences between v_i and g_i are included in estimates of l_i of Hayman (1954b), and of h_i of Gardner and Eberhart's Analysis II. In fact, it is evident that $h_i = 2\ l_i/p$. The s_{ij} of Gardner and Eberhart's Analysis II, the l_{ij} of Hayman, and the s_{ij} of Griffing's Method 4 are all identical to the specific combining ability effects (s_{ij}) of Analysis III. The difference between the mean of the progeny (m_c) and the mean of the parents (m_v) provides a measure of average heterosis. An estimate of this quantity is provided by l in Hayman's analysis and by h in Gardner and Eberhart's Analysis II. The specific combining abilities of gametes with themselves (s_{ii}) and with gametes from other parents (s_{ij}), as estimated in Method 2 of Griffing, are rather complex functions of all parameters in the Analysis III model.

From the above results, it is apparent that all statistical parameters can be expressed as linear functions of the parameters in Gardner and Eberhart's Analysis III. Therefore, for the purposes of this study, all results will be derived for this one diallel analysis

method (i.e. Analysis III). For this method of analysis, the statistical parameters that need be considered are the mean of the F_1 progeny (m_c), the mean of the inbred parents (m_v), the difference between the value of the i^{th} parent and the mean of the parents (i.e. the variety effect, v_i), the difference between the mean of the progeny from the i^{th} parent and the mean of all the progeny (i.e. the general combining ability effect, g_i), and the value of the ij^{th} progeny minus the value of the general combining ability effects for the i^{th} and j^{th} parents (i.e. the specific combining ability effect, s_{ij}). For completeness, the genetic composition of the difference between m_c and m_v (a measure of average heterosis) and the difference between g_i and v_i (which provides a measure of average heterosis contributed by the i^{th} parent) will also be investigated.

4. SIMULATION OF DIALLEL EXPERIMENTS

4.1. Characterization of Genetic Models

Consideration of two genetic loci allows the study of additive, dominance and two-locus epistatic effects. Nine different genotypes are possible when there is segregation at the two loci. Using the notation of Mather (1967), the genotypic values of the nine possible genotypes can be completely described with nine terms which describe various types of gene action. Van der Veen (1959) has attributed the use and definition of these terms to Hayman (1954a). This method of representing genotypic values has been termed the "F_∞-metric" or "pure-line-metric". The nine possible genotypes for two segregating loci, A-a and B-b, and their genotypic values (expressed in terms of Hayman's "pure-line-metric") are given in Table 4.1. The nine terms of the "pure-line-metric" are: m, the mean of the homozygous genotypes AABB, AAbb, aaBB and aabb; d_a and d_b which represent the differences between the homozygous loci A-a and B-b, respectively; h_a and h_b which represent the dominance effects at each locus; i_{ab} which represents the interaction between d_a and d_b; j_{ab} and j_{ba} which represent the interactions between d_a and h_b and d_b and h_a, respectively; l_{ab} which represents the interaction between the heterozygous loci Aa and Bb.

Arbitrary values were assigned to each of these nine terms in specifying models which included additive, completely dominant and various types of epistatic gene action (Table 4.2). The first five

TABLE 4.1. Genotypic values of the nine genotypes possible from the segregation of two loci.

Genotype	Genotypic value [#]
AABB	$Y_{22} = m + d_a + d_b + i_{ab}$
AABb	$Y_{21} = m + d_a + h_b + j_{ab}$
AAbb	$Y_{20} = m + d_a - d_b - i_{ab}$
AaBB	$Y_{12} = m + h_a + d_b + j_{ba}$
AaBb	$Y_{11} = m + h_a + h_b + l_{ab}$
Aabb	$Y_{10} = m + h_a - d_b - j_{ba}$
aaBB	$Y_{02} = m - d_a + d_b - i_{ab}$
aaBb	$Y_{01} = m - d_a + h_b - j_{ab}$
aabb	$Y_{00} = m - d_a - d_b - i_{ab}$

[#] Y_{ij} $(0 \leq i \leq 2,\ 0 \leq j \leq 2)$ = the value of a genotype with i "plus" (A) genes at the A-a locus and j "plus" (B) genes at the B-b locus.

The terms, m, d_a, d_b, etc., refer to additive, dominance and epistatic genetic effects as described in text.

TABLE 4.2. Specification of ten genetic models used in simulations.

Model	Description [#]	Genetic effects [##]								
		m	d_a	d_b	h_a	h_b	i_{ab}	j_{ab}	j_{ba}	l_{ab}
I	additive effects	0	3	3	0	0	0	0	0	0
II	additive plus dominance effects	0	3	3	3	3	0	0	0	0
III	additive plus additive x additive effects	0	3	3	0	0	3	0	0	0
IV	additive plus additive x dominance effects	0	3	3	0	0	0	3	3	0
V	additive plus dominance x dominance effects	0	3	3	0	0	0	0	0	3
VI	recessive epistasis	0	2	3	2	3	2	2	2	2
VII	complementary epistasis	0	3	3	3	3	3	3	3	3
VIII	inhibitory epistasis	0	3	-3	3	-3	3	3	3	3
IX	duplicate epistasis	0	3	3	3	3	-3	-3	-3	-3
X	dominant epistasis	0	2	3	2	3	-3	-3	-3	-3

[#] See text for further description.

[##] The terms, m, d_a, d_b, etc., refer to additive, dominance and epistatic genetic effects as described in text.

models all include additive effects. Model I has only additive effects. Model II includes additive and dominance effects. Models III, IV and V include additive effects plus one of the three types of two-locus epistatic effects. Models VI to X specify the five classical types of epistasis identified by Jana (1972).

If the frequencies of the nine genotypes are the same as those found in an F_2 population with no linkage, the total genetic variance can be subdivided into variation due to additive, dominance and epistatic effects by using the method of Cockerham (1954). For each of the models in Table 4.2, the genetic variance was subdivided into variation due to additive and dominance effects, additive x additive, additive x dominance, dominance x additive and dominance x dominance epistatic effects (Table 4.3).

Examination of Table 4.3 reveals that in the models studied, variation due to additive effects ranges from 100 percent (Model I - additive effects) to 18 percent (Model X - dominant epistatis). Dominance variation ranges from 0 to 33.3 percent and epistatic variation from 0 to 73 percent. Results in Table 4.3 are presented as a method by which the ten genetic models can be characterized with respect to the type of genetic variation present in each.

4.2. Method of Simulating Data for a Diallel Experiment

When dealing with two loci, only four possible inbred parents exist in a diallel experiment. The genotypes of these four parents, their genotypic values and their frequencies are presented in Table 4.4. This method of specifying the parental frequencies was also used by

TABLE 4.3. Percentage of genetic variation due to additive ($d_a + d_b$), dominance ($h_a + h_b$) and epistatic (i_{ab}, $j_{ab} + j_{ba}$, l_{ab}) effects in ten genetic models.

