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Review on the Application of Mating Designs and Estimation of Genetic Variances in Plant Breeding

Zewdu Asrat* Mastewal Gojjam

Ethiopian Institute of Agricultural Research, Chiro National Sorghum Research and Training
Center P. O. Box190, Chiro, Ethiopia

*Corresponding author: zewduasrat07@gmail.com

Abstract

Breeders and geneticists use different mating designs and arrangements to produce improved plants. Even though Success in plant breeding is based the selection of suitable parents and good mating designs, there are several factors affecting the choices of mating design. Each mating design has its own significance, merits and demerits according to conditions of experiment space, time, objectives of study and problems. Theoretically, differences between maternal groups measure variation in their general combining ability. Specific combining ability (SCA) refers to combinations or crosses that do relatively better or worse than would be expected based on the average performance of the lines involved, it is therefore due to non-additive gene action. For a successful plant breeding, the information vis-à-vis the estimates of combining ability and genes actions are very important.

Keywords: Crop improvement, Gene-action, Pollination, and Allele.

Introduction

Breeders and geneticists use various mating designs and arrangements to produce improved plants. Even though Success in plant breeding is based the selection of suitable parents and good mating designs, there are several factors affecting the choices of mating designs (Khan *et al.*, 2009). Those are; the type of pollination (self- or cross-pollinated), the type of crossing to be used (artificial or natural), the type of pollen dissemination (wind or insect); the presence of a male-sterility system, the purpose of the project

(for breeding or genetic studies) and the size of the population required (Acquaah, 2012). Breeders have interests in discovering the answer to the following questions in making various crosses: how significant is genetic variation? How much of the variation is heritable? And what types of gene affecting that significance? However, these are answered by comparing the variances of the segregating and the non-segregating generations (Kearsey and Pooni, 1996).

Another interest of the breeder is identifying plants with superior genotypes as judged by the performance of their progeny. Suitable inbreds or lines are selected based on combining ability effects with better mean performance. Combining ability depends on the gene action controlling the trait to be improved. General combining ability (GCA) is the average performance of a line in hybrid combinations and is due to additive genes action. The estimation of GCA for a particular line depends upon the mating design, but essentially, it is the deviation of its progeny mean from the mean of all lines included in the trial (Acquaah, 2012).

Thus, theoretically, differences between maternal groups measure variation in their general combining ability. Specific combining ability (SCA) refers to combinations or crosses that do relatively better or worse than would be expected based on the average performance of the lines involved, it is therefore due to non-additive gene action (Falconer and Mackay, 1996; Acquaah, 2012). For a successful plant breeding, the information vis-à-vis the estimates of combining ability and genes actions is very important (Panhwaret *et al.*, 2008). Therefore, the objective of this paper is to review the different form of mating designs and estimation of genetic variances for those designs.

Genetic assumptions as steppingstone for mating designs

Before discussing the mating designs, it is very important to understand the genetic assumptions (Hill *et al.*, 1998): (a) Diploid behavior at meiosis; this assumption applies to all designs, but it doesn't rule out the investigation of polyploidy species provided they behave as functional diploids, with disomic inheritance. (b) Uncorrelated genes distribution. The genes controlling the character should be independently distributed among the parents. (c) Absence of non-allelic interactions. In the triple test and diallel crosses epistasis can be detected and its effects including in prediction. (d) No multiple alleles at those loci controlling the character. (e)

Absence of reciprocal differences. Again this assumption can be tested in several designs and appropriate measure taken. (f) Ideally the diallel cross should be restricted to crosses among homozygous lines. Heterozygous can be catered for, but it complicated the interpretation of the results. (g) Absence of genotype-environment interaction. Their presence merely emphasizes the need for wide scale testing of material in order to determine the extent of such interaction.

Use of mating designs

Plant breeding experiments use two types of designs. Namely, mating and experimental design which should march with its statistical components analysis and interpretation. Those mating designs have four critical uses,

- (1) To provide information on the genetic control of the character under investigation
- (2) To generate a breeding population to be used as a basis for the selection and development of potential varieties
- (3) To provide estimates of genetic gain and
- (4) To provide information for evaluating the parents used in the breeding program (Acquaah, 2012).

Mating designs in plant breeding

Mating design refers to the procedure of producing the progenies. In plant breeding, breeders use different form of mating designs and arrangements for targeted purpose. However, the choice of a mating design for estimating genetic variances should be dictated by the objectives of the study, time, space, cost and other biological limitations.

