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# Common Mating Designs in Agricultural Research and Their Reliability in Estimation of Genetic Parameters

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***Abstract:*** *Population development and hybridization are important for improvement of both quantitative and qualitative traits of different crops and are determined by proper selection of mating designs as well as the parents to be mated. Mating design refers to schematic cross between the groups or strains of plants and has been extensively used in agriculture and biological sciences. The mating design in plant breeding has two main objectives: (1) to obtain information and understand the genetic control of a trait or behavior that is observed, and (2) to get the base population for the development of plant cultivars. Analysis of variance in offspring plants resulting from mating designs is used to understand the additive and dominant effects, epistasis and heritability. Various mating designs are available and have been effectively utilized to create different kinds of relatives and to estimate the additive as well as other genetic variance components. Choice of a mating design is based on the breeding objectives and the available capacity such as time, space and cost. It is assumed that individuals used in a mating design are selected at random and crossed to form progenies that are related to each other as half-sibs or full-sibs. Variations among the progenies (sibs) can be assessed using analysis of variance procedures. Mating designs most used are those that can be easily analyzed by normal statistical procedures and provide components of variance that can be translated into covariance of relatives. Although various mating schemes have been introduced, very few of them have been maximized in crop improvement. This is because majority of breeders and geneticists are disadvantaged by inadequate knowledge about the specificity of value each scheme could offer to crop improvement. The objective of this review was to underscore the different forms of mating designs and to shed some light on their implications in plant breeding and genetic studies. The review may provide easy and quick insight of the different forms of mating designs and some statistical components involved for successful plant breeding.*

***Keywords:*** *Sib mating, genetic variance, crosses, statistics, progeny, population*

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## I. Introduction

Various experimental mating designs are developed for the purpose of estimating genetic variance, based on correlation between relatives and how they are used to partition the variations into different genetic components using second degree statistics [1], [2]. Major roles of mating designs are: (1) to provide information on the genetics of the character under investigation; (2) to generate a breeding population to be used as a basis for 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 [3]. Various levels of relatedness among relative progenies are determined by making series of crosses among individuals of random mating population. These generate different statistical components of variation from which genetic variances can be estimated. The genetic components of the variance are used to estimate relationships among the relatives [1].

Evaluation of the progenies in multi environments using appropriate experimental designs and statistical analyses provides good understanding of genotype, environment and genotype x environment interaction effects and reduces error. In addition, the additive model allows estimation of components of variance. Precision of estimates of genetic variance for any mating design depends on number of replications and environments, level of inbreeding of the parents and number of progenies involved [1], [4]. Experiments are analyzed to estimate experimental error in which expectations of expected mean squares (EMS) are expressed in terms of components of variance. These components of variance are then translated into covariance of relatives

depending on the mating design used. The information generated is important in guiding selection processes [5]. Selection can be enhanced by the advances in molecular marker technology where multi factorial or complex traits can be analyzed with much more accuracy [6]. The QTL analysis and marker-assisted selection provide more precise information on QTL locations, their contribution to variations as well as selection of markers associated with them [2], [7]–[9]. Correct selection of mating design is important and it depends on several factors that can be summarized into the following two points: 1) the kind of relatives that will be developed for analysis. This is because certain relatives are observed more readily in certain species than in others, and some kind of phenotypic convariances between relatives are more likely to approximate the desired quantities than others; 2) optimum experimental design: the degree of precision that can be achieved in the quantitative genetic estimates is the function of the number of individuals measured and the way in which effort is allocated to number of families versus number of individuals within families [2].

Adequate interpretation of the genetic composition of covariance of relatives across mating designs is determined by a number of genetic assumptions which include: 1) normal Mendelian diploid inheritance; 2) no maternal effects; 3) no linkage; 4) non-inbred relatives; 5) random selection of parents and relatives; 6) no correlation of environmental effects with relatives; 7) arbitrary allelic frequencies, and 8) no epistasis [3], [5]. These assumptions however, put some restrictions on application of mating designs for assessment of genetic variance. Therefore, use of best linear unbiased prediction (BLUP) is a remedy where breeding values of the parents are estimated from the entire breeding population rather than from a specific mating design. Breeders should have enough understanding of phenotypes and genotypes of the selected parents before any decision to cross [10]. The choice may depend on the following information: (i) the phenotypes of the potential parents, (ii) the genotypes of the potential parents with regards to traits with known genetic control, (iii) the differences between the potential parents with regard to their geographic origin, their pedigrees and their values for a set of traits, (iv) the performance as a parent of the pursued genotype (s), and (v) the performance of early generation progenies from crosses involving the potential parents [11]. Complex alleles of economic importance require special methods for incorporation into elite breeding populations and breeders should use design(s) that ensure fair representation of the parents in pedigrees as quick as possible. The experimental designs are analyzed to estimate experimental error (multi locations and replicated trials) and obtain unbiased results which can be translated into covariance of relatives, depending on the mating design utilized. Finally, genetic parameters are estimated and used to make inferences about the populations. Although various mating schemes have been introduced, very few of them have been maximized in crop improvement. This is because majority of breeders and geneticists are disadvantaged by inadequate knowledge about the specificity of value each scheme could offer to crop improvement. The objective of this review was to underscore the different forms of mating designs and to shed some light on their implications in plant breeding and genetic studies. The review may provide easy and quick insight of the different forms of mating designs and some light on statistical components involved for successful plant breeding.

## II. Biparental Mating (Full-Sib Families)

This is one of the simplest mating designs used for estimation of genetic variance in a reference population as was termed by Mather in 1949. The mating design provides opportunity for creating variability with minimum effort and cost (e.g., cross-pollinated species) and also provides information needed to determine whether the variation within a population is significant for a long term selection program [5]. However, the design cannot give information on the type of genetic variation. Bi-parental mating design involves pairs of individuals chosen randomly from a random mating population then mated (Figure 1). Normally, individual pairs of plants can be crossed reciprocally to produce progenies which can be bulked for evaluation across environments. Many crosses are required to allow accurate measurements and adequate interpretations relative to the reference population. If *n* parents are used the total number of crosses = *n*/2 [3], [5], [12].

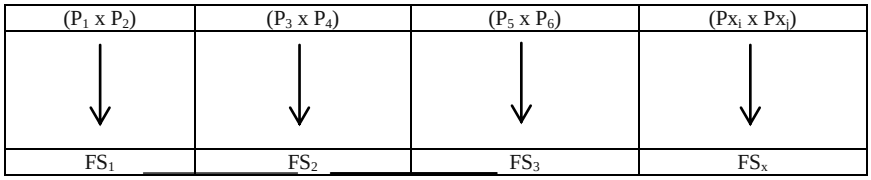


**Figure 1. Schematic presentation of biparental progeny development**

Analysis of variance of *among* and *within* bi-parental crosses is shown below (Table 1). *F*-test of differences among crosses can be made to determine if they are greater than within-cross variations. Alternatively, chi-square test is used for testing the variation among crosses [5]. Intraclass correlation ($r_I$) between *among* and *within* crosses can be calculated from the analysis of variance as follow:

$$r_I = \sigma^2_c / (\sigma^2_c + \sigma^2_w) \quad (1)$$

where $\sigma^2_c$ = variance among crosses and $\sigma^2_w$ = variance within-group.

**Table 1. Analysis of variance of *among* and *within* bi-parental crosses tested in replications**

| Source of variation | Df | Mean Squares | Expected Mean Squares | |
|---|---|---|---|---|
| | | | Components of variance | Covariance of relatives |
| Replication | *r -1* | | | |
| Among crosses | *(n/2) - 1* | *M3* | $\sigma^2_w + k\sigma^2_P + rk\sigma^2_c$ | $\sigma^2_w + k\sigma^2_P + rkCovFS$ |
| Error | *(r-1)[(n/2)-1]* | *M2* | $\sigma^2_w + k\sigma^2_P$ | $\sigma^2_w + k\sigma^2_P$ |
| Total | *r(n/2)-1* | | | |
| Within crosses | *r(n/2)(k-1)* | *M1* | $\sigma^2_w$ | $\sigma^2_w + (\sigma^2_G - CovFS)$ |

*r, n, k* refer to number of replications, parents and plants.

If the variation among crosses is not significantly different from zero ($F = 0$) then the *among-group* variance is equal to the covariance of individuals within the groups (CovFS) and the covariance among crosses is given as:

$$\sigma^2_c = CovFS = {}^1/_2\,\sigma^2_A + {}^1/_4\sigma^2_D = {}^1/_2\,\sigma^2_A + {}^1/_4\sigma^2_D + \sigma^2_P \quad (2)$$

where $\sigma^2_P = (M_2 - M_1)/k$; then variance component within-crosses can be obtained as:

$$\sigma^2_w = [\sigma^2_G - CovFS] + \sigma^2_{we} = {}^1/_2\,\sigma^2_A + {}^3/_4\sigma^2_D + \sigma^2_{we} \quad (3)$$

where $\sigma^2_{we}$ is the environmental source of variation within crosses, and if $\sigma^2_D = 0$, then $\sigma^2_c = ({}^1/_2)\sigma^2_A$, $\sigma^2_A = 2\sigma^2_c$ and $\sigma^2_{we} = (\sigma^2_w + \sigma^2_c)$ respectively. Bi-parental mating design does not detect what kind of genetic variation exists and the ANOVA does not provide estimates for the *within-crosses* component of environmental source of variation ($\sigma^2_{we}$). Therefore, to estimate heritability ($h^2$) in absence of dominant effect ($D$=0), the population variance can be approximated as follow [5]:

Broad sense heritability based on FS family means ($H^2$) $= \sigma^2_c / (\sigma^2_c + \sigma^2_P/r + \sigma^2_{we}/rk)$ (4)

Narrow sense heritability based on FS family means ($h^2$) $= {}^1/_2\sigma^2_A / (\sigma^2_c + \sigma^2_P/r + \sigma^2_w/rk)$ (5)

where *r, k* are the number of replications and number of plants respectively. Standard error (SE) of broad sense heritability is obtained as follow:

$$SE(H^2) = 2SE(\sigma^2_c)(2\,\sigma^2_c + \sigma^2_P + \sigma^2_{we}) \quad (6)$$

As mentioned earlier, bi-parental is one of the simplest mating designs but it generates progenies with limited informationon on the relative importance of additive genetic variance which can be used to decide if indeed sufficient genetic variability exists [5].

## III. Triple testcross (TTC)

Triple testcross design was developed by Kearsey and Jinks (1968) as an extension of Comstock and Robinson's (1952) NC Design III [13], [14]. The design is able to detect epistatic effects (additive × additive, additive × dominance, dominance × dominance) for quantitative traits, and also provides estimates of additive and dominance genetic variances in the absence of epistasis [5], [15]. In TTC, a random sample of male individuals from the $F_2$ generation obtained by crossing two inbred lines P1 and P2 are backcrossed to three testers: $P_1$, $P_2$ and $F_1$. This will generate 3 families where $P_1 \times F_2 = L_{1i}$, $P_2 \times F_2 = L_{2i}$, and $F_1 \times F_2 = L_{3i}$ (Figure 2). Each family is tested in replicated trials and individual family means obtained. The means are used to calculate the epistatic deviation from the means of the parental lines [13], [16], [17].

