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Gene Action and Heterotic Response of Elite Maize Varieties under Varying Growing Conditions in Rain-Forest Agro-Ecology of Nigeria

A THESIS

IN THE RURAL POLYTECHNIC INSTITUTE OF TRAINING AND APPLIED RESEARCH IN PARTNERSHIP WITH THE WEST AFRICAN SCIENCE SERVICE CENTRE ON CLIMATE CHANGE AND ADAPTED LAND USE (WASCAL), SUBMITTED TO THE SCHOOL OF POSTGRADUATE STUDIES, IN PARTIAL FULFILMENT OF THE REQUIREMENT FOR THE AWARD OF THE DEGREE OF DOCTOR OF PHILOSOPHY IN CLIMATE CHANGE AND AGRICULTURE OF THE UNIVERSITY OF SCIENCES, TECHNIQUES AND TECHNOLOGIES OF BAMAKO (USTTB)

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DEDICATION

This work is dedicated to the Almighty God and To my wife, Melody EZE To my daughter, Princess EZE To my mother, Esther EZE To my father, Ignatius EZE (of blessed memory)

DECLARATION

I, Chinedu Emmanuel EZE, declare that this PhD thesis entitled "GENE ACTION AND HETEROTIC RESPONSE OF MAIZE POPULATIONS UNDER VARYING GROWING CONDITIONS IN RAIN-FOREST AGRO-ECOLOGY OF NIGERIA" is my own work except for quotations and citations which have been duly acknowledged. I also declare that it has not been previously, and it is not concurrently submitted for any other degree at the University of Sciences, Techniques and Technologies of Bamako or at any other institution.

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LIST OF ACRONYMS AND ABBREVIATIONS

- ADAA Additive, Dominance and Additive x Additive
- BLUE Best Linear Unbiased Estimate
- BLUP Best Linear Unbiased Prediction
- DAP Days after planting
- DNA Deoxyribonucleic acid
- FAO Food and Agriculture Organisation
- G x E Genotype by Environment
- GCA General Combining Ability
- GEAN Gardener and Eberhart Analysis
- HSGCA Heterotic grouping based on Specific and General Combining Ability
- HGCAMT Heterotic grouping based on the GCA of Multiple Traits
- IITA International Institute of Tropical Agriculture
- QTL Quantitative Trait Loci
- SCA Specific Combining Ability
- SNP Single Nucleotide Polymorphism
- SSA sub-Saharan Africa
- WCA Western and Central Africa

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RÉSUMÉ

Plusieurs programmes de sélection de maïs utilisent des variétés à pollinisation libre (OPV) comme source de variabilité génétique et d'allèles favorables des caractères cibles. Des hybrides de maïs tolérants à la sécheresse et à la provitamine A (PVA) sont nécessaires pour lutter contre la malnutrition et l'insécurité alimentaire en Afrique subsaharienne (SSA). En réponse à ce besoin, des OPV ayant des antécédents génétiques tolérants à la sécheresse et à la PVA ont été développés grâce aux efforts du Programme d'amélioration du maïs de l'Institut International d'Agriculture Tropicale (IITA-MIP) pour le développement hybride et la commercialisation, en particulier en faveur des petits agriculteurs ruraux. Les objectifs de l'étude étaient de: (i) évaluer la variabilité génétique entre 14 variétés de maïs élite à pollinisation libre (OP) à l'aide de la méthode génétique, (ii) déterminer le mode d'action des gènes contrôlant le rendement en grains et d'autres traits agronomiques (iii) classer les parents de variétés de maïs en groupes hétérotiques, et (iv) analyser la stabilité du rendement des parents et de leurs hybrides dans des environnements contrastés. Quatre-vingt-onze hybrides générés à partir de 14 parents de maïs élite OP selon un dispositif de croisement diallèle et trois témoins ont été évalués dans des conditions pluviométriques marginales, de sécheresse et d'environnements optimaux au Nigéria entre 2017 et 2018. L'expérience a été réalisée avec un dispositif en blocs incomplets randomisés (9 x 12 réseaux alpha) avec trois réplications dans chaque environnement. L'analyse de variance combinée a montré une grande variabilité génétique parmi les génotypes évalués. Sur les 91 hybrides, 41 ont donné des rendements supérieurs à la moyenne $(2,31 \text{ t} \text{ ha}^{-1})$. Environ 18% des hybrides pourraient être sélectionnés sur la base du seuil de score 3 pour les aspects des épis et des plantes. Par l'analyse séquentielle du coefficient de chemin, l'aspect de la plante et celui de l'épi ont été considérés comme des indices de sélection importants pour l'amélioration visant à développer des OPV à haut rendement dans la région subsaharienne. Les effets génétiques non additifs étaient plus importants que les additifs pour le rendement en grains et d'autres caractères agronomiques dans tous les environnements étudiés. La classification de certains des parents ayant des antécédents génétiques similaires ensemble dans le même groupe à travers chaque environnement de test a indiqué que le regroupement des OPV repose en grande partie sur leur pedigree. En utilisant la méthode HSGCA, les groupes TZL Comp - 3 C3 DT (P6) et White DT STR SYN / IWD C3 SYN F2 (P9) ont été systématiquement regroupés différemment à travers tous les environnements de test, ce qui suggére leur potentiel hétérotique. Les génotypes ont été divisés en trois groupes, contenant soit les parents, les hybrides ou les variétés de référence, pour estimer la variance de la stabilité et du rendement en grains. La différence entre l'environnement à rendement le plus bas et le plus élevé était de 3,2 t ha⁻¹, tandis que la répétabilité des essais de rendement céréalier variait de 35% pour les conditions de précipitations marginales à Ile-Ife à 80% pour les conditions optimales à Umudike. Le rendement céréalier moyen des hybrides était nettement supérieur à celui des parents et des variétés témoins. Les hybrides étaient également plus stables que les parents et les variétés de référence. Cette étude a établi une grande variabilité génétique entre les variétés parentales et la prépondérance de la variance non additive sur la variance additive pour l'hérédité de la plupart des caractères. Un certain nombre d'hybrides de variétés à haut rendement et stables ont été identifiés et pourraient être mis à la disposition des agriculteurs. L'approche des marqueurs moléculaires de ce travail est recommandée pour l'avenir afin de valider les résultats phénotypiques qui ont été obtenus dans cette étude.

Mots-clés: maïs; variétés à pollinisation libre; action des gènes; diallèle; rendement en grains.