Model #	% Variation due to				
	additive effects	dominance effects	epistatic effects		
	$d_a + d_b$	$h_a + h_b$	i_{ab}	$j_{ab} + j_{ba}$	l_{ab}
I	100.0	0.0	0.0	0.0	0.0
II	66.7	33.3	0.0	0.0	0.0
III	80.0	0.0	20.0	0.0	0.0
IV	90.0	0.0	0.0	10.0	0.0
V	84.2	10.5	0.0	0.0	5.3
VI	59.5	29.8	4.7	4.8	1.2
VII	57.1	28.6	6.3	6.4	1.6
VIII	51.3	25.6	10.3	10.2	2.6
IX	26.7	13.3	26.7	26.6	6.7
X	18.0	9.0	32.4	32.5	8.1

Description of genetic models in text.

TABLE 4.4. Genotypes, genotypic values and frequencies of inbred parents in simulated diallel experiments.

Parental genotype	Genotypic value [#]	Frequency [##]
AABB	$m + d_a + d_b + i_{ab}$	$k_1 = p_a p_b + d$
AAbb	$m + d_a - d_b - i_{ab}$	$k_2 = p_a q_b - d$
aaBB	$m - d_a + d_b - i_{ab}$	$k_3 = q_a p_b - d$
aabb	$m - d_a - d_b + i_{ab}$	$k_4 = q_a q_b + d$

[#] The terms, m, d_a, d_b, etc., refer to additive, dominance and epistatic genetic effects as described in text.

[##] p_a = the frequency of the A-allele in the parent population = $k_1 + k_2$; $q_a = 1 - p_a = k_3 + k_4$;
p_b = the frequency of the B-allele in the parent population = $k_1 + k_3$; $q_b = 1 - p_b = k_2 + k_4$.

d = a measure of association between genes at the A-a and B-b loci (see text).

Coughtrey and Mather (1970). With respect to the parental genotypes in Table 4.4, the frequency of the A-allele ($k_1 + k_2$) can be represented by p_a while the frequency of the a-allele ($k_3 + k_4$) can be represented by q_a ($= 1 - p_a$). Similarly, for the B-b locus the frequencies of the B ($k_1 + k_3$) and b ($k_2 + k_4$) alleles can be represented by p_b and q_b ($= 1 - p_b$), respectively. The parameter, $d = k_1k_4 - k_2k_3$, is a measure of the degree of non-random distribution of genes (i.e. association and dispersion) in the parents. When genotypes of the AABB and aabb types predominate in the parent population, the genes are said to be associated and d is positive. When the AAbb and aaBB genotypes predominate, the genes are said to be dispersed and d is negative.

Wright (1969) has provided a formula which measures the degree of non-random distribution of genes in terms of the correlation between gene frequencies at each locus. The correlation presented by Wright (1969) is equivalent to

$$r = \frac{d}{\sqrt{p_a q_a p_b q_b}} .$$

Therefore, it should be apparent that the correlation is positive with gene association, negative with gene dispersion, and zero when genes are randomly distributed in the parent population.

The use of the d parameter in the specification of the parental frequencies allows one to investigate the assumption of random distribution of genes in the parent population. In the present study, the value of d was set at -0.1875, -0.125, 0, 0.125 and 0.1875. With a population of sixteen parents and gene frequencies equal to 0.5 (i.e. $p_a = p_b = 0.5$) the five disequilibrium levels used correspond to correlations between loci of -0.75, -0.5, 0, 0.5 and 0.75. To obtain

a correlation as high as 0.75 and to avoid fractional numbers of each type of parent, sixteen parents were used. The use of more than sixteen parents would be unreasonable from a practical standpoint. For these reasons, all simulations were for diallel experiments involving sixteen parents.

If the four parental genotypes (Table 4.4) are considered as the parents of a diallel cross, where p is the number of parents, there will be pk_1 parents with genotype AABB, pk_2 with genotype AAbb, pk_3 with genotype aaBB and pk_4 with genotype aabb. These parents can then be considered in all possible combinations to simulate a diallel cross. For the purpose of this study, progeny derived from selfing and reciprocal matings were not considered. In this case, there will be pk_1 x $(pk_1 - 1)/2$ matings involving parents with genotype AABB with other parents of the same genotype. Similarly, there will be pk_1 x pk_2 matings of the type AABB x AAbb. The numbers of each possible mating, the genotypes of the parents involved, the genotypes of the resultant progeny and the genetic values of these progeny appear in Table 4.5.

Using the formulae discussed in this section, diallel cross data can be generated in the following manner. First, the number of parents (p), the frequencies of the A and B alleles (p_a and p_b, respectively) and the degree of non-random gene distribution in the parents (d) are used in conjunction with Table 4.4, to calculate the frequencies of the four parental genotypes. These frequencies are then used to calculate the number of each type of progeny as indicated in Table 4.5. The values of the different genetic parameters (i.e. m, d_a, d_b, h_a, h_b, i_{ab}, j_{ab}, j_{ba}, l_{ab}) are then used to calculate the genotypic values of the parents (Table 4.4) and of the progeny (Table 4.5) of the diallel experiment.

TABLE 4.5. Parental mating types, resultant progeny genotypes, genotypic values and numbers in simulated diallel experiments.

Mating type of parents	Progeny		
	Genotypes	Genotypic value [#]	Number [##]
AABB x AABB	AABB	$m + d_a + d_b + i_{ab}$	$pk_1 (pk_1 - 1)/2$
AABB x AAbb	AABb	$m + d_a + h_b + j_{ab}$	$p^2k_1k_2$
AABB x aaBB	AaBB	$m + h_a + d_b + j_{ba}$	$p^2k_1k_3$
AABB x aabb	AaBb	$m + h_a + h_b + l_{ab}$	$p^2k_1k_4$
AAbb x AAbb	AAbb	$m + d_a - d_b - i_{ab}$	$pk_2 (pk_2 - 1)/2$
AAbb x aaBB	AaBb	$m + h_a + h_b + l_{ab}$	$p^2k_2k_3$
AAbb x aabb	Aabb	$m + h_a - d_b - j_{ba}$	$p^2k_2k_4$
aaBB x aaBB	aaBB	$m - d_a + d_b - i_{ab}$	$pk_3 (pk_3 - 1)/2$
aaBB x aabb	aaBb	$m - d_a + h_b - j_{ab}$	$p^2k_3k_4$
aabb x aabb	aabb	$m - d_a - d_b + i_{ab}$	$pk_4 (pk_4 - 1)/2$

[#] The terms, m, d_a, d_b, etc., refer to additive, dominance and epistatic genetic effects as described in text.

[##] See text for further description.

The simulated data can then be subjected to Gardner and Eberhart's (1966) Analysis III.

In this study, 16 parents were considered in all simulations for reasons previously expressed. To study the impact of non-random distribution of genes in the parents, correlations between loci of -0.75 to 0.75 were simulated for gene frequencies of 0.5. The effect of gene frequencies other than 0.5 was studied by simulating gene frequency combinations from 0.25 to 0.75 with zero correlation between loci.

