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Chapter

Heterosis and Heterotic Grouping among Tropical Maize Germplasm

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Abstract

Maize (*Zea mays* L.) is the most important staple cereal cultivated in sub-Saharan Africa but its productivity is considerable low due to several factors. Development and deployment of maize hybrids have been reported as one of the crucial options in achieving sustainable maize production in sub-Saharan Africa. Information on the heterotic response among available genetic materials in a breeding program is valuable before commencement of any hybrid development program. Unlike the temperate germplasm, maize tropical germplasm is characterized with wide genetic base and genetic complexities and thus, proper organization of the pools, populations, varieties and inbreds that can serve as parental materials for hybrid development through identification of a distinct heterotic groups and patterns among tropical germplasm becomes very essential. This paper reviewed past research efforts at characterizing heterotic response among tropical maize genetic materials with a view to point out merits and demerits in the methods used and future direction towards achieving sustainable hybrid cultivation and enhancing food security in the sub-region.

Keywords: combining ability, gene action, heterotic grouping, hybrids, tropical maize

1. Introduction

The term 'heterosis', as first introduced by Shull in 1909, was used to describe the phenomenon when the mean of any character or characters in a hybrid exceeds the mean of its descendants obtained by any system of close inbreeding. Four hypotheses were proposed to explain this; the dominance hypothesis which postulates that the increase in vigor after crossing results from the combination of different dominant alleles contributed by each parent [1]. The heterozygosis hypothesis attributes the increase in vigor to the existence of loci at which the heterozygous state is superior to either homozygotes [2, 3]; the pseudo-overdominance hypothesis that attributes the hybrid vigor to the effect of tightly linked genes with favorable dominant alleles in repulsion phase in the parental lines resulting in an apparent overdominance when combined in the hybrid [4] and epistasis hypothesis which explains the increased vigor in the light of the interaction of favorable alleles from two parents at different loci that show additive, dominant and/or overdominant action [5]. Among these hypotheses, heterozygosis gained prominence. Milborrow [6] asserted, from physiology view point, that even though the growth of a plant may be limited by the genes that regulate certain metabolic pathway down to a lower level than the maximum possible, heterozygous plants may partially escape the growth regulation, thereby giving them advantage over the homozygous

individuals. Brieger [7] explained that heterosis is easily obtained when the parents from which the hybrids are produced are inbreds or purelines and that heterosis does not affect the individual plant as a whole, but the expression of each of the traits that are heterotic. For instance, characters in maize that are affected by heterosis include plant and ear heights, size of leaves, intensity, size and strength of root system, amount of pollen shed, number and size of kernels and response to biotic and abiotic stresses [7]. Characters such as earliness to maturity, row number of the ear, plant and kernel color are not heterotic characters.

Two types of heterosis have been described in literatures. Falconer and Mackay [8] defined mid-parent heterosis as the difference between the hybrid and the mean of the two parents. They also defined high- or best-parent heterosis as the difference between the hybrid mean and the mean of either of the parent. Mid-parent heterosis value has been of more importance because it provides the basis for the identification of heterotic patterns among a fixed set of populations/inbred lines [9]. Melani and Carena [10] asserted that the utilization of mid-parent values is an effective practical method to identify heterotic responses among parents.

A heterotic group has been defined as a collection of germplasm that, when crossed with germplasm from an external group, tends to exhibit a higher degree of heterosis (on the average) than when crossed with a member of its own group [11]. Melchinger and Gumber [12] also defined heterotic group as a collection of related or unrelated genotypes from the same or different populations, which display similar combining ability and heterotic response when crossed with genotypes from other genetically distinct germplasm groups. Heterotic pattern refers to a specific pair of two heterotic groups, which express high heterosis and consequently high hybrid performance in their cross. Melchinger and Gumbler [12] recommended the following criteria for the choice of heterotic pattern in hybrid breeding; (i) high mean performance and large genetic variance in the hybrid population; (ii) high *per se* performance and good adaption of the parent population to the target regions; and (iii) low inbreeding depression, if hybrids are produced from inbred lines. Establishing heterotic pattern is of prime importance in the development of a successful maize hybrid program [13].

2. Heterotic grouping methods for maize germplasm.

After establishing significant genetic variability among parental materials to use, plant breeders employ several methods for classifying the parents into heterotic groups. The methods include morphological traits, pedigree method, multivariate technique, genetic methods involving mating designs and the use of molecular markers. At advanced stage of breeding, genetic and molecular methods are preferred because of their high level of precision since their results are minimally influenced by environmental factors. Among several mating designs in plant breeding, three are prominent for classifying parents into heterotic groups. Where proven testers exist in a breeding program, a line x tester mating design is embraced in which each tester represent a heterotic group. Where there is no proven testers, diallel method and North Carolina Design II become better alternatives. In studies where such designs are employed, information on heterotic groups as well as identification of testers are usually the prime objectives. The advent of molecular markers has offered a less-stressful, faster, smarter and somewhat cheaper alternative through the use of genetic distance. Examples of markers for popularly used this purpose are Amplified Fragment Length Polymorphism (AFLPs), Simple Sequence Repeats (SSRs) and Single Nucleotide Polymorphism (SNPs) markers. The qualities

of these markers that make them suitable for this purpose include the following: high throughput, they are highly reproducible and they are relatively easy to assay. In more recent times, SNPs markers has become the most popular and marker technologies include Microarray and DarT and DarTSeq have been developed on the basis of SNPs.