ABSTRACT

Several maize breeding programs use open-pollinated varieties (OPVs) as a source of genetic variability and favourable alleles of target traits. Drought tolerant and provitamin A (PVA) maize hybrids are needed to address malnutrition and food insecurity in sub-Saharan Africa (SSA). In response to this need, OPVs with drought tolerant and PVA genetic backgrounds were developed through the effort of the International Institute of Tropical Agriculture Maize Improvement Programme (IITA-MIP) for hybrid development and commercialization especially among the small holder rural farmers. The objectives of the study were to (i) assess genetic variability among 14 elite maize OPVs using genetic method, (ii) determine the mode of gene action controlling grain yield and other agronomic traits (iii) classify the maize varietal parents into distinct heterotic groups, and (iv) analyse yield stability of the parents and their hybrids across contrasting environments. Ninety-one hybrids generated from 14 elite OPV parents in a diallel mating design plus three checks, were evaluated under marginal rainfall, drought, and optimal environments in Nigeria from 2017 to 2018. The experiment was laid out in a randomized incomplete block design (9 x 12 alpha lattice) with three replications in each environment. The combined analysis of variance showed wide genetic variability among the evaluated genotypes. Out of the 91 hybrids, 41 yielded above average $(2.31 \text{ t} \text{ ha}^{-1})$. Based on threshold score of 3 for both ear and plant aspects, about 18% of the hybrids could be selected. From the sequential path coefficient analysis, plant aspect and ear aspect were considered important selection indices for improvement aimed at developing high yielding OPVs in the sub-Saharan region. Non-additive genetic effects were more important than additive for grain yield and other agronomic traits across all the the research environments. The classification of some of the parents with similar genetic backgrounds together in the same group in each and across test environments indicated that the grouping of the OPVs was based largely on their pedigree. Using HSGCA method, TZL Comp - 3 C3 DT (P6) and White DT STR SYN/IWD C3 SYN F2 (P9) were consistently grouped differently under all the test environments suggesting their heterotic potential. The genotypes were divided into three groups, containing either the parents, hybrids or checks, for estimating the stability variance and grain yield. The difference between the lowest and highest yielding environment was 3.2 t ha⁻¹, while the repeatability of the grain yield trials ranged from 35% for marginal rainfall condition at Ile-Ife to 80% for optimal condition at Umudike. The average grain yield of the hybrids was significantly higher than that of the parents and the check varieties. The hybrids were also more stable than both the parents and the checks. This study established wide genetic variability among the parental varieties and preponderance of non-additive variance over additive variance for inheritance of most traits. A number of high yielding and stable variety hybrids were identified which are potential candidate for release to farmers. Molecular markers approach to this work is recommended for the future in order to validate the phenotypic results that have been achieved in this present study.

Keywords: maize; open-pollinated varieties; gene action; diallel; grain yield.

CHAPTER I

INTRODUCTION

1.1 Background of study

Information relating to heterosis is of utmost concern to breeders of cross-pollinated crops such as maize (*Zea mays* L.). Its exploitation is considered one of the outstanding achievements of plant breeding. Among germplasm sources, heterotic response is critical for determining the best method of absorbing germplasm with desirable traits into agronomically accepted populations. Several authors have reported heterosis (hybrid vigour) in maize as a key feature underlying the expression of grain yield in hybrids (Springer and Stupar, 2007; Troyer and Weillen, 2009; Munaro *et al*., 2011). Combining ability and nature of gene action are valuable in determining whether such heterosis is predictable or fixable (Tiwari *et al*., 2011). Hence, to know the inheritance pattern of some morphological traits in maize, hybrids alongside their parents are usually evaluated in different environments to identify best heterotic combinations. Variation in mean heterosis over a range of environments is expected when maize hybrids respond differently to environmental stimuli. However, the magnitude and nature of the heterosis x environment interaction (H×E) has not been described sufficiently in the recent past (Munaro *et al*., 2011).

The hypotheses to explain heterosis were laid out a century ago, however, mechanisms of heterosis largely remain unclear or poorly understood (Goodnight, 1999; Wang *et al*., 2015; Zhang *et al*., 2016). Among several mating designs available, diallel design is the most commonly used experimental approach in studying combining ability. Diallel analysis of quantitative traits has contributed immensely in improving crops and understanding heterosis. In 1942, Sprague and Tatum introduced the concepts of general combining ability (GCA) and specific combining ability (SCA) in the diallel analysis. It will be of interest to plant breeders to know if genetic parameters or statistics obtained from different diallel methods according to Griffing (1956a) and Gardner and Eberhart (1966) would yield same, similar or varying results. Such information would be valuable for breeders in choosing the most appropriate diallel method and also in determining whether the results from other diallel studies with varying number and sets of parental lines could be used as reference for crop breeding programs in West Africa. Hayman (1954b) proposed a method of analysis that includes the parents, F_1 crosses, and the reciprocal F_1 crosses. Jones (1965) later modified Hayman's model so that it could be used without the reciprocal F_1 crosses. Griffing's methods (1956a) of analysing different diallel mating designs have become popular among plant breeders in determining the GCA and SCA effects in maize (Fan *et al*., 2013; Yao *et al*., 2013; Ahmad *et* al., 2016; Zhang *et al*., 2016; Kahriman *et al*., 2017). It described statistical procedures for analysing four different methods of diallel for use in plants. Zhang *et al*. (2005) stated that the methods define clearly GCA and SCA thereby making it possible to understand statistical models and develop software tools. Other major diallel mating models utilized in combining ability analyses are that relative to Gardener and Eberhart (1966) analysis II (GEANII) and analysis III (GEANIII). Although these methods were developed to obtain additional information (for instance, on heterosis, inbreeding depression, additive gene action, epistasis and dominance), due to the fact that additional resources were required for their implementation, they were not widely adopted (Yao *et al*., 2013). Authors(Sughroue and Hallauer, 1997; Fan *et al*., 2002; Melani and Carena, 2005; Barata and Carena, 2006; Fan *et al*., 2013) have further reported the use of the GCA and SCA effects for genetic diversity evaluation, inbred line selection, heterotic pattern classification, heterosis estimation and hybrid development.

The knowledge of various traits and identification of superior parents are important prerequisites for carrying out efficient and effective breeding programme. Combining ability analyses provide information on additive and non-additive variations (dominance and epistasis) which are important to decide the best parents for hybridization in order to produce superior hybrids. In 1999, Xu and Zhu proposed a method for predicting potential heterosis of crop hybrids by an additive, dominance and additive x additive model (ADAA). By using unbiased predictors of additive and dominance, as well as additive x additive effects, they derived general formulae for predicting heterosis over mid-parent and over better parent for different generations. However, the ADAA model did not include the effects of additive x dominance epistasis and dominance x dominance epistasis as it assumes that these effects are complicated, negligible and will likely decline quickly as the generations increase. In contradiction, recent studies with molecular markers have clearly revealed that epistasis has a significant role in the inheritance of quantitative traits as well as plant growth and development (e Sousa *et al*., 2017). In their study carried out with single cross maize hybrid SR52, Musimwa and Derera (2017) reported that epistasis contributed 49.7% to the gene action sum of squares of the hundredkernel weight. The selection of parents based on only phenotypic performance is not a sound practice as phenotypically superior parents may yield poor recombination. Therefore, it is essential that parents should be chosen based on their genetic value.

With advancement in the use of molecular markers, the selection for important traits such as grain yield, which was originally performed on by phenotypic information, can now be performed using the molecular marker's information (Cantelmo *et al*., 2017). A justification for the use of molecular markers as reported by Meuwissen *et al*. (2001) is the expectation that information on genomic constitution of the individuals may bring greater genetic gain than when only phenotypic data are used. By combining the information from molecular markers and phenotypic data, Bernardo (1994) proposed a model for prediction of maize hybrids using best linear unbiased prediction (BLUP). This takes the information from considered molecular markers for the construction of the pedigree of the parental lines. According to Mi *et al*. (2011), by using BLUP, information from genetically related candidates is combined to obtain more precise estimates of genotypic values of test candidates, thereby, increasing progress from selection. The use of such unbiased methods to assess single-cross performance with high accuracy can greatly increase the efficiency of maize breeding programs (Mendes and Souza, 2016). In plant breeding, the application of BLUP approach was advocated by Bernardo (1996) and Piepho *et al*. (2008) because it has a good prediction accuracy and promises to enhance the efficiency of selection. Bernardo (1996) stated that the prediction of breeding values using BLUP is based on known genetic relationships among genotypes and the available phenotypic data of related genotypes. However, investigation by Piepho *et al*. (2008) revealed that BLUP is rarely used in plant breeding.

There is an increasing demand for hybrid seeds which is driving the emergence of several seed companies in the sub-region. These companies depend on public breeding programs for their supply of germplasm. There is, therefore, an urgent need for maize programs in public institutions to identify diverse lines that seed companies could use to produce commercial hybrids. Therefore, there is need for understanding the mode of gene action governing the inheritance of economic traits and heterotic patterns of genotypes derived from different germplasm sources for successful and sustainable hybrid production in the sub region in the face of the changing climate.

