

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

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Michael James Sokol

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## 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  $i^{\text{th}}$  parent,  $l_i$  measures the difference in performance of gametes of the  $i^{\text{th}}$  parent in combination with themselves and with gametes of other parents, and  $l_{ij}$  measures the specific interaction of gametes from the  $i^{\text{th}}$  and  $j^{\text{th}}$  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  $i^{\text{th}}$  and  $j^{\text{th}}$  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

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

where  $Y_{ii}$  is the average performance of the  $i^{\text{th}}$  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  $i^{\text{th}}$  parent (both in inbred and hybrid combination),  $l_i$  measures the difference in performance of gametes of the  $i^{\text{th}}$  parent in combination with themselves and with gametes from other parents, and  $l_{ij}$  measures the specific

interaction between gametes from the  $i^{\text{th}}$  and  $j^{\text{th}}$  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

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

where  $m$  is the mean of the parents plus progeny,  $g_i$  and  $g_j$  are the general combining ability of gametes from the  $i^{\text{th}}$  and  $j^{\text{th}}$  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  $i^{\text{th}}$  and  $j^{\text{th}}$  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

$$Y_{ij} = m_c + g_i + g_j + s_{ij} \quad \dots (3)$$

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

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

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  $i^{\text{th}}$  parent in combination with themselves and with gametes from other parents, and  $s_{ij}$  is the specific combining ability of gametes from the