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# Assessing Mating Designs Utilized in Cassava Population Improvement

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## Abstract

Cassava breeders are curious about appropriate breeding strategies utilized to generate elite genotypes with desired complimentary traits or genes from parents used in crossing. Use of appropriate mating design is influenced by a good understanding of the flower biology of the putative parent plants, type of pollination, crossing technique, pollen dissemination, the presence of male-sterility system, the purpose of the project (that is either breeding or genetic studies), and the size of population needed. The objective of this book chapter is to assess the current knowledge on mating designs, their applications and limitations in cassava improvement. This book chapter discusses the floral biology, genetic improvement, breeding procedures and mating designs in cassava. The information utilized in this study were obtained from various sources including documentary search of the journals, books and websites of relevant stakeholder organizations. Empirical findings of selected mating designs in cassava and their impacts were discussed. Findings serve as a good guide for selection of appropriate mating arrangement to obtain useful information on parents and progenies. Findings are relevant to scientists, researchers, scholars, lecturers and other relevant stakeholders.

**Keywords:** cassava, breeding, genetics, mating designs, gene action

## 1. Introduction

Breeders and geneticists have used different mating designs for development of improved genotypes of plants [1]. Mating designs are principles involved in arranging different cross combinations and altering the genetics of plants to satisfy human needs [1, 2]. The original intent of developing these designs was to estimate additive- and/or dominance- variance genetic parameters. Successful plant breeding involves selection of appropriate mating design and parents [1, 3]. However, selection of appropriate mating designs is influenced by the type of crossing used (artificial or natural), type of pollination (self or cross pollinated), type of pollen dissemination (insect or wind), the purpose of project (genetic or breeding studies), the presence of male sterility system and the size of population desired. Selection of mating design for the estimation of genetic diversity depends on the objective of study, time, space and biological limiting factors. A suitable mating arrangement is imperative for successful plant breeding programme [4].

Mating and experimental designs are critically important in plant breeding. The four main significance of mating designs include (i) generation of information on genetic control of character, (ii) serves as basis for selection and development of elite genotypes in breeding population, (iii) estimation of genetic gain, and (iv) generation of information for evaluation of parents in breeding program [5–8]. Use of any particular mating design lies in its ability to adequately address research questions of plant breeders such as: Are genetic variabilities significant? How much of the variation is heritable or due to environment? And what types of gene(s) influence significance? Comparison of variances of both segregating and the non-segregating generations provides a good resolve of the above questions [9]. Generally, for a given number of parents, the mating design that permits larger number of crossings will produce smaller sampling variance. Path coefficient analysis, generation mean analysis, stability analysis, heritability and genetic advance, combining ability, heterosis and inbreeding depression, gene action in plant breeding, triple test cross analysis, correlation and regression analyses are also used to answer various research questions [10, 11]. The statistical components and interpretations should match the mating and experimental designs used in plant breeding experiments [6].

This book chapter focuses on the floral biology, genetic improvement, breeding procedures and mating designs in cassava. The objective was to provide updated information on breeding procedures and mating designs in cassava. This information would contribute to effectively guide scientists, researchers, students and research and development partners in the selection of adequate design for improved efficiency in cassava breeding.

## **2. Floral biology of cassava**

Cassava belongs the genus *Manihot* of the family Euphorbiaceae. The genus comprises two sections, viz., the Fructicosae, which contains low-growing shrubs adapted to savannah grassland or desert conditions and the Arborae, containing tree species [12, 13]. There are about 98 species in the genus *Manihot*, all of which are confined to the tropical Americas [14]. Cultivated cassava belongs to the section Fructicosae, often considered as an unknown cultigen in the wild [14]. All known species of *Manihot* are polyploids with  $2n = 36$  chromosomes, although they exhibit regular bivalent pairing, thereby behaving as diploids [15].

Cassava is monoecious with both male (pistillate) and female (staminate) flowers borne on the same plant [16]. The female cassava flowers are usually borne on the lower part of the inflorescence and are fewer than the male flowers, which are borne on the upper part of the inflorescence [17, 18]. The female and male flowers on the same inflorescence open at different times, a condition known as protogyny. The female flowers open one to two weeks before the male flowers. However, female and male flowers on different branches of the same plant can open at the same time. Cassava is a cross-pollinating root crop producing highly heterozygous plants [13, 17]. Self-pollination has been noted, although the proportions of self- and cross-pollinated seeds generated depends on the genotype, the type of pollinating insect present and the plant design [13]. Inbreeding and inbreeding depression have been reported in cassava [19, 20].

Cassava exhibits varying flowering patterns ranging from those with frequent flowering pattern to types that do not flower [21]. Flowering may begin at six weeks after planting in the early types, depending on the genotype and the environment used [13]. Flowering initiation is preceded by reproductive branching known as forking. The time of forking depends on the genotype and agroecological conditions. Optimum flowering occurs at moderate temperatures of about 24 °C [17].

Since cassava does not flower during a long dry season, Kawano [18] suggested that cassava crossing blocks should be irrigated during the dry season. A good understanding of the optimum flowering period and duration of flowering is important for successful crossing.

Flowering in cassava is controlled by the complex interaction of a range of genetic and environmental factors [17]. Moreover, the control of flowering and flowering itself are major challenges in cassava breeding. For instance, genotype(s) possessing valuable complementary traits of interest may not be used in breeding due to its shyness and non-synchronized flowering [22]. Flowering synchronization of genotypes for crossing may present a problem. However, flowering on a single plant usually lasts for more than two months [13]. Since male flowers are more numerous than female flowers, the limiting factor for large production of hybrid cassava seeds is lack of sufficient female flowers [17]. Thus, genotypes intended to be used as female parents should be planted sequentially and in higher numbers than the males [18]. The number of seeds set per female flower significantly differ per genotype. This necessitates the selection of highly fertile genotypes as female parents.