1.2 Problem and Justification

Maize is a major food security crop supporting millions of people in sub-Saharan Africa (SSA) and further regions of the developing world. The low maize yield in SSA $(1.5 - 2.0 t \text{ ha}^{-1})$ in comparison to developed countries is primarily attributed to production constraints, which include several abiotic stress factors and low adaptation of exotic germplasm to target environments in the major maize production agro-ecological regions of the SSA Savannahs (Badu-Apraku *et al*., 2011c; Adebayo *et al*., 2017). Strong effects of genotype-by-environment interaction as well as a general scarcity of improved cultivars (Abakemal *et al*., 2016) furthermore impair the yield potential of maize in these regions. These dynamic environmental conditions are particularly evident in Nigeria, where small-scale farmers who largely lack the capacity to influence the plant production environments with inputs like synthetic fertilizers and pesticides (Oluwatusin *et al*., 2017) are cultivating the majority of the country´s maize acreage. Hence, there is a considerable need for the development of high yielding and stable genotypes that are accepted by farmers who are exposed to a diverse range of growing conditions.

In developing countries, open pollinated (OP) maize cultivars have been useful for providing low-priced and farm-saved seeds, and dependable yields to farmers, although they generally produce lower grain yield compared to well adapted single cross hybrid cultivars. However, hybrid seed is comparably expensive and therefore not easily accessible for small-scale famers. These qualities of OP maize make them sustainable alternatives (Kutka, 2011), while improved maize populations and population-derived hybrids can both be valuable alternatives to commercial single-cross hybrids as well as good elite sources of novel inbred lines (Carena, 2005). Although rarely used, several studies have shown that population hybrids show some heterotic increase in productivity across stressed and non-stressed environments when exploiting heterotic patterns among them (Carena, 2005, 2007; Gabriel *et al*., 2009). Future climate scenarios suggest that maize yields in some regions will decline by up to 10% by 2050 (Tesfaye *et al*., 2015). Therefore, exploiting the putative higher yield stability of such heterogeneous and heterozygous variety types would moreover represent a significant step in coping with the increasing abiotic stress factors expected from climate change.

1.3 State of knowledge

1.3.1 Maize production and utilization in Nigeria and the rest of sub-Saharan Africa

Maize (*Zea mays* L.) is an important cereal crop grown worldwide for various purposes. It occupies the second position after wheat in terms of area of production but represents the most important cereal crop in terms of quantity produced worldwide (FAOSTAT, 2015). Maize is Nigeria's most important cereal crop and is grown by the vast majority of rural households. According to FAO data (Figure 1), maize production in Nigeria has increased nearly ten-fold between 1961 and 2014, resulting in Nigeria becoming the largest maize producer in sub-Sahara Africa (SSA) and $11th$ largest producer in the World accounting for over 0.9% of the world production (FAOSTAT, 2014). However, the increased production is mainly due to increase in the area under maize production, rather than changes in yield (Figure 1). Average yield levels increased approximately from 0.9 t/ha in 1961 to 2.0 t/ha in 2014 with an average yield of 1.4 t/ha during that period. This figure is approximately 75 % lower than the world average yield (5.5 tha^{-1}) and much lower (~90%) compared to the yield obtained in countries, such as USA (7.8 tha⁻¹), Canada (7.2 tha⁻¹) and South Africa (2.6 tha⁻¹) (Figure 2). Nevertheless, FAO (2009) noted that under irrigation system, a good commercial maize variety yield is 6 to 9 t/ha. Several authors (Nagy, 2003; Nagy, 2010; Muyiwa and Mikkah, 2012) have identified irrigation as a practice which can increase the yield of maize considerably. Babatunde *et al*. (2008) noted that production of maize in Nigeria is mainly under the rain-fed system and has been insufficient in meeting the demand of the increasing population particularly during the dry season.

Figure 1: Maize production and area harvested in Nigeria from 1961-2014 (source: FAOstat3.fao.org)

Figure 2: Yield of Maize in four countries from 1961-2014 (source: FAOstat3.fao.org)

Maize is an important part of the daily diet in Nigeria and it is consumed in different forms such as boiled, roasted and as porridges in all parts of the country. According to a survey conducted by Maziya-Dixon *et al*. (2006) and reported in Iyanda *et al* (2014), maize is estimated to account for 20% of the total staple food consumption. About 55 % of maize produced is used as food, 31% as feed and 2% is processed (Cadoni and Angelucci, 2013) in industries.

1.3.2 Constraints to maize production in sub-Saharan Africa

Stress factors, such as droughts, floods, and pests as outlined in IPCC (2001) have been identified (Regh *et al*., 2014) as one of the complex interactions that can lead to variability in food availability. These events are associated with global warming and its effects which have changed the weather pattern in SSA. Badu-Apraku *et al*. (2016a) identified recurrent drought and low soil nitrogen (Low-N) as the two major constraints militating against the achievement of food security in West Africa (WA). The annual loss in maize production due to lack or insufficient rainfall is estimated at several billion US dollars (Badu-Apraku *et al*., 2016a). Edmeades *et al.* (1995) and Badu-Apraku and Akinwale (2011) estimated the annual maize yield loss from drought stress in the savanna of WCA at 15% of total maize production and pointed out that localized losses may be much higher in the marginal areas, where the annual rainfall is less than 500 mm and soils are sandy or shallow.

Bänziger *et al*. (2006) pointed out Low-N stress as one of the most important factors frequently limiting maize production, food security, and economic growth in sub-Saharan Africa. Badu-Apraku *et al.* (2016a) confirmed the work of Wolfe *et al*. (1988) that the estimated yield losses from Low-N stress alone vary from 10 to 50% in West Africa and are attributable to inadequate or no application of inorganic fertilizer by farmers and rapid mineralization of organic matter in the soil. According to Cechin and Press (1993); Kim and Adetimirin (1997); Badu-Apraku *et al*., (2011b) and Badu-Apraku *et al*., (2016a), drought, Striga infestation, and soil nutrient deficiency can occur simultaneously in the farmer's field with a devastating combined effect. Therefore, maize varieties targeted to the Striga-prone areas of WCA must also be resistant or at least tolerant to drought and Low-N.

The low maize yield in SSA (Figure 3) compared to the rest of the world is primarily attributed to production constraints such as poor soil nutrient status, especially nitrogen (N) and phosphorus (P) (Sanchez, 2002; Jibrin *et al.*, 2012)**,** parasitism by weeds such as *Striga hermonthica* (Tambo and Abdoulaye, 2011), poor adherence to improved agronomic practices (especially sowing dates and densities), low use of improved inputs such as fertilizers and seeds and frequent droughts caused by erratic rainfall patterns in the major maize production ecoregions of the Savannas of SSA (Badu-Apraku *et al.,* 2011a; Kamara *et al*., 2011). Production of maize is severely constrained by recurrent drought in the maize belt of Africa with farmers encountering losses close to 90% in severe instances (IITA, 2013).

Figure 3: Relative yield losses from agronomic causes in maize crops in SSA Soil fertility includes low soil organic matter, deficiencies in zinc, phosphorus and potassium, and soil acidity, but not low nitrogen status. Source: Gibbon *et al*. (2007).

1.3.3 Breeding for drought tolerance in maize

Improving grain yield is the major objective in maize breeding. Selection and breeding have always been conducted to achieve high yield and better quality of crops under stressful conditions (Niu *et al*., 2012). Grain yield and its response to stress are highly complex traits involving a long-term interaction between the environment and plant characteristics and regulatory pathways at different scales of organization (Araus *et al*., 2012). The trait most frequently associated with genetic yield improvement in maize under post-flowering drought condition is delayed leaf senescence or ''stay green'' (Duvick, 1997b; Nguyen and Blum, 2004).

