Diallel Analysis and its Applications in Plant Breeding

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Introduction

Three biometrical techniques, viz., diallel, partial and line x tester crosses are known as mating designs. These biometrical techniques are extensively used in crop improvement programmes for evaluating inbred lines in terms of genetic components of variation and evaluate several single crosses at a time. Diallel mating design is used to evaluate several inbred lines in terms of combining ability variances and effects. Diallel cross refers to mating of selected parents in all possible combinations and evaluation of a set of diallel crosses is known as diallel analysis. Diallel is a Greek word and introduced by Schmidt in 1919. Procedures of diallel cross analysis for the study of polygenic traits in self pollinated species was developed by Jinks and Hayman in 1954.

Types of Diallel Cross

The diallel mating design involves three types of materials, namely, direct crosses or one way crosses, reciprocals and parents. Depending upon number of crosses to be made diallel cross is of two types as given below:

Plan of crossing for a Diallel Design

<table>
<thead>
<tr>
<th>Parents</th>
<th>P1</th>
<th>P2</th>
<th>P3</th>
<th>P4</th>
<th>P5</th>
</tr>
</thead>
<tbody>
<tr>
<td>P1</td>
<td>¶</td>
<td>#</td>
<td>#</td>
<td>#</td>
<td>#</td>
</tr>
<tr>
<td>P2</td>
<td>x</td>
<td>¶</td>
<td>#</td>
<td>#</td>
<td>#</td>
</tr>
<tr>
<td>P3</td>
<td>x</td>
<td>X</td>
<td>¶</td>
<td>#</td>
<td>#</td>
</tr>
<tr>
<td>P4</td>
<td>x</td>
<td>X</td>
<td>x</td>
<td>¶</td>
<td>#</td>
</tr>
<tr>
<td>P5</td>
<td>x</td>
<td>X</td>
<td>X</td>
<td>¶</td>
<td>#</td>
</tr>
</tbody>
</table>

Where, ¶, x and # = direct crosses, reciprocals and parents (selfings), respectively.

Full Diallel

In this design, all possible matings among the selected parents are made in both directions, i.e. direct and reciprocals. In a full diallel, each parent is used as male and female for each mating.

Main features of full diallel:

- Total number of single crosses in a full diallel is equal to $P(P-1)$, where $P$ is the number of parents used.
- Full diallel is used when, a) reciprocal differences are significant and b) parents do not have male sterility or self incompatibility.
- Permits estimation of maternal effects.
- Each parent is used as male and female in the mating.
- There are two methods for evaluation of full diallel crosses i.e. with parents and without parents as described below:
  a. Full diallel with Parents ($F_1$s, Reciprocals and Parents)
     This includes both way crosses and parents. The total number of entries to be evaluated is equal to $P^2$ where $P =$ number of parents. This used when do not have self incompatibility or male sterility. The inclusion of parents permits the estimation of heterosis.
  b. Full diallel without Parents ($F_1$s and Reciprocals)
This includes all possible single crosses made among P parents in both the directions i.e. direct or reciprocal crosses. The total number of single crosses is equal to P(P-1). This method can be used when the presence of self incompatibility or male sterility prevent the inclusion of parents in the experiment and does not permit estimation of heterosis.

Advantage of Full Diallel
1. Each parent has equal chance of mating as male and female with every other parent.
2. It measures the maternal effects.

Disadvantage of Full Diallel
1. Double mating are required i.e. P(P-1), which limits the number of parents for evaluation.
2. More experimental area is required for evaluation.

Half Diallel
- In this design, all possible crosses among the selected parents are made in one direction only i.e. direct crosses.

Main features of half diallel
- In half diallel, parent is used either as male or as female in the mating.
- The number of single crosses required is equal to P(P-1)/2, where P is the number of parents used.
- Half diallel is used when reciprocal differences are not significant.
- It can be used when parents have male sterility or self incompatibility.
- It can be evaluated in two ways i.e. with parents and without parents as given below:
  a. Half Diallel with Parents (F₁s and Parents)
     This includes one way crosses and parents. The total number of entries to be evaluated is equal to P(P+1)/2, where P = number of parents. This can be used when parents do not have self incompatibility or male sterility. The inclusion of parents in the experiment permits the estimates of heterosis.
  b. Half Diallel without Parents (F₁s only)
     This includes all possible single crosses made in one direction only. The single crosses required is equal to P(P-1)/2. This design can be used when the presence of self incompatibility or male sterility prevents the inclusion of parents in the experiment. Thus estimates of heterosis are not possible in this method.