The design is effective for predicting the properties of recombinant inbred lines used in the triple test cross [18], [19]. Understanding traits and their genetic correlations can aid efficient selection through recombination of favorable alleles and will improve genetic gains. Triple testcross has been intensively used in the area of genetic components and correlation studies in various crops [16]. Statistical model for detection of epistasis is as described by Kearsey and Jinks (1968) and is given by:

$$Y_{ijk} = u + g_{ij} + r_k + \mathbf{e_{ijk}} \quad (7)$$

where $Y_{ijk}$ = phenotypic value of cross between tester *i* and line *j* in *k* replication, *u* = overall mean of all single and three-way crosses, genotypic value of cross between tester *i* and line *j*, $r_k$ = effect of $k^{th}$ replication, and $e_{ijk}$ = environmental error. The theory underlying TTC is that $F_1$ progenies produce recombinant gametes, whose average associated gene expression will deviate from that of the mean of the parental line gametes if epistasis interactions are significant. The epistasis deviation can be detected as below [18], [20]:

$$L_{1i} + L_{2i} - 2L_{3i} = D \quad (8)$$

where $L_{1i}$ = mean of testcross between tester 1 and male $i^{th}$, $L_{2i}$ = mean of testcross between tester *2* and male $i^{th}$, $L_{3i}$ = mean of testcross between tester 3 and male $i^{th}$, and $D$ = epistatic deviation from the parental means. If epistasis is absent then the $D$ will equal zero, and in presence of epistasis $D$ will significantly differ from zero. The test for significant epistatic variance may also be used in one-way ANOVA to detect whether the *among* observed family values is greater than that expected from sampling error. Thus, triple testcross is capable of detecting epistasis involving the entire sample of the population for which the tester lines differ. However, in absence of epistasis, it is advisable to use NC Design III to estimate the degree of dominance [18], [19]. Reference is made to the work of Wolf (1965) for table of analysis of variance for TTC.

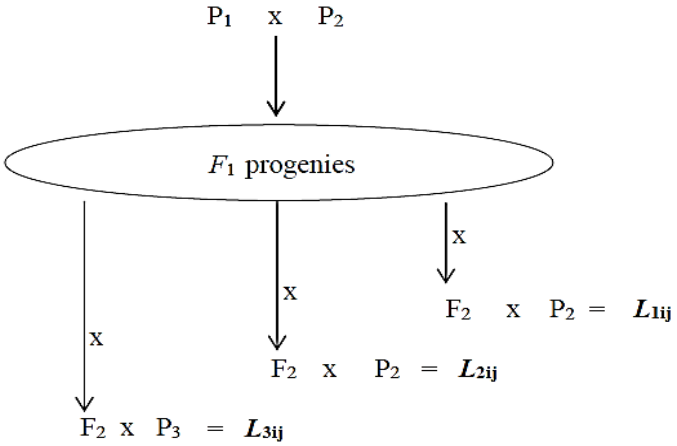


**Figure 2. Generation of test cross progenies involving three testers $P_1$, $P_2$ and $F_1$ (females), and a set of $F_2$ individuals (males)**

Analysis of variance for the TTC provides two *F*-tests for the presence of epistasis: the source of variation due to tester which can be partitioned into two orthogonal contrasts of which one is $L_{1i} + L_{2i} - 2L_{3i}$ where the contrast is designated as epistasis; and tests for the presence of additive by additive epistatic effects. These two sources of epistatic variations are also tested for their interaction with environments. The epistasis source of variation from the TTC analysis and epistatic deviation are both based on the comparison of testcross means across $F_2$ males. Therefore, positive and negative epistatic effects will cancel and only net epistasis will be detected. For epistasis by male, positive and negative effects will not cancel because variation in effects between males is tested [14], [21]. Genetic variance components of TTC include additive variance ($\sigma^2_A$), additive x environment variance ($\sigma^2_{AE)}$, dominance variance ($\sigma^2_D$) and dominance x environment variance ($\sigma^2_{DE}$), which can similarly be obtained according to [13]:

$$\sigma^2_M = \text{CovHS} = {}^1/_4\,\sigma^2_A \quad (9)$$

$$\sigma^2_{ME} = {}^1/_4\,\sigma^2_{AE} \quad (10)$$

$$\sigma^2_{MT} = \sigma^2_D \quad (11)$$

$$\sigma^2_{MTE} = \sigma^2_{DE}. \quad (12)$$

The genetic estimates of ($\sigma^2_A$) and ($\sigma^2_D$) obtained above can be used to calculate average level of dominance as: $d = (\sigma^2_{MT}/ 2\sigma^2_M)^{1/2} = (2\,\sigma^2_D / \sigma^2_A)^{1/2}$. If dominance is complete then the ratio $\sigma^2_M / \sigma^2_{MT}$ will be equal to unity. Similarly, genetic covariance between half-sib and $S_1$ progeny can be obtained as:

$$\sigma^2_{XY} = {}^1/_2\,\sigma^2_A = {}^1/_2\sigma^2_{AE}. \quad (13)$$

## IV. Pure line progenies

Pure lines are the basis of most breeding programs where homozygous lines such as DH (doubled haploid), RILs (recombinant inbred lines) and NILs (near isogenic lines) are used. The concept (Johanssons 1903) is based on production of progenies from crosses between two parents and advanced to later stage of inbreeding (e.g at $S_8$) through selfing or backcrossing, followed by selection of highly homozygous progenies (Figure 3). At this stage the reference population is assumed to compose of complete homozygous inbred lines containing additive and additive-by-additive types of epistatic variances [3], [22].

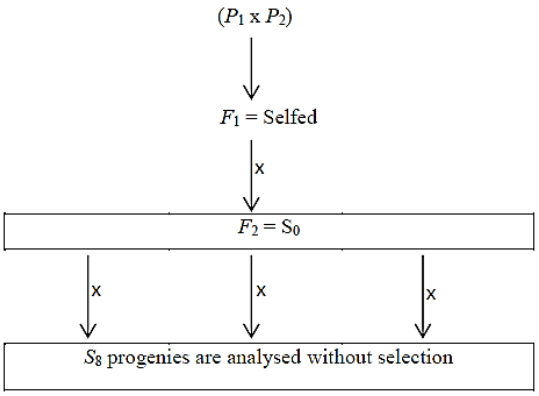


**Figure 3. Stages of pure line progeny development**

Since the lines are pure, they can be multiplied without changes in their genetic compositions and thus are the best materilas to be considered for biological studies aimed at estimation of genetic variances [23]. Frequency of alleles at heterozygous locus at $F_2$ is given $p$=$q$=0.5. However, the genetic coefficient for convariances of relatives $F \approx 1$ at the later inbreeding stage [5]. Similarly, variance component ($\sigma^2 g$) is equivalent to additive component ($\sigma^2_A$). Therefore, heterosis within pure line is not important because at the advanced inbreeding stage, dominance (difference in allele frequency between loci) is minimized or lost [24]. Seed of selected homozygous (pure) lines can be multiplied without alteration and evaluated in replicated experiments across locations (Table 2).

**Table 2. The analysis of variance for pure line progenies tested in replicated trials across locations**

| Source of variation | Df | Mean Squares | Expected Mean Squares |
|---|---|---|---|
| Environment | *e* | | |
| Replication/environment | *e(r-1)* | | |
| Progeny | *g-1* | $M_2$ | $\sigma^2 + r\sigma^2_{ge} + re\sigma^2_g$ |
| Progeny x environment | *(g-1)(e-1)* | $M_2$ | $\sigma^2 + r\sigma^2_{ge}$ |
| Pooled error | *(r - 1)(g - 1)* | $M_1$ | $\sigma^2$ |

Narrow sense heritability based on progenies mean is calculated as [5]:

$$h^2 = 2\sigma^2_A / (\sigma^2/re + r\sigma^2_{ge}/e + \sigma^2_g) \quad (14)$$

Similarly, the approximate standard error of the heritability is obtained as:

$$SE(h^2) = SE(\sigma^2_g) / (\sigma^2/re + r\sigma^2_{ge}/e + \sigma^2_g) \quad (15)$$

## V. Parent-offspring regression analysis

The resemblance between a parent and its offspring was employed by Robinson (1949) for estimation of genetic variance and heritability [1]. A set of male parents randomly chosen from a reference population ($S_0$) are mated to a set of females randomly chosen from another reference population ($S_0$). The reference population can be $S_0$ population obtained from open-pollinated crops or the $F_2$ population derived from a cross of two inbred lines [5]. The progenies produced are used to determine estimates of parent-offspring regressions by (1) regression of offspring on one parent (half-sib method), (2) regression of offspring on the mean of two parents (full-sib method), and (3) regression of selfed progeny on parents (selfing method). Measurements of traits of interests are made on individual plants from the reference population and on the offspring. This allows good determination of the degree of association between the traits measured in the parents and in their respective offspring [5]. Progenies from the crosses are evaluated in trials and the same traits are measured in the replicated progeny trials (Table 3).

**Table 3. Analysis of variance for parent-offspring based on fixed and random effect models**

| Source of variation | DF | Mean Squares | Expected Mean Squares | |
|---|---|---|---|---|
| | | | Model I | Model II |
| Replications | r-1 | | | |
| Genotypes | g-1 | $M_2$ | $\sigma^2 + rK^2_g$ | $\sigma^2 + r\sigma^2_g$ |
| Error | (r-1)(g-1) | $M_1$ | $\sigma^2$ | |

In the half-sib method $n$ progeny measurements ($Y$, the dependent variable) are regressed on a single $S_0$ parental plant measurements ($X$, the independent variable). The standard regression model is given by:

$$Yi = a + bX_i + e_i \quad (16)$$

where $Y_i$ is the mean measurement of the offspring, $X_i$ is the measurement of the parental $S_0$ plant, $b$ is the regression (slope) of $Y_i$ on $X_i$, and $e_i$ is the error associated with the $Y_i$. The regression ($b$) can be obtained from:

$$b = \sum xy / \sum x^2 = \sum(X_i - \bar{X})(Y_i - \bar{Y}) / \sum X_i - \bar{X})^2 = \sigma^2_{xy} / \sigma^2 x. \quad (17)$$

If $F = 0$ and we assume that there is no epistasis then:

$$b = (^1/_2)\sigma^2_A / \sigma^2_x = \sigma^2_A / 2\sigma^2_x \quad (18)$$

Therefore, eestimate of heritability on an individual plant basis of the traits can be obtained from parent-offspring regression as:

$$h^2 = 2b = \sigma^2_A/2\sigma^2_x \quad (19)$$

Standard error (SE) of the heritability estimate on an individual can be obtained as:

$$SE(h^2) = 2SE(b) = (\sigma^2 / \sum_i x_i^2)^{1/2} \quad (20)$$

When two parents are crossed to produce offspring (full-sib method) then regression of the offspring will be made on mean of the two parents as [5]:

$$b = (1/2)\,\sigma^2_A / [(1/2)\sigma^2_x] = \sigma^2_A / \sigma^2_x = h^2 \quad (21)$$

Thus, the covariance or mid parent-offspring regression ($b$) will be similar to heritability ($h^2$) and mid-parent value is given by:

$$\mu = (X_1 + X_2)/2 \quad (22)$$

where $\mu$ = mean of mid-parent, $X_1$ = mean of parent 1, and $X_2$ = mean of parent 2. If inbred generations are used to estimate heritability, adjustments are needed to account for the level of inbreeding and relatedness of the parents [1], [18]. The parents are considered fixed (model I) if the parents used are the whole genotypes in a reference population, and considered random (model II) when parents are a random set of genotypes sampled from a random mating (reference) population [4]. Analysis of variance can be performed for each model in replicated trials.

## VI. North Carolina designs

This mating design was developed by Comstock and Robinson (1948) and has since been one of the most useful mating designs for estimation of genetic variance and crop selection. The mating design produces large number of progenies and is also useful for self-pollinated crops with multiple flowers. North Carolina design has three different mating schemes and these include NC Design I, NC Design II and NC Design III respectively [5], [25].