4.3. Results

4.3.1. General Combining Ability Effects

A total of 100 simulations were performed in order to assess the effects of (a) different genetic models, (b) non-random distribution of genes in the parents and (c) varying gene frequencies on the genetic interpretation of diallel analyses. Fifty of these were used to determine the genetic make-up of a particular set of statistical effects in the following way. An additive genetic model (Model I) was used as the standard. The statistical effects were calculated for Model I and their values were compared to the statistical effects calculated under genetic models II, III, IV and V. These four models contain dominance, additive x additive, additive x dominance and dominance x dominance effects, respectively, in addition to additive effects. If the value of the statistical effects under any model differed from the strictly additive model, it was concluded that the dominance or epistasis of that particular model contributed to the genetic make-up.

The general combining ability effects (g_i), calculated for varying

gene frequencies and correlations between loci, are presented in Table 4.6 for the additive and additive plus dominance models. The results show that the general combining ability effects for the additive model are the same as those for the additive plus dominance model when gene frequencies equal 0.5. This result does not depend on the correlation between loci.

From the lower half of Table 4.6, it is apparent that dominance does contribute to estimates of g_i effects when gene frequencies do not equal 0.5. This result agrees with the statement by Hayman and Mather (1955) that dominance and additive effects are confounded when gene frequencies in the parents do not equal one-half.

The comparisons of general combining ability effects (g_i) for an additive model with a model that includes both additive and additive x additive epistasis are given in Table 4.7. When additive x additive epistasis is present, the general combining ability effects are composed of additive and additive x additive epistatic effects, regardless of the gene frequencies or correlation between loci. Similar conclusions hold for the effect of additive x dominance epistasis (Table 4.8) and of dominance x dominance epistasis (Table 4.9). It is apparent that general combining ability is a measure of additive effects only when gene frequencies are 0.5 and when epistasis is not present.

4.3.2. Variety Effects

In the analysis of Gardner and Eberhart (1966), the variety effects (v_i) measure the difference between the value of a particular parent and the mean of all parents. To investigate the genetic make-up of the variety effects, simulations were performed under five genetic models.

TABLE 4.6. General combining ability effects (g_i) calculated under an additive model (I) and an additive plus dominance model (II) at various gene frequencies (p_a and p_b) and correlations between loci (r).

			g_1 #		g_2		g_3		g_4	
p_a	p_b	r	I	II	I	II	I	II	I	II
0.5	0.5	-0.75	3.0	3.0	0	0	0	0	-3.0	-3.0
0.5	0.5	-0.5	3.0	3.0	0	0	0	0	-3.0	-3.0
0.5	0.5	0	3.0	3.0	0	0	0	0	-3.0	-3.0
0.5	0.5	0.5	3.0	3.0	0	0	0	0	-3.0	-3.0
0.5	0.5	0.75	3.0	3.0	0	0	0	0	-3.0	-3.0
0.75	0.5	0	2.2	1.8	-0.7	-1.2	-0.7	0.5	-3.7	-2.5
0.75	0.25	0	3.0	3.8	0	-0.8	0	2.6	-3.0	-2.1
0.75	0.75	0	1.5	0.6	-1.5	-0.6	-1.5	-0.6	-4.5	-1.9
0.25	0.25	0	4.5	7.1	1.5	2.3	1.5	2.3	-1.5	-2.3
0.5	0.25	0	3.7	5.0	0.7	0.3	0.7	2.0	-2.2	-2.7

g_1, g_2, g_3 and g_4 are the general combining ability effects of parents with genotypes AABB, AAbb, aaBB and aabb, respectively.

TABLE 4.7. General combining ability effects (g_i) calculated under an additive model (I) and an additive plus additive x additive epistatic model (III) at various gene frequencies (p_a and p_b) and correlations between loci (r).

			g_1 #		g_2		g_3		g_4	
p_a	p_b	r	I	III	I	III	I	III	I	III
0.5	0.5	-0.75	3.0	4.1	0	-0.2	0	-0.2	-3.0	-1.9
0.5	0.5	-0.5	3.0	4.0	0	-0.3	0	-0.3	-3.0	-2.0
0.5	0.5	0	3.0	3.6	0	-0.6	0	-0.6	-3.0	-2.3
0.5	0.5	0.5	3.0	3.3	0	-1.0	0	-1.0	-3.0	-2.7
0.5	0.5	0.75	3.0	3.2	0	-1.1	0	-1.1	-3.0	-2.8
0.75	0.5	0	2.2	3.3	-0.7	-1.8	-0.7	-1.0	-3.7	-3.5
0.75	0.25	0	3.0	4.2	0	-0.9	0	0.8	-3.0	-1.8
0.75	0.75	0	1.5	2.4	-1.5	-2.7	-1.5	-2.7	-4.5	-5.3
0.25	0.25	0	4.5	3.7	1.5	0.3	1.5	0.3	-1.5	-0.6
0.5	0.25	0	3.7	4.0	0.7	-0.3	0.7	0.5	-2.2	-1.2

g_1, g_2, g_3 and g_4 are the general combining ability effects of parents with genotypes AABB, AAbb, aaBB and aabb, respectively.

TABLE 4.8. General combining ability effects (g_i) calculated under an additive model (I) and an additive plus additive x dominance epistatic model (IV) at various gene frequencies (p_a and p_b) and correlations between loci (r).

			g_1 #		g_2		g_3		g_4	
p_a	p_b	r	I	IV	I	IV	I	IV	I	IV
0.5	0.5	-0.75	3.0	6.0	0	0	0	0	-3.0	-6.0
0.5	0.5	-0.5	3.0	5.6	0	0	0	0	-3.0	-5.6
0.5	0.5	0	3.0	4.7	0	0	0	0	-3.0	-4.7
0.5	0.5	0.5	3.0	3.8	0	0	0	0	-3.0	-3.8
0.5	0.5	0.75	3.0	3.4	0	0	0	0	-3.0	-3.4
0.75	0.5	0	2.2	3.1	-0.7	-0.7	-0.7	-0.7	-3.7	-6.3
0.75	0.25	0	3.0	5.1	0	0	0	0	-3.0	-5.1
0.75	0.75	0	1.5	1.5	-1.5	-1.1	-1.5	-1.1	-4.5	-7.1
0.25	0.25	0	4.5	7.1	1.5	1.1	1.5	1.1	-1.5	-1.5
0.5	0.25	0	3.7	6.3	0.7	0.7	0.7	0.7	-2.2	-3.1

g_1, g_2, g_3 and g_4 are the general combining ability effects of parents with genotypes AABB, AAbb, aaBB and aabb, respectively.