3. Classifying tropical maize germplasm into heterotic groups and identifying heterotic pattern

In temperate maize germplasm, distinct heterotic groups and establishing clear heterotic patterns such as European flint x US Lancaster, which is commonly used in Europe and Reid Yellow Dent x Lancaster extensively exploited in US, China [14, 15] and many parts of the world ([10, 16]). Paterniani [17] noted that there is lack of information on the heterotic response among tropical maize germplasm and that might be due to the existence of the large number of races and cultivars that were yet to be studied, thus making it difficult to have well-defined heterotic patterns in tropical maize. By then, only a few studies have been conducted to establish heterotic patterns of the tropical maize germplasm [18]. An earlier study reported a combination of Tuxpeno with Eto and other Carribean flints as a promising heterotic pattern [19]. The study also established Tuson x Tuxpeno, Cuban flint × Tuxpeno, and Suwan 1 x Tuxpeno as promising combinations for hybrid production in the tropics. Previous studies on the heterotic pattern using late/intermediate maturing inbred lines from IITA could not establish clear heterotic patterns [20–22]. The reason adduced for the results was that the inbred lines were derived from source populations formed by mixing different germplasm without taking into consideration the need to maintain heterotic groups intact [22]. Menkir *et al.* [20] recommended a combination of divergent testers with molecular markers as a better alternative to classifying tropical maize inbred lines. On this basis, Menkir *et al.* [23] attempted to classify 38 tropical maize inbred lines into heterotic groups using two testers (TZMI102 and TZMI 1407) and molecular markers. The testers successfully classified 23 out of 38 inbreds into two heterotic groups. The results of the classification based on AFLP and SSR markers were found to be largely consistent with each other but the molecular markers classified the same inbreds into groups different from those classified by the testers. The authors concluded that the line x testers method used was found to be more efficient in classifying the inbreds than the molecular markers and recommended that the molecular marker-based grouping might at best serve as a basis for designing and carrying out combining ability studies in the field for tropical maize germplasm. However with the advent of more efficient markers for genetic diversity assessment, the result appears more promising.

A similar study by Barata and Carena, [13] in their comparative analysis of heterotic grouping of maize inbreds using diallel analysis method and SSR markers corroborated the above findings and recommended extensive field evaluation as being more appropriate in assigning unrelated maize inbred lines into heterotic groups.

Breeders at national and international research institutes in sub-Saharan Africa have developed thousands of inbred lines over years and several efforts have been made to identify defined heterotic groups that can be utilized in the sub-region.

Badu-Apraku *et al*. (2005) used multivariate techniques to classify 47 inbreds based on morphological traits and 4 groups were identified. They however, considered the grouping to be preliminary since morphological traits can be greatly influenced by environmental factors. Badu-Apraku et al. [24] also selected promising

inbred parents based on multiple morphological traits under stress and non-stress environments using genotype main effect and genotype by environment interaction (GGE) biplot.

Wu *et al.* [25] classified 27 maize inbreds into four distinct heterotic groups using North Carolina Design II. Agbaje *et al.* [26] used a line x tester method to classify 35 early maturing yellow endosperm inbred lines into heterotic groups with two testers, TZi 4001 and Ku1414 evaluated under *Striga*-infested and *Striga*-free conditions at Mokwa and Abuja and in *Strig*a-free environment at Ile-Ife, Nigeria. None of the inbred lines could be classified into heterotic groups under any of the evaluation environments, evidently because the testers were not sufficiently effective to discriminate among the inbreds. Furthermore, Badu-Apraku *et al.* [27] could neither identify definite heterotic groups, nor identify ideal testers in a diallel study among nine yellow-grained early maize inbreds using the genotype main effect plus genotype-by-environment interaction (GGE) biplot analysis. The reason they adduced for this was the overdominating effect of SCA relative to GCA effects. Nevertheless, distinct tester groups were identified. In their study of heterosis and genetic distance among 17 lowland white-grained tropical maize under drought stress and non-stress conditions using diallel and RFLP markers, Betran *et al.* [28] found that the degree of inbreeding of the parental lines could affect their response to stress. They also observed that the environment significantly affected the correlations of genetic distance with lower values observed under more stressed conditions. They equally opined that optimal nonstress environments where grain yield is maximal could be more appropriate to measure SCA effects and the predictive value of genetic distance.