### **3. Genetic improvement in cassava**

#### **3.1 Parental selection and hybridization in cassava**

Genetic improvement in root and tuber crops begin with the assembly and evaluation of broad-based germplasm or source populations [23]. Genotypes with high frequencies of genes associated with desirable complementary traits are selected from the source populations and utilized as parents for the generation of new recombinant genotypes [20, 23]. Since cassava is highly heterozygous, selection of suitable parents for hybridization is among the most critical steps in a breeding programme. Parental selection for a cassava hybridization programme is often based on known performances of putative genotypes. However, parental selection based on phenotypic performances alone is not a sound procedure, since phenotypically superior clones may produce poor recombinants in the segregating population [24]. This led to the suggestion of selecting elite parents on the basis of genetic value [25]. Genotypic performances in hybridization programmes depend on their combining ability and the effectiveness in transmitting heredity traits to their progeny [26]. In a breeding programme where general combining ability (GCA) is more important, a small number of parents with good GCA should be utilized. If the specific combining ability (SCA) is more important, a large number of parents should be used to produce a large number of the first filial generation ( $F_1$ ) families [25]. A good understanding of existing profiled parental traits is imperative to guide effective parental selection and genetic improvement of current breeding populations. Genetic improvement through hybridization consists of selection of parents, generation of  $F_1$  progeny and selection of superior clones [25]. Clonally propagated crops such as cassava, yam, sweetpotato, etc. are generally improved by crossing two or more clones possessing desirable complementary traits, followed by selection in the  $F_1$  progeny. Controlled pairwise-crossing could be done manually to produce full-sib families, or naturally in polycross nurseries that allow open pollination to produce half-sib families [23, 27]. The breeding procedure of clonally propagated crops is known as clonal selection [28].

#### **3.2 Breeding procedures**

The main objective of breeding is to improve the characteristic of plants to obtain new genotypes that are more desirable agronomically and economically



[25, 29]. However, improving some specific traits of certain crops may be among key priority objectives for various agronomic and/or economic reasons. Some of the common breeding methods in cassava include: clonal selection, recurrent selection and backcross breeding. Backcross breeding has been used to incorporate genes for disease resistance [23, 30].

### 3.3 Clonal selection

A clone is a group of genetically identical vegetative propagule obtained from a single plant [31]. Hybridization of parental clones with superior traits produces a source population that may be utilized for the selection of new clones [32]. Hybridization creates genetic variability in progeny obtained through gene recombination of parental clones used. Botanical seeds obtained from crosses are grown in seedling nurseries. The growing seedlings are exposed to major diseases and pests such as cassava mosaic disease (CMD), cassava brown-streak disease (CBSD), and cassava bacterial blight (CBB) for selection against susceptible seedlings [30]. The clonal selection is based on visual observations and on breeders' judgment of the genetic value of the clones [25]. The replicated preliminary yield trial (PYT) should involve both the selected clones and suitable standard check(s). A few clones with desirable superior performances are selected for the yield trial stages. Replicated yield trials should be conducted in several locations along with suitable standard check(s). The best clones with desirable high yield, quality and disease resistance are then multiplied and released as a new variety [28, 30]. Alternatively, the superior clones may be isolated and grown as a variety from a genetically mixed population of an asexually propagated crop. The demerit of this technique is that genetic progress is limited to the isolation of the best genotype present [28]. Moreover, the phenotypic values the clones are contingent upon include the effects of the genotype, the environment and the genotype  $\times$  environment interactions [33]. During the early stages of clonal selection, single plants or single plots are used with the emphasis of eliminating weak and undesirable plants [30]. The later clonal selection stages involving replicated yield trials, yield and yield attributes are considered, with the emphasis of identifying and selecting superior clones [16].

### 3.4 Recurrent selection

Recurrent selection involves the selection of a number of plants with desirable phenotype, growing, evaluating and selecting seedling-derived clones obtained from seeds, and intercrossing the progenies in all possible combinations [25, 32]. At IITA, recurrent selection has been utilized for the genetic improvement of cassava breeding populations for CMD resistance and other agronomic traits [34]. Genetic improvement for CMD resistance alone was accomplished in one cycle (1–2 years). However, combination of CMD resistance with high yield potential trait took about 4–5 years. The introgression of exotic sources from other continents, especially Latin America, into IITA breeding populations was achieved after obtaining adequate resistance to CMD [34].

### 3.5 Backcross breeding

Backcross breeding involves repeated backcrossing of the hybrid and the progenies in subsequent generations to one of the parents [28]. The progenies obtained are increasingly similar to the recurrent parent. Interspecific hybridization between cultivated cassava (*M. esculenta*) and other related *Manihot* species such as *M. glaziovii* has been reported [35]. Backcrossing of progenies to cultivated cassava (the

recurrent parent) to recover positive agronomic traits and resistance to CMD produced variable results regarding fertility. However, the second backcross generation had improved fertility. Controlled back-crossing of progenies to cultivated female cassava parents successfully produced F<sub>3</sub> generation [15, 35].

Transfer of high protein content of tuberous roots of cassava from wild species (*M. tristis* subsp. *saxiola*) was achieved through backcrossing of hybrids obtained between cassava and *M. tristis* subsp. *saxiola* to the recurrent parent [35, 36]. However, breeding efforts to increase favorable alleles protein content in cassava roots were unsuccessful since the high protein contents in the initial hybrids were not maintained in the backcross progenies [37].

### 3.6 Inbreeding in cassava

Inbreeding reduces the genetic load of deleterious genes thereby increasing the frequency of desirable genes [23] and improving selection efficiency [38]. In sweetpotato, inbreeding depression was noted for storage root yield, storage root number and vine length [39]. To develop new genotypes with high dry matter content and high storage root yield, it has been suggested to develop high dry matter inbred lines for crossing among themselves or with superior cultivars. Development of genotypes with high starch content requires concentration of genes controlling starch content in the genotype [39]. In cassava breeding, inbreeding is seldom practiced due to the lengthy duration required to obtain high levels of inbreeding (9–10 years) and high level of inbreeding depression [23]. Tolerance to inbreeding depression can be bred into crops. Fifth generation inbred lines of cassava were developed at IITA [40]. In India, Easwari-Amma et al. [38] reported reasonable homozygosity in successive generations of inbred lines of cassava in four generations.