### 1. North Carolina (NC Design I)

NC Design I is adequate only for estimating genetic variance of a reference population which is assumed to be a random mating population and is in linkage equilibrium. The $S_0$ plants are chosen from the reference population, then plants are divided into two groups of males (*m*) and females (*f*). Each male is crossed to a different set of females (independent sample) to produce progenies for evaluation (Figure 4). The genetic structure of the progenies will include full-sibs that have both parents in common and half-sibs that have a male parent in common. As a result, expected mean squares are expressed as covariance of relatives.

| | | |
|---|---|---|
| Male1 x Female1 | Male2 x Female6 | Male3 x Female11 |
| Male1 x Female2 | Male2 x Female7 | Male3 x Female12 |
| Male1 x Female3 | Male2 x Female8 | Male3 x Female13 |
| Male1 x Female4 | Male2 x Female9 | Male3 x Female14 |
| Male1 x Female5 | Male2 x Female10 | Male3 x Female15 |

**Figure 4. Mating procedures in NC Design I**

The mathematical equation for estimation of mean performance of offspring generated by NC Design I is given by:

$$Y_{ijk} = u + m_i + f_{ij} + r_k + e_{ijk} \quad (23)$$

where $\mu$ is the mean, $m_i$ is the effect of the *i*th male, $f_{ij}$ is the effect of the *j*th female mated to the *i*th male, $r_k$ is the replication effect, and $e_{ijk}$ is the experimental error. As shown above, the mating design is nested and progenies have different genetic structures. Therefore, expected mean squares are obtained and can be expressed as covariance of relatives (Table 4).

**Table 4. Analysis of variance for NC Design 1 replicated in one environment**

| Source of variation | Df | Mean Squares | Expected Mean Squares | |
|---|---|---|---|---|
| | | | Variance component | Covariance of relatives |
| Replications | *r*-1 | | | |
| Males | *m*-1 | *M4* | $\sigma^2 + r\sigma^2_{f/m} + rf\sigma^2_m$ | $\sigma^2 + r$ [CovFS - CovHS] + $rf$ CovHS |
| Females(males) | *m*(*f*-1) | *M3* | $\sigma^2 + r\sigma^2_{f/m}$ | $\sigma^2 + r$[CovFS - CovHS] |
| Error | (*r*-1)(*mf*-1) | *M2* | $\sigma^2$ | $\sigma^2$ |
| Within | *rmf* (*k*-1) | *M1* | | |
| Total | *rmf*-1 | | | |

where *r*, *m*, *f*, and *k* refer to number of replications, males, females within males, and plants within plots; and:

$$M_1 = \sigma^2_w = (\sigma^2_{we} + \sigma^2_{wg}) = [\sigma^2_{we} + (\sigma^2_G - CovFS)] \quad (24)$$

$$M_2 = \sigma^2 = [\sigma^2_{we} + (\sigma^2_G - CovFS)]/k + \sigma^2_P \quad (25)$$

where $\sigma^2_P$ is the experimental plot error. The same concept observed in biparental progenies applies to NC Design I in which the differences among males are equal to the similarities between half-sib families within males ($\sigma^2_m$ = CovHS). This is because the higher the association within groups, the greater the differences among groups [5]. For NC Design I, each male is matted to a different group of females and therefore only one half-sib relationship exists, and the variance component for female-within-males is: CovFS – CovHS = (1/4) $\sigma^2_A$ + (1/4) $\sigma^2_D$ where $F = 0$.

Direct *F*-tests can be made for males and *females-within-males* mean squares, and males and *females-within-males* components of variances can be estimated from the appropriate mean squares. The male component is genetically the same as GCA of the diallel, and among males and among females of NC Design II. The *among-females-within-males* component, however, has a different expectation compared to other designs. To reduce replication size and attempt to increase the precision of experiment, progenies are grouped into sets

by males. For example, 40 full-sib progenies can be obtained from crosses between 10 males and 4 females respectively. The experiment can be arranged in the field in (1) replications within sets or (2) sets (as sub-blocks) within replications [5]. The analysis of variance for NC Design I experiment repeated over environments is shown in Table 5 from where components of variance can be translated into covariances of relatives. *F*-tests and estimation of components of variance can be made directly for all sources of variation except males within sets. NC Design I is more suitable for extensive sampling of $S_0$ plants in a population compared to other mating designs. The nested structure of the progenies makes this design amenable by grouping them into sets, and the pooling across sets is straightforward. Estimates of additive genetic ($V_A$) variance and total genetic variance ($V_G$), assuming no epistasis, are obtained directly from the mean squares of the analysis of variance. Similarly, the design provides GCA for males which allow early selection of superior males. Heritability estimates based on the mean of *r* plots can be determined from components of variance as:

$$h^2 = 4\sigma^2_m / (\sigma^2/r + 4\sigma^2_{f/m}) \quad (26)$$

where f/*m* = female-within-males sets; and

$$SE(h^2) = 4SE(\sigma^2_m) / (\sigma^2_w + \sigma^2_P + 4\sigma^2_{f/m} + \sigma^2_m) \quad (27)$$

where $SE(h^2)$ = standard error of heritability.

The estimate of heritability based on half-sib progeny means can be obtained following the procedure used by Nyquist and Baker (1991): $h^2 = \sigma^2_m / (\sigma^2/rf + \sigma^2_{f/m}/f + \sigma^2_m)$. If parents used are homozygous or partially inbred (i.e $F$=1), then only narrow sense heritability is calculated as a result of changes in the coefficient used for calculating additive variance. Estimates of additive genetic variance ($\sigma^2_A$) and total genetic variance ($\sigma^2_G$), assuming no epistasis, are obtained from the mean squares of the analysis of variance. Estimate of dominance ($\sigma^2_D$) is obtained as the difference between the *females-within-males* and the male components of variance. NC Design I analysis provides information on GCA for males thus, male plants are self-pollinated and early testing conducted to select males with superior GCA to be used as $S_0$ progenies. Average dominance of genes is determined as:

$$\sigma^2_m = CovHS = (^1/_4)\sigma^2_A \text{ where } \sigma^2_A = (^1/_2)\sum d^2_i \quad (28)$$

$$\sigma^2_{f/m} = CovFS - CovHS = (^1/_4)\sigma^2_A + (^1/_4)\sigma^2_D \text{ where } \sigma^2_D = (^1/_4)\sum d^2_i \quad (29)$$

Thus, the average gene dominance ($\bar{d}$) is: $\bar{d} = [2(\sigma^2_{f/m} - \sigma^2_m) / \sigma^2_m]^{1/2} = [(2\sigma^2_D) / \sigma^2_A]^{1/2}$

Heritability based on mean of *r* plots can be obtained from the components of variance as:

$$h^2 = 4\sigma^2_m / (\sigma^2/r + 4\sigma^2_{f/m} \quad (30)$$

Variance components for non-inbred parents with no epistasis are [26]:

$$\text{Male parent} = \sigma^2_m = (¼)/\sigma^2_A, \quad (31)$$

$$\text{Female parent} = \sigma^2_{f/m} = [(¼)/\sigma^2_A + (¼)/\sigma^2_D] \quad (32)$$

**2. North Carolina (NC Design II)**

Is one of the useful mating design also known as *factorial design*, in which parents are divided into one group (males) and the other group (females). Each member of a group has equal chance to cross with a member from the other group [1]. For example, in a two-factor design if 1, 2 and 3 are male parents and 4 and 5 are female parents then factorial design will be: (1x4), (1x5), (2x4), (2x5), (3x4), and (3x5) respectively. Depending on the capacity and availability of resources, the breeder can use more than 2 factorial schemes where crosses among three or more groups of parents are involved (Table 5). Although the assumptions for NC Design II are similar as those for NC Design I, NC Design II has greater precision, it is more applicable to self-pollinated crops, and has a direct estimate of the level of dominance [5].

**Table 5. Arrangement of NC Design II for possible crosses**

| | Male parents | | | |
|---|---|---|---|---|
| Female parents | 1 | 2 | 3 | 4 |
| 5 | 5x1 | 5x2 | 5x3 | 5x4 |
| 6 | 6x1 | 6x2 | 6x3 | 6x4 |
| 7 | 7x1 | 7x2 | 7x3 | 7x4 |
| 8 | 8x1 | 8x2 | 8x3 | 8x4 |

Therefore, NC Design II with four parents in each group produces 16 crosses. The number of crosses increases as the number of parents per group increases. If the number of experimental units is fixed, the number of parents used can be doubled in the experiment. This is an advantage of NC Design II, and it allows for estimation of genetic parameters of a reference population. NC Design II is considered as a cross-classification design for analysis where sources of variation are partitioned into males, females, and the interaction of males with females. In this case, a factorial design is used to obtain expected mean squares in the ANOVA (Table 6). The linear model for the phenotype of the NC Design II offspring can be expressed as:

$$Y_{ijk} = \mu + s_i + d_j + i_{ij} + e_{ijk} \quad (33)$$

where $\mu$ *is the* population mean, $s_i$ and $d_j$ are the additive effects (breeding values) of the $i^{th}$ site and $j^{th}$ plot, $i_{ij}$ is the non-additive effects due to the combination of genes from parents *i* and *j*, and $e_{ijk}$ is the deviation from the observed mean of $k^{th}$ offspring of the parents *i* and *j*.

**Table 6. Analysis of variance where males are crossed with females in NC Design II and progenies evaluated in replicated trials within environment**

| Source of variation | Df | Mean Squares | Expected Mean Squares | |
|---|---|---|---|---|
| | | | Variance component | Covariance of relatives |
| Replications | *r*-1 | | | |
| Males (M) | *m*-1 | *M5* | $\sigma^2 + r\sigma^2_{fm} + rf\sigma^2_m$ | $\sigma^2 + r$ [CovFS – $CovHS_f$ - $CovHS_m$] + *rf* $CovHS_m$ |
| Females (F) | *m*(*f*-1) | *M4* | $\sigma^2 + r\sigma^2_{fm} + rm\sigma^2_f$ | $\sigma^2 + r$[CovFS – CovHSf - $CovHS_m$] + *rm*$CovHS_f$ |
| M x F | *(m-1)(f-1)* | *M3* | $\sigma^2 + r\sigma^2_{fm}$ | $\sigma^2 + r$[CovFS – CovHSf - $CovHS_m$] |
| Error | (*r*-1)(*mf*-1) | *M2* | $\sigma^2$ | $\sigma^2$ |
| Within | *rmf* (*k*-1) | *M1* | | |
| Total | *rmf*-1 | | | |

*M*= within-plot mean square and it includes within-plot genetic variance and within-plot error variance.

NC Design II has the following advantages over diallel designs if one is interested in estimating components of variance of a reference population: (1) more parents can be included for a given level of resources, (2) two independent estimates of additive variance are available, (3) an estimate of dominance variance is determined directly from the mean squares, and (4) a greater number of parents can be included by subdividing parents into sets. The grouping of parents into sets permits pooling the sums of squares over sets. Emphasis is based on estimates of components of variance rather than comparisons of means. The analysis of variance for parents grouped in sets includes a source due to sets with the expectations of the mean squares of males, females, and male × female remain the same for the components of variance and the covariance of relatives. The analysis is conducted on each set, and sums of squares and degrees of freedom are pooled over sets.