Thus, several studies (Griffing, 1956b; Kearsey and Pooni, 1996; Hallauer *et al.*, 2010; Acquaah, 2012) described and contrasted different mating designs and six types of mating designs have been described so far: (1) bi-parental progenies (BIP), polycross, topcross, North Carolina (I, III, III), Diallels (I, II, III, IV) and Line X tester design. In all mating designs, the individuals are taken randomly and crossed to produce progenies which are related to each other as half-sibs or full-sibs.

A form of multivariate analysis or the analysis of variance can be adopted to estimate the components of variances.

Diallel Mating Design

There are two types of diallel cross (1) Full diallel: (Full diallel with parents and Full diallel without parents.) (Griffing, 1956). (2) Half diallel: (Half diallel with parents and half diallel without parents.) (Griffing 1956). Diallel cross analysis involve these steps (1) Involve all possible single crosses among 'n' parents $N(n-1)/2$, (2) Calculation is complex, (3) Results have high precision, (4) Help in choice of parents and breeding procedures, (5) May included direct and reciprocal crosses (6) Sampling of cross is not required, (7) 10 to 12 parents can be evaluating (7) Planting arrangement for diallel by unpaired parents and paired parents (8) Graphical analysis is also possible. (Vr-Wr graph) (9) It is called mating design (Acquaah, 2012; Griffing 1956, Hayman and Jinks, 1977). Some merits of diallel cross are (1) Each parents have equal chance for mating and recombine with other parents (2) If F₂ population is required then inbreeding depression also worked out (3) Evaluation of single crosses in term of genetic component of variance (Nduwumuremyiet *al.*, 2013). Some demerits of diallel cross are (1) By hand its analysis is complex (2) Limited number of parents can be test at a time.

A complete diallel mating design is one that allows the parents to be crossed in all possible combinations (Schlegel, 2010), including selfs and reciprocals. This is the kind of mating scheme required to achieve Hardy–Weinberg equilibrium in a population (Acquaah, 2012). The diallel is the most used and abused of all mating designs in obtaining various genetic information (Hallauer *et al.*, 2010). Much of its abuse could probably be due to the presence of two models for diallel analysis; random and fixed models (Griffing, 1956b). Random model involves parents that are random members of a random mating population. Random model is useful for estimating GCA and SCA variances.

In contrast, when parents are considered fixed effects, the aim is to measure the GCA effect for each parent and the SCA effect for each pair of parents. These effects only apply to the set of parents in the diallel. It is also widely used for developing breeding populations for recurrent selection (Acquaah, 2012). In addition, Johnson and King (1998), reported that diallel mating designs are deployed to provide the maximum opportunity to manage co-ancestry in breeding population and maximize selection differential. However, in practice, a diallel with selfs and reciprocals is neither practical nor useful for several reasons. Selfing does not contribute to the recombination of genes between parents. Furthermore, recombination is achieved by crossing in one direction making reciprocals unnecessary (Acquaah, 2012). Because of the extensive mating patterns, the number of parents that can be mated this way is limited.

Nursery arrangements for the application vary depending either complete or partial diallel design and four methods under the diallel mating design have been so far described. The number of progenies generated from each method are different, the number of progeny families (pf) for methods 1 through 4 are: $pf = n^2$, $pf = 1/2n(n + 1)$, $pf = n(n - 1)$, and $pf = 1/2n(n - 1)$, respectively (Acquaah, 2012).

Method I or Full diallel mating design

The method I or full diallel design consisted by parents, one set of F₁'s and reciprocal F₁'s. The system gives n^2 genotypes (Griffing, 1956b). The mathematical models for combining ability analysis for the fixed and random effects are given by;

Fixed effect model or model I: $Y_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{bc} \sum \sum \epsilon_{ijkl}$, where, μ is the population mean, g_i, g_j is the general combining ability effect for the i th and j th parents, s_{ij} is the specific combining ability effect of the cross between the i th and j th parents such that $s_{ij} = s_{ji}$, r_{ij} is the reciprocal effect involving the reciprocal crosses

between the i th and j th parents such that $r_{ij} = r_{ji}$ and ε_{ijkl} is the experimental error due to environmental effect associated with the $ijkl$ th, which is assumed to be uncorrelated and normally distributed with zero mean and variance,

$$\text{Random effect model or Model II: } Y_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{bc} \sum (bv)_{ijk} + \frac{1}{bc} \sum \varepsilon_{ijkl}$$