### 3.7 Gene action and inheritance

Gene is known as the basic unit of inheritance. Genes are responsible for the transmission of characteristics from one generation to the next [29]. Gene action and gene inheritance are involved in crop improvement process. From physiology perspective, gene action is the reflection of gene differences that provide the basis for the selection of desirable genotypes in plant breeding [41]. Gene action also determines the expression of characteristics of plants including its morphology, response to environments, and yielding ability. Gene inheritance is the transmission of genetic material or information to succeeding generations [42]. According to Klug and Cummings [43] the classical Mendelian genetic pattern of inheritance reveals the expression of one dominant, when two contrasting characters are brought together in a cross and one recessive (latent) in F<sub>1</sub> and in F<sub>2</sub> the two characters segregate and express themselves phenotypically. Knowledge of gene inheritance is relevant for the efficient recovery and maintenance of desirable genes transmitted from selected parents to their progeny [26].

Multiple genes are known to influence the phenotypic expression of a quantitative trait. The four gene actions in the phenotypic expression of traits are: additive, dominance, epistatic and overdominance. Additive genes are genes that act additively or cumulatively to a quantitative character, whereas dominance gene effects are deviations from additive effects [44]. Epistatic gene effects are non-allelic gene interactions; and over-dominance gene effects occur when the contribution of the combined alleles is greater than the separate effect of either allele [26].

Most of the physiological characters such as yield, dry matter content and disease resistance are inherited quantitatively [32]. Quantitatively inherited

characters are controlled by polygenes with small individual effects and environmental effect [42]. The varied expression of quantitatively inherited characters is continuous and measurable [45].

Different mating designs possess different genetic parameters that can be estimated. For instance, the diallel or North Carolina II mating design permits for the estimation of two key genetic parameters for the set of genotypes used [42]. The two genetic parameters include: the average performance of parents in crosses, which estimates the breeding value of a given genotype due to additive gene effects, also known as general combining ability (GCA); and the deviation of individual crosses from the mean performance of parents, due to specific allelic combinations or dominance effects, also referred to as specific combining ability (SCA). A high GCA/SCA variance ratio indicates the importance of additive gene action effects, whereas a low ratio suggests the presence of dominant and/or epistatic gene effects [46]. If the SCA is smaller than the GCA, the performance of the single cross progeny is affirmed based on the GCA of the parents.

### **3.8 Estimation of genetic variances**

The phenotype is a combined expression of the genotype and environment effects. The breeder is mainly interested in determining the proportion of the phenotypic expression that is due to genotypic and environmental effects [24]. The genotypic effect of a genotype is the difference between the mean of all the phenotypes with that genotype and the mean of all the phenotypes in the population [42]. Prediction of genetic improvement expected from crossing and inbreeding requires estimation of variances between crosses. Thus, selection of a mating design for the development of progenies and their evaluation depends on its efficiency in estimating variance components [42].

The main purposes of using mating designs are: to inform breeders with vital information on the genetic control of the character under investigation; and to generate breeding population(s) that can be utilized as a source population for the selection and development of potential genotypes [47]. These purposes enable the breeder to choose an appropriate breeding strategy, thereby evaluating the genetic progress that can be expected for a given selection intensity [48].

### **3.9 Selection and evaluation stages in cassava**

Early cassava breeding efforts mostly focused on improvement of the crop for staple food for humans [13]. During this period, intensive selection was done for disease resistance and root yield potential, thereby restricting the availability of genetic variability for starch and dry matter content [49]. The general breeding objectives considered were high yield, root characteristics, adaptability to a wide range of environmental conditions, early maturity resistance to major insect pests and diseases [23, 30]. Early generation testing is a pre-requisite in self- and cross-pollinated crops to permit the estimation of the genetic potential of an individual [50]. The early generation testing and selection in cassava involves seedling and clonal (single row) stages on the basis of high heritability obtained in traits such as plant type, branching habits and reaction to certain diseases [51] and harvest index [52]. Selection can also be done on the basis of single plant performance [23]. Seedlings are usually exposed to key cassava diseases such as CMD, CBSD and CBB using spreader varieties, and susceptible seedlings are eliminated.

The selection criteria for the seedlings includes short neck (1–3 cm), fat roots that are uniform, short, and compact as well as low cyanide content [49, 53]. Seedlings that are low branching (50–100 cm) are also discarded since they are

associated with high branching habit that tends to produce low harvest index and yield [20]. Sometimes root dry matter is also used as a selection criterion [49]. The relevance of root dry matter was observed by Byrne [21] that significant correlations ( $r = 0.48^{**}$ ) exist between dry matter content in seedling and single row trials, and suggested that evaluation for this trait was feasible at the  $F_1$  stage. The selected seedlings are harvested at 12 months after planting and screened for conformation and root characteristics. Visual evaluation with few data collection is often used at the early stages of selection involving large number of materials for easy handling at reduced costs [23]. Low planting densities have been suggested for seedling population establishment to allow equal opportunity of all plants to express their genetic potential and to minimize the effects of intergenotypic competition [54]. At the clonal evaluation trial stage, competition between neighboring genotypes may favor more vigorous plant architectures [55].

At the later stages of selection, the emphasis of selection shifts from highly heritable traits to those of low heritability such as yield. At the preliminary yield trial (PYT), advanced yield trial (AYT) and regional trial (RT) stages of selection, each plot is replicated at least twice [23]. The selection is done on the basis of yield per plot, dry matter content, CNP levels, consumer acceptance, and adaptation of the crop [30]. Multi-environments trials (METs) covering a wide range of environments are done to identify clones with reasonable stability for desired traits across METs. Superior clones are evaluated on-farm for farm level testing and farmer evaluation. The clones that are the most popular with farmers are recommended for rapid multiplication, distribution and release.