If epistatic effect is negligible and the reference population is in linkage equilibrium ($p = q = 0.5$), the components of genetic variance are estimated and the average dominance ($\bar{d}$) of genes conditioning the trait can be obtained from below [27], [28]:

$$\bar{d} = (2\sigma^2_{mf} / \sigma^2_m)^{1/2} = (2\sigma^2_{mf} / \sigma^2_f)^{1/2}. \quad (34)$$

Population size is important, large random mating population has minimal linkage bias while an $F_2$ population created from two inbred lines shows linkage disequilibrium. Repulsion phase linkages cause an upward or positive bias in the estimate of dominance variance similar to coupling phase linkages. However, repulsion phase linkages can also cause a downward or negative bias in estimates of additive variance. The levels of dominance of genes conditioning the variability can be determined: 0 is no dominance, 0 to 1 is partial dominance, 1 is complete dominance, and a value that exceeds 1 is termed overdominance. Heritability estimates can be calculated from the estimates of male and female components of variance. Assuming non-inbred parents and no epistasis, an estimate of $h^2$ based on the mean of *r* plots for one environment and standard error are:

$$h^2 = (4\sigma^2_m) / (\sigma^2/r + 4\sigma^2_{mf} + 4\sigma^2_m), \quad (35)$$

$$SE(h^2) = (4SE\sigma^2_m) / (\sigma^2/r + 4\sigma^2_{mf} + 4\sigma^2_m) \quad (36)$$

Similarly, $h^2$ estimate and standard error based on individual plant are calculated as:

$$h^2 = (4\sigma^2_m) / (\sigma^2/w + \sigma^2_p + \sigma^2_{mf} + \sigma^2_f + \sigma^2_m) \quad (37)$$

$$SE(h^2) = (4SE\sigma^2_m) / (\sigma^2_w + \sigma^2_p + \sigma^2_{mf} + \sigma^2_f + \sigma^2_m) \quad (38)$$

A reliable estimate of heritability can be obtained by pooling male and female sums of squares and more meaningful and reliable estimates of heritability are those based on half-sib and full-sib family means. Estimate of heritability for half-sib family means for the male source of variation is: $h^2 = (\sigma^2_m)/(\sigma^2/ref + \sigma^2_{efm}/e + \sigma^2_{fm}/f + \sigma^2_m)$. Similarly, estimate of heritability can be calculated from the female source of variation with *m* as the divisor in the denominator components of variance. Male x female sources of variation are pooled to estimate heritability on full-sib family means as:

$$h^2 = (\sigma^2_{fm})/(\sigma^2/re + \sigma^2_{efm}/r + \sigma^2_{fm}) \quad (39)$$

Estimates based on half-sib or full-sib family means are essential for genetic selection [5][3].

### 3. North Carolina (NC Design III)

NC Design III is one of the mating designs developed to estimate the average level of dominance of genes affecting traits in pedigree breeding. It is also used to detect the effects of linkages on the estimates of additive and dominance variance for $F_2$ population [29]. As explained earlier, estimates of average level of dominance depends on linkage equilibrium of the populations. If linkage is present, both additive and dominance variances are positively (upward) biased. However, linkage bias for additive variance depends on the phase of linkage. For repulsion phase linkage effect on additive variance is underestimated whereas for coupling

phase linkages are overestimated [5]. A reference population ($F_2$) is used to develop progenies by backcrossing randomly chosen males ($S_0$) from the $F_2$ population to each of the parents (females) of the $F_2$ (Figure 5).

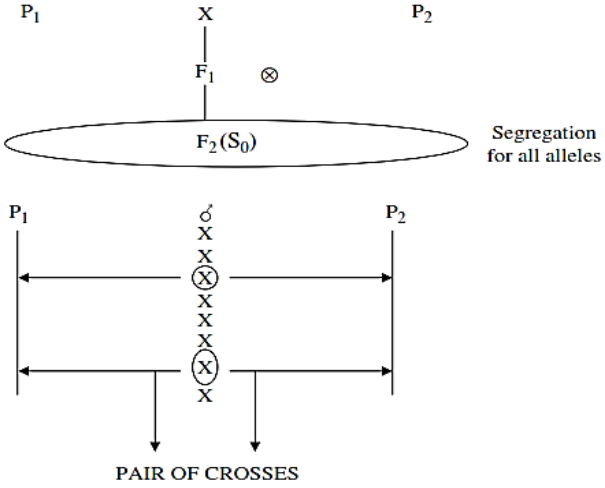


**Figure 5. Diagram for generation of progenies using NC Design III**

The focus on expected mean squares is based on the component of variance among males and the one for the interaction of males and inbred parents [29], [30]. The design provides exact *F*-tests of two hypotheses concerning the relative importance of dominance effects: (1) that dominance is not present (this can be tested by comparison of the $M_1$ and $M_2$ mean squares (Table 7); and (2) that dominance is complete. Sufficient sampling of the $F_2$ population is required so as to obtain valid estimates of components of variance to determine average level of dominance. However, to make proper sampling the number of progenies produced may get huge. Therefore, local control of error can be done by grouping the pairs of progenies into sets. Analysis is done for each set and the sums of squares and degrees of freedom across sets are pooled to estimates the variance components. These components are important for estimating narrow-sense heritability in the $F_2$ populations. Estimate of narrow-sense heritability based on the mean of *r* plots in one environment can be determined as follows:

$$h^2 = (4\sigma^2_m) / (\sigma^2/r + \sigma^2_{mp} + 4\sigma^2_m) \quad (40)$$

**Table 7. Analysis of variance for NC Design III progenies**

| Source of variation | Df | Mean Squares | Expected Mean Squares (Model II) |
|---|---|---|---|
| Replications | *r-1* | | |
| Parents (p) | *1* | *M4* | $\sigma^2 + r\sigma^2_{mp} + rmK^2_p$ |
| Males (m) | *m-1* | *M3* | $\sigma^2 + 2r\sigma^2_m$ |
| m x p | *m-1* | *M2* | $\sigma^2 + r\sigma^2_m$ |
| Error | *(m-1)(2m-1)* | *M1* | $\sigma^2$ |
| Total | *2mr-1* | | |

*r* and *m* refer to number of replications and male parents respectively.

Combined analyses across environments provide estimates of the interaction of the additive and dominance effects with environments. Direct *F*-tests can be obtained for each mean square and components of variance can be calculated directly from the mean squares with their appropriate standard errors (Table 10). In addition to providing a measure of the dominance of genes for the expression of a trait, NC Design III also is an excellent mating design for estimation of additive and dominance variances for $F_2$ populations (assuming both linkage and epistasis are absent) [29]. The estimate of narrow-sense heritability based on the mean of progenies pooled over sets and across environments is given as:

$$h^2 = (4\sigma^2_m) / (\sigma^2/re + \sigma^2_{mpe}/e + \sigma^2_{mp} + 4\sigma^2_{me})/e + 4\sigma^2_m) \quad (41)$$

Normally, individual $F_2$ plants are males crossed to both inbred (female) parents, and the differences among male means are covariance of half-sib families. The heritability estimates based on half-sib family means are:

$$\text{Heritability within environment} = h^2 = (\sigma^2_m) / (\sigma^2/r + \sigma^2_m) \quad (42)$$

$$\text{Heritability across environments} = h^2 = (\sigma^2_m) / (\sigma^2/2re + \sigma^2_{mpe}/2e + \sigma^2_{me}/e + \sigma^2_m) \quad (43)$$

NC Design III is widely used in testing for presence of dominance effects, though linkage biases may affect the estimation of additive and dominance variance for the $F_2$ populations where effects of linkage are expected to be maximum [31], [32]. However, linkage equilibrium can be reached by allowing $F_2$ populations to randomly mate without male and female selection; to develop first random mating population (e.g synthetic 1). The synthetic 1 is then allowed to advance to successive synthetic generations (e.g synthetic 8) by random

mating where linkage disequilibrium is minimized. The attainment of linkage equilibrium state depends on the rate of recombination, tightly linked genes may require many generations of random mating. The synthetic and the original $F_2$ populations are tested each in replicated trials so as to detect the effects of overdominance and bias by linkage disequilibrium among loci in the populations [5]. The restriction in this design is that there may be a situation where the gene frequencies are equal which is limiting. However, where the technique is applicable, major advantage is that it provides estimates for additive and dominance components of variance with equal precision compared to other designs [29], [32]. In addition, the ratio of the variance among differences to the additive variance provides weighted estimte of the squatted degree of dominance, with expectation identical to that of Design II. However, violation of the above assumptions results in inflated estimates of the degree of dominance [18].

## VII. Dialel mating designs

Diallel mating design first presented by Schmidt (1919) became an important tool used to produce crosses for evaluation of genetic variances [4], [33], [34]. Crosses are generated from parents ranging from inbred lines to broad genetic base varieties where progenies are developed from all possible combinations of parents involved. Analysis of diallel progenies allows inference about heterosis (Gardner & Eberhart, 1966), estimation of general and specific combining ability (Griffing, 1956) and study of genetic control of traits [33], [35], [36]. Two models designated as model I and model II by Eisenhart (1947) are available and have been equally used in diallel mating with each having its own assumptions [37], [38]. Model I is a fixed model based on the assumption that the parents used have undergone selection for a period of time and have become a complete population. The model measures only GCA and SCA effects because the parents are fixed. Model II is where parents are random, taken from a random mating population. It is assumed that the effects in the model *u* are randomly distributed with mean zero and variance $\sigma^2_\theta$ where $\theta = b, g, s, r$. As a result, model I is used for selection of parents based on the GCA and SCA results. Model II is appropriate for estimating GCA and SCA variances, and to compute the standard errors for differences between effects, considering epistatic is negligible or absent. It is therefore, assumed that the error terms $e_{ijkl}$ are normally distributed with mean *zero* and variance $\sigma^2$. Thus, expected mean squares are expressed in terms of genetic relationships of relatives, and translated from the covariances of relatives to the genetic components of variance [4], [5].

Four main methods of diallel mating design (Table 8) have been developed by Griffing (1956) and they include: (i) Full diallel where parents, one set of $F_1$ and reciprocal $F_1$ are included (number of crosses = $p^2$ where $p$ is the number of parent lines); (ii ) Half diallel where only parents and one set of $F_1$ are included (number of crosses = $^1/_2p(p+1)$); (iii) Full diallel where only one set of $F_1$ and reciprocals are included (number of crosses = p(p-1)); and (iv) Half diallel where only one set of $F_1$ are included and the number of crosses = $^1/_2p(p-1)$. Choice among the four methods depends on inbreeding depression of the parents. For pure inbred lines use of parents in the crosses will not be necessary. However, if the parents are synthetics or a set of non-inbred (species with less inbreeding depression) it is important to include the parents so that comparison between performances of heterosis and mean is made [4], [28], [39].