Table 1. Skeleton of ANOVA for method I Diallel design

Expected mean squares					
Source	Df	SS	MS	Model I	Model II
GCA	p-1	S_g	M_g	$\sigma^2 + 2p(\frac{1}{p-1}) \sum g_i^2$	$\sigma^2 + 2(\frac{p-1}{p}) \sigma_g^2 + 2p \sigma_g^2$
SCA	p(p-1)/2	S_s	M_s	$\sigma^2 + \frac{2}{p(p-1)} \sum \sum s_{ij}^2$	$\sigma^2 + 2(\frac{p^2-p+1}{p^2}) \sigma_s^2$
Reciprocal eff.	p(p-1)/2	S_r	M_r	$\sigma^2 + 2(\frac{2}{p(p-1)}) \sum \sum r_{ij}^2$	$\sigma^2 + 2 \sigma_r^2$
Error	m	S_e	M_e	σ^2	

Source: Griffing (1956b)

Method II or half diallel design

This method includes parents and one set of F1's without reciprocals F1's. This design gives p(p+1)/2 genotypes. The mathematical models for combining ability for fixed model is: $Y_{ij} = \mu + g_i + g_j + s_{ij} + \frac{1}{bc} \sum \varepsilon_{ijkl}$ Where, μ is the population mean, g_i , g_j is the general combining ability effect for the i th and j th parents, s_{ij} is the specific

combining ability effect of the cross between the i th and j th parents such that $s_{ij} = s_{ji}$ and ε_{ijkl} is the experimental error due to environmental effect associated with the $ijkl$ th. The mathematical equation for analysis of combining ability for random model is: $Y_{ij} = \mu + g_i + g_j + s_{ij} + \frac{1}{b} \sum b + \frac{1}{b} \sum (bv)_{ijk} + \frac{1}{bc} \sum \varepsilon_{ijkl}$

Table 2. The analysis of variance for method II

Expected mean squares					
Source	Df	SS	MS	Model I	Model II
GCA	p-1	S_g	M_g	$\sigma^2 + (2+p)(\frac{1}{p-1}) \sum g_i^2$	$\sigma^2 + \sigma_s^2 + (p+2) \sigma_g^2$
SCA	p(p-1)/2	S_s	M_s	$\sigma^2 + \frac{2}{p(p-1)} \sum \sum s_{ij}^2$	$\sigma^2 + \sigma_s^2$
Error	m	S_e	M_e	σ^2	

Source: Griffing (1956b)

Method III

In this method, one set of F1's and the reciprocals are included. This mating design gives rise to a = p (p-1) different number of genotypes. As for methods I and II, also it has both fixed and random effect models. Fixed model: $Y_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{bc} \sum \sum \epsilon_{ijkl}$, Where, μ is the population mean, g_i , g_j is the general combining ability effect

for the i^{th} and j^{th} parents, s_{ij} is the specific combining ability effect of the cross between the i^{th} and j^{th} parents such that $s_{ij} = s_{ji}$, r_{ij} is the reciprocal genotypic effects such that $r_{ij} = r_{ji}$ and ϵ_{ijkl} is the experimental error due to environmental effect associated with the $ijkl^{th}$ (Griffing, 1956b). Random model: $Y_{ij} = \mu + g_i + g_j + s_{ij} + r_{ij} + \frac{1}{b} \sum b + \frac{1}{b} \sum (bv)_{ijk} + \frac{1}{bc} \sum \sum \epsilon_{ijkl}$.

Table 3.Skeleton of ANOVA of Diallel method III.

Expected mean squares					
Source	Df	SS	MS	Model I	Model II
GCA	p-1	S_g	M_g	$\sigma^2 + 2p(p-2)(\frac{1}{p-1}) \sum g_i^2$	$\sigma^2 + 2 \sigma_s^2 + 2(p-2) \sigma_g^2$
SCA	p(p-3)/2	S_s	M_s	$\sigma^2 + \frac{2}{p(p-3)} \sum \sum s_{ij}^2$	$\sigma^2 + 2 \sigma_s^2$
Reciprocal eff.	p(p-1)/2	S_r	M_r	$\sigma^2 + 2(\frac{2}{p(p-1)}) \sum \sum r_{ij}^2$	$\sigma^2 + 2 \sigma_r^2$
Error	M	S_e	M_e	σ^2	σ^2

Source: Griffing (1956b)

Method IV

In this method, only one set of F1's are included. It is the most common of the diallel crossing systems. There are a = p (p-1)/2 different genotypes evaluated. As for other diallel methods, there are two models. Fixed model: $Y_{ij} = \mu + g_i + g_j + s_{ij} + \frac{1}{bc} \sum \sum \epsilon_{ijkl}$, where, μ is the population mean, g_i , g_j is the general combining ability effect for the i^{th} and j^{th} parents, s_{ij} is the specific combining ability effect of the cross between the

i^{th} and j^{th} parents such that $s_{ij} = s_{ji}$ and ϵ_{ijkl} is the experimental error due to environmental effect unique to the $ijkl^{th}$ (Griffing, 1956b).