Breeding for tolerance to drought has been a major strategy to increase maize production and productivity in this region during the last three decades (Badu-Apraku *et al*., 2015a). Measures being adopted by researchers to prevent the negative consequences of drought include the development of top cross hybrids and the development of drought tolerant cultivars that possess drought tolerance genes. A possible approach to reduce N deficiency in the soil is to lower crop demand for N through selection for low N tolerance (Smith *et al*., 1994). This has brought about the development of inbred lines, open pollinated (OP) and hybrid varieties capable of utilizing the available N in the soil. The improved varieties could enhance productivity in N poor soils and reduce reliance on inorganic N fertilizers thereby reducing the toxic impact on the soil because of excess dependent on inorganic fertilizers.

Drought, like many other environmental stresses, has adverse effects on crop yield including maize. Low water availability is one of the major causes for maize yield reductions affecting the majority of the farmed regions around the world. Therefore, the development of droughttolerant lines becomes increasingly more important. In maize, a major effect of water stress is a delay in silking, resulting in an increase in the anthesis-silking interval, which is an important cause of yield failures. Diverse strategies are used by breeding programs to improve drought tolerance. Conventional breeding has improved the drought tolerance of temperate maize hybrids and the use of managed drought environments, accurate phenotyping, and the identification and deployment of secondary traits has been effective in improving the drought tolerance of tropical maize populations and hybrids as well. The contribution of molecular biology is potential to identify key genes involved in metabolic pathways related to the stress response. Functional genomics, reverse and forward genetics, and comparative genomics are all being deployed with a view to achieving these goals. However, a multidisciplinary approach, which ties together breeding, physiology and molecular genetics, can bring a synergistic understanding to the response of maize to water deficit and improve the breeding efficiency (Maazou *et al*., 2016).

According to Witcombe *et al*. (2007), drought and salinity are two of the most complex stress tolerances to breed for as the type (combinations of heat and drought or sodicity and salinity), timing in relation to plant growth stage and intensity of stress can all vary considerably. There is no unified abiotic stress resistance mechanism for drought at the level of the whole plant or the single gene (Blum, 2004). The traits associated with avoidance and tolerance can be constitutive (differing between genotypes) or adaptive (vary with the stage of the life cycle). Drought avoidance and drought tolerance involve different mechanisms and processes, and phenology is the single most important factor influencing whether a plant avoids drought. Drought stress is highly variable in its timing, duration and severity, and this results in high environmental variation and $G \times E$ variation. The whole-plant response to stress is complex because it is determined by component traits that interact and differ in their individual responses to the intensity and duration of water deficits and temperature. The use of managed stress environments can be very effective in breeding for drought tolerance, however, it is important to apply sufficient drought stress intensity to maximize *G*×*E* [\(Bänziger](http://rstb.royalsocietypublishing.org/content/363/1492/703.short#ref-15) *et al*., 2006).

1.3.4 Secondary Traits for Selection under Drought Conditions

Secondary traits are those other than economic yield itself, which can provide a measure of plant performance (Lafitte *et al*., 2003). An ideal secondary trait would be genetically correlated with grain yield in the target environment, genetically variable, have a high level of heritability, be simple, cheap, non-destructive and fast to assay, be stable throughout the measurement period and would not be associated with any yield loss under non-stressed conditions (Ribaut *et al*., 2009). Under drought stress conditions, breeding progress is impeded by a significant level of $G \times E$ (both with respect to cropping season and with respect to location). Given the poor heritability of grain yield under drought stress conditions, genetic progress is hard to achieve via direct selection. However, because under drought, both the heritability (h^2) of at least some secondary traits remains high and the genetic correlation between grain yield and these traits increases significantly, recourse to indirect selection becomes an attractive strategy (Lafitte *et al*., 2003). Selection based on secondary traits, which reflect the direct effects of drought, can improve the response, since it avoids the confounding effects of other stresses, such as poor soil fertility, micronutrient deficiency and pathogen presence. Application of this strategy has generated genetic gains under a range of environmental conditions (Ribaut *et al*., 2009).

After evaluation of a total of 3509 inbred progenies (S1 to S3 level) in 50 separate yield trials under two or three water regimes, Bolaños and Edmeades reported a general tendency to decrease with increasing moisture stress in the heritability for grain yield from around 0.60 in well-watered environments to values of 0.40 or less at very low yield levels (Bolaños and Edmeades, 1996). The heritability (h^2) of kernels ear⁻¹and weight kernel⁻¹ was around 0.60 under well-watered conditions, but also decreased with increasing stress. In contrast, the heritability for anthesis-silking interval (ASI) and ears per plant either increased or remained fairly constant with in- creasing moisture stress and declining yield levels. The $h²$ for days to anthesis remained fairly constant across all moisture regimes. They suggested that earlierflowering progenies were associated with high grain yields and similarly, a short ASI was linked to high grain yield under stress. This perception was reinforced by findings of Magorokosho *et al*. who found that a phenotypic correlation between grain yield and ASI were small ($r = -0.08$ to -0.21 *) under adequate moisture conditions and became much larger ($r =$ −0.40** to −0.43**) at moisture-stressed sites (Magorokosho *et al*., 2003). Similarly, the relationship between ears per plant (EPP) and grain yield, also became stronger with increasing moisture stress (from 0.08 to 0.24^{**} without stress, to 0.40^{**} to 0.45^{**} with moisture stress). In a later study using similar methods, Ziyomo and Bernardo observed a significant decrease in h^2 for grain yield under drought (0.60 in the control experiment and 0.37 under drought) but not for ASI and leaf senescence (Ziyomo and Bernardo, 2013). They observed a higher h^2 and genetic variance for ASI and leaf senescence under drought stress. Furthermore, in this drought experiments, the strongest genetic correlation was observed between grain yield and ASI (−0.77). In summary, compared with direct selection for grain yield under drought, indirect selection based on grain yield in the control experiments had a relative efficiency of 0.78, indirect selection based on ASI had a relative efficiency of 1.04, and indirect selection based on leaf senescence had a relative efficiency of 0.98. These results indicate that ASI, leaf senescence and EPP are useful secondary traits for the selection of grain yield at moisture stressed sites. Therefore, the use of this strategy can increase selection efficiency.

1.3.5 Diallel mating design

Plant breeders have several mating designs to select from to investigate the genetic properties of plant populations, but study conducted by Sughroue (1995) has shown that none of them has caused as much controversy and debate as the diallel mating design. According to Hallauer and Miranda (1988), "the diallel mating design has been used and abused more extensively than any other in maize and other plant species". A full diallel mating design requires that all the parents be crossed in all possible pairwise combinations to produce hybrids in all possible combinations. Variations of the full diallel may include partial diallels with parents or without parents. A full diallel requires twice as many crosses and entries in experiments, but both maternal and paternal effects are tested for (Crusio, 1987). When reciprocal effects are assumed to be minor a half diallel without reciprocals can be done.

Sprague and Tatum (1942) introduced the diallel cross concept to plant breeding by making all possible crosses among a set of maize (*Zea mays* L.) inbred lines. The diallel mating design has been used successfully for over 50 years in plant breeding to estimate the relative combining ability of lines (Sughroue, 1995). From the diallel mating design, plant breeders can estimate general combining ability (GCA) and specific combining ability (SCA). Sprague and Tatum (1942) defined GCA as "the average performance of a line in hybrid combinations" and defined SCA as "those cases in which certain combinations do relatively better or worse than would be expected on the basis of the average performance of the lines involved."