TABLE 4.9. General combining ability effects (g_i) calculated under an additive model (I) and an additive plus dominance x dominance epistatic model (V) at various gene frequencies (p_a and p_b) and correlations between loci (r).

			g_1 #		g_2		g_3		g_4	
p_a	p_b	r	I	V	I	V	I	V	I	V
0.5	0.5	-0.75	3.0	1.9	0	0.2	0	0.2	-3.0	-4.1
0.5	0.5	-0.5	3.0	2.3	0	0.2	0	0.2	-3.0	-3.6
0.5	0.5	0	3.0	3.0	0	0	0	0	-3.0	-3.0
0.5	0.5	0.5	3.0	3.2	0	-0.6	0	-0.6	-3.0	-2.8
0.5	0.5	0.75	3.0	3.2	0	-1.1	0	-1.1	-3.0	-2.8
0.75	0.5	0	2.2	2.0	-0.7	-1.0	-0.7	-0.1	-3.7	-3.1
0.75	0.25	0	3.0	3.2	0	-0.3	0	1.4	-3.0	-2.8
0.75	0.75	0	1.5	1.2	-1.5	-1.3	-1.5	-1.3	-4.5	-3.0
0.25	0.25	0	4.5	5.9	1.5	1.7	1.5	1.7	-1.5	-1.8
0.5	0.25	0	3.7	4.4	0.7	0.5	0.7	1.4	-2.2	-2.5

g_1, g_2, g_3 and g_4 are the general combining ability effects of parents with genotypes AABB, AAbb, aaBB and aabb, respectively.

Table 4.10 provides a comparison of the variety effects calculated for an additive model with those calculated for a model that included additive and dominance effects. The results show that the values for the variety effects are the same for both genetic models regardless of the gene frequencies or correlations between loci. Similar conclusions hold for the effects of additive x dominance epistasis (Table 4.11) and dominance x dominance epistasis (Table 4.12) on the value of the variety effects. In comparing an additive model to one that includes additive and additive x additive epistatic effects (Table 4.13) it is found that the variety effects differ between the two models in every case. This means that additive x additive epistasis contributes to the values of the variety effects.

4.3.3. Correlation Between General Combining Ability and Variety Effects

Both the general combining ability and variety effects represent a measure of the value of individual parents. To investigate the possibility that variety effects could be used as indicators of general combining ability, the correlations between them were calculated (Table 4.14).

Results in Table 4.14 reveal that, at gene frequencies equal to 0.5, the correlation between v_i and g_i is lower than 0.73 in only three of the cases presented. When gene frequencies other than 0.5 are considered (lower half of Table 4.14), the correlation between v_i and g_i is lower than 0.81 in only two of the cases presented. Of the 100 correlations presented in Table 4.14, only five are less than 0.73. Of these five, the two for the duplicate epistatis, model IX ($p_a = p_b = 0.5$, $r = -0.75$; $p_a = p_b = 0.75$, $r = 0.0$) are zero because there was no

TABLE 4.10. Variety effects (v_i) calculated under an additive model (I) and an additive plus dominance model (II) at various gene frequencies (p_a and p_b) and correlations between loci (r).

			v_1 [#]		v_2		v_3		v_4	
p_a	p_b	r	I	II	I	II	I	II	I	II
0.5	0.5	-0.75	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	-0.5	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	0	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	-0.5	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	0.75	6.0	6.0	0	0	0	0	-6.0	-6.0
0.75	0.5	0	4.5	4.5	-1.5	-1.5	-1.5	-1.5	-7.5	-7.5
0.75	0.25	0	6.0	6.0	0	0	0	0	-6.0	-6.0
0.75	0.75	0	3.0	3.0	-3.0	-3.0	-3.0	-3.0	-9.0	-9.0
0.25	0.25	0	9.0	9.0	3.0	3.0	3.0	3.0	-3.0	-3.0
0.5	0.25	0	7.5	7.5	1.5	1.5	1.5	1.5	-4.5	-4.5

[#] v_1, v_2, v_3 and v_4 are the variety effects of parents with genotypes AABB, AAbb, aaBB and aabb, respectively.

TABLE 4.11. Variety effects (v_i) calculated under an additive model (I) and an additive plus additive x dominance epistatic model (IV) at various gene frequencies (p_a and p_b) and correlations between loci (r).

			v_1 #		v_2		v_3		v_4	
p_a	p_b	r	I	IV	I	IV	I	IV	I	IV
0.5	0.5	-0.75	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	-0.5	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	0	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	-0.5	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	0.75	6.0	6.0	0	0	0	0	-6.0	-6.0
0.75	0.5	0	4.5	4.5	-1.5	-1.5	-1.5	-1.5	-7.5	-7.5
0.75	0.25	0	6.0	6.0	0	0	0	0	-6.0	-6.0
0.75	0.75	0	3.0	3.0	-3.0	-3.0	-3.0	-3.0	-9.0	-9.0
0.25	0.25	0	9.0	9.0	3.0	3.0	3.0	3.0	-3.0	-3.0
0.5	0.25	0	7.5	7.5	1.5	1.5	1.5	1.5	-4.5	-4.5

v_1, v_2, v_3 and v_4 are the variety effects of parents with genotypes AABB, AAbb, aaBB and aabb, respectively.

TABLE 4.12. Variety effects (v_i) calculated under an additive model (I) and an additive plus dominance x dominance epistatic model (V) at various gene frequencies (p_a and p_b) and correlations between loci (r).

			v_1 #		v_2		v_3		v_4	
p_a	p_b	r	I	V	I	V	I	V	I	V
0.5	0.5	-0.75	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	-0.5	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	0	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	-0.5	6.0	6.0	0	0	0	0	-6.0	-6.0
0.5	0.5	0.75	6.0	6.0	0	0	0	0	-6.0	-6.0
0.75	0.5	0	4.5	4.5	-1.5	-1.5	-1.5	-1.5	-7.5	-7.5
0.75	0.25	0	6.0	6.0	0	0	0	0	-6.0	-6.0
0.75	0.75	0	3.0	3.0	-3.0	-3.0	-3.0	-3.0	-9.0	-9.0
0.25	0.25	0	9.0	9.0	3.0	3.0	3.0	3.0	-3.0	-3.0
0.5	0.25	0	7.5	7.5	1.5	1.5	1.5	1.5	-4.5	-4.5

v_1, v_2, v_3 and v_4 are the variety effects of parents with genotypes AABB, AAbb, aaBB and aabb, respectively.

TABLE 4.13. Variety effects (v_i) calculated under an additive model (I) and an additive plus additive x additive epistatic model (III) at various gene frequencies (p_a and p_b) and correlations between loci (r).

			v_1 #		v_2		v_3		v_4	
p_a	p_b	r	I	III	I	III	I	III	I	III
0.5	0.5	-0.75	6.0	11.2	0	-0.7	0	-0.7	-6.0	-0.7
0.5	0.5	-0.5	6.0	10.5	0	-1.5	0	-1.5	-6.0	-1.5
0.5	0.5	0	6.0	9.0	0	-3.0	0	-3.0	-6.0	-3.0
0.5	0.5	0.5	6.0	7.5	0	-4.5	0	-4.5	-6.0	-4.5
0.5	0.5	0.75	6.0	6.7	0	-5.2	0	-5.2	-6.0	-5.2
0.75	0.5	0	4.5	7.5	-1.5	-4.5	-1.5	-4.5	-7.5	-4.5
0.75	0.25	0	6.0	9.7	0	-2.0	0	-2.2	-6.0	-2.2
0.75	0.75	0	3.0	5.2	-3.0	-6.7	-3.0	-6.7	-9.0	-6.7
0.25	0.25	0	9.0	11.2	3.0	-0.7	3.0	-0.7	-3.0	-0.7
0.5	0.25	0	7.5	10.5	1.5	-1.5	1.5	-1.5	-4.5	-1.5

v_1, v_2, v_3 and v_4 are the variety effects of parents with genotypes AABB, AAbb, aaBB and aabb, respectively.