This mating design provides information on GCA and SCA (Griffing, 1956b). However, the fixed model of method 3 or 4 is the most appropriate for obtaining unbiased estimates of combining abilities and gene action (Shattuck *et al.*, 1993). This method is most suitable when there are no genotypic reciprocal effects (Griffing, 1956b).

Table 4.Skeleton of ANOVA for Diallel method IV.

Expected mean squares					
Source	Df	SS	MS	Model I	Model II
GCA	p-1	S_g	M_g	$\sigma^2 + (p-2)(\frac{1}{p-1}) \sum g_i^2$	$\sigma^2 + 2 \sigma_s^2 + (p-2) \sigma_g^2$
SCA	p(p-3)/2	S_s	M_s	$\sigma^2 + \frac{2}{p(p-3)} \sum \sum s_{ij}^2$	$\sigma^2 + 2 \sigma_s^2$
Error	M	S_e	M_e	σ^2	σ^2

Source: Griffing (1956b)

Estimation of combining ability

In plant breeding concept of combining ability is a very important and it can be used to compare and investigate how two in bredlines can be combined together to produce a productive hybrid or to breed new in bredlines. Selection and development of parentallines or inbreeds with strong combining ability is one of the most important breeding objectives, no matter whether the goal is to create a hybrid with strong vigour or develop a pure-line cultivar with improved characteristics compared to their parental lines. In maize breeding, Sprague and Tatum (1942) partitioned the genetic variability among crosses into effects due to primarily either additive or non-additive effects, which correspond to two categories of combining ability, general combining ability (GCA) and special combining ability (SCA).

The relative importance of GCA and SCA depends on the extent of previous testing of the parents included in the crosses. Although these concepts were developed for breeding maize, an open-pollinated crop, they are generally applicable to self-pollinated crops. The GCA for an inbred line or a cultivar can be evaluated by the average performance of yield or other economic traits in a set of hybrid combinations. The SCA for a cross combination can be evaluated by the deviation in its performance from the value expected from the GCA of its two parental lines.

If the crosses among a set of inbred lines are made in such a way that each line is crossed with several other lines in a systematic manner, the total variation among crosses can be partitioned into two components ascribable to GCA and SCA. For calculating the general combining ability (GCA) and specific combining ability (SCA) the mother plants are tested with the same set of testers. The tester can be lines (inbred tester), populations (broad based tester) or hybrids. According to the performance the best hybrids are selected.

$Y = \mu + GCA_i + GCA_j + SCA_{ij}$; i is the father, j is the mother plant

The expected value of a cross with a specific male (or female) can be calculated as:

$Y_i = \text{mean}(Y) + GCA_1$; Y is the yield of all crosses, GCA_1 is the GCA of male 1

Where, $GCA_1 = \text{mean}(Y_i) - \text{mean}(Y)$; Y_i is the yield of all crosses with male 1

The expected SCA can be calculated as:

$SCA_{12} = Y_{12} - GCA_1 - GCA_2 - \text{mean}(Y)$; Y_{12} is the yield of the cross between father 1 and mother 2

Griffing (1956) defined diallel crosses, which have been used extensively in plant breeding. However, general and specific combining ability effects are commonly based on the average effect of the parent when it is used as a female or a male in its hybrid combinations assuming that they are likely to be similar as proposed by Yates, (1947). Griffing's methods 1 and 3 where crosses and their reciprocals are included, the fixed models, only one GCA effect value for each parent and one SCA effect value for each cross combination are estimated. These estimated effects do not, separately, show the contribution of each parent to the cross combination when this particular parent is used as a male or, alternatively, female. Partitioning of the general and specific combining ability effects would provide additional information about each parent when it is used as a female or a male in its hybrid combinations (Mahgoub, 2004). It should, also provide precise information about the nature of the interaction between the best combinations among parents. Therefore, a proposed model is presented as follows:

i) Griffing's method 1 model I (all crosses, their reciprocals and parents are included) $n = p^2$. Various effects are estimated according to Griffing (1956) as follows:

$$g_i = \frac{1}{2p}(X_{i.} + X_{.i}) - \left(\frac{1}{p^2}\right)X_{..},$$

$$s_{ij} = \left(\frac{1}{2}\right)(x_{ij} + x_{ji}) - \left(\frac{1}{2p}\right)(X_{i.} + X_{.i} + X_{.j} + X_{j.}) + \left(\frac{1}{p^2}\right)X_{..},$$