In the 1950s, however, the diallel mating design was extended to estimate genetic variance components, and with this use of diallel mating design came criticism, controversy, and debate about its usefulness in supplying such information. The controversy is centred around whether it is proper and valid to estimate genetic variance components from parents of a diallel that cannot be considered to be a random sample of a defined population. One of the assumptions required to estimate genetic parameters using the diallel mating design is that the genes in the parents must be independently distributed. Previous theoretical and computer simulation studies found that the failure of this assumption often resulted in the average level of dominance being overestimated (Hayman, 1954b; Nassar, 1965).

The theory and statistical analysis of the diallel mating design have been investigated in depth by several researchers (Jinks and Hayman, 1953; Hayman, 1954a, 1954b, 1958, 1960; Griffing 1956a, 1956b; Kempthorne, 1956; Gardner and Eberhart, 1966). Various forms of the diallel crossing system and analysis have been developed since its conception. Kempthorne and Curnow (1961) developed the partial diallel as a way of increasing the number of parents that could be used in a diallel. A partial diallel requires fewer crosses per parent than does a regular diallel. Gardner and Eberhart (1966) developed a model to investigate the genetic properties of open-pollinated varieties and their crosses.

Hayman (1954a) proposed a method of analysis that includes the parents, crosses, and the reciprocal crosses. Jones (1965) later modified Hayman's model so that it could be used without the reciprocal F_1 crosses.

Gardner and Eberhart (1966) proposed three methods of analyses. Analysis I is only for varieties and includes the parent varieties, selfed progenies of the varieties, and the variety crosses. Analysis II and Analysis III can be used with either varieties or with homozygous lines. Analysis II includes the parent varieties and the variety crosses while Analysis III includes only the variety crosses. Following Gardner–Eberhart Analysis II, Laude and Carena (2014) estimated the variety (v_i) and heterosis (h_{ii}) genetic effects for grain yield and grain quality traits in a sample of sixteen maize populations adapted to the northern U.S. Corn Belt. The Specific heterosis (*sij*) and predicted means of population crosses for grain yield were then used to evaluate the heterotic relationships among the populations.

Griffing (1956a) proposed four different methods of analysing a diallel based on whether the parents, their reciprocal F_1 crosses, or both, are included in the evaluation with the F_1 crosses: (1) F_1 crosses with parents and reciprocal F_1 crosses (n^2) ; (2) F_1 crosses and parents $[n(n+1)/2]$; (3) F_1 crosses and reciprocal F_1 crosses n(n-l); (4) F_1 crosses only $[n(n-1)/2]$ (Griffing, 1956a).

From the proposed types of analyses of diallel crosses, Griffing's methods two and four, Hayman's method, and Gardner and Eberhart's Analyses II and III can be used to analyze the same type of data. Sokol (1976; cited by Baker, 1978) demonstrated that the statistical parameters of Griffing's methods two and four, Hayman's method, and Gardner and Eberhart's Analysis II are all linear functions of the parameters in Gardner and Eberhart's Analysis III (1966).

For each Griffing's method, a different form of analysis is applied. Different sampling assumptions give rise to different estimation problems regarding combining ability effects. In situations where (1) parent lines are randomly sampled from a population, or (2) where lines are chosen for specific phenotypic traits, the assumptions are expressed differently. In the second case, the lines cannot be regarded as representative of the entire population thus; no valid interpretations can be made (Griffing, 1956a).

For the plant breeder, it is important to know if a pure line has a good GCA with regard to a tester population and if or not two pure lines possesses good SCA. It is therefore clear that the interest, when analysing the GCA and SCA, is in the parents and not their off-spring. In this respect, a diallel cross analysis is a unique type of progeny testing (Bos and Caligan, 1995).

Analysing methods commonly utilise general linear models to detect heterotic groups (Griffing, 1956a), estimate GCA and SCA (Gardner and Eberhart, 1966), determine interactions with testing environments and to estimates additive, dominant, and epistatic genetic effects (Sprague and Tatum, 1942; Hayman, 1954a) and genetic correlations (Crusio, 1993).

Situations where parent lines were randomly selected from a population, and where deliberate parent selections were made, should be clearly distinguished. The two situations give rise to different estimation problems with regard to combining ability effects (Griffing, 1956a). In the first scenario, the genotypic effects are considered to be random variables where in the second case they are seen to be constants (Dey, 2002).

The progeny of the crosses can either be planted in random- or constant block designs. The randomised-block design is commonly used for this type of study. Such a design contains '*a'* varieties, each assigned at random to each of '*b'* blocks with '*c'* individuals in the '*ab'* plots (Griffing, 1956a). The mathematical formula for the *ijklth* observation is expressed as:

$$
x_{ijkl} = u + v_{ij} + b_k + (bv)_{ijk} + e_{ijkl}
$$
 (Equation 1.1)

where $u =$ population mean effect, v_{ij} is the effect for the *ijth* genotype, b_k is the *kth* block effect, $(bv)_{ijk}$ is the interaction between the *ijth* genotype and the *kth* block, and e_{ijkl} is the environmental effect atypical to the *ijklth* individual (Griffing, 1956a).

Double subscript notation is used for the variety effect. The genotypic means in the combining ability analyses is indicated as x_{ij} , where x_{ii} is the mean for the *ith* parent, and x_{ij} is the mean for the F¹ following cross between the *ith* and *jth* parents. In the combining ability analyses for methods in which reciprocal F1s are included, the variety effects are expressed in terms of GCA and SCA ability effects as:

$$
v_{ij} = g_i + g_j + s_{ij} + r_{ij}
$$
 (Equation 1.2)

where g_i and g_j is the GCA effect of the parents, s_{ij} is the SCA effect for the cross between the *ith* and *jth* parents and *rij*, the reciprocal effect between the *ith* and *jth* parents (Griffing, 1956a).

The correct analysis of the combining ability effects and variance depends on the particular diallel method applied, the assumptions regarding the experimental material, and the conditions imposed on the combining ability effects. According to Griffing (1956a), four sets of assumptions are considered with regard to the variety and block effects and are summarised as follow:

1. The variety and block effects are constant (model I)

2. The variety effects are random variables and the block effects are constants (model II) or (mixed A)

3. The variety effects are constants and the block effects are random variables (model III) or (mixed B)

4. The variety and block effects are both random variables (model IV).

From assumption 1, a model (model I) is presented in which all effects, excluding the error, are regarded as constants. The last set, assumption 4, leads to a second model, (model IV) where all effects except *u* (population mean effect) are random variables. Assumptions 2 and 3 lead to mixed models which are designated as mixed A and mixed B (Eisenhart, 1947).

The objectives in model I are to compare combining abilities of the parents where the parents are used as testers and to identify higher yield combinations. Thus, the experimental material is to be regarded as the population about which inferences are to be made (Griffing, 1956a). The importance is in estimating combining ability effects and calculating standard errors for differences between effects. For testing procedures, the assumption is that the *eijkl* are normally and independently distributed with mean zero and variance σe^2 (Griffing, 1956a). The mathematical formula for combining ability analysis is:

$$
x_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + 1/bc_{kl} \Sigma \Sigma e_{ijkl}
$$
 (Equation 1.3)

where $u =$ population mean; g_i (g_j) = GCA for the *ith* (*jth*) parents and $s_{ij} = s_{ji}$; $r_{ij} =$ reciprocal effect involving the reciprocal crosses between the *ith* and *jth* parents and $r_{ij} = r_{ji}$; $e_{ijkl} =$ environmental effect associated with the ijklth individual observation (Griffing, 1956a).