## **4. Mating or breeding designs in cassava**

Many mating designs have been developed to enable breeders and geneticists to extract more genetic information from parents and progenies. These mating designs are broadly categorized into two [56]. The first is based on control over parents involved in a cross. This group is sub-divided into two: (i) control over seed parents only. Examples include top cross and polycross designs; and (ii) control over both parents and examples include diallel, partial diallel, line  $\times$  tester, North Carolina and bi-parental designs. The second broad category is based on control over parents per progeny. This is sub-divided into four including (i) one-factor designs such as top cross and polycross; (ii) two-factors designs such as bi-parental, diallel, partial diallel, line  $\times$  tester designs and generations; (iii) three factors design such as triallel design; and (iv) four factors design such as quadriallel design. Mating designs offer different hierarchical structures, such as half-, full-sib family, and individuals within family, in the progeny population. Of the mating designs highlighted above, the key ones that are often utilized in cassava breeding are discussed below.

### **4.1 Biparental mating design**

Bi-parental mating design involves selection and paired random mating of a large number of parents ( $n$ ) to obtain  $\frac{1}{2n}$  full-sib families [5]. The features of the design include (i) it is viewed as the simplest mating design [57]; (ii) it involves  $F_2$ ,  $P_1$  and  $P_2$  generations of a single cross; (iii) it requires 3 cropping seasons for generation of materials and the fourth season for evaluation; (iv) analysis is based on second order statistics and (v) it consists of full sibs or unrelated progeny. The genetic assumptions of bi-parental design are (i) random distribution of genotypes in relation to variation; (ii) random selection of plants for mating; (iii) regular



diploid segregation; (iii) absence of epistasis; (iv) equal survival of all genotypes; (v) absence of linkage; (vi) absence of maternal effects; and (vii) lack of multiple allelism.

The merits of bi-parental design are (i) it provides information on additive and dominance components of genetic variance; (ii) it is useful in selecting breeding procedure for genetic improvement of polygenic characters. The demerits of this design include: (i) it lacks the ability of providing information for estimation of all genetic parameters; (ii) use of unjustifiable assumption where critical genetic and environmental parameters are needed [48]; and (iii) overestimation of genetic component compared to environmental component where unjustified assumptions are used. Although family plots may be allotted by randomization of individual plants in the experiment to increase precision of overestimates, it is however, practically more expensive. The simpler alternative is direct estimation of VEC from families  $\times$  replicates interaction mean square in an adequately replicated trial. The layout, statistical model and analysis of variance of the bi-parental mating design are reviewed in Nduwumuremyi et al. [6].

## 4.2 Diallel mating design

Diallel mating design is a mating arrangement used in both plant and animal breeding to investigate the genetics of qualitative and quantitative trait inheritance [58]. Diallel design is the most widely used and abused of all mating designs in estimating genetic parameters [58]. The abuse is possibly related to the presence of random and fixed models used in diallel analysis [59]. In the random model, parents are random members of a random mating population, and is useful to estimate the general combining ability (GCA) and the specific combining ability (SCA) variances. The GCA estimates the mean performance of a line in hybrid combinations and is due to additive gene action. It is also the deviation of progeny mean from the mean of all lines in the experiment [5]. The variations between maternal groups are essentially due to variations in their general combining ability. The SCA measures specific hybrid crosses that perform relatively better or worse than expected mean performance of lines involved and is due to non-additive gene action [5]. It measures the dominance deviation from the additive model. Information of GCA and SCA (the types of gene action influencing various traits) enables evaluation of parental entries and selection of the best breeding system for maximum improvement of trait [60]. In this mating scheme, the general linear models are commonly used for identification of heterotic groups [59], estimation of general or specific combining ability [61], interactions with environments and years, or estimation of additive, dominance and epistatic genetic effects and genetic correlations [62].

There are essentially four main types of diallel mating design that have been reported [60]. These include: Full diallel involving parents and reciprocal crosses along with  $F_1$ , half diallel with parent and without reciprocal crosses, Full diallel without inclusion of parents, and Half diallel without parents and reciprocal crosses. In full diallel mating design, all parents, reciprocals and  $F_1$ s are mated in all possible combinations to generate hybrids [63]. The features of this design include (i) it requires twice as many crosses and entries in experiments; (ii) it permits testing for maternal and paternal effects [60]; (iii) it is required for Hardy-Weinberg equilibrium in a population [5]. The half diallel without reciprocals is effectively applied where reciprocal effects are assumed to be negligible in a diallel mating system. Other forms of diallel mating design include partial or fractional diallel mating design and disconnected half diallel mating design.

The partial diallel or fractional diallel mating design is a technique in which part of all possible crosses are made from a diallel analysis [1]. It is usually utilized in

plant breeding to evaluate parents for their combining ability [64]. Partial diallel mating design involves omission of certain crosses thereby reducing number of crosses per parent ( $n - 1$ ) without losing much precision. In the symmetric partial diallel mating,  $s$  number of crosses per parent ( $P$ ) are sampled from  $n$  number of crossing parents ( $P = 1, \dots, n$ ). The value of  $s$  is:  $2 < s < n-1$ , where  $s$  and  $n$  are number of parents and sample crosses, respectively. The  $s$  and  $n$  differentially odd and even (i.e.  $s$  is even where  $n$  is odd and vice versa, but  $s \neq n-1$ ). The number of crosses generated for selected  $s$  and  $n$  is:  $C = \frac{ns}{2}$ . The  $C$  is developed based on the sampling constant  $K = \frac{n+1-s}{2}$ , which is an absolute number variance between one parent and other parents to be crossed with the former [56]. The features of partial diallel analysis are (i) it uses one type of analysis (ii) it uses one method of combining ability (iii) it involves direct crosses; (iv) it involves sampling of crosses (v) it evaluates more parents than diallel; and (vi) helps in selection of parents and breeding procedures [64].