TABLE 4.14. Correlations between general combining ability and variety effects simulated at various gene frequencies (p_a and p_b) and correlations between loci (r).

			Genetic models #									
p_a	p_b	r	I	II	III	IV	V	VI	VII	VIII	IX	X
0.5	0.5	-0.75	1.00	1.00	0.93	1.00	0.93	0.82	0.73	0.88	0.00	0.09
0.5	0.5	-0.5	1.00	1.00	0.94	1.00	0.97	0.86	0.80	0.83	1.00	0.44
0.5	0.5	0	1.00	1.00	0.95	1.00	1.00	0.94	0.91	0.83	1.00	0.96
0.5	0.5	0.5	1.00	1.00	0.97	1.00	0.99	0.99	0.98	0.91	1.00	1.00
0.5	0.5	0.75	1.00	1.00	0.98	1.00	0.99	0.99	1.00	0.96	1.00	1.00
0.75	0.5	0	1.00	0.94	0.97	0.99	0.99	0.93	0.90	0.81	1.00	0.87
0.75	0.25	0	1.00	0.87	0.96	1.00	0.97	0.94	0.90	0.87	1.00	1.00
0.75	0.75	0	1.00	1.00	0.98	0.96	0.99	0.94	0.93	0.83	0.00	-0.16
0.25	0.25	0	1.00	1.00	0.92	0.96	1.00	0.95	0.91	0.94	1.00	1.00
0.5	0.25	0	1.00	0.97	0.94	0.99	0.99	0.94	0.90	0.91	1.00	1.00

Description of genetic models in text.

variation due to general combining ability. These same two cases of parental genotype frequencies also gave very low correlations for the dominant epistasis, model X. For most of the cases considered, variety performance was a fairly good indicator of general combining ability.

4.3.4. Average Heterosis

The difference between the mean of the progeny (m_c) and the mean of the parents (m_v) was considered by Hayman (1954b) and Gardner and Eberhart (1966) to measure average heterosis. To investigate the genetic make-up of this measure of average heterosis, $m_c - m_v$, its value was determined under five genetic models. The results (Table 4.15) show that additive effects and additive x additive epistatic effects never contribute to average heterosis. Further, additive x dominance epistasis contributes to average heterosis only when gene frequencies do not equal 0.5. Dominance effects and dominance x dominance epistatic effects always contribute to average heterosis.

4.3.5. Percentage of the Total Sum of Squares Due to General Combining Ability

A measure of the amount of general combining ability (relative to specific combining ability) is the ratio of the sum of squares due to general combining ability (GCA) to the total sum of squares expressed as a percentage. Considering only those cases where gene frequencies were 0.5 and there was random distribution of genes in the parents, the relationship between this percentage and the amount of additive

TABLE 4.15. The value of the difference between the mean of the progeny and the mean of the parents calculated under five genetic models at varying gene frequencies (p_a and p_b) and correlations between loci (r).

			Model #				
p_a	p_b	r	I	II	III	IV	V
0.5	0.5	-0.75	0	3.2	0	0	1.2
0.5	0.5	-0.5	0	3.2	0	0	1.0
0.5	0.5	0	0	3.2	0	0	0.8
0.5	0.5	0.5	0	3.2	0	0	1.0
0.5	0.5	0.75	0	3.2	0	0	1.2
0.75	0.5	0	0	2.8	0	0.8	0.6
0.75	0.25	0	0	2.4	0	0	0.4
0.75	0.75	0	0	2.4	0	1.2	0.4
0.25	0.25	0	0	2.4	0	-1.2	0.4
0.5	0.25	0	0	2.8	0	-0.8	0.6

See text for description of genetic models I, II, III, IV and V.

variation, or additive plus additive x additive epistatic variation is illustrated in Fig. 4.1.

Examination of this figure reveals that the amount of GCA correlates most closely with additive plus additive x additive genetic variation (Fig. 4.1 b). It is apparent that the amount of general combining ability does not represent strictly additive variation. In the presence of epistasis, the GCA sum of squares (expressed as a percent of the total sum of squares) tends to overestimate the amount of additive genetic variation in the ten models studied.

The above results apply only when genes are randomly distributed in the parents. To investigate the effect of non-random gene distribution in the parents on the amount of general combining ability, five levels of non-random gene distribution were simulated under the ten genetic models listed in Table 4.2. For each simulation the GCA sum of squares was expressed as a percentage of the total sum of squares. The results of these simulations appear in Fig. 4.2 a and b. Examination of this figure reveals that no general trend exists for the effect of non-random distribution of genes on the sum of squares due to general combining ability. It should be noted, however, that in the presence of strictly additive genetic effects, the amount of the total sum of squares due to general combining ability is not affected by non-random distribution of genes. When dominance and epistasis are present, non-random gene distribution can affect the amount of the total sum of squares due to general combining ability.

Some authors (Hayman and Mather, 1955; Gardner and Eberhart, 1966) have stated that valid information can be derived from the diallel