Advantage of Half Diallel
1. Each parent has equal opportunity to mate and recombine with every other parent.
2. It requires half mating than full diallel.
3. Requires less experimental area for evaluation of material.

Disadvantage of Half Diallel
1. Maternal effect cannot be measured.

Assumptions of Diallel Analysis
- Normal diploid segregation
- Lack of maternal effects
- Absence of multiple alleles
- Homozygosity of parents
- Absence of linkage
- Lack of epistasis
- Random mating

Approaches of Diallel Analysis
There are two approaches of diallel analysis
- Hayman’s approach
- Griffing’s approach
- Hayman’s graphical approach
It was initially developed by Jinks and Hayman in 1954. This approach is based on the estimation of components of variation.

**Main features of Hayman’s approach:**

- This is a graphical approach which involves Vr-Wr graph
- The analysis is based on the estimation of components of variance
- The following six components of variation are estimated:
  
- \( D = \) additive genetic variance
- \( H_1 = \) dominance variance
- \( H_2 = H_1 [(1 – (U-V)^2)] \), Where \( u \) and \( v \) are proportions of positive and negative genes respectively in the parents
- \( E = \) expected environmental component of variance
- \( F = \) mean of Fr over the arrays, where Fr is the covariance of additive and dominance effects in a single array
- \( h^2 = \) dominance effect, as algebraic sum over all the loci in heterozygous phase in all the crosses.

**Estimation of Genetic Ratios**

1) Average degree of dominance = \( (H_1/D)^{1/2} \)
   - If the value of this ratio is 0 = no dominance, >0<1 = partial dominance, 1 = complete dominance and >1 = over dominance

2) The ratio of dominant and recessive genes in the parents is estimated as follows:
   
   \[
   \frac{\left[4DH_1 + F\right]}{\left[4DH_1 + F\right]} / \left[4DH_1 - F\right]
   \]

   - If this ratio: 1 = dominant and recessive genes in the parent are in equal proportions, <1 = excess of recessive genes and >1 = an excess of dominant genes is indicated.

3) The number of gene groups, which control the character and exhibit dominance is given by the following formula:
   
   Number of gene groups = \( h^2 / H_2 \)

4) The proportion of genes with positive and negative effects in the parents is estimated using the following formula:

   - Genes with – and + effects = \( H_2/4H_1 \)
   - If the positive and negative alleles are symmetrically distributed, this ratio equals 0.25.
   - The above components are estimated from the data on \( F_1 \) generation of a diallel cross.
   - In 1956, Jinks gave the procedure for estimating these components, from \( F_2 \) data as well. The coefficient of \( H_1 \) and \( H_2 \) are \( 1/4 \) in \( F_2 \), while they are 1 in \( F_1 \).

The \( h^2 \) and \( F \) have a co-efficient of \( 1/4 \) because of the one generation of inbreeding to attain \( F_2 \).

Therefore, the genetic ratios in \( F_2 \) are worked out as follows:

   i) Degree of dominance = \( \left[\frac{1}{4}(H_1/D)\right]^{1/2} \)

   ii) Proportion of dominant and recessive genes in the parents is estimated as follows:

   \[
   \left[\frac{H_2}{4H_1}\right]^{1/2} + \frac{1}{2} F / \left[\frac{H_2}{4H_1} - \frac{1}{2} F\right]
   \]

   The proportions of genes with positive and negative effects in the parents = \( (H_2/4H_1) \), and the number of gene groups which control the character and exhibit dominance are the same in \( F_2 \) as those in \( F_1 \).

**Vr-Wr Graph**

In the hayman’s approach of diallel analysis a graph is drawn with the help of variances of arrays (Vr) and covariances between parents and their offspring (Wr). This graph is known as Vr-Wr graph.