$$r_{ij} = \left(\frac{1}{2}\right)(x_{ij} - x_{ji})$$

Maternal effect is estimated using Griffing's notations as follows: $m_i = \left(\frac{X_{i.} - X_{.i}}{2p}\right)$ where $X_{i.}$ is the

sum of the i^{th} female over all males; $X_{.i}$ is the sum of the i^{th} male over all females; $X_{.j}$ is the sum of the j^{th} female over all males; $X_{j.}$ is the sum of the j^{th} male over all females; x_{ij} is the mean for the F1 resulting from crossing the i^{th} female and the j^{th} male parents, x_{ji} is the mean for the F1 resulting from crossing the j^{th} female and the i^{th} male parents; g_i is the general combining ability effect of the i^{th} parent, s_{ij} is the specific combining ability effect for the cross between the i^{th} female and the j^{th} male parents ($s_{ij} = s_{ji}$); r_{ij} is the reciprocal effect involving the i^{th} and j^{th} parents, m_i is the maternal effect of the i^{th} parent, s_{ij} is the SCA effect of the i^{th} female and the j^{th} male parent, and s_{ji} is the SCA effect of the reciprocal, the j^{th} female and the i^{th} male parent, and $X_{..}$ is the grand total.

A proposed model where GCA effect g_i is partitioned to estimate GCA effect for the parent when it is used as a female in its hybrid combination g_{fi} ; and GCA effect for the parent when it is used as a male in its hybrid combination g_{mi} as follows:

$$g_{fi} = \frac{1}{p}(X_{i.}) - \left(\frac{1}{p^2}\right)X_{..},$$

$g_{mi} = \frac{1}{p}(X_{.i}) - \left(\frac{1}{p^2}\right)X_{..}$, where g_{fi} is the deviation of the mean performance of the i^{th} parent when it is used as a female, averaged over a set of P males, from the grand mean and g_{mi} is the deviation of the mean performance of the i^{th} parent when it is used as a male, averaged over a set of P females, from the grand mean where: $g_i = \frac{1}{2}(g_{fi} + g_{mi})$ and

$$\frac{1}{2}(g_{fi} - g_{mi}) = \frac{1}{2p}(X_{i.} - X_{.i})$$

This proves that the average of the difference between g_{fi} and g_{mi} is exactly equal to maternal effect. In other words, estimation of $g_{fi} - g_{mi}$ would

provide precise estimation for the maternal effect. General combining ability effect provides estimation for the additive effect. Therefore, maternal effect is mainly additive and expresses how much additive effect is involved. Specific combining ability effect is partitioned to estimate SCA effect for the cross s_{ij} and for its reciprocal s_{ji} as follows:

$$s_{ij} = x_{ij} - \left(\frac{1}{2p}\right)(X_{i.} + X_{.i} + X_{.j} + X_{j.}) + \left(\frac{1}{p^2}\right)X_{..},$$

$$s_{ji} = x_{ji} - \left(\frac{1}{2p}\right)(X_{i.} + X_{.i} + X_{.j} + X_{j.}) + \left(\frac{1}{p^2}\right)X_{..},$$

Therefore, $\left(\frac{1}{2}\right)(s_{ij} - s_{ji}) = \left(\frac{1}{2}\right)(x_{ij} - x_{ji}) =$ reciprocal effect

This proves that the average of the difference between SCA effect of the cross and its reciprocal is exactly equal to the estimated reciprocal effect. Accordingly, this difference provides precise estimation for the reciprocal effect.

ii) Griffing's method 3 model I(all crosses and their reciprocals, excluding parents) $n=p(p-1)$ Various effects are estimated according to Griffing's method 3 as follows:

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

$$s_{ij} = \left(\frac{1}{2}\right)(x_{ij} + x_{ji}) - \left(\frac{1}{2(p-2)}\right)(X_{i.} + X_{.i} + X_{.j} + X_{j.}) + \left(\frac{1}{(p-1)(p-2)}\right)X_{..},$$

$$r_{ij} = \left(\frac{1}{2}\right)(x_{ij} - x_{ji})$$

Estimated effects after partitioning according to the proposed model are calculated as follows:

$$g_{fi} = \left(\frac{X_{i.}}{p-2}\right) - \left(\frac{X_{..}}{p(p-2)}\right),$$

$$g_{mi} = \left(\frac{X_{.i}}{p-2}\right) - \left(\frac{X_{..}}{p(p-2)}\right),$$

$$g_i = \left(\frac{1}{2}\right)(g_{fi} + g_{mi})$$

$$g_{fi} - g_{mi} = \left[\left(\frac{X_{i.}}{p-2}\right) - \left(\frac{X_{..}}{p(p-2)}\right) - \left(\frac{X_{.i}}{p-2}\right) + \left(\frac{X_{..}}{p(p-2)}\right)\right],$$

$$\frac{1}{2}(g_{fi} - g_{mi}) = \frac{1}{2(p-2)}\left(\frac{X_{i.} - X_{.i}}{2}\right)\left(\frac{p-1}{p-2}\right)$$