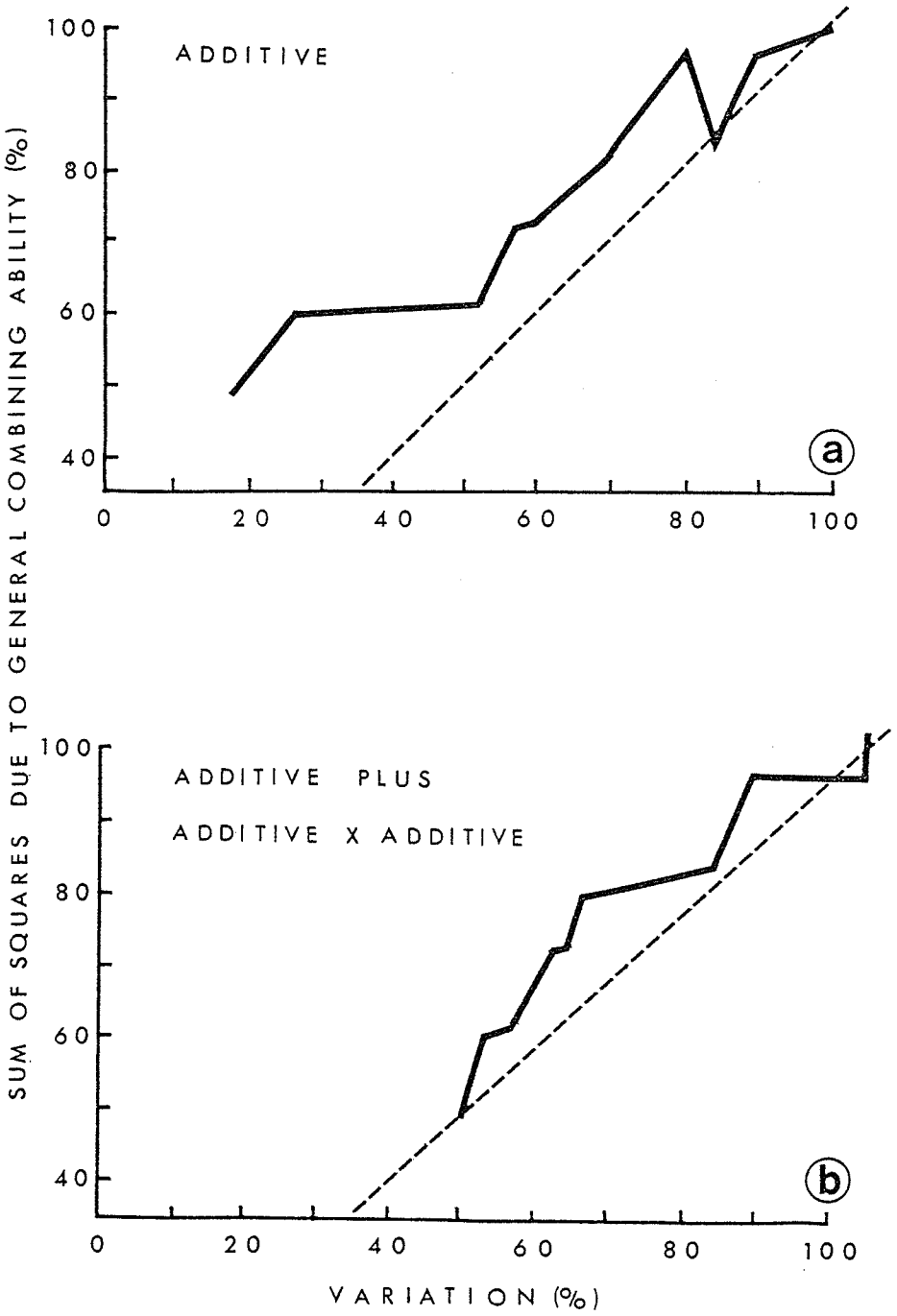

Figure 4.1. Relationship between the percentage of the sum of squares due to general combining ability and the percent of different types of genetic variation. Broken line represents a one-to-one correspondence and is simply for comparison.

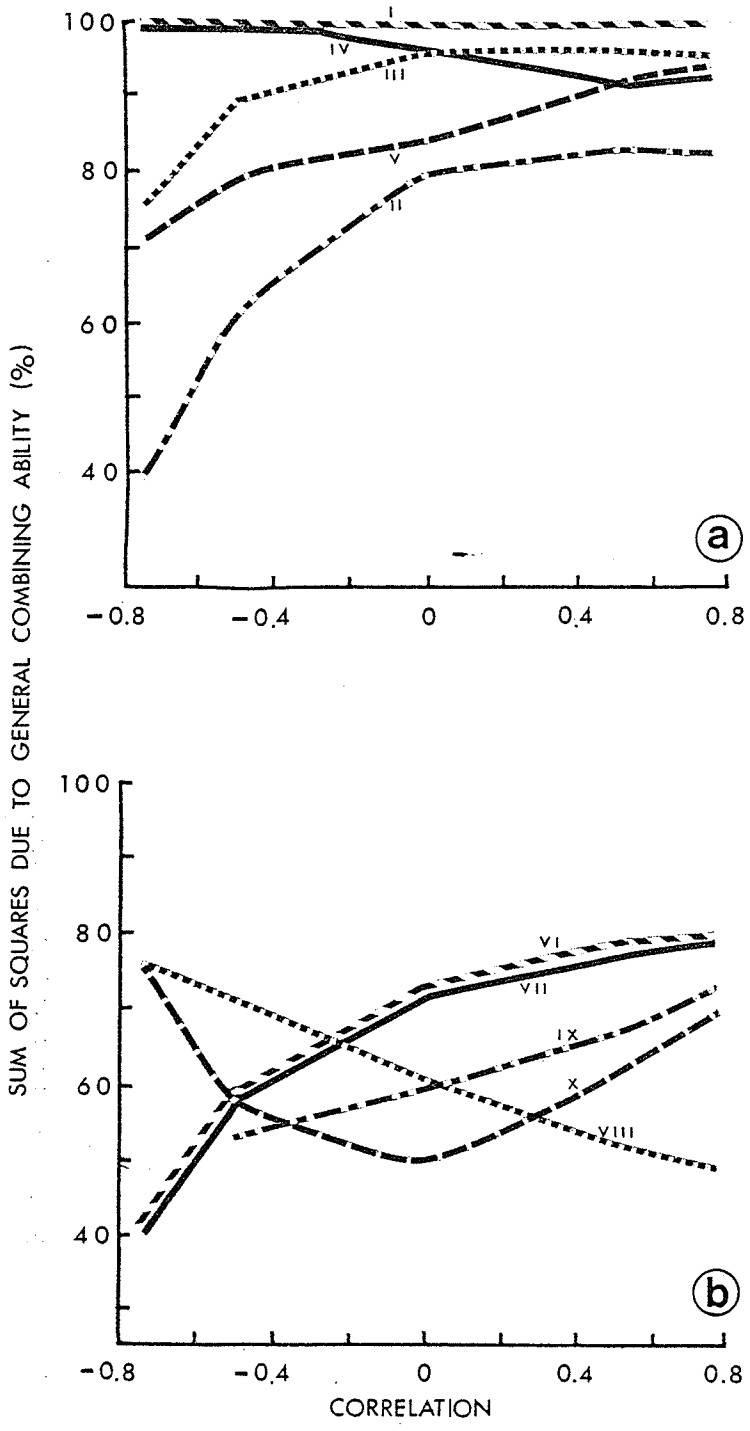

Figure 4.2. Effect of correlations between loci on the percentage of the sum of squares due to general combining ability for ten genetic models.

results only when gene frequencies equal 0.5. In the present study, the effect of gene frequencies other than 0.5 on the amount of general combining ability was examined. Table 4.16 shows what happens to the amount of the total sum of squares due to general combining ability under each of ten models, when gene frequencies differ from 0.5. Under the additive model (Model I), the amount of general combining ability is constant for all gene frequencies. However, in the presence of dominance and/or epistasis (Models II-X), the amount of general combining ability varies with the gene frequency. It would appear from the results in Table 4.16 (upper half) that for models II, V, VI, VII, VIII, IX and X, a decrease in the gene frequencies from 0.75 to 0.25 causes the amount of general combining ability to increase. For model III, an increase in the gene frequencies causes the amount of general combining ability to increase, while for model IV, the amount of general combining ability decreases for frequencies of 0.25 and 0.75. In the lower half of Table 4.16, the trends, with respect to the amount of general combining ability, are similar to those in the upper half for $p_a = 0.5$, $p_b = 0.25$ and $p_a = 0.75$, $p_b = 0.5$.