**Array:** The array refers to the crosses in which a particular parent is common.

**Construction of Vr-Wr Graph:**

- Graph begin with Vr values are taken on the x-axis and Wr values on the Y-axis.
- Wri values are estimated for all the arrays with the help of following formula:

\[
Wri = \left(Vri \times V_{0L_0}\right)^{1/2}
\]

Where, Vri is the variance of \( r^{th} \) array and \( V_{0L_0} \) is variance of parents.
• These Wri values are used to draw the limiting parabola. For drawing regression line, the expected values of Wrei are required.

• These Wrei values are obtained for all the arrays separately with the help of following formula:
\[ Wrei = W_r - bV_r + bV_{ri} \]

Where, \( W_r \) is array mean of covariances, \( V_r \) array mean of variances and \( b = \) regression coefficient.

Inferences from the \( V_r – W_r \) graph
1) The position of regression line on \( V_r-W_r \) graph provides information about the average degree of dominance.
   - When the regression line passes through the origin it indicates complete dominance (\( D = H_1 \))
   - When the regression line passes above the origin cutting \( W_r \) axis, it shows the existence of partial dominance (\( D>H_1 \))
   - When it passes above the origin, cutting the \( W_r \) axis and touching the limiting parabola, it suggests absence of dominance.
   - But when the regression line passes below the origin, cutting the \( V_r \) axis, it denotes the presence of over dominance.

2) The position of parental points along the regression line indicates the dominance order of the parents. The parents with more dominant genes are located nearer to the origin, while those with more recessive genes fall farther from the origin. The parents with equal frequencies of dominant and recessive genes occupy an intermediate position.

Griffing’s Numerical Approach
This approach of diallel analysis was developed by Griffing in 1956. This is based on the estimation of general combining ability (GCA) and specific combining ability (SCA) variances and effects. Griffing (1956) gave four different methods of diallel analysis depending on the material (s) included in the experimentation:

<table>
<thead>
<tr>
<th>Methods</th>
<th>Materials included in the experiment of entries in the experiment (( F_1 )’s + parents)</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>Method 1</td>
<td>Parents, ( F_1 )’s and Reciprocals</td>
<td>( \sqrt{n} )</td>
</tr>
<tr>
<td>Method 2</td>
<td>Parents and ( F_1 )’s (w/o Reciprocals)</td>
<td>( n(n + 1)/2 )</td>
</tr>
<tr>
<td>Method 3</td>
<td>( F_1 )’s and Reciprocals (w/o Parents)</td>
<td>( n(n – 1) )</td>
</tr>
<tr>
<td>Method 4</td>
<td>( F_1 )’s (w/o parents &amp; w/o Reciprocals)</td>
<td>( n(n – 1)/2 )</td>
</tr>
</tbody>
</table>

- Method 2 which utilizes direct crosses and parents in the analysis is in the most common use.
- In their approach, gene action is deducted through the estimates of GCA and SCA variances and
The GCA component is primarily a function of additive genetic variance. However, if epistasis is present, the GCA will include the additive x additive interaction as well. On the other hand, the SCA variance is mainly a function of dominance variance but it would include all the three types of epistatic interaction component; if epistasis is present.

**Features of Griffing’s approach:**
- This is a numerical approach which is based on the estimates of combining ability variance and effects.
- Provide information about D and H components through gca and sca variances and effects.
- Analysis is possible even when parents are not included.
- Helps in selection of desirable parents and cross combinations.
- Calculation of various genetic ratios is not possible in this approach.