The merits of partial diallel analysis include (i) it estimates heritability, genetic advance and heterosis; (ii) it is also utilized in open pollinated species with problem of male sterility [64]; (iii) the GCA of the parents are estimated with less precision, but larger gains may result from intense selection among a larger number of parents; (iv) selection can be done among crosses from many parents; and (v) where the parents represent a population, the variance for general combining ability can be estimated more accurately [65]. Some demerits of partial diallel analysis are: (i) each parent equal chance of mating and recombining with every other parent [64]; (ii) its analysis is complex; (iii) it does not estimate difference between each pair of GCA effects with same precision; and (iv) an unsuccessful cross further creates imbalance in partial diallel mating, whereas such missing cross can be tolerated without significant loss of balance in diallel design [56].

### 4.3 Polycross mating designs

Polycross is the natural intermating or crossing among group of genotypes in isolated block [6]. It was first used by Tysdal, Kiesselbach and Westover in 1942, in relation to progenies obtained from outcrossed plants in a nursery [48]. Polycross design has been used for various plants that are obligate crossers such as tree crops, forage grasses, sugarcane, legumes and especially roots and tubers that are propagated by vegetative means, i.e. cassava, sweet potato and yam [5]. Polycross design accords equal chance of natural intermating among plants thereby eliminating the possibility of selfing and hand pollination [56]. Although polycross design in cassava breeding does not prevent self-pollination, however, it produces more cross-bred botanical seeds than controlled pairwise pollination techniques [13]. Self-pollination can be minimized in polycross blocks by emasculating plants located near an intercrossing population [13]. The genetic basis of polycross is similar to topcross, but differing with its characteristic wider genetic background of pollen source.

The features of a polycross nursery include: (i) it is adequately isolated to safeguard against foreign pollen grains; (ii) it consists of small plot size and highly replicated compact blocks to permit large number of test genotypes; (iii) plots and blocks are arranged in all directions that permit random pollination by wind; and (iv) two to three border rows of seed mixture of test inbreds.

The mating arrangement of putative candidates or entries is critical for successful random mating in the polycross block [26]. Latin square design has been considered most appropriate for equal random intermating among entries in a polycross nursery [66], however, where entries are more than 10, completely randomized block design could be used [5]. About 20–30 replications are used in the crossing block of the two designs. Ideal criteria for use of polycross is practically

hard to fulfill due to several limitations such as cross incompatibility, male sterility, irregular- and non-flowering and lack of flowering synchronization, nonrandom dispersal of pollen, among others cause deviation from random mating. Plant breeders often use sequential planting of genotypes with different flowering dates for synchronization of flowering and crossing.

The progenies of each of the test genotypes are half-sib families. They are collected separately and mixed over replications and evaluated. For instance, if six inbreds will produce six polycross bulk seed samples, these samples and parental seeds are grown in replicated randomized complete blocks design. Data are collected in the same fashion as the top cross mating trial [56]. The covariance within the families is estimated as:  $Cov(HS) = \frac{1+F}{4} \sigma_A^2$  where F is the inbreeding coefficient of the genotypes being tested. The statistical models for  $r_{OP}$ ,  $b_{OP}$  and  $b_{AP}$  are similar to those of top cross design. In polycross,  $b_{AP} = \frac{Cov(AP)}{2 var(P)}$  since only one parent is known [56].

The merits of polycross design lie in its applications such as in the development of synthetic cultivars, recombination of selected entries in recurrent selection breeding, or evaluation of GCA of entries [5]. It is used for identification of maternal parents with superior genotypes based on general combining ability reflected in the performances of the progenies [6]. Conventionally, half sibs are developed from individual maternal parent. However, paternal parents could be identified using DNA fingerprinting and parentage analysis. Polycross is useful in determining variance components, GCA and heritability. The variance components and GCA are determined from the average performance of the progenies of individual maternal parents. Variations measured in a progeny are partitioned into within and between maternal parents [26]. The estimated heritability obtained reveals the usefulness of polycross and guides the choice of progenies in breeding programme [56].

The demerits of polycross include insufficient statistics to estimate all genetic parameters, expected genetic gains are reduced by half since the components of variance are estimated from maternal half sibs; information about the males is lost, there is no control over the pollen source; nonrandom mating may occur due to lack of flowering synchronization, unequal pollen production and/or position effects within crossing block [6]. Environmental variability greatly influences flowering and performances of the parents and progenies possibly due to their diverse origins and heritability of traits [6, 66]. These factors could affect the accuracy of GCA and heritability estimates suggesting a cautionary note on their use.

#### 4.4 Line $\times$ tester mating design

The line  $\times$  tester mating design involves mating between lines (f) and testers to generate 'fm' hybrids [56]. It is the simplest design that simultaneously provides full-sibs and half-sibs compared to topcross which only exhibits half-sibs. The line  $\times$  tester technique was introduced by Kempthorne [67] as one of the powerful tools used to estimate the combining ability effects and assist selection of desirable parents and crosses for pedigree breeding [68].

The main features of the lines  $\times$  tester design are (i) mf crosses are needed in which 'm' is male and 'f' is female; (ii) it provides information on germplasm lines; (iii) it consists of simple analysis compared to complex designs; and (iv) it follows both first and second order statistics [56].

The main features of a good tester include (i) broad genetic base; (ii) wider adaptability; (iii) low yield potential; and (iv) low performance of other traits [56].

The linear model for line  $\times$  tester design is:  $Y_{ijk} = \mu + g_i + g_j + S_{ij} + r_k + e_{ijkl}$  where:  $Y_{ijk}$  = observed value of the cross  $i \times j$  in the  $k^{\text{th}}$  replication;  $\mu$  = population

mean effect;  $g_i$  = GCA effect of  $i^{\text{th}}$  tester;  $g_j$  = GCA effect of  $j^{\text{th}}$  line;  $S_{ij}$  = SCA effect of the cross  $i \times j$ ;  $r_k$  = effect of the  $k^{\text{th}}$  block;  $e_{ijkl}$  = experimental error due to  $(ijk)^{\text{th}}$  individual. Detailed explanation of the model is reported in Karim et al. [69].