The SCA effects are partitioned as follows:

$$s_{ij} = x_{ij} - \left(\frac{1}{2(p-2)} \right) (X_{i.} + X_{.i} + X_{j.} + X_{.j}) + \left(\frac{1}{(p-1)(p-2)} \right) X_{...}$$

$$s_{ji} = x_{ji} - \left(\frac{1}{2(p-2)} \right) (X_{i.} + X_{.i} + X_{j.} + X_{.j}) + \left(\frac{1}{(p-1)(p-2)} \right) X_{...}$$

$$s_{ij} - s_{ji} = x_{ij} - x_{ji}$$

Therefore, $\frac{1}{2}(s_{ij} - s_{ji}) = \frac{1}{2}(x_{ij} - x_{ji}) =$ reciprocal effect

Thus, the average of the difference between s_{ij} and s_{ji} is equal to the estimated reciprocal effect as indicated above in method 1. Improving the precision of the statistical model used for estimating GCA and SCA effects may provide a precise tool for selecting the breeding method as well as the paired populations to be used in a reciprocal recurrent selection program.

Non-allelic interaction

Genes are independent of one another in the contribution that they made to the various statistics, means, variances and co variances - in the form of, for example, scaling tests in the analysis of means or tests of the constancy of W_r - v , in diallel analysis. In non-allelic interaction, means of explicitly accommodating the consequences of non-independence in the analysis is valuable to solve problems. genes may show non-independence in two ways. First, they may be influenced by one another in their expression, i.e. they may interact in producing their effects.

Secondly, they may be correlated with one another in their distribution among the individuals whose phenotypes are under investigation (Hayman and Jinks, 1977).

In the absence of dominance individuals heterozygous for the gene Aa , would display a phenotype midway between those of the homozygotes AA and aa . The effect of substituting allele A for a would be independent of whether the allelic gene also present was A or a : the effects of the alleles would be simply additive and there would be no need to incorporate h into the model. The incorporation of h is at once a recognition that alleles need not be independent of each other in exerting their effects, and the provision of a parameter by which their interaction can be accommodated and measured. Dominance is thus the interaction of allelic genes and h is the parameter by which this allelic interaction is measured. So, it is important to note that, corresponding means of representing and measuring the interaction of non-allelic genes, or non-allelic interaction as it is often called (Hayman and Jinks, 1977).

Consider the simplest case of two gene pairs, Aa and Bb . These can give rise to nine different genotypes each with its own phenotypic characteristics as shown in Table below. The differences among these phenotypes can therefore be completely described by eight parameters, which correspond of course to the 8df among the nine observations (Hayman and Jinks, 1977).

Table 5. Phenotypes from the nine genotypes comprising all combinations of A-a and B-b

	AA	Aa	aa
BB	$d_a + d_b$ $+ i_{ab}$	$h_a + d_b$ $+ j_{ba}$	$-d_a + d_b$ $- i_{ab}$
Bb	$d_a + h_b$ $+ j_{ab}$	$h_a + h_b$ $+ l_{ab}$	$d_a + h_b$ $- j_{ab}$
bb	$d_a + d_b$ $- i_{ab}$	$h_a + d_b$ $- j_{ba}$	$-d_a - d_b$ $+ i_{ab}$

Source: (Hayman and Jinks, 1977)

Four of these parameters defined above, namely d_a , d_b , h_a and h_b . The remaining four parameters can then be conveniently defined as representing respectively the interactions of d_a and d_b , d_a and h_b , h_a and d_b and h_a and h_b . Now d_a measures the difference in phenotype between AA and aa, and similarly d_b that between BB and bb. If d_a and d_b are independent, d_a will be the same whether the difference AA-aa is measured in BB or bb individuals (Hayman and Jinks, 1977). Thus with independence $AABB - aaBB = AAbb - aabb$ or $AABB - aaBB - AAbb + aabb = 0$, where AABB is the phenotype of AABB etc. Similarly in respect of d_b $AABB - AAbb = aaBB - aabb$ or $AABB - aaBB - AAbb + aabb = 0$, as before. We can therefore accommodate prospective interaction of d_a and d_b by including a further parameter i_{ab} such that the phenotype of AABB is $d_a + d_b + i_{ab}$, that of AAbb is $d_a - d_b - i_{ab}$, that of aaBB is $-d_a + d_b - i_{ab}$ and that of aabb is $-d_a - d_b + i_{ab}$ (Hayman and Jinks, 1977).