**Table 8. Schematic diagrams of 4 methods of diallel mating scheme showing crosses between 5 parents**

*Method I* - Full diallel crosses including parents and reciprocals: number of crosses = $p^2 = 25$

| | Male | | | | |
|---|---|---|---|---|---|
| Female | 1 | 2 | 3 | 4 | 5 |
| 1 | 1x1 | 1x2 | 1x3 | 1x4 | 1x5 |
| 2 | 2x1 | 2x2 | 2x3 | 2x4 | 2x5 |
| 3 | 3x1 | 3x2 | 3x3 | 3x4 | 3x5 |
| 4 | 4x1 | 4x2 | 4x3 | 4x4 | 4x5 |
| 5 | 5x1 | 5x2 | 5x3 | 5x4 | 5x5 |

*Method II* – Half diallel crosses including parents and no reciprocals: number of crosses = p(p+1)/2 = 15

| | Male | | | | |
|---|---|---|---|---|---|
| Female | 1 | 2 | 3 | 4 | 5 |
| 1 | 1x1 | - | - | - | - |
| 2 | 2x1 | 2x2 | - | - | - |
| 3 | 3x1 | 3x2 | 3x3 | - | - |
| 4 | 4x1 | 4X2 | 4x3 | 4x4 | - |
| 5 | 5x1 | 5x2 | 5x3 | 5x4 | 5x5 |

*Method III* - Full diallel crosses with no parents: number of crosses = $p(p-1) = 20$

| | Male | | | | |
|---|---|---|---|---|---|
| Female | 1 | 2 | 3 | 4 | 5 |
| 1 | - | 1x2 | 1x3 | 1x4 | 1x5 |
| 2 | 2x1 | - | 2x3 | 2x4 | 2x5 |
| 3 | 3x1 | 3x2 | - | 3x4 | 3x5 |
| 4 | 4x1 | 4X2 | 4x3 | - | 4x5 |
| 5 | 5x1 | 5x2 | 5x3 | 5x4 | - |

*Method IV*– Half diallel with no parents and no reciprocals: number of crosses = $p(p-1)/2 = 10$

| | Male | | | | |
|---|---|---|---|---|---|
| Female | 1 | 2 | 3 | 4 | 5 |
| 1 | - | - | - | - | - |
| 2 | 2x1 | - | - | - | - |
| 3 | 3x1 | 3x2 | - | - | - |
| 4 | 4x1 | 4X2 | 4x3 | - | - |
| 5 | 5x1 | 5x2 | 5x3 | 5x4 | - |

**1. Method I: Full diallel crosses including parents and reciprocals**

This is a full diallel mating design where parents, one set of $F_1$ and reciprocal $F_1$ are included (number of crosses = $p^2$ where $p$ is the number of parent lines) [40]. The fixed effect assumption for model I for the analysis of combining ability is given by:

$$Y_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + 1/bc\sum\sum e_{ijkl} \quad (44)$$

where $u$ = population mean, $g_i$ and $g_j$ = GCA effects of $i^{th}$ and $j^{th}$ parents, $s_{ij}$ = SCA effect of the cross between $i^{th}$ and $j^{th}$ parents ($s_{ij} = s_{ji}$), $r_{ij}$ = reciprocal effect involving reciprocal crosses between $i^{th}$ and $j^{th}$ parents ($r_{ij} = -r_{ji}$), $b$ = number of blocks, $c$ = number of crosses, and $e_{ijkl}$ = environmental effect associated with the $ijkl^{th}$ individual observation. The random effect assumption for model II for the analysis of combining ability is given by:

$$Y_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + 1/bc\sum b_k + 1/bc\sum bv_{ijk} + 1/bc\sum\sum e_{ijkl} \quad (45)$$

where $v$ = number of parents. Analysis of variance for the combining ability and expected mean squares based on model I and model II is shown below (Table 9).

**Table 9. Anaysis of vriance for method I showing expectations of mean squares for model 1 & II**

| Source of variation | Df | Mean Squares | Expected Mean Squarres | |
|---|---|---|---|---|
| | | | Model I | Modeel II |
| GCA | $p$-1 | $M_g$ | $\sigma^2 + 2p\,[1/(p\text{-}1)]\,\sum g_i^2$ | $\sigma^2 + [2(p\text{-}1)/p]\,\sigma^2_s + 2p\,\sigma^2_g$ |
| SCA | $p(p\text{-}1)/2$ | $M_s$ | $\sigma^2 + [2/p(p\text{-}1)]\,\sum\sum s_{ij}^2$ | $\sigma^2 + [2(p^2 - p + 1)/p^2]\,\sigma^2_s$ |
| Reciprocal effects | $p(p\text{-}1)/2$ | $M_r$ | $\sigma^2 + 2[2/p(p\text{-}1)]\,\sum\sum r_{ij}^2$ | $\sigma^2 + 2\sigma^2_r$ |
| Error | $m$ | $M_e$ | $\sigma^2$ | $\sigma^2$ |

From the above analysis, test for the overall differences among the classes of effects can be done. Also, variances of effects and of differences between effects can be estimated.

**2. Method II: Half diallel crosses including parents and no reciprocals**

This is a half diallel cross where only the parents and one set of $F_1$ are included in the analysis, with total number of crosses = $p(p+1)/2$ [41], [42]. Estimates of variance are interpreted relative to some reference population from which the sample genotypes were obtained. Unlike model I where estimation of heritability and genetic gains are not possible when limited sample size is used, model II provided enough genetic information especially for GCA and SCA effects [5]. Normally if crosses mean of squares is detected to be significant then an orthogonal subdivision of sum of squares for the crosses can be made which allows partitioning of GCA and SCA effects. Analysis of variance for Method II is shown below (Table 10).

**Table 10. Analysis of variance for Method II showing expected mean squares for model I and II**

| Source of variation | Df | Mean Squares | Expected Mean Squares | |
|---|---|---|---|---|
| | | | Model I | Modeel II |
| GCA | $p$-1 | $M_g$ | $\sigma^2 + 2p\,[1/(p\text{-}1)]\,\sum g_i^2$ | $\sigma^2 + \sigma^2_s + (p+2)\sigma^2_g$ |
| SCA | $p(p\text{-}1)/2$ | $M_s$ | $\sigma^2 + [2/p(p\text{-}1)]\,\sum\sum s_{ij}^2$ | $\sigma^2 + \sigma^2_s$ |
| Error | $m$ | $M_e$ | $\sigma^2$ | $\sigma^2$ |

The $F$-test for genotype variance is obtained by $M_g/M_s$ and interaction variance is tested by $M_s/M_e$ respectively, where $M_g$, $M_s$, $M_e$ are mean squares for genotype, interaction between genotypes, and environment. Similarly, fixed effect $F$-test is conducted using interactions mean squares whereas for random effects error variance is used. Model for fixed effects for Method II is given by:

$$Y_{ij} = u + g_i + g_j + s_{ij} + {}^1/bc\sum\sum e_{ijkl} \quad (46)$$

where $u$ = population mean, $g_i$ and $g_j$ = GCA effects of $i^{th}$ and $j^{th}$ parents, $s_{ij}$ = SCA effect of the cross between $i^{th}$ and $j^{th}$ parents ($s_{ij} = s_{ji}$), $b$ = number of blocks, $c$ = number of crosses, and $e_{ijkl}$ = environmental effect associated with the $ijkl^{th}$ individual observation. The mathematical model for combining ability analysis for model II is written as:

$$Y_{ij} = u + g_i + g_j + s_{ij} + 1/b_k\sum b_k + {}^1/b_k\sum(bv)_{ijk} + 1/bc\sum\sum e_{ijkl} \quad (47)$$

The variance components for GCA and SCA can be estimated as: $\sigma^2_g = [1/(p+2)]\,(M_g - M_s)$, $\sigma^2_s = M_s - M_e$

**3. Method III: Full diallel crosses with no parents**

In this method one set of $F_{1s}$ and the reciprocal progenies are included and without parents [43]. The total number of crosses = $p(p\text{-}1)$. The fixed model for the analysis of combining ability is given by:

$$Y_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + {}^1/bc\sum\sum e_{ijkl} \quad (48)$$

where $u$= population mean, $g_i$ and $g_j$ = *GCA* and *SCA* effects, $sij$ = *SCA* effect ($s_i = s_j$), $r_{ij}$ = reciprocal effect ($r_{ij} = -r_{ji}$), and $e_{ijkl}$ = error effect for the $ijkl^{th}$ observation. The combining ability effects are restricted such that $\sum g_i = 0$ *and* $\sum s_i = 0$. The Anaalysis of vriance is shown below(Table 11).

**Table 11. Aalysis of variance for Method II showing expeted mean squares for the assumptions of model I ad II**

| Source of variation | Df | Mean Squares | Expected Mean Squares | |
|---|---|---|---|---|
| | | | Model I | Modeel II |
| GCA | $p$-1 | $M_g$ | $\sigma^2 + 2(p\text{-}2)[1/(\text{p-}1)]\sum g_i^2$ | $\sigma^2 + 2\sigma^2_s + 2(p\text{-}2)\,\sigma^2_g$ |
| SCA | $p(p\text{-}1)/2$ | $M_s$ | $\sigma^2 + 2[2/p(p\text{-}3)]\,\sum\sum s_{ij}^2$ | $\sigma^2 + 2\sigma^2_s$ |
| Reciprocal effects | $p(p\text{-}1)/2$ | $M_r$ | $\sigma^2 + 2[2/p(p\text{-}1)]\,\sum\sum r_{ij}^2$ | $\sigma^2 + 2\sigma^2_r$ |
| Error | $m$ | $M_e$ | $\sigma^2$ | $\sigma^2$ |

Differences within classes of effects can be tested using *F*-test ratios and effects are estimated. The vriancees of effects and of differences between effects can also be calculated based on the procedure used by Griffing (1965). Random model for analysis of combining ability is as provided below:

$$Y_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + 1/b_k\sum b_k + {}^1/b_k\sum(bv)_{ijk} + 1/bc\sum\sum e_{ijkl.} \quad (49)$$

where all variables are random with the exception of mean *u*.

## 4. Method IV: Half diallel with no parents and no reciprocals

The method involves use of $F_{1s}$ without parents nor reciprocals thus, total number of crosses is $p(p\text{-}1)/2$. It is one of the most common methods of diallel mating used for generating segregating populations for genetic analysis [8], [35], [44]. The fixed model for the analysis is:

$$Y_{ij} = u + g_i + g_j + s_{ij} + {}^1/bc\sum\sum e_{ijkl} \quad (50)$$

where $u$ = population mean, $g_i$ and $g_j$ = GCA effects of $i^{th}$ and $j^{th}$ parents, $s_{ij}$ = SCA effect of the cross between $i^{th}$ and $j^{th}$ parents ($s_{ij} = s_{ji}$), $b$ = number of blocks, $c$ = number of crosses, and $e_{ijkl}$ = environmental effect associated with the $ijkl^{th}$ individual observation [35]. The random model is given by:

$$Y_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + 1/b_k\sum b_k + {}^1/b_k\sum(bv)_{ijk} + 1/bc\sum\sum e_{ijkl.} \quad (51)$$

where all variables except *u* are considered random. Analysis of variance for Method IV is shown below (Table 12).

**Table 12. Analysis of variance for Method IV showing expectations of mean squares for assumptions of model I and II**

| Source of variation | Df | Mean Squares | Expected Mean Squares | |
|---|---|---|---|---|
| | | | Model I | Modeel II |
| GCA | $p$-1 | $M_g$ | $\sigma^2 + (p\text{-}2)\,[1/(\text{p-}1)]\,\sum g_i^2$ | $\sigma^2 + \sigma^2_s + (\text{p} - 2)\sigma^2_g$ |
| SCA | $p(p\text{-}3)/2$ | $M_s$ | $\sigma^2 + [2/\text{p}(p\text{-}3)]\,\sum\sum s_{ij}^2$ | $\sigma^2 + \sigma^2_s$ |
| Error | $m$ | $M_e$ | $\sigma^2$ | $\sigma^2$ |

## 5. Hayman's (1954) numerical approach (maximum likelihood method)

In case where there is only two alleles per segregating locus, complete dialel can provide useful information for inference about the degree of dominance in a population. The concept was intruducd by Hayman (1954) in which the parental lines used were fully inbreds [18]. The approach is based on the following assumptions [34], [36], [37]:

1. Parents are homozygous.
2. Normal diploid segregation.
3. Absence of multiple alleles.
4. Lack of maternal effect.
5. Absence of linkage among genes affecting the character.
6. Random mating.
7. Lack of epistasis.