Model IV deals with random samples from a parent population in order to make assumptions about the parameters in the parent population and not individual lines. Thus, the importance is in estimating the genetic and environmental components of the population variance. The assumption is that the effects in this model are normally and independently distributed with means = zero and variances $\sigma\theta^2$ where $\theta = b$, *g*, *s* or *r*. Component estimations for variance are obtained for any given diallel crossing method by equating the observed to the expected mean squares in the appropriate analysis of variance. Standard errors for variance component estimates are then calculated from the variances of the appropriate mean squares (Griffing, 1956a). The mathematical formula for combining ability analysis is:

$$
xij = u + gi + gj + sij + rij + (1/b_k)\Sigma b_k + (1/b_k)\Sigma (bv)_{ijk} + (1/bc_k)\Sigma \Sigma e_{ijkl}
$$
 (Equation 1.4)

where all except *u* are considered random variables (Griffing, 1956a).

Interpretation of combining ability effects and variance depends on the diallel method used, assumptions regarding the experimental material, as well as the conditions imposed on the combining ability effects (Griffing, 1956a). Thus, where model I is used; the equation for calculating combining ability depends on the applicable diallel method.

When using model IV, valid inferences will depend on the specific diallel crossing method applied as well as the nature of the population from which the lines were drawn (Griffing, 1956a). Mixed model A can be used for all four diallel crossing methods. For the methods that

exclude reciprocal F_1s , the mathematical formula for calculating combining ability is:

$$
x_{ij} = u + g_i + g_j + s_{ij} + (1/bc_{kl})\Sigma \Sigma e_{ijkl}
$$
 (Equation 1.5)

For those diallel methods including the reciprocal F_1 's the formula is as follows:

$$
x_{ij} = u + g_i + g_j + s_{ij} + r_{ij} + (1/bc_{kl})\Sigma \Sigma e_{ijkl}
$$
 (Equation 1.6)

In both cases, all except *u* are considered random variables (Griffing, 1956a).

Mixed model B is used when the 'mixed' elements (bv)ijk are introduced into the calculation of combining ability. For the methods that exclude reciprocal F1's the mathematical formula for calculating combining ability is:

$$
xij = u + gi + gj + sij + (1/b_k)\Sigma b_k + (1/b_k)\Sigma (bv)_{ijk} + (1/bc_k)\Sigma \Sigma e_{ijkl}
$$
 (Equation 1.7)

and for those diallel methods including the reciprocal F_1 's, the formula is as follows (Griffing, 1956a):

$$
xij = u + gi + gj + sij + r_{ij} + (1/b_k)\Sigma b_k + (1/b_k)\Sigma (bv)_{ijk} + (1/bc_{kl})\Sigma \Sigma e_{ijkl}
$$
 (Equation 1.8)

In the recent past, diallel studies have routinely been performed on a number of crops including maize (Malik *et al*., 2004), wheat (Ahmad *et al*., 2006), rice (Ahangar *et al*., 2008) and rye (Goncharenko *et al*., 2013) and so on.

Goncharenko *et al*. (2013) analysed grain quality traits in inbred winter rye lines in a full diallel design. Five inbred lines were selected to determine their combining ability and genetic characteristics for the following traits: grain test weight, water extraction viscosity, falling number, protein content, hearth bread form ration and pan loaf volume. The parent lines, as well as their F1 hybrids, were found to differ greatly with regard to quality traits. This enables them to identify lines with high GCA estimates for traits like high falling number and higher water extract viscosity and to calculate combining ability on the basis of the value of quality traits.

Olfati *et al*. (2012) compared two forms of half-diallel (Griffing's model I, method 2 and 4) analysis in cucumber. They found the methods to be interrelated. However, according to them, method 4 partitioned heterosis into different components as well as gave information about combining ability and also had some advantages over the other. Their results further indicated that using parental generations in the Griffing method 2 may cause biased estimate of the GCA and SCA variances. Therefore, they concluded that using Griffing method 4 is more suitable than the other methods in reducing time, cost, and facilities, and as a result recommended it as an applicable method.

Despite the wide perception that the inclusion of reciprocal crosses in a diallel does not have significant impact on the estimates of maize grain yield, GCA and SCA effects, the study by Fan *et al*. (2013) has suggested otherwise. They evaluated a 12-parent maize diallel cross in three environments using Griffing's Methods 3 and 4. Their results showed that inclusion of reciprocal crosses in a diallel greatly impacted grain yield and estimates of GCA and SCA effects. Under the assumption of a random-effects model, the inclusion of reciprocal crosses caused the residual and GCA variances to decrease and the SCA variances to increase as the number of parental lines increased in a diallel cross. Because inclusion of reciprocal crosses impacted grain yield and SCA estimates, reciprocal crosses would have great impact on maize heterotic group classification (Fan *et al*., 2013).

1.3.6 Heterosis, heterotic pattern and heterotic group in maize

Hybrid vigour or heterosis is the phenomenon in which progeny of crosses between inbred lines or purebred populations are better than the expected average of the two populations or inbred lines for a particular trait (Kwena, 2008). Heterosis observed in various crosses is the average expression of heterosis of the hybrids formed by crossing a sample of genotypes from each of the two populations (Hallauer and Miranda, 1988). The manifestation of heterosis usually depends on genetic divergence of the two parental varieties. Information on heterosis and heterotic groups is important in the development of high performance hybrids and improvement of populations from collections. Heterosis is credited for large increase in production per unit area, thus sparing large amounts of land for other uses such as environmentally benign nature preserves (Duvick, 1997a). Although many hypotheses to explain heterosis have been suggested, the genetical, physiological, and biochemical bases of heterosis still remain largely unexplained. Theoretical and experimental arguments are given suggesting that grouping of germplasm into divergent heterotic groups is advantageous due to (i) a higher mean heterosis and hybrid performance and (ii) a reduced specific combining ability (SCA) variance and a lower ratio of SCA to general combining ability (GCA) variance. Thus, early testing becomes more effective and superior hybrids can be identified and selected mainly based on their prediction from GCA effects (Reif *et al*., 2005).

Netravati *et al*. (2013) studied the 91 F1s of maize derived by diallel mating design involving fourteen inbred lines (excluding reciprocals) to investigate heterosis over best check NK 6240 for maturity characters, yield characters and quality parameters. Four crosses showed desirable heterosis for earliness viz; for days to 50% tassel and for 50% maturity. For the character, grain yield plant⁻¹, five crosses showed significant heterosis over better parent and standard check in positive direction. These better performing crosses/hybrids can be exploited for hybrid vigour. Six crosses showed heterosis in favourable direction over better parent and standard check for grain yield.

Jain and Bharadwaj (2014) reported standard heterosis in thirty-six crosses of maize. These crosses showed marked variations in the expression of standard heterosis for yield and yield contributing characters. Grain yield manifested highly significant standard heterosis in three crosses in the positive direction. Standard heterosis ranged from -27.15 to 38.80 for grain yield. The highest heterotic effect among the yield components was observed for number of ears plant⁻¹ followed by ear length, grain rows ear⁻¹ and ear weight respectively. The maximum significant positive heterosis was obtained in 1541-1 x R9303 (38.8) followed by 1394-1 x HKI-163 (21.69) and 1204-1 x HKI-193-1 (13.83) for grain yield.

Zemach *et al*. (2014) evaluated one hundred thirty-four genotypes using BHQ542 maize variety and other checks at two locations. The study objective was to determine the heterosis and heterotic patterns of the inbred lines and to identify promising crosses for future advanced trial. Based on the mean value of grain yield, sixteen crosses at Awassa and only four crosses at Melkassa were superior to hybrid (BHQ542) but no crosses out yielded this check in the combined data. Heterosis value varied highly for most of the traits studied at individual location and across locations. The highest heterosis over mid and better parent for grain yield was 189.47% (L36 x T2) and 100.8% (L36 x T2) at Awassa and 172.22% (L18 x T2) and 62.65% (L35 x T2) at Melkassa, respectively.