Then the difference of AA and aa taken over both BB and bb genotypes is $(AABB - aaBB) + (AAbb - aabb) = 4d_a$. Similarly the overall difference of BB and bb is $(AABB - AAbb) + (aaBB - aabb) = 4d_b$, and the interaction of these differences is $(AABB - aaBB - AAbb + aabb) = 4i_{ab}$. The relation of these four completely homozygous classes has been described completely by the introduction of the new parameter i_{ab} representing the interaction of d_a and d_b . When there is no such interaction $i_{ab} = 0$ since $(AABB - aaBB - AAbb - aabb) = 4i_{ab} = 0$ (Hayman and Jinks, 1977).

Turning to the relation of d_a and h_b since d_a represents the difference between AA and aa, absence of interaction implies that h_b will be the same whether measured in individuals that are AA or individuals that are aa. In the presence of interaction between d_a and h_b , these two measurements will not be the same, and we can accommodate the interaction by including a new parameter j_{ab} such that it is added in the specification of AABb which is basically $d_a + h_b$ but subtracted in the specification of aaBb, which is basically $-d_a + h_b$. In the absence of interaction $j_{ab} = 0$, and its value provides a

measure of any interaction that may be present between d_a and h_b . A corresponding parameter j_{ba} can be similarly incorporated into the specifications of AaBB and Aabb to represent and provide a measure of the interaction between h_a and d_b . The last of the four interactions, between h_a and h_b is covered by a fourth parameter l_{ab} which is incorporated into the specification of AaBb, where h_a and h_b appear together (Hayman and Jinks, 1977).

Components and significance of diallel analysis

Diallel cross analysis is one way to obtain genetic information. According to Johnson (1963), this method is experimentally a systematic approach, and analytically a comprehensive genetic evaluation approach that is useful in identifying potential cross for the best selection in early generations. Diallel analysis is useful in intersecting the suspect of the general combining ability (GCA) and the specific combining ability (SCA). This analysis is also useful to predict additive and dominant effects of a population which can then be used to predict the genetic variability and heritability. The combining ability analysis can be conducted using the Griffing Method (Griffing 1956), whereas to study the action of genes, genetic components and heritability can use the Hayman Method (Hayman 1954). Griffing and Hayman data analysis are often used together for complementary data interpretation.

North Carolina

North Carolina design was developed after using long time diallel. However, the later require much labour. Therefore, in order to obtain more information about combining ability but without much labour comparing to full diallel, Comstock and Robinson in 1952, introduced the North Carolina designs I, II, and III.

North Carolina Design I

Each male mated to different group of female. It has set of 'f' crosses where f is female plants. Variance between males provides an estimate of additive variance. If variance between female it

provide dominance and additive variance estimation. It is influenced by maternal effects. it require 10 to 12 time more area. It is a least powerful design. It involve F2 plant in crossing. Variance id divided between two fractions, male and female (Acquaah, 2012).

Table7. ANOVA for North Carolina design I (Acquaah, 2012)

Source of variation	Df	MS	Expected mean squares
Males	(m - 1)	1 M	$\sigma^2_w + r \sigma^2_{mf} + rf \sigma^2_m$
Females	m(f - 1)	2 M	$\sigma^2_w + r \sigma^2_{mf}$
Within plots	mf(r - 1)	1 M	σ^2_w
Total	rmf - 1		

North Carolina Design II

Each male is mated with same group of female. It has mf set of crosses in which 'm' is male and 'f' is female plant. Due to male and female variance it provides additive effects. It also provides dominance variance if male $\times$ female variance (Acquaah, 2012). It also influenced by maternal

effects. It requires 2 to 4 time more area. It is an intermediate design which involved F2 plants in crossing. Variance is divided in three fractions due to males and females and due to male $\times$ female cross (Acquaah, 2012). It does not provide epistasis test or G $\times$ E interaction (Kearsey and Pooni, 1996).

Table 8.ANOVA for NC II(Acquaah, 2012).