Conventionally in quantitative genetics, SCA effects of inbreds have always been used to classify genetic materials into heterotic groups. This is based on the assumption that SCA of two lines from different heterotic groups is greater than those from the same group. However, the reliability of this method is dependent on the number of materials investigated and adequate sampling of the genetic background. Fan *et al.* (2008) used heterotic group's Specific and General Combining Ability (HSGCA), a combination of SCA and GCA effects, to assign some tropical maize inbreds into heterotic groups instead of the traditional method involving SCA effects only. This proposition was on the basis that SCA effects were often greatly influenced by the interaction between two inbred lines and between hybrids and environments, which often times lead to assigning the same inbred line into different heterotic groups under different studies (Fan *et al.*, 2008). Results of the study showed that HSGCA method was more effective than the use of SCA and molecular marker methods in classifying tropical maize germplasm into distinct heterotic groups. Akinwale et al. [29] attempted to classify 28 tropical inbred lines into heterotic groups using SCA yield, HSGCA and SSR-based molecular markers and reported that HSGCA was most efficient. They also reported that classifying inbreds based on SCA-yield under non-stress environment was closely related to the groups established by SSR markers.

Because yield is a complex trait and possesses low heritability, improvement progress based on direct selection is usually very slow. Most of the methods used for heterotic grouping are based on single trait, yield. Therefore, Badu-Apraku et al. [30] devise another method, heterotic groups based on General Combining Ability of Multiple Traits (HGCAMT), which integrate general combining ability effects of multiple traits especially where additive gene effects are predominant over non-additive effects for such traits. Comparing the HGCAMT method with other grouping methods, it was reported that results obtained were consistent with those of HSGCA, yield-SCA and SNP marker-based genetic distance under stress environment and even more effective than other methods across multiple stress

environments [31, 32]. Badu-Apraku and Akinwale [33] in another line by tester study among 63 lines by 4 testers using GGE biplot concluded that the GGE biplot method was efficient in classifying the inbreds.

It should be noted that heterotic grouping of tropical maize germplasm is greatly influenced by factors. The amount of genetic diversity among parental lines evaluated is a major factor. Badu-Apraku et al. [27] reported in a diallel study among nine yellow maize inbreds that the genetic diversity was small and therefore distinct heterotic groups could not be identified. The inbreds could only be classified into tester groups. In another similar study with white inbreds, significant genetic diversity was recorded and two clear heterotic groups were identified among set of 9 inbreds [34]. Another important factor affecting heterotic grouping is the type of gene action preponderant in the set of parents under study. Heterotic groups are clearly identified when both additive and non-additive gene action are significant and there is preponderant of additive gene action over non-additive gene action [31, 32, 35]. In any study where these conditions are not met, distinct heterotic groups cannot be identified. The third factor that affects heterotic grouping among tropical germplasm is the type of mating design and heterotic grouping method used in the study. Heterotic grouping are conventionally based on combining ability effects, which are obtained from different mating designs employed in various genetic studies. It should be noted that among all mating designs, cross classification/ factorial mating designs are the only type of design that are useful for heterotic grouping combining ability effects of the parents and hybrids can only be estimated using this type of mating designs. Examples of these designs are diallel, North Carolina Design II and line x tester design. Among these designs, diallel mating design has proved to be the most valuable design and most popularly used especially when evaluating a sizable number of parents for the purpose of heterotic grouping and identification of testers ([29]: [27, 34]). North Carolina design II added the advantage of being able to classify more parents more efficiently. Based on the type of combining ability effect used in the classification, three grouping methods are commonly used; yield's specific combining ability effects (SCA) [20], heterotic group's general and specific combining ability effects (GCA + SCA) [36] and heterotic group's general combining ability effects of multiple traits (HGCAMT) [30]. Each of these grouping methods gives different heterotic groups and the efficiency of these methods differ depending on the mode of gene action prevalent for the trait(s) under study. For instance, the use of HGCAMT (which is predominantly based on additive gene action for classification) is grossly inappropriate where non-additive gene action is prevalent. The fourth factor affecting heterotic grouping is the environmental complexes including environmental stresses such as drought, striga infestation, insect infestation, and low soil N, which characterize production environment in the sub-Saharan Africa. Different groups, in terms of number of groups and constitution of each group, are created among the same set of parents but under different research environments ([29]: [31, 32, 35]: [33]). These factors and their interaction are very important in grouping tropical maize germplasm and to establish a clear heterotic pattern with broad application to tropical germplasm, which in turn will greatly facilitate development and deployment of superior maize hybrid in the sub-region. It is therefore recommended that research efforts should be intensified to study these factors and how some of them interact in order to decipher the genetic complexities and environmental complexes that characterize maize production and productivity in sub-Saharan Africa.

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