Due to the above assumptions, there is a likelihood that not all of them can be satisfied at the same time thus, causing biasness in the precision of estimates of genetic sources of variations. Therefore, Hayman's method can be used to fulfill some of these hypotheses. The linear models for reciprocal and maternal effects are presented in two forms as below [40], [45], [46]:

Reciprocal effect model:

$$Y_r = m + 2j_r - (n\text{-}1)l - (n\text{-}2)l_r \;\; (\text{if } r = s \quad (52)$$

$$Y_{rs} = m + j_r + j_s + j_{rs} + k_r - k_s + k_{rs} \; (\text{if } r \neq s) \quad (53)$$

where $Y_{rs}$ is the entry of the $r^{th}$ row (females) and $s^{th}$ column (males) in the diallel table. If $r \neq s$ then, $Y_{rs}$ represents all progenies of the inbred crosses. If $r = s$ then $Y_r$ represents the progenies of the within-lines crosses in the diallel table. Maternal effect model:

$$Yr = m + 2j_r + k_r \; (\text{if } r = s) \quad (54)$$

$$Y_{rs} = m + j_r + j_s + l + l_r + l_s + l_{rs} + k_r \; (\text{if } r \neq s) \quad (55)$$

The maternal effect model assumes no interaction between maternal effects and own-genotype effects since $k_{rs}$ did not show up in the model. Parameters used in the above linear models are $m$ = grand mean; $j_r = a$ =

variation due to additive genes; $l = b_1$ = mean dominance divination (directional dominance); $l_r = b_2$ = further dominance deviation due to the *r*th parent line; $l_{rs} = b_3$ = residual dominance deviation; $k_r = c$ = average maternal effects of each parent line; and $k_{rs} = d$ = variation in the reciprocal differences not due to *c*. General components of genetic variations are obtained as following [34].

1. Additive variance: $D = (V_P - E)$ where $V_p$ and $E$ are variances of parents and environment.
2. Dominance variance: $H_1 = [Vp - 4Wr - 4Vr] [(3n - 2E)/n]$ where *Vr*, *Wr* and *n* are means of the array variance, mean of the covariances between parents and arrays, and number of parents respectively.
3. Variation due to dominance effects of genes correlation: $H_2 = 4Wr - 4Vr - 2E$ where *E* is the environmental variance.
4. Relative frequency of dominant and recessive alleles: $F = 2V_P - 4Wr - [2(n-2)E]/n$. If *F* is positive then dominance alleles are more frequent than recessive alleles.
5. Environmental variance: E = [(Error SS + Rep SS)/No. Rep] / (Error d.f + Rep d.f).
6. Overall dominant effect of heterozygous loci: $h^2 = 4(ML1 - ML0)^{1/2} - [4(n - 1)E]/n^2$

where $(ML1 - ML0)^2 = 1/n [(GT/n) - \sum$parental values], and GT = Grand total of all observations. The effect ($h^2$) is the algebraic sum over all the loci in heterozygous phase in all the crosses. It provides direction of dominance where positive indicates increasing gene dominance at most of the loci and negative shows decreasing gene dominance.

The genetic ratios based on $F_1$ generation include the following [46], [47]:

1. Average dominance: $D = (H_1/D)^{1/2}$ and the value is explained as:

0 = no dominance
> 0 < 1 = partial dominance
1.0 = complete dominance
>1 = over dominance

2. Proportion of gene groups that show dominance characteristics = $h^2/H_2$ and is explained below.
3. Propotion of genes with positive and negative effects = $[4DH1)^{1/2} + F]/ 4DH1)^{1/2} - F$**]**. If the ratio $H_2 / 4H_1$ is equal to 0.25 then the frequency of positive alleles (*u* ) and the negative alleles (v) are symmetrically distributed between the parents i.e $u = v = 0.5$.

Genetic ratio based on $F_2$ generation was also introduced by Jinks (1956) where the coefficients of $H_1$ and $H_2$ are ¼ in $F_2$ compared to the 1 in $F_1$. This is because both $h^2$ and $F_1$ have the coefficient of ½ due to the inbreeding to attain $F_2$. Thus, the genetic ratios in $F_2$ are obtained as follow:

$$\text{Degree of dominance} = [1/4(H_1/D)]^{1/2} \quad (56)$$

$$\text{Proportion of dominance and recessive} = [{}^1/_4(4D)^{1/2} + ½ F]/[(4H1)^{1/2} - ½F] \quad (57)$$

The formula for proportions of genes with positive and negative effects in the parents, and for the number of groups of genes which control the character and exhibit dominance are the same as those in $F_1$ [37], [47]. Hayman's numerical approach for analysis of variance and covariance components with error variance homogeneous over crosses is shown below (Table 13).

**Table 13. Hayman's analysis of variance and covariance components with error variance homogeneous over crosses**

| Source of variation | Df | Mean Squares | Covariance of relatives |
|---|---|---|---|
| $jr = a$ | $n$-1 | $Var(a) = [(n-1)/4n]\sigma^2$ | $Cov(j_r, j_s) = [(-1/4n)\ \sigma^2$ |
| $l = b_1$ | 1 | $Var(b_1) = [(1/n-1)]\sigma^2$ | - |
| $lr = b_2$ | $n$-1) | $Var(b_2) = [(n-1)/4(n-2)]\sigma^2$ | $Cov(l_r, l_s) = [-1/4(n-2)]\ \sigma^2$ |
| $lrs = b_3$ | ½$n$($n$-3) | $Var(b_3) = [(n-3)/2(n-1)]\sigma^2$ | $Cov(l_{rs}, l_{rt}) = [-(n-3)/(2(n-1)(n-2)]\ \sigma^2$ |
| | | | $Cov(l_{rs}, l_{tu}) = [1/(n-1)(n-2)]\ \sigma^2$ |
| $kr = c$ | ($n$-1) | $Var(c) = [(n-1)/2n^2]\sigma^2$ | $Cov(k_r, k_s) = [-1/2n^2]\ \sigma^2$ |
| $krs = d$ | ½($n$-1)($n$-2) | $Var(d) = [(n-2)/2n]\sigma^2$ | $Cov(k_{rs}, k_{rt}) = [-1/2n]\ \sigma^2$ |
| | | | $Cov(k_{rs}, k_{tu}) = 0$ |
| Error | | $\sigma^2$ | |
| Total | | | |

The heritability estimates are obtained according to [47]:

$$\text{Broad sense heritability: } H^2 = [((D+H_1)/2) - 0.25H_2 - 0.5F)] /[((D+H_1)/2) - 0.25H_2 - 0.5F + E] \quad (58)$$

$$\text{Narrow sense heritability: } h^2 = [((D+H_1)/2) - 0.5H_2 - 0.5F)] /[((D+H_1)/2) - 0.25H_2 - 0.5F + E] \quad (59)$$

The correlation between parental lines ($Y_r$) and $V_r+W_r$ is given by:

$$r = [Cov(Y_r, - V_r+W_r)]/[Var_{Yr} . Var_{Vr+Wr}]^{1/2} \quad (60)$$

where positive *r* value indicates dominance and negative value implies that recessive genes are responsible for the expression of the phenotypes.

**6. Hayman's (1954) graphical approach**

As for the case of numerical approach this approach also uses the following components of variance to perform graphical analysis:

D = additive variance, $H_1$ = dominance variance, $H_2$ = Variation due to dominance effects of genes correlation, E= expected environmental variance, F= mean of Fr over the arrays where *Fr* is the covariance of additive and dominance effects in a single array, and $h^2$ = dominance effects of all loci in heterozygous phase in all the crosses. The analysis involves *Vr*-*Wr* graph constructed with the help of variances of arrays (*Vr*) and covariances (*Wr*) between parents and their offspring. The array refers to the crosses in which a particular parent is common. The *Vr*-*Wr* distribution is used to simultaneously study the genetical properties of homogeneous parents [45], [48], [49]. The *Wri* values used for constructing limiting parabola curve is obtained by the formula:

$$\text{Wri} = (\text{Vri} \times V_{0L0})^{1/2} \quad (61)$$

where *Vri* is the variance of $r^{th}$ array and $V_{0L0}$ is the variance of parents. Similarly, *Wrei* values used for contracting regression line are obtained by the formula:

$$\text{Wrei} = \text{Wr} - b\,(\text{Vr} + \text{Vri}) \quad (62)$$

where *Wr* is array mean of covariances, *Vr* is array mean of variances and b = regression coefficient. The *Vr* - *Wr* regression is used to explain the graphical relationship between the offspring and the parents in which main inferences are mentioned below:

1. when regression line passes through the origin, there is complete dominance ($D = H_1$);
2. when regression line passes above the origin and cutting the *W*r axis, there is partial dominance ($D > H_1$);
3. when regression line passes above the origin, cutting *Wr* axis and touching the limiting parabola, there is no dominance; and
4. when regression line passes below the origin and cutting the *Vr* axis, there is over dominance.

The above genetic estimates can be represented by a *Vr*-*Wr* graph where *Vr* is the variance of the *r*th array, and *Wr* is the covariance between the parents and the offspring on the *r*th array (Figure 6). The points *Vr* and *Wr* are distributed along the corresponding straight line inside the limiting parabola, based on the value of the ratio $H_1/D$ [34], [46], [48]. If a sloping straight line cuts *Wr* at *A*, and another parallel tangent to the parabola cuts it at *B*, then the line is determined by $AB/OB = H_1/D$. The line marked *A* in the diagram represent diallel cross with $H_1/D = 4$. The position of *Vr*, *Wr* on the line indicates the relative proportion of dominant and recessive genes in the $r^{th}$ parent. For any diallel cross, the point corresponding to a parent containing *p*% dominants and *q*% recessive lies on the curve labeled *p : q*. Completely recessive parents correspond to points at the upper ends of the sloping lines on the part of the limiting parabola labeled 0:100, and completely dominant parents to points at the lower ends on the part labeled 1:0 [36], [39], [47]. In an experiment where there is no dominance, the points coincide at ($^1/_4$D, $^1/_2$D) where $H_1 = 0$ (Figure 6).

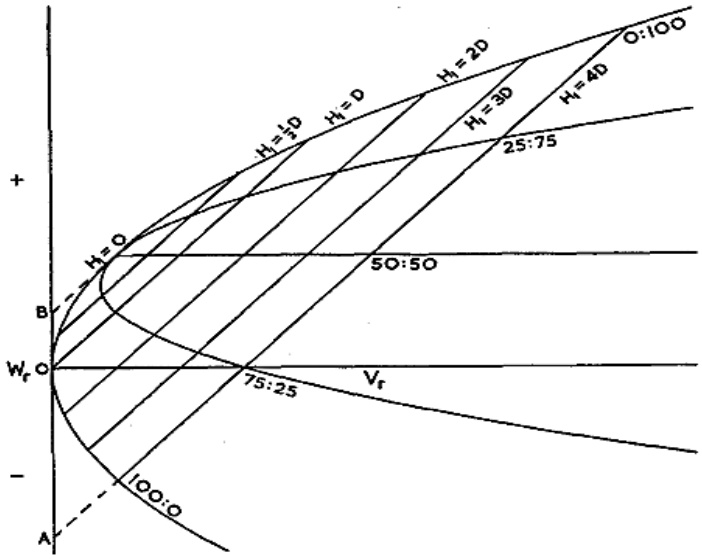


**Figure 6. Diallel cross dominance relationship when environmental variation neglected**

**7. Gardner and Eberhart model**

Gardner and Eberhart (1966) proposed a statistical genetic model to obtain the maximum possible genetic heterosis from a fixed set of random mating varieties involved in a diallel cross [35]. The model is more suitable for used when the parents are open-pollinated populations [50]. They deduced three kinds of ANOVA (Analysis 1, 2 & 3) where heterosis is partitioned into three components (average, variety and specific). The statistical model is repsented as:

$$Y_{ij} = \mu v + (v_i + v_j)/2 + \theta(h + h_i + h_j + h_{eij}) \quad (63)$$

where $Y_{ij}$ = mean of parent when $i=j$ or mean of single cross when $i \neq j$; $\mu v$=mean of all parents; $v_i$, $v_j$=effect of parent $i$ measured as deviation from $\mu v$ so that $\sum v_i$ or $\sum v_j$=0; $hij$=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 crosses and $\mu v$,$h_i$; $h_i$=mean heterosis of $v_i$ or $v_j$ in all crosses, also named varietal heterosis, measured as deviation 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; $\theta$=*0 when i = j = 1 or i ≠ j.* The heterosis with respect to the best parent (hbp) is obtained by the difference between the cross *vi*,*vj* and the highest parent mean [38].