### Comparision of Hayman’s and Griffing’s Approaches:

<table>
<thead>
<tr>
<th>S.No.</th>
<th>Particulars</th>
<th>Hayman’s approach</th>
<th>Griffing’s approach</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td>Type of approach</td>
<td>Graphical</td>
<td>Numerical</td>
</tr>
<tr>
<td>2.</td>
<td>Estimates obtained</td>
<td>Components of variance</td>
<td>Combining ability effects &amp; variances</td>
</tr>
<tr>
<td>3.</td>
<td>Components estimated</td>
<td>D, H&lt;sub&gt;1&lt;/sub&gt;, H&lt;sub&gt;2&lt;/sub&gt;, E, F &amp; h&lt;sup&gt;2&lt;/sup&gt;</td>
<td>D &amp; H</td>
</tr>
<tr>
<td>4.</td>
<td>Estimation of genetic ratios</td>
<td>Possible</td>
<td>Not possible</td>
</tr>
<tr>
<td>5.</td>
<td>Inclusion of parents in the analysis</td>
<td>Essential</td>
<td>Not essential</td>
</tr>
<tr>
<td>6.</td>
<td>Identification of superior cross combinations</td>
<td>Not possible</td>
<td>Possible</td>
</tr>
</tbody>
</table>

### Models of Combining Ability Analysis

**Fixed Effect Model:** Also known as model no. 1 which is used with diallel set of crosses made among fixed sample of inbred lines. In this model, the experimental material includes a set of fixed genotypes, say a set of inbreds or varieties. Such a set of genotypes is considered as a population and inferences are drawn about individual line/variety.

**Random Effect Model:** Also known as model no. 2 which is used with diallel set of crosses made among random samples of individuals from random mating population. In this case, inferences cannot be drawn about individual line but about the parent population as a whole.

### Application of Diallel Analysis
- Diallel cross is used for evaluation of several single crosses in terms of genetic components of variance.
- It provides information about gca and sca variances and effects and additive (D) and dominance (H) components of genetic variance.
- The estimates of heterosis, heritability and genetic advances can also be worked out.
- If F<sub>2</sub> population is available, inbreeding depression can be worked out.
- Diallel analysis helps in the selection of suitable parents for use in the hybridization programme as well as the choice of appropriate breeding/procedure for the genetic improvement of various quantitative traits in a crop species.
- Diallel analysis has been extensively used in both self and cross-pollinated species to understand the nature or gene action involved in the expression of quantitative traits.

### Breeding procedures in relation to gene action:

<table>
<thead>
<tr>
<th>Types of gene action</th>
<th>Breeding procedure to be adopted</th>
<th>Possible outcome</th>
</tr>
</thead>
</table>
### a) Self-pollinated species

<table>
<thead>
<tr>
<th></th>
<th>Additive</th>
<th>Non-additive</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pure line selection</td>
<td>Pure line variety</td>
<td>Heterosis breeding</td>
</tr>
<tr>
<td>Mass selection</td>
<td>Mass selected variety</td>
<td>Hybrid variety</td>
</tr>
<tr>
<td>Progeny selection</td>
<td>New variety</td>
<td></td>
</tr>
<tr>
<td>Hybridization &amp; selection</td>
<td>Superior segregant or new variety</td>
<td></td>
</tr>
<tr>
<td>Heterosis breeding</td>
<td>Hybrid variety</td>
<td></td>
</tr>
</tbody>
</table>

### b) Cross-pollinated species

<table>
<thead>
<tr>
<th></th>
<th>Additive</th>
<th>Non-additive</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recurrent selection for GCA</td>
<td>Population improvement</td>
<td>Heterosis breeding</td>
</tr>
<tr>
<td>Synthetic breeding</td>
<td>Synthetic variety</td>
<td></td>
</tr>
<tr>
<td>Composite breeding</td>
<td>Composite variety</td>
<td></td>
</tr>
<tr>
<td>Recurrent selection for SCA</td>
<td>Population improvement</td>
<td>Reciprocal Recurrent</td>
</tr>
<tr>
<td>Reciprocal Recurrent</td>
<td>Population improvement selection</td>
<td></td>
</tr>
</tbody>
</table>

**Interpretation of Gene Action**

- If gca variances are higher than sca variances, it means that there is preponderance of additive gene action and progeny selection will be effective for the genetic improvement of such traits.
- If sca variances are higher than gca variances, it indicates that there is preponderance of non-additive gene action (dominance & epistasis) and therefore, heterosis breeding may be rewarding.
- If both gca & sca variances are of equal magnitude, it shows that additive and non-additive genes are equally important in the expression of character then we use reciprocal recurrent selection.

**References (if any)**

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