Some merits of line  $\times$  tester design are (i) it facilitates selection of desirable parents and breeding procedure via measurement of genetic components of variance; (ii) it is good for estimation of genetic gains from both  $V_A$  and  $V_D$  and evaluation of germplasm; (iii) it provides heterosis, heritability and genetic advance estimates [56]; (iv) it is useful in determining types of gene actions involved in the expression of quantitative traits [70]. Some demerits of the line  $\times$  tester design are (i) it does not estimate epistasis variance, (ii) it lacks equal change of random mating [56]; (iii) limited selection intensity; and (iv) high cost.

#### 4.5 North Carolina mating designs

The North Carolina designs were developed to improve the efficiency and save time that restrained diallel mating design. The North Carolina designs I, II, and III were developed in 1952 by Comstock and Robinson.

The general features of the NC designs include:

- i. Effective in breaking undesirable linkages – mating randomly selected plants in segregating population.
- ii. Selection of suitable breeding procedure for polygenic traits.
- iii. Useful for self- and cross-pollinated species.
- iv. Used in the generation of variability – creating heterozygosity.
- v. The bi-parental mating permits evaluation of segregating ( $F_2$  or later generation) population of individual cross made between two inbred lines.
- vi. It provides information on two components of genetic variance i.e. additive and dominance variance.
- vii. It is useful in the selection of suitable breeding procedures.

Despite these applications, the North Carolina designs are (i) not applicable to the segregating populations of three way, double and multiple crosses; (ii) does not permit several simultaneous segregating crosses; (iii) does not provide information on the epistatic variance; and (iv) analysis is difficult as it is based on second order statistics.

The specific characteristics and applications of the various NC designs are summarized in **Table 1**.

Of the three North Carolina designs summarized in **Table 1**, NC I and II are often utilized in root and tuber breeding programmes. The North Carolina I mating design (nested design) is a hierarchical design that involves mating between each common male and different sets of female parents. It is widely applicable in theoretical and practical plant breeding [5]. The statistical model for NC I design is:  $Y_{ijk} = \mu + m_i + bf_{ij} + r_k + \mathcal{E}_{ijk}$  where  $Y_{ijk}$  = observed value from each experimental unit;  $\mu$  = population mean;  $m_i$  = effect of the  $i^{\text{th}}$  male;  $f_{ij}$  = effect of the  $j^{\text{th}}$  female mated to the  $i^{\text{th}}$  male,  $r_k$  = replication effect, and  $\mathcal{E}_{ijk}$  = experimental error [58].

The merits of this design include (i) it is useful for both self- and cross-pollinated species; (ii) it is utilized for estimation of additive and dominance variances; (iii) it is



| No. | North Carolina Design I (NC I)  | North Carolina Design II (NC II)   | North Carolina Design III (NC III)  |
|-----|---|--|---|
| 1   | Each male is mated to a different group of females.   | Each male is mated to the same group of females.                                     | Each male is mated to both inbred parents of original cross.                        |
| 2   | ‘f’ crosses are obtained.   | ‘mf’ crosses are obtained.   | ‘2 m’crosses are obtained.  |
| 3   | Variance is divided into 2 parts: males and females.  | Variance is divided into 3 parts: males, females and male × female.                  | Variance is divided into 2 parts: male and male × female.                           |
| 4   | Variance due to male provides an estimate of additive variance ( $V_A$ ).                           | Variance due to male and female provides an estimate of additive variance ( $V_A$ ). | Variance due to male provides an estimate of additive variance ( $V_A$ ).           |
| 5   | Variance due to female provides an estimate of additive ( $V_A$ ) and dominance variance ( $V_D$ ). | Variance due to male × female provides an estimate of dominance variance ( $V_D$ ).  | Variance due to male × female provides an estimate of dominance variance ( $V_D$ ). |
| 6   | It requires 10–12 times more area than design 3.  | It requires 2–3 times more area than design 3.                                       | It requires much less area than designs 1 and 2.                                    |
| 7   | It is influenced by the presence of maternal effects.   | It is influenced by the presence of maternal effects.                                | It is not affected by the presence of maternal effects.                             |
| 8.  | It involves $F_2$ plants in crossing.   | It involves $F_2$ plants in crossing.  | It involves $F_2$ , $P_1$ and $P_2$ plants in crossing.                             |
| 9.  | It is least powerful design.  | It is intermediate design.   | It is most powerful design.   |

Source: *Acquaah* [5].

**Table 1.**  
*Characteristics of North Carolina designs.*

used to evaluate full- and half-sibs in recurrent selection; (iv) it is widely used in animal studies, as well as maize breeding for determination of genetic variances [5]; (v) its merit over biparental and polycross designs, is that it gives three statistics, whereas biparental and polycross designs give two statistics [71].

The demerits of NC I are (i) it is practically inapplicable in breeding species that produce few amounts of seed, since the technique requires sufficient seeds for replicated evaluation trials; and (ii) it does not account for epistatic variance.

The North Carolina II (NC II) mating design is a factorial design that has been modified from NC I design by Comstock and Robinson [72]. In the NC II design, each progeny family exhibits half-sib relationships through common male and common female. It is most adapted to plants with multiple flowering that facilitate repeated use of each as male and female parents.

The NC II is used to estimate genetic variances and to assess inbred lines for combining ability [73]. In NC II, an equal number of different sets of females and males is randomly selected from an  $F_2$  population, with each male mated with a female to create female half-sib (HS) groups and male HS groups [46]. This is achieved through systematic crossing of  $n_1$  male and  $n_2$  female in all possible mating combinations to give  $n_1n_2$  progeny families [5]. Reciprocal crosses are if the objective is to analyze for maternal effects [48]. The mean squares for the female and male sets produce separate and independent estimates of the additive component of variation. The additive variance estimates obtained include variance due to males, and variance due to females. This technique also produces an estimate of non-additive genetic variance (dominance variance) from the interaction mean squares obtained between the males and females.

The difference between the mean performance of the progeny of a given male and the mean of the progeny of all the males used in the crosses is the GCA. The GCA gives an indication of how well the genes combine, on average, to produce the best progeny when crossed to a random sample of females in the population. The GCA is often obtained from the mean square (MS) between HS family groups. The occurrence of significant deviation from the mean performance of the progeny is attributable to dominance or epistatic effects. The deviations of specific individual crosses are estimated from the 'male  $\times$  females' MS in the ANOVA of the NC II [46].