**8. Partial diallel**

Complete diallel mating designs have been instrumental in progeny generation for genetic analysis. Kempthorne and Curnow (1961) had introduced partial dialel mating design as a modification of complete diallel. However, breeders find the use of the design cumbersome especially for big number of parents in which all possible combinations are expected. In partial diallel the number of parents is increased but the parents are not mated in all possible combinations as shown in Table 14 below [33].

**Table 14. Partial diallel crosses with number of parents (*n*) = 11 and number of crosses per parent (*s*) =4**

| Parent | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | | | | x | x | x | x | | | |
| 2 | | | | | x | x | x | x | | |
| 3 | | | | | | x | x | x | x | |
| 4 | | | | | | | x | x | x | x |
| 5 | | | | | | | | x | x | x |
| 6 | | | | | | | | | x | x |
| 7 | | | | | | | | | | x |

*P* = patent line

The major difference between partial and complete diallels is that more parents are involved to produce same number of crosses as in a complete diallel [5]. For example, in a half-diallel method, 16 parents are needed to produce 120 crosses while for partial diallel 80 parents can be used to generate the same 120 crosses. This gives an advantage over other mating designs because more parents can be investigated and genetic variance can be estimated with limited resources (Table 12). Total number of crosses in partial diallel is obtained as*:* $ns/2$ where $n$ = number of parents and $s$ = whole number (≥2).
Table 15.

**Table 15. Comparison of number of crosses obtained from 100-parent maize populations using diallel, NC Design II, and partial diallel**

| Diallel | NC Design II | Partial diallel |
|---|---|---|
| n(n-1)/2 | 50x50 | ns/2 |
| 4950 | 2500 | 150 (if *s*=3) |

The statistical model for partial diallel is given by:

$$Y_{ijkl} = u + g_i + s_{ij} + b_k + r_l + rb_{kl} + e_{ijkl} \quad (64)$$

where $u$ = population mean, $g_i$ = GCA effects of $i^{th}$ parents, $s_{ij}$ = SCA effect of the cross between $i^{th}$ and $j^{th}$ parents, $b_k$ = block effect, $r_i$ = replication effect, $rb_{kl}$ = block effect within replication, and $e_{ijkl}$ = environmental effect associated with the $ijkl^{th}$ individual observation. Rest of the analysis of variance is similar to the diallel mating design except that the degrees of freedom and coefficients of expected mean squares are different because of the sampling of crosses among parents (Table 16). The use of large number of parents is advantageous to partial diallel due to more even distribution of degrees of freedom and high precision for GCA and SCA.

**Table 16. Analysis of variance of partial diallel evaluated in one environment, model II**

| Source of variation | Df | Mean Squares | Expected Mean Squares |
|---|---|---|---|
| Replications | $r$ - 1 | | |
| Crosses | ($ns$/2) - 1 | $M3$ | $\sigma^2 + r\sigma^2_c$ |
| GCA | $n$ -1 | $M3,1$ | $\sigma^2 + r\sigma^2_s + [rs(n-2)/(n-1)]\sigma^2_g$ |

| | | | |
|---|---|---|---|
| SCA | $n(s/2 - 1)$ | $M3,2$ | $\sigma^2 + r\sigma^2_s$ |
| Error | $(r\text{-}1)[(ns/2) - 1]$ | $M2$ | $\sigma^2$ |
| Total | $(rns/2) - 1$ | | |
| Within | $r(ns/2)(k\text{-}1)$ | $M1$ | |

*r*, *n*, *s*, and *k* refer to the number of replications, parents, crosses per parent, and plants within a plot.

If individual plant data is used, then:

$$\sigma^2 = [(\sigma^2_{g} - {}_{CovFS)} + \sigma^2_{w}/k + \sigma^2_{p}] \quad (65)$$

where *k* is the number of plants measured per plot and $\sigma^2_p$ is the experimental plot error. Partial diallel is also used to test single crosses among selected inbred lines. Data from partial diallel is used in best linear unbiased prediction (BLUP) and best linear unbiased estimation (BLUE) analyses to predict the untested single crosses. Generally, partial diallel mating design is more appropriate compared to diallel for estimation of genetic components of variance with similar accuracy (e.g., GCA and SCA). In addition, a greater number of parents can be included with the same resources available [1]. Although partial diallel provides good alternatives, the design is not commonly used in breeding. This is because complete diallel gives more information than partial diallel when dealing with smaller number of parents. Similarly, for large number of parents NC Design II is very simple and easy to manage than partial diallel [5].

## 9. Triallel and quadrallel

Cockerham (1961) produced triallel (three-way crosses) and quadrallel (double-cross hybrids) crosses from a group of parents that originated from the same population. He determined the variances and covariances between all possible pairs of the hybrid relatives among single cross, three-way, and double cross hybrids [5]. Analysis of triallel and quadrallel can provide useful information on the estimates of genetic components of variance [5]. Population size is important for example if we have *n* lines, then number of possible three-way combinations will be $n(n - 1)(n - 2)/6$, and assuming no reciprocal crosses, three possible arrangement of the three-way crosses will be $3*[ n(n - 1)(n - 2)/6]$. Similry, if we have *n* parents the possible number of quadrallel (double-crosses) is $n(n - 1)(n - 2)(n - 3)/24$, and three possible arrangement of double-crosses will be $3*[n(n - 1)(n - 2)(n - 3)/24]$ respectively.

Basic models and analyses of variance of triallel and quadrallel designs repeated over environments are the same as those given for the diallel model II. Direct *F*-tests of crosses and crosses with environment mean squares are used to determine if further partitioning of the crosses sums of squares is required. If the crosses mean square is non-significant, further analysis should not be done [5]. Orthogonal partitioning of the triallel and the quadrallel is similar to that of complete diallel and depends on the number of lines common among crosses and the arrangement of lines within crosses. For example, $12[(4 \times 3 \times 2)/2]$ three-way crosses can be generated from four parent lines (A, B, C, and D) as shown below (Table 17).

**Table 17. Possible threeway cross combinations that can be generated from four parent lines (A, B, C and D)**

| | | | | | |
|---|---|---|---|---|---|
| 1. | (AxB)C | 5. | (AxD)B | 9. | (BxD)A |
| 2. | (AxB)D | 6. | (AxD)C | 10. | (BxD)C |
| 3. | (AxC)B | 7. | (BxC)A | 11. | (CxD)A |
| 4. | (AxC)D | 8. | (BxC)D | 12. | (CxD)B |

Basic model for triallel is given by:

$$Y_{ijkl} = u + r_i + C_{ijk} + e_{ijkl} \quad (66)$$

where $C_{ijk}$ is the cross sums of squares, defined as the liner function of uncorrelated effects which can be partitioned as below [5]:

$$C_{ijk} = (g_i+g_j+g_k) +(s_{2ij} + s_{2ik} + s_{2jk}) +s_{3ijk} + 0_{1i} + 0_{1j} + 0_{ik} +(0_{2aij} + 0_{2aik} + 0_{2ajk}) +(0_{2bij} + 0_{2bik})+ 0_{3ijk}. \quad (67)$$

The expected mean squares are expressed in terms of components of variance (Table 18) and can be interpreted according to the descriptions below.

$\sigma^2_g$ = effect of lines averaged over all orders for A.
$\sigma^2_{s2}$ = two-line interaction effect averaged over all orders for AxB.
$\sigma^2_{s3}$ = three-line interaction effect averaged over all orders for (AxB)C.
$\sigma^2_{01}$ = one-line order effect of lines as a parent A
$\sigma^2_{02a}$ = two-line order interaction effects averaged over orders for A and B.
$\sigma^2_{02b}$ = two-line order interaction effects of parents and grandparents due to A and B.
$\sigma^2_{03a}$ = three-line order interaction effects of parents and grandparents due to (AxB)C.

The GCA (g) and SCA ($s_2$, $s_3$) effects are similar to those for diallel analyses. The only difference in triallel and quadrallel is the addition of order effects ($0_1$, $0_{2a}$, $0_{2b}$, $0_3$) which occur due to the arrangement of parents and line ancestry in three-way crosses.

**Table 18. Analysis of variance for the triallel**

| Source of variation | Df | Mean Squares | Expected Mean Squares |
|---|---|---|---|
| Three-way crosses | $3pC_3$ -1 | $C$ | |
| One-line general | $p$ - 1 | $G$ | $\sigma^2 + 3r\sigma^2_{s3} + 6rp\sigma^2_{s2} + (3rp2p3/2)\,\sigma^2_g$ |
| Two-line specific | $pp_3/2$ | $S_2$ | $\sigma^2 + 3r\sigma^2_{s3} + 3rp_4\sigma^2_{s2}$ |
| Three-line specific | $pp_1p_5/6$ | $S_3$ | $\sigma^2 + 3r\sigma^2_{s3}$ |
| One-line order | $p_1$ | $O_1$ | $\sigma^2 + r\sigma^2_{o3} + 3rp_2\sigma^2_{ob2} + (rp/3)r\sigma^2_{2a} + (rpp_2/3)\sigma^2_{o1}$ |
| Two-line order (a) | $pp_3/2$ | $O_{2a}$ | $\sigma^2 + r\sigma^2_{o3} + (2rp_1/3)\sigma^2_{2a}$ |
| Two-line order (b) | $p_1p_2/2$ | $O_{2b}$ | $\sigma^2 + r\sigma^2_{o3} + 2rp_3\sigma^2_{o2b}$ |
| Three-line order | $pp_2p_4/3$ | $O_3$ | $\sigma^2 + r\sigma^2_{o3}$ |
| Error | (r-1)($3pC_3$-1) | $E$ | $\sigma^2$ |

*F*-tests for significance is made direct for all except one-line order effects where expected mean squares (EMS) are expressed in terms of covariances of relatives because their composition can be determined in terms of genetic components of variance [5]. The components of variance ($\sigma^2_g$) and ($\sigma^2_{01}$) include only additive effects and additive x additive epistatic effects. Variance components ($\sigma^2_{s2}$) and ($\sigma^2_{02a}$) include dominance and all kinds of epistasis or deviations from all-additive model; $\sigma^2_{s3}$ includes all types of epistasis effects except additive x additive. Tests of hypothesis of appropriate mean squares and their genetic interpretations are similar to those of the diallel [51]. Level of genetic variance increases as we advance from single cross to threeway cross and double cross when common parents are used with $F = 0$ (Table 19).

**Table 19. Coefficients of components of genetic variance among unrelated single, threeway, and double crosses**

| | Coefficients of genetic components of variance for $F = 1$ | | | | | |
|---|---|---|---|---|---|---|
| Type of cross | $\sigma^2_A$ | $\sigma^2_D$ | $\sigma^2_{AA}$ | $\sigma^2_{AD}$ | $\sigma^2_{DD}$ | $\sigma^2_{AAA}$ |
| Single cross | 1 | 1 | 1 | 1 | 1 | 1 |
| Threeway cross | 3/4 | 1/2 | 9/16 | 3/8 | 1/4 | 27/64 |
| Double cross | 1/2 | 1/4 | 1/4 | 1/8 | 1/16 | 1/8 |

If only additive genetic effects are assumed, the relative advantage of single, threeway, and double crosses is 1:3/4: 1/2 i.e. variation among single crosses will be twice that of quadrallel and only additive effects are important. If non-additive variance is important then the relative advantage increases for single crosses over both triallel and quadrallel [5].