Moneam *et al*. (2014) obtained highest grain yield from P4 x P1 and P5 x P4 in combined, these crosses significantly out yielded the two checks, SC 155, and SC 162 at 5% level. Moreover, crosses P1 x P4, P1 x P5, P6 x P1, P4 x P2, P2 x P3 and P3 x P6 were significantly better than the checks. The highest positive significant heterosis over mid-parents for 100 kernels weight was recorded by 14 crosses. Cross P1 x P2 showed maximum positive and significant heterosis over better parent and mid parents and only one cross P1 x P4 gave positive and significant heterosis over check varieties for 100 kernels weight.

Kumar *et al*. (2014) estimated heterosis in 60 hybrids obtained by crossing 20 inbred lines with three testers in maize. Sixty hybrids along with 20 parents and three standard checks were evaluated for twelve characters. All the 60 hybrids showed earliness for days to 50% tassel and days to 50% silk over mid parent and 39 hybrids showed earliness over standard checks for days to maturity. The hybrid MRC 13 x BML 14 recorded positive significant heterosis over three standard checks DHM 117, 900M Gold and NK 6240 for grain yield (14.67%, 12.94% and 11.89%, respectively). Over standard check NK 6240, it showed desirable significant heterosis for grain yield plant⁻¹, number of kernels row⁻¹, number of kernel rows ear⁻¹ and ear length.

According to Goff (2011) the dominance and over-dominance theories remain the best models to explain heterosis, especially for single gene or single trait heterosis and are not mutually exclusive while the epistasis which is the interaction between different genes, explain hybrid vigour. Maize grain yield in the United States of America has increased by about 100 kg/ha/year or 2% per year from the start of large-scale adoption of hybrids by maize growers in the late 1930s until the first decade of the $21st$ century and about 75% of the yield improvement has been attributed to genetic gain (Tollenaar and Lee, 2006). Germplasm are thus classified into specific heterotic groups or patterns depending on their similarity in combining ability and heterotic response when crossed with genotypes from other genetically distinct germplasm groups (Kwena, 2008). Heterosis and combining ability are prerequisites for developing a good economically viable hybrid maize variety (Izhar and Chakraborty, 2013). Today the concept of heterotic groups and patterns is fundamental to hybrid breeding theory and practice. To systematically exploit heterosis in hybrid breeding program, the concept of heterotic groups and patterns was suggested by Reif *et al*. (2005). The term heterotic pattern refers to a specific pair of two heterotic groups, which express high heterosis and consequently high hybrid performance in their cross. The concept of heterotic patterns includes the subdivision of the germplasm available in a hybrid-breeding program in at least two divergent populations, which are improved with inter-population selection methods (Reif *et al*., 2005). Conventional methods, based on testcross data, have been widely used to estimate heterosis between populations or inbred lines and group them into heterotic groups or patterns (Menkir *et al*., 2003; Welcker *et al*., 2005; Badu-Apraku *et al*., 2013a; Qurban *et al*., 2014).

According to Melchinger and Gumber (1998), a heterotic group is a group 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. In most private sectors, breeders develop their heterotic groups by using elite inbred lines as testers. The general process is to cross two inbreds with different desirable traits but which both combine well with an elite tester. The F1 of this self-cross is to produce a source population from which new inbreds will be developed. The new inbreds are selected by evaluating hybrids between them and the tester. Any tester hybrids that outperform the best commercial check hybrid by 10% or more are advanced and the new inbred is classed into an anti-tester heterotic group (Mikel and Dudley, 2006). Heterotic groups in dent corn have been subdivided into Iowa Stiff Stalk Synthetic (BSSS) and non- BSSS (Lu and Bernardo, 2001). In practice, commercial corn hybrids consist of crosses of two unrelated inbreds each derived from different families or heterotic groups; there is much less diversity within heterotic groups, but diversity increases on pooling germplasm from different heterotic groups (Mikel, 2008).

Vasal *et al*. (1992) assigned inbred lines to heterotic groups using the traditional method of specific combining ability. Lines in genetically different heterotic groups are usually identified by positive SCA effects between them while inbred lines in the same heterotic group have a tendency to exhibit negative SCA effects when crossed.

Shnable and Springer (2013) reported that although, heterosis or hybrid vigour is widely exploited in agriculture, a complete description of its molecular underpinnings has remained elusive despite extensive investigation. It appears that there is not a single, simple explanation for heterosis. Instead, it is likely that heterosis arises in crosses between genetically distinct individuals as a result of a diversity of mechanisms. Heterosis generally results from the action of multiple loci, and different loci affect heterosis for different traits and in different hybrids. Hence, multigene models are likely to prove most informative for understanding heterosis. Several other intriguing hypotheses are also under investigation. Shnable and Springer (2013) went further to suggest that heterosis in crops must be considered within the context of the genomic impacts of prior selection for agronomic traits.

1.3.7 Gene action, general and specific combining ability effects

Sprague and Tatum (1942) introduced first the concepts of general and specific combining ability in relation to single cross maize. Combining ability study is very commonly used to understand the nature of gene action of different yield contributing characters in crop plants and to identify desirable parents in order to exploit heterosis. General combining ability (GCA) is defined as an average performance of a line in hybrid combination and specific combining ability (SCA) is the deviation of crosses on the basis of average performance of the lines involved.

Diallel analysis is used to estimate GCA and SCA effects and their implications in breeding (Griffing, 1956a; Gardner and Eberhart, 1966; Baker, 1978). Griffing (1956a) proposed an analysis for diallel mating systems that estimate the general and specific combining abilities of lines and hybrids. Combining ability for different yield and yield contributing traits in maize has been investigated by several authors (Betrán *et al*., 2003; Long *et al*., 2004; Menkir and Ayodele, 2005; Badu-Apraku *et al*., 2013a; Badu-Apraku *et al*., 2015a). GCA is associated to additive genetic effects (additive variance and additive \times additive variance) while specific combining ability is associated to non-additive genetic effects (dominance variance, additive \times dominance variance and dominance \times dominance variance).

Hemalatha *et al*. (2014) reported that the general and specific combining ability variances were highly significant for almost all the characters except for anthesis-silk interval. Based on GCA effects the parents, P4-TQPM 34-1 and P3-QPM 46-3 were early and contributed maximum favourable genes for maturity characters and P3-QPM 46-3 and P10-QPM 89-4 were good general combiners for plant height and ear height while the crosses viz; P1 x P9 and P4 x P9 for earliness and P4 x P6 and P3 x P6 for plant height and ear height are the best specific combiners, involving either both the parents or one of the parents as good general combiners.

Rovaris *et al*. (2014) assessed male flowering (MF), female flowering (FF), plant height, ear height, percentage of broken and lodged plants $(Ld + Br)$ and grain yield. The P7, P1, P3 and P2 genotypes presented the best general combining ability for all the traits assessed. The best estimates for specific combining ability were observed in the P6 x P9, P2 x P9 and P7 x P8 hybrids indicating dominant loci systems in the genetic control of the traits plant height, ear height and grain yield.

Kumar *et al*. (2014) studied combining ability of twenty newly developed inbred lines in maize. The resulting 60 crosses along with parents and standard checks were evaluated in a randomized block design replicated three times. They recorded highly significant estimates of GCA and SCA effects on twelve quantitative characters namely, plant height, ear height, ear
length, ear girth, number of kernel rows ear⁻¹, number of kernels row⁻¹, 100 kernels weight and grain yield per plant⁻¹.