TABLE 4.16. Percentage of the total sum of squares due to general combining ability under ten genetic models at various gene frequencies (p_a and p_b) and with zero correlation between loci.

		Genetic models [#]									
p_a	p_b	I	II	III	IV	V	VI	VII	VIII	IX	X
0.25	0.25	100.0	93.4	82.0	85.6	92.3	79.0	72.9	73.5	78.1	74.4
0.5	0.5	100.0	79.9	95.4	95.9	83.7	72.8	71.6	60.6	60.0	48.6
0.75	0.75	100.0	51.4	97.1	85.6	83.5	51.1	51.4	43.9	0.0	43.9
0.5	0.25	100.0	87.5	90.9	93.9	89.4	83.3	78.7	52.1	66.8	61.0
0.75	0.25	100.0	88.4	95.0	98.0	89.5	89.3	87.4	24.4	56.3	47.7
0.75	0.5	100.0	73.7	96.5	93.9	83.9	73.1	71.4	32.9	52.6	29.3

[#] See text for description of genetic models.

5. FACTORS AFFECTING RESPONSE TO SELECTION IN SELF-POLLINATING SPECIES

According to Pederson (1969), the expected response to selection in self-pollinated crops is proportional to the correlation between individuals in the population in which selection is practised. Further, Pederson has stated that, in the absence of epistasis, this correlation is proportional to the amount of additive variation. In the absence of any information of the effect of epistasis on the magnitude of intergeneration correlations, it was decided to investigate the genetic nature of such correlations for the case of two loci. Because the effect of epistasis is most pronounced in the F_2, the correlation between the individuals in this generation and the inbred progeny derived from them, was examined.

In an F_2 population, nine different two-locus genotypes are possible. These nine genotypes and their genotypic values appear in Table 5.1. If each of the nine genotypes is inbred to complete homozygosity (F_∞), only additive effects and additive by additive epistatic effects contribute to the mean genotypic values of the inbred families (Table 5.1). Dominance and some epistatic effects decrease with each generation of inbreeding, while additive effects and additive x additive epistatic effects are expressed in inbred lines.

By substituting values for the genetic parameters (i.e. m, d_a, d_b, h_a, h_b, i_{ab}, j_{ab}, j_{ba} and l_{ab}) into the expressions in Table 5.1, numerical values can be obtained. These numerical values can then be

TABLE 5.1. Genotypes, frequencies and genotypic values of F_2 plants and mean genotypic values of their inbred progeny.

Genotype	Frequency	Genotypic value [#]	
		F_2 plants	Inbred progeny mean
AABB	1/16	$m + d_a + d_b + i_{ab}$	$m + d_a + d_b + i_{ab}$
AABb	1/8	$m + d_a + h_b + j_{ab}$	$m + d_a$
AAbb	1/16	$m + d_a - d_b - i_{ab}$	$m + d_a - d_b - i_{ab}$
AaBB	1/8	$m + h_a + d_b + j_{ba}$	$m + d_b$
AaBb	1/4	$m + h_a + h_b + l_{ab}$	m
Aabb	1/8	$m + h_a - d_b - j_{ba}$	$m - d_b$
aaBB	1/16	$m - d_a + d_b - i_{ab}$	$m - d_a + d_b - i_{ab}$
aaBb	1/8	$m - d_a + h_b - j_{ab}$	$m - d_a$
aabb	1/16	$m - d_a - d_b + i_{ab}$	$m - d_a - d_b + i_{ab}$

[#] The terms, m, d_a, d_b, etc., refer to additive, dominance and epistatic genetic effects as described in text.

substituted into standard formulae for variances and covariances of frequency tables. The resulting variances and covariances give rise to the correlations summarized in Table 5.2.

The percentage of the total sum of squares due to GCA (also tabulated in Table 5.2) provides the same ranking of the genetic models (except for Models III and IV) as the correlation between F_2 and F_∞. It would appear that, in a diallel experiment, the percentage of the sum of squares due to general combining ability, might provide an estimate of the relative magnitude of intergeneration correlation to be expected in an ensuing breeding program.

TABLE 5.2. Correlations between F_2 plants and their inbred family means (F_∞) and the percentage of the total sum of squares due to general combining ability (gca) for ten genetic models.

Model [#]	Correlation (F_2 and F_∞)	Sum of squares due to general combining ability (%)
I	1.00	100.0
II	0.82	79.9
III	1.00	95.4
IV	0.95	95.9
V	0.92	83.7
VI	0.80	72.8
VII	0.79	71.6
VIII	0.72	60.6
IX	0.69	60.0
X	0.64	48.6

[#] See text for description of genetic models I - X.

6. DISCUSSION

In the present study, conclusions have been based on results derived with only two genetic loci. Extension of the study to more loci might cause specific estimates to change in magnitude. However, consideration of more than two loci would not alter the general conclusion that statistics of the diallel analysis depend on gene frequency, on the correlation between loci and on the types of gene action. The types of gene action (i.e. additive, dominance and epistatic) that contribute to the make-up of the various statistics under a two-locus model should also contribute under models with more than two loci. For example, the general combining ability effects would be composed of additive genetic effects only in the absence of epistasis and with gene frequencies equal to 0.5, regardless of the number of loci considered.

A second possible weakness of the present study is that only a fixed effects model was simulated. Although the genetic content of variance components was not considered, variance components of a random effects model should contain the same genetic elements as their corresponding fixed effects. Mean squares, from which variance components are estimated, are simply functions of the sum of squares of the same deviations used to calculate the fixed effects considered in the present study.

The validity of random effects models, when dealing with breeding material, has been questioned. When considering self-pollinated crops, most of the plant material of interest to the breeder has been highly selected for traits of economic importance. Eberhart and Gardner (1966) are of the opinion that parents selected from such material cannot be

considered as a random sample. They conclude that estimation of variance components in self-pollinated crops does not provide any useful information.

There appears to be some confusion in the literature with respect to this last point. Some workers (Upadhyaya and Rasmusson, 1967; Briggs, 1974 a, b; Gritton, 1975; Sampson, 1971; and others) have conducted diallel experiments using established self-pollinated varieties as parents. In some of these cases, parents were assumed to represent a random sample of the crop concerned; hence, a random effects model was specified. In other studies, information about the specific set of parents was desired. Therefore, a fixed effects model was specified for these cases. However, in all studies cited, components of variance were estimated. According to Eberhart and Gardner (1966), such estimates have no value.