## VIII. Top cross

The top cross design was proposed by Jenkins and Brunsen (1932) for testing inbred lines of maize in cross-bred combinations and later renamed top cross by Tysdal and Grandall (1948). The cross is made between a plant (line, clone, etc) selected as female and a common male tester of a known performance (variety, inbred line or single cross). Possible number of crosses that can be made is $n$ x 1, where $n$ is number of inbreds. Top cross scheme is effective for testing big number of elite lines especially when crossed to a tester with wide or narrow genetic base [33], [51]. However, the most appropriate tester used for top cross is single cross hybrid ($F_1$) because of its uniformity. Top cross, sometimes referred to as inbred variety cross, is mostly suitable for preliminary evaluation of combining ability of new inbred lines before pairing them into single cross hybrids. The parental pair-wise combinations are estimated based on: i) parental performance in pair wise combinations; ii) direct contribution of each parent to the progeny mean through additive gene action; and iii) reliability of the results being obtained is independent of the quantity of the data [33], [51]. Narrow-sense heritability is obtained as:

$$h^2 = \sigma^2_A / \sigma^2_P \tag{68}$$

where $h^2$ = narrow-sense heritability, $\sigma^2_A$ = additive variance, and $\sigma^2_P$= phenotypic variance. Correlation coefficient (r) between specific crosses involving one parental line and its performance in the test cross may be low (r = 0.5), especially when the tester has a broad genetic base. Therefore, when a higher stringency is expected on the combining ability tests, a tester with a narrow genetic base should be used so as to elevate the correlation coefficients (r = 0.7) [33]. The analysis of variance for top cross progenies is given below (Table 20).

**Table 20. Analysis of variance for top cross progenies**

| Source of variation | Df | Mean Squares | Expected Mean Squares | Variance of relatives |
|---|---|---|---|---|
| Progenies | $g$ -1 | $M_1$ | $\sigma^2_e + r\sigma^2_{prog}$ | $\sigma^2_{prog} = CovHS = [(1+F)/4]\,\sigma^2_A$ |
| Blocks | $r$ -1 | $M_2$ | - | - |

| | | | | |
|---|---|---|---|---|
| Error | *(g – 1)(r – 1)* | $M_e$ | $\sigma^2_e$ | $\sigma^2_e = \sigma^2$ |

When the parents are non-inbred then $F = 0$ and the variance component = $\sigma^2_{prog} = (1+F)/4a^2_A$, also $\sigma^2_{prog} = V(m_1) + V(m_2)$. The analysis of top cross progenies can only provide information on GCA rather than on SCA [51].

## IX. Line x Tester

Line x tester was first introduced by Kempthorne (1957) and it involves crosses between lines (used as females) and wide based testers (used as males) in all possible combinations to produce one to one fashion generating $F_1$ hybrids. It is the simplest mating design that provides both full-sibs and half-sibs simultaneously as opposed to top cross where only half-sibs are generated [51], [52]. The statistical model for Line x Tester is given by:

$$Y_{ijkl} = u + a_i + b_{kl} + v_{ij} + (av)_{ijl} + e_{ijkl} \quad (69)$$

where $Y_{ijkl}$ = observed phenotypic value of each experimental unit, $u$ = population mean, $a_i$ = location effect, $b_{kl}$ = block or replication effect within each location, $v_{ij} = F_1$ hybrid effect. The $F_1$ hybrid effect can further be partitioned into: $V_{ij} = g_i + g_j + s_{ij}$ where $g_i$ = GCA effect for the $i^{th}$ parent line, $g_j$ = GCA effect for the $j^{th}$ tester, $s_{ij}$ = SCA for the $ij^{th}$ hybrid and $l^{th}$ location, and $e_{ijkl}$ = environmental error effect. Analysis of variance is presented below (Table 21). The variances for general and specific combining ability are tested against their respective error variances, derived from the analysis of variance of the different traits as follows [52]:

$$\text{Covariance of half-sib of line} = \text{CovHS (line)} = (M_l - M_{lt})/rt \quad (70)$$

$$\text{Covariance of half-sib tester} = \text{CovHS (tester)} = (M_t - M_{lt})/rl \quad (71)$$

$$\text{Covariance of full-sib} = \text{CovFS} = [(M_l M_e)+(M_t-M_e)+(M_{lt}-M_e)] /3r+[6r\text{CoHS}-r(l+t)\text{CovHS}]/3r \quad (72)$$

where *l, t, r* are number of lines, testers and replication.

**Table 21. Presentation of analysis of variance for Lin x Tester design**

| SOV | Df | Mean Squares | Expected Mean Squares | |
|---|---|---|---|---|
| | | | Model I | Modeel II |
| Replications | *r* - 1 | | | |
| Lines (L) | *m* - 1 | $M_1$ | $\sigma^2 + rf[1/(m-1)] + \sum g_i^2$ | $\sigma^2 + \sigma^2_{sca} + rf_{gca(m)}$ |
| Testers (T) | *f - 1* | $M_2$ | $\sigma^2 + rm[1/(f-1)] \sum g_j^2$ | $\sigma^2 + r\sigma^2_{sca} + rm_{gca(f)}$ |
| L x T | *(m-1)(f-1)* | $M_3$ | $\sigma^2 + r[1/(m-1)(f-1)]\sum\sum s_{ij}^2$ | $\sigma^2 + r\sigma^2_{sca}$ |
| Error | *(r-1)(mf-1)* | $M_e$ | $\sigma^2$ | |

Average covariance of half-sib is given as:

$$\text{CovHS (average)} = \{[1/r\,(2lt - l - t)]\,[M_1(l - 1) + M_t(t - 1)] / (l + t - 1)\} - M_{lt} \quad (73)$$

If it is assumed that there is no epistasis and breeding coefficient equals unity ($F$=1), then variance components of GCA and SCA are estimated based on the following:

$$\text{GCA variance component} = \sigma^2_{GCA} = \text{CovHS} = [(1+F)/4]\sigma^2_A \quad (74)$$

$$\text{SCA variance component} = \sigma^2_{SCA} = [(1+F)/2]^2\sigma^2_D \quad (75)$$

The breeding coefficient is considered to be 1 when both line and tester are inbreds and therefore, the relative importance of additive effects in conditioning the phenotypic variance is termed the narrow sense heritability and given by the ratio [3], [52]:

$$h^2 = \sigma^2_{GCA}/\sigma^2_{SCA} \quad (76)$$

To detect whether the GCA and SCA effects are significant, they are subjected to *t*-test.

## X. Ploy cross

The term polycross was coined by Tysdal and Kiesselbach (1942), to indicate progeny from seed of a line that was subject to out crossing with other selected lines growing in the same nursery [51], [53]. The design allows a group of cultivars to undergo natural crossing in isolated block. The main aim of polycross is to improve homozygosity of open pollinated variety while at the same time maintaining the high level of heterozygosity. It is most suited to species that are obligate cross-pollinaters (e.g., vegetables, forage grasses and legumes, sugarcane, sweet potato) [11], [22], [54]. Statistical model for polycross is fitted as follow:

$$Y_{ij} = \mu + G_i + B_j + E_{ij} \quad (77)$$

where $\mu$ is the global mean, $G_i$ is the effect of genotype i, $B_j$ is the effect of replication (four replications), and $E_{ij}$ is the error term. In polycross additive effect is insignificant therefore, heritability is estimated on broad sense basis and is given by:

$$H^2 = \sigma^2 g/(\sigma^2 g + \sigma^2 e) \quad (78)$$

where $\sigma^2 g$ is the genetic variance and $\sigma^2 e$ is the error variance. Proper design and randomization in the polycross block are critical. Latin square design is the most used where entries are exposed to random intermating in the polycross nursery. Nevertheless, when the entries number is more than 10, the completely randomized block design may be used instead [22]. If all the entries do not flower together, mating will not be

random. Non-random dispersal of pollen may lead to concentrations of common pollen in the crossing block. To avoid this, the breeder may plant late flowering entries earlier. The mean performance of progenies of any female parent in the polycross is used to determine the variance components and consequently, the general combining ability [11]. The general combining abilities estimated are basically for maternal parents and the variations measured in a progeny can be partitioned into *within* and *between* maternal parents and therefore, the general combining ability is used for estimating heritability (Table 22). Heritability can be estimated to provide guidance for usefulness of polycross in breeding program. However, since the parents are of different origin and the crop is sensitive to environmental changes, the performance of the parental lines and their progenies such as flowering is likely to be affected [51].

**Table 22. Analysis of polycross progenies in replicated trials**

| Source of variation | Df | Mean Squares | Eespeced Mean Squares | |
|---|---|---|---|---|
| | | | Variance | Variance of relatives |
| Progenies | $g$ -1 | $M_1$ | $\sigma^2_e + r\sigma^2_{prog}$ | $\sigma^2_{prog} = CovHS = [(1+F)/4]\ \sigma^2_A$ |
| Blocks | $r$ -1 | $M_2$ | - | - |
| Error | $(g-1)(r-1)$ | $M_e$ | $\sigma^2_e$ | $\sigma^2_e = \sigma^2$ |

$F$ = beeding depression = 0.

Comparison of the coefficients indicates that precision of estimate is lower for the topcross or polycross than for covariance between parents and offspring. The precision is increased if the tested genotypes are inbred. It is convenient to use polycross design in cross-pollinated species when evaluating a large number of genotypes. The selection is then applied based on half-sib progeny means [11]. However, polycross design has a number of limitations such as random mating; insufficient statistics to estimate all the parameters; the components of variance are only estimated from the maternal half sibs; information about the males is lost; no control over the pollen source; expected genetic gains are reduced by half; the non-randomness of mating (due to lack of synchronization of flowering); and unequal pollen production and position effects in the crossing block). The polycross is ideally suited for identifying mother plants with superior genotypes from the performance of their progeny general combining ability [55].

## XI. Conclusion

Mating designs generate various kinds of progenies and genetic relationships that permit estimation of multiple components of variance with high precisions. Various designs have been introduced for genetic improvement of crops and no single one of them can satisfy all the breeding objectives. Diallel analysis gives more precision of both additive and dominance components of variance compared to NC Design II. Similarly, partial diallel is more effective than complete diallel when dealing with fixed effects. This is because partial diallel can sample many genotypes. However, most genetic models, particularly those for second-degree statistics, do not provide a valid test for epistasis. If the presence of epistasis is ignored in populations, then information on epistasis is lost and the estimates of additive and dominance components will be biased and misleading. Further, detection and estimation of epistasis will enable breeders to determine genetic cause of heterosis with greater reliance.

Although Hayman's model of diallel analysis provides huge information on genetic variance and covariance of relatives, the model has met some criticisms. Firstly, the analysis appears to have been calculated using a progressive fitting of the unknown parameters; in this way, a truly non-orthogonal analysis of variance is made orthogonal, with the component sums of squares adding up to the total sum of squares. Secondly, Hayman's representation of the maternal effects makes his analysis to appear more of reciprocal effects than the maternal effects.

Triallel and quadrallel mating designs have not been used extensively because they (1) are relatively new in development; (2) are complex mating designs with complex analyses; (3) require a large number of crosses to sample the population adequately; and (4) require two or more growing seasons to produce crosses before they can be tested. In addition, it seems the potential of triallel and quadrallel for estimation of genetic variances in a reference population is limited because of complexity in obtaining parents and crosses. In addition, such selected lines are of diverse origins, and the estimates of genetic variances would not be valid. Generally (especially for unbalance data), there is no single crossing scheme that fit all. Therefore, based on the resource availability, choice of a suitable mating design depends on ability of the method to partition the various model effects which allows calculation of the sum of squares associated with each individual factor. Breeders need to make right decision when choosing a mating design for generation of progeny for genetic analysis.

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