If the number of males and females are the same ( $n_1 = n_2$ ), the magnitude of the maternal effects is estimated from the variance ratio MSF/MSM [46]. The NC II design provides additive and dominance variance estimates ( $V_A$  and  $V_D$ ) and a test of significance, thereby permitting the estimation of heritability [46].

The merits of NC I mating design are: (i) the NC II is useful for estimation of both GCA and SCA [5]; (ii) there is possibility of analyzing for maternal effects using reciprocal crosses [48]; (iii) the design is useful for evaluation of inbred lines for their combining abilities; (iv) it provides estimates of genetic gains from both  $V_A$  and  $V_D$ ; and (v) it provides good information for parents and full-sib families. The demerits of this design include: (i) it lacks estimate of epistasis or  $G \times E$  interaction effect [46]; (ii) limited selection intensity; and (iii) high cost.

## 5. Conclusions and future prospects

This chapter articulates features, applications, analysis, merits, demerits, the role and progressive modifications of mating designs in explaining the nature of quantitative variation for their use in plant breeding and genetics. The choice of appropriate parents and mating design depends on critical factors of genetic, environmental, interaction between the genotype and environment, etc. A good knowledge of the flower and pollination biology, total genetic variance due to genetic and environmental influence guides meaningful decision on resource allocation and expected response to selection. Moreover, the use of appropriate experimental design and statistical technique would help plant breeders to estimate and explain the type of gene action existing in parents and progenies. Half-sibs generated in some of the designs can be resolved using DNA fingerprinting or parentage analysis. The use of integrated conventional-molecular techniques increases precision and efficiency in plant breeding. However, as efficient molecular techniques emerge, economic phenotyping of mega trials still remains a challenge.

## Acknowledgements

The authors are thankfully grateful to scientists at the International Institute of Tropical Agriculture (IITA) and lecturers at the University of Ghana whose supports have been tremendous in building our careers.

## Conflict of interest

The author declares no conflict of interest.

Appendices

Appendix 1. Analysis of variance (ANOVA) for bi-parental mating design

| Source of variation | Degree of freedom               | Mean square | Expected mean square        |
|---------------------|---------------------------------|-------------|-----------------------------|
| Between families    | $\left(\frac{a}{b}n\right) - 1$ | $M_1$       | $\sigma_w^2 + r \sigma_b^2$ |
| Within families     | $\frac{a}{b}n(r - 1)$           | $M_2$       | $\sigma_w^2$                |
| Total               | $\frac{a}{b}nr - 1$             |             |                             |

Source: Acquaah [5].

Appendix 2. Analysis of variance (ANOVA) for full diallel mating design (Method I)

| Source of variation | Degree of freedom  | Sum of squares | Mean squares | Expected mean squares  |  |
|---------------------|--------------------|----------------|--------------|--|--|
|                     |                    |                |              | Model I  | Model II   |
| GCA                 | $(p - 1)$          | $S_g$          | $M_g$        | $\sigma^2 + 2p\left(\frac{1}{p-1}\right)\sum g_i^2$              | $\sigma^2 + \frac{p(p-1)}{2}\sigma_s^2 + 2p\sigma_g^2$ |
| SCA                 | $\frac{p(p-1)}{2}$ | $S_s$          | $M_s$        | $\sigma^2 + \frac{2}{p(p-1)}\sum\sum S_{ij}^2$                   | $\sigma^2 + \frac{2(p^2-p+1)}{p^2}\sigma_s^2$          |
| Reciprocal eff.     | $\frac{p(p-1)}{2}$ | $S_r$          | $M_r$        | $\sigma^2 + 2\left(\frac{2}{p(p-1)}\right)\sum_{i < j} r_{ij}^2$ | $\sigma^2 + 2\sigma^2r$                                |
| Error               | $m$                | $S_e$          | $M_e$        | $\sigma^2$   |  |

Source: Griffing [59].

Appendix 3. Analysis of variance (ANOVA) for half diallel with parents and without reciprocal crosses mating design (Method II)

| Source of variation | Degree of freedom  | Sum of squares | Mean squares | Expected mean squares                                    |                                |
|---------------------|--------------------|----------------|--------------|--|--------------------------------|
|                     |                    |                |              | Model I  | Model II                       |
| GCA                 | $(p - 1)$          | $S_g$          | $M_g$        | $\sigma^2 + (2 + p)\left(\frac{1}{p-1}\right)\sum g_i^2$ | $\sigma^2 + (p + 2)\sigma_g^2$ |
| SCA                 | $\frac{p(p-1)}{2}$ | $S_s$          | $M_s$        | $\sigma^2 + \frac{2}{p(p-1)}\sum\sum S_{ij}^2$           | $\sigma^2 + \sigma_s^2$        |
| Error               | $M$                | $S_e$          | $M_e$        | $\sigma^2$   |                                |

Source: Griffing [59].

Appendix 4. Analysis of variance (ANOVA) for full diallel without inclusion of parents mating design (Method III)

| Source of variation | Degree of freedom    | Sum of squares | Mean squares | Expected mean squares   |                                  |
|---------------------|----------------------|----------------|--------------|---|----------------------------------|
|                     |                      |                |              | Model I   | Model II                         |
| GCA                 | $(p - 1)$            | $S_g$          | $M_g$        | $\sigma^2 + 2p(p - 2)\left(\frac{1}{p - 1}\right) \sum g_i^2$       | $\sigma^2 + 2(p - 2) \sigma_g^2$ |
| SCA                 | $\frac{p(p - 3)}{2}$ | $S_s$          | $M_s$        | $\sigma^2 + \frac{2}{p(p - 3)} \sum \sum S_{ij}^2$                  | $\sigma^2 + 2 \sigma_s^2$        |
| Reciprocal eff.     | $\frac{p(p - 1)}{2}$ | $S_r$          | $M_r$        | $\sigma^2 + 2\left(\frac{2}{p(p - 1)}\right) \sum_{i < j} r_{ij}^2$ | $\sigma^2 + 2 \sigma^2 r$        |
| Error               | $M$                  | $S_e$          | $M_{e'}$     | $\sigma^2$  | $\sigma^2$                       |

Source: Griffing [59].