In the present study, the effect of environment has not been considered in the simulation and interpretation of results. Of the results obtained, the percentage of the total sum of squares due to general combining ability is the only item that would be affected by environmental influences. The effect of environmental variation on this percentage will depend on the relative amounts of general and specific combining ability, of environmental variation and on the number of parents in the diallel experiment.

Some papers in the literature (Hayes and Paroda, 1974; Lim, 1975; Paschal and Wilcox, 1975; Thaden et al., 1975) have used one of Griffing's (1956b) analysis methods, and assumed a fixed effects model (Model I) to apply to their material. In these papers (as well as others)

the mean square due to general combining ability is compared to the mean square due to specific combining ability to determine which is the more important of the two. It is clear from the expected mean squares provided by Griffing (1956b) that such a comparison is affected by the design (i.e. number of parents) of the experiment and, therefore, does not give a valid measure of the relative importance of general and specific combining ability.

It is apparent that all of the diallel methods presented are highly interrelated. All five analyses are measuring the same things, but expressing the results in slightly different terms. Because of this, it is difficult to say that any one method is better or worse than another for analyzing results of diallel experiments.

In this study, it was found that the most critical assumption, with respect to the genetic content of diallel estimates, was that gene frequencies were 0.5 at all loci. Kempthorne (1956) identified the requirement for random distribution of genes among the parents as being most important for the valid genetic interpretation of diallel results. One possible explanation for this discrepancy in assessment of genetic assumptions could be due to the difference in genetic models used in each study. The model used in the present study (i.e. the "pure-line-metric") allows individual genotypic values to be expressed without reference to other genotypes in the population. The model used by Kempthorne (1956) (also Falconer, 1960; and others), however, describes the genotypic value of an individual relative to the frequency of other genotypes in the population. Under such a model, the definition of genetic effects (i.e. additive, dominance and epistatic) changes from one population to another. For example, an additive effect, in

Kempthorne's terminology, could contain only additive gene effects (according to the "pure-line-metric") in one population but may contain additive and dominance genetic effects in another. Although the genetic constitution of an individual plant is the same in both populations, the definitions of the genotypic effects vary under Kempthorne's model. The "pure-line-metric" was chosen for the present study because it reflects biological relationships rather than statistical relationships.

Rojas and Sprague (1952) stated that general combining ability is associated with genes which are additive in their effects. Results of the present study show that this statement is true only under the very restricted conditions that gene frequencies equal 0.5 and that there is no epistasis. Sprague (1967) commented that limited benefit is derived from estimates of additive, dominance and epistatic effects, if the final product is to be a pure line. This statement is supported by the present results which revealed that the amount of general combining ability provided an indication of the presence of genetic effects important in breeding pure lines (i.e. additive and additive x additive effects).

Gilbert (1958) and Sprague (1966) have examined the genetic assumptions required for valid interpretation of diallel results. Their conclusion was that some of the assumptions required would be difficult, if not impossible, to fulfill. It appears that assumptions concerning the frequency and distribution of genes among the parents are most critical to the valid genetic interpretation of diallel experiments. To be assured that these assumptions apply, one must use a random sample of inbred lines from a population developed by random mating in

a cross of two inbred lines. For a self-pollinated species, much work is involved in deriving parents in this fashion. The amount of work required is probably the reason why the bulk of diallel experiments reported in the literature have not used parents derived in this fashion. Genetic conclusions derived from these experiments are of little value.

Assuming that there is no epistasis seems to be biologically unrealistic. There is considerable evidence to suggest that epistasis is a common genetic phenomenon.

From equation 19.4 (Falconer, 1960), it is clear that, in developing inbred lines, the expected response to selection among F_2 plants is proportional to the genetic correlation between F_2 plants and their inbred progeny. Pederson (1969) considered the factors that enter the genetic covariance between generations and concluded that, in the absence of epistasis, the genetic covariance depends only on additive genetic effects.

In the present investigation, it was shown that epistasis can markedly reduce the genetic correlation between F_2 plants and their inbred progeny. Models containing strictly additive x additive epistatic and/or additive variation yielded the highest correlations. If F_3 or F_4 plants were considered (instead of F_2 plants), the correlation with inbreds would be higher. This increase in correlation would be due to the decrease in dominance, additive x dominance and dominance x dominance gene effects during inbreeding.

In discussing epistasis, Crow and Kimura (1970) suggest that, in practical problems, "the breeder usually estimates the heritability and then uses this value as a guide to selection programs." Such

estimates are usually derived from various correlations between relatives. Under a complementary gene model, Crow and Kimura state that epistasis "... doesn't cause a very large error in heritability measurements or predictions based on these (estimates)". Therefore, Crow and Kimura feel that breeders ignore epistasis for this reason as well as the practical difficulty involved in measuring epistasis.

General combining ability has been used for the selection of parents. Stuthman and Stucker (1975) have recommended that, when expression of a trait is due to strictly additive effects, selection of parents can be made on the basis of their own performance. Results of the present study (correlation between general combining ability and variety effects) suggest that parents can be selected on the basis of their own performance when additive plus additive x additive epistatic effects are present. However, breeders of self-pollinated crops are interested in superior lines and not cross means. Diallel experiments do not provide information about the variability within a cross. Stuthman and Stucker (1975) have suggested that once the progeny with the best mean performance have been identified, several lines should be selected to measure the potential variability of the cross.

7. SUMMARY AND CONCLUSIONS

Five methods for analyzing diallel experiments in self-pollinated crops were examined and compared. All five methods measure the same basic parameters but express them in different terms. The basic measurements of a diallel experiment include (i) the difference between progeny and parental means, (ii) parental performance, (iii) general combining ability, and (iv) specific combining ability in the progeny. None of the methods appears to have any particular advantage for analyzing results of a diallel experiment.

The genetic content of diallel statistics was examined. General combining ability, variety effects and average heterosis can be attributed to individual types of gene action only when gene frequencies equal 0.5 at all loci and when there is no epistasis.

The percentage of the total sum of squares due to general combining ability was used to assess the effects of gene frequency, distribution of genes in the parents and type of gene action on the relative amounts of general and specific combining ability. It was shown that all three factors, alone or in combination, can alter the relative amounts of the two types of combining ability. When gene frequencies were 0.5 at all loci and there was zero correlation between loci, the amount of general combining ability reflected the amount of variation due to additive plus additive x additive epistatic gene action.

The genetic assumptions required for valid interpretation of diallel results were studied. Results suggested that the assumption that gene

frequencies are equal to 0.5 is the most critical with respect to the genetic content of diallel estimates.

Correlations between the general combining ability and variety effects were calculated under ten genetic models that contained different amounts and types of epistasis. For the models studied, it was concluded that the variety effects could be used as indicators of the general combining ability effects.

Response to selection in the presence of epistasis was examined. For developing inbred lines, it appears that parents can be chosen on the basis of their own performance rather than on the basis of their general combining ability. However, neither variety performance nor diallel analysis estimates can predict the amount of genetic variation within crosses.

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