Source of variation	Df	MS	Expected mean squares
Replication	r-1		
Male	m-1	M1	$\sigma^2_w + r \sigma^2_{mf} + rf \sigma^2_m$
Female	f-1	M2	$\sigma^2_w + r \sigma^2_{mf} + rm \sigma^2_f$
MaleX Female	(m-1)(f-1)	M3	$\sigma^2_w + r \sigma^2_{mf}$
Within progenies	mf(r-1)	M4	σ^2_w
Error	(r-1)(mf-1)	M5	σ^2
Total	rmf-1		

North Carolina Design III

Each male is mated to both inbred parents of original cross. It consists of 2m cross where m is number of male. It is capable of testing epistasis, additive and dominance variances. This is more

powerful design and involves F2, F1 and P2 plants during crossing. Variance is divided into two fraction due to male and due to male×female (Acquaah, 2012). It is also called as triple test cross because a third tester is included in this (Hill *et al.*, 1998).

Table 9. ANOVA for NC III(Acquaah, 2012).

Source of variation	Df	MS	Expected mean squares
Testers, P	1	M4	$\sigma^2 + r \sigma^2_{mp} + rm K2p$
Males(F2)	m- 1	M3	$\sigma^2_w + r \sigma^2_{mf}$
Testers X Parents	m-1	M2	$\sigma^2 + r \sigma^2_{mp}$
Within FS families/error	(r-1) (2m-1)	M1	σ^2
Total	2mr-1		

Heterosis

Heterosis is the hybrid vigor manifested in hybrids and represents the superiority in performance of hybrid individuals compared with their parents. Heterosis is a phenomenon not well understood but has been exploited extensively in breeding and commercially. Hybrid cultivars are used for commercial production in crops in which heterosis expression is important. The commercial use of hybrid is restricted to those crops in which the amount of heterosis is sufficient to justify the extra cost required to produce hybrid seed. Hybrid vigor in maize is manifested in the offspring of inbred lines with high specific combining ability (SCA).

Heterosis was first applied by the proposed hybridization of complex hybrid mixtures made by farmers in the 1800s (Enfield, 1866). However, public scientists E. M. East and G. H. Shull developed the concept of hybrid vigor or heterosis in maize independently in the early 1900s (Shull, 1952). It was realized that genetic divergence of parental crosses was important for hybrid vigor expression (Collins, 1910). But, the range of genetic divergence limited the expression of heterosis (Moll *et al.*, 1965). Heterosis can be inferred from heterotic patterns (Hallauer and

Carena, 2009). A heterotic pattern is the cross between known genotypes that expresses a high level of heterosis (Carena and Hallauer, 2001).

The analysis II proposed by Gardner and Eberhart was used by Excel package to estimate several types of heterosis, as described by the following model:

$Y_{ij} = \mu v + (v_i + v_j)/2 + \phi h_{ij} = \mu v + (v_i + v_j)/2 + \phi (h + h_i + h_j + h_{eij})$, where Y_{ij} = mean of a parent when $i = j$, or mean of a single cross when $i \neq j$; μv = mean of all parents; v_i, v_j = effect of parent i or j , measured as deviation from μv , so that $\sum v_i$ or $\sum v_j = 0$; h_{ij} = heterosis of the cross $v_i v_j$, estimated as the difference between the cross and the average of its two parents, so that $\sum h_{ij} = 0$; h = mean heterosis, estimated by the difference between the average of all crosses and μv ; h_i, h_j = mean heterosis of v_i or v_j in all crosses, also named varietal heterosis, measured as deviations from h , so that $\sum h_i$ or $\sum h_j = 0$; h_{eij} = specific heterosis of the cross $v_i v_j$, estimated as the difference $h_{ij} - (h + h_i + h_j)$, so that $\sum h_{eij} = 0$; ϕ = zero when $i = j$, or = 1 when $i \neq j$. Heterosis with respect to the best parent (hbp) was estimated by the difference between the cross $v_i v_j$ and the highest parent mean.

Conclusion

For the success of any experiment the choice of suitable mating design is very important. Design types, its merits and demerits are basic for this choice. Each mating design has its own significance, merits and demerits according to conditions of experiment i.e., space, time, objectives of study and problems. For example path coefficient analysis is done for measuring correlation between a dependent and an independent variable. If information about presence and absence of epistasis besides of estimation of additives and dominance variations and effects is to be checked generation mean analysis is used. If crossing of randomly selected plants from F₂ or subsequent generation in a definite fashion is needed the bi-parental design is used. If the effect of tester is to be checked with different lines then line $\times$ tester design is used. If degree and direction of relationship between two or more variable is to be checked then correlation is used. If crossing of all plants in all possible combinations is needed then diallel analysis is used and if part of all possible combinations are needed then partial diallel analysis is used and discriminate function technique is used for development of selection on various character combinations where plant breeder indirectly selects the genetic material in yield. Experiments with diallel crosses provide a powerful method of investigating polygenic systems.

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