Appendix 5. Analysis of variance (ANOVA) for half diallel without parents and reciprocal crosses mating design (Method IV)

| Source of variation | Degree of freedom    | Sum of squares | Mean squares | Expected mean squares                                       |  |
|---------------------|----------------------|----------------|--------------|---|--|
|                     |                      |                |              | Model I   | Model II                                   |
| GCA                 | $(p - 1)$            | $S_g$          | $M_g$        | $\sigma^2 + (p - 2)\left(\frac{1}{p - 1}\right) \sum g_i^2$ | $\sigma^2 + \frac{p(p - 1)}{2} \sigma_g^2$ |
| SCA                 | $\frac{p(p - 3)}{2}$ | $S_s$          | $M_s$        | $\sigma^2 + \frac{2}{p(p - 3)} \sum \sum S_{ij}^2$          | $\sigma^2 + \sigma_s^2$                    |
| Error               | $M$                  | $S_e$          | $M_{e'}$     | $\sigma^2$  | $\sigma^2$                                 |

Source: Griffing [59].

Appendix 6. Skeleton Analysis of variance (ANOVA) for partial or fractional diallel mating design

| Source of variation | Degree of freedom | Sum of square | Mean square | Expected mean square   |
|---------------------|-------------------|---------------|-------------|--|
| Replication (r)     | $(r - 1)$         | $rSS$         | $rMS$       | —  |
| Crosses (c)         | $(c - 1)$         | $cSS$         | $cMS$       | —  |
| GCA (n)             | $(n - 1)$         | $gSS$         | $gMS$       | $\sigma_r^2 + r \sigma_s^2 + \frac{rs(n - 2)}{(n - 1)} r \sigma_s^2$ |
| SCA (s)             | $(c - n)$         | $sSS$         | $sMS$       | $\sigma_r^2 + r \sigma_s^2$  |
| Error (e)           | $(c - 1)(r - 1)$  | $eSS$         | $eMS$       | $\sigma_r^2$   |
| Total               | $(cr - 1)$        | $TSS$         |             |  |

Source: Sharma [56].



Appendix 7. Analysis of variance (ANOVA) for polycross mating design

| Source of variation | Degree of freedom | Mean square | Expected mean square                    | Variance components  |
|---------------------|-------------------|-------------|---|--|
| Progenies           | $(g - 1)$         | $M_1$       | $\sigma_e^2 + r \sigma_{\text{prog}}^2$ | $\sigma_{\text{prog}}^2 = \text{Cov}(HS) = \frac{1+F}{4} \sigma_A^2$ |
| Blocks              | $(r - 1)$         | $M_2$       | —                                       | —  |
| Error               | $(g - 1)(r - 1)$  | $M_3$       | $\sigma_e^2$                            | $\sigma_e^2 = \sigma^2$  |

Source: Nduwumuremyi et al. [6]; Wricke and Weber [74].

Appendix 8. Analysis of variance (ANOVA) for line × tester mating design

| Source of variation | Degree of freedom | Mean square | Expected mean square   |                                     |
|---------------------|-------------------|-------------|--|-------------------------------------|
|                     |                   |             | Model I  | Model II                            |
| Replication ( $r$ ) | $(r - 1)$         |             |  |                                     |
| Genotype ( $g$ )    | $(g - 1)$         | $MS_2$      |  |                                     |
| Parents ( $p$ )     | $(p - 1)$         |             |  |                                     |
| Crosses ( $c$ )     | $(c - 1)$         |             |  |                                     |
| Lines ( $m$ )       | $(m - 1)$         | $M_m$       | $\sigma^2 + rf\left(\frac{1}{m-1}\right) + \sum g_i^2$                   | $\sigma^2 + v_{sca} + rf_{gca(m)}$  |
| Testers ( $f$ )     | $(f - 1)$         | $M_f$       | $\sigma^2 + rm\left(\frac{1}{f-1}\right) + \sum q_j^2$                   | $\sigma^2 + rv_{sca} + rm_{gca(f)}$ |
| Lines × testers     | $(m - 1)(f - 1)$  | $M_{mxf}$   | $\sigma^2 + r\left[\frac{1}{(m-1)(f-1)}\right] + \sum_i \sum_j q_{ij}^2$ | $\sigma^2 + rv_{sca}$               |
| Error               | $(r - 1)(mf - 1)$ | $MS_1$      | $\sigma^2$   | $\sigma^2$                          |

Where  $MS_2$  = genotypic mean square,  $M_m$  = line mean square,  $M_f$  = tester mean square,  $M_{mxf}$  = line × tester mean square, and error  $MS_1$  = mean square. Adapted from Nduwumuremyi et al. [6] and Fellahi et al. [75].

Appendix 9. Analysis of variance (ANOVA) for North Carolina design II

| Source of variation | Degree of freedom | Mean square | Expected mean square                           |
|---------------------|-------------------|-------------|--|
| Replication         | $(r - 1)$         |             |  |
| Males               | $(m - 1)$         | $M_1$       | $\sigma_w^2 + r \sigma_{mf}^2 + rf \sigma_m^2$ |
| Females             | $(f - 1)$         | $M_2$       | $\sigma_w^2 + r \sigma_{mf}^2 + rm \sigma_f^2$ |
| Males × females     | $(m - 1)(f - 1)$  | $M_3$       | $\sigma_w^2 + r \sigma_{mf}^2$                 |
| Within progenies    | $mf(r - 1)$       | $M_4$       | $\sigma^2$                                     |
| Error               | $(mf - 1)(r - 1)$ | $M_5$       | $\sigma_w^2$                                   |
| Total               | $rmf - 1$         |             |  |

Source: Kearsey and Pooni [52].

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