In a study carried out by Badu-Apraku *et al.* (2015a), 91 diallel crosses derived from 14 early maturing yellow endosperm QPM inbreds were evaluated under Striga infested, drought, low-N and optimal environments in Nigeria. They reported that the GCA and SCA effects were important in the inheritance of grain yield and other traits of the inbreds. However, they recorded that GCA was more important than SCA under each contrasting environment and across environments suggesting that the additive gene action was more important than the nonadditive in the set of inbreds. Similar results were initially recorded by Badu-Apraku *et al.* (2013) in a study to determine the combining ability of 20 extra-early yellow inbred lines conducted at four locations in Nigeria.

1.3.8 Prediction of hybrid performance: best linear unbiased prediction (BLUP)

Non-additive genetic effects such as dominance and epistasis are necessary for heterosis to occur. Some traits can show a strong non-additive inheritance. If the relative magnitude of these components is known by plant breeders, more accurate selection could be practiced (Santos *et al*., 2015). In the breeding of commercial maize, a very large number of new inbreds and hybrids is generated in each breeding cycle. Selection of the best ones is a challenge and, therefore, should be based on the most reliable criterion for the true performance of genotypes. In addition, resources (such as human resources, finances, and infrastructure) are limited and, therefore, their optimum allocation is of crucial importance for the efficiency and competitiveness of breeding programs. Furthermore, the effect of environment in a quantitative trait like grain yield is expressive, interfering on the efficiency of estimating single-crosses breeding values. Therefore, the use of unbiased methods to assess single-cross performance with high accuracy can greatly increase the efficiency of maize breeding programs (Mendes and Souza Junior, 2016). For optimal progress from selection, a plant breeder has to strike a balance among the number of (1) parental crosses, (2) test candidates within each cross, and (3) test environments as well as field replications (Mi *et al*., 2011).

In the past, estimation of the genotypic value is commonly based on the phenotypic value of the tested candidate itself, whereas information on related genotypes is largely neglected. With BLUP, information from genetically related candidates is combined to obtain more precise estimates of genotypic values of test candidates and thereby increase progress from selection (Mi *et al*., 2011). The best linear unbiased prediction (BLUP) method was originally developed to estimate breeding values in animal breeding (Robinson, 1991). The prediction of breeding values using BLUP is based on (1) known genetic relationships among genotypes and (2) the available phenotypic data of related genotypes (Bernardo, 1996). It also enables users to cope with unbalanced data sets. Because of its good prediction accuracy and enhanced efficiency of selection it offers, Bernardo (1996) and Piepho *et al*. (2008) advocated its application in plant breeding. However, BLUP is rarely used in plant breeding (Piepho *et al*., 2008).

With advancement in the use of molecular markers, the selection for important traits such as grain yield, which was originally performed on by phenotypic information, can now be performed using the molecular marker's information (Cantelmo *et al*., 2017). A justification for the use of molecular markers as reported by Meuwissen *et al*. (2001) is the expectation that information on genomic constitution of the individuals may bring greater genetic gain than when only phenotypic data are used.

By combining the information from molecular markers and phenotypic data, Bernardo (1994) proposed a model for prediction of maize hybrids using best linear unbiased prediction (BLUP). It takes the information from molecular markers into consideration for construction of the pedigree of the parental lines. Although the correlation between the predicted genotypic performance and its phenotypic value is moderate in most cases, there were advantages to this approach (Bernardo1994). Several authors (Bernardo, 1995, 1996; Massman *et al*., 2013; Cantelmo *et al*., 2016; Cantelmo *et al*., 2017) in their studies have proved this approach to effective.

Some of the objectives of the study carried out by Mi *et al*. (2011) were to compare the progress from selection using BLUP and conventional phenotypic selection based on mean performance solely of the candidates and also to analyse the potential of BLUP for further improving the progress from selection. According to them, the progress from selection was slightly higher with BLUP compared to conventional phenotypic selection, for both the selection gain and the probability to select the best genotypes. They concluded that selection based on BLUPs rather than phenotypic values had a positive, though small, effect on progress from selection in the two breeding schemes used. It was then suggested that further research is warranted to study the effect of BLUP on the progress from selection through the additional integration of marker information.

In the reports of Heffner *et al*. (2011) and Massman *et al*. (2013), empirical and simulation evidence suggests that genomic prediction (GP) can produce greater genetic gain per unit time than phenotypic selection in plant breeding with the use of year-round nurseries and highthroughput genotyping technology. GP can utilize all available genomic markers simultaneously to predict quantitative traits; many GP models assume that the performance of trait is a product of all loci in the genome. VanRaden (2008) proposed the genomic best linear unbiased prediction (GBLUP) model, and it has been widely used in plant breeding (Crossa *et al*., 2013). The GBLUP uses genomic covariance to estimate the genetic merit of an individual. For that purpose, a genomic relationship matrix estimated from information from molecular markers is used to recover information in related individuals (VanRaden, 2008; Hayes *et al*., 2009a, b; Crossa *et al*., 2013; Santos *et al*., 2015). Results indicate advantages of the GBLUP model in relation to marker models due to its relative simplicity and shorter computational time, which, in addition to the already well-known properties of the mixed models of selection, makes this a very attractive approach from the genetic and statistical perspective (VanRaden *et al*., 2009; Heslot *et al*., 2014).

Cantelmo *et al*. (2017) performed genome-wide selection using a set of Dart-seq markers associated to the additive-dominant genomic best linear unbiased prediction (GBLUP) model to predict maize grain yield in different crop seasons and locations. They used the different crop seasons as training and validation populations to estimate the predictive accuracy. The magnitude of the correlations between predicted and observed hybrids ranged from 0.82 to 0.89 in the winter crop season and from 0.56 to 0.76 in the summer crop season. Their results showed that the predictive ability was highly influenced by the genetic background and also by the interaction between crop seasons. In terms of discard, the coincidences between the genomic values of the summer crop and winter crop were 89 and 90%. This result indicates the possibility of using genomic prediction in breeding programs for initial discard of low-yielding genotypes. They concluded that GBLUP method was able to generate high correlations between predicted and observed hybrids in different test environments.

1.3.9 Grain yield stability and genotype by environment interaction

Evans (1993) defined crop yield potential as the yield of a cultivar when grown in environments to which it is adapted with non-limiting nutrients and water and with pests, diseases, weeds, lodging, and other stresses effectively controlled. Hence, a more functional definition of yield potential is the yield obtained when an adapted cultivar is grown with the minimal possible stressthat can be achieved with best management practices (Cassman, 1999). Improvements in maize stress tolerance have contributed to an increase in grain yield (GY). Grain yield in maize is determined by kernel number per plant (KNP) and kernel weight (KW) (Cerrudo *et al*., 2012). Yield improvement has been associated with increase in stress tolerance and heterosis, but the nature of the enhanced stress tolerance remains elusive. Yield improvement is the result of changes underlying physiological processes (Tollenaar and Lee, 2006).

Environment is the sum total of physical, chemical and biological factors (Nath *et al*., 2013). Genotype x environment interactions (GEI) are of major importance to plant breeders in developing improved genotypes because they cause difficulties in selecting genotypes evaluated in diverse environments. When G×E interaction is significant, its cause, nature, and implications must be carefully considered because it reduces the correlation between phenotypic and genotypic values, and has been shown to hinder the selection progress (Khalil *et al*., 2011). Grain yield is quantitative in nature and routinely exhibits genotype x environment interactions and necessitates genotype evaluation in multi-environments trials in the advanced stages of selection (Singh *et al*., 2009; Kandus *et al*., 2010). The GxE interaction allows the classification of genotypes by their behaviour in two different situations, either stable or adapted to a particular environment in terms of the yield or some other interesting agronomic feature (Kandus *et al*., 2010; Badu-Apraku *et al*., 2011a; Adu *et al*., 2013; Jorge de Oliveira *et al*., 2014).

By partitioning yield components of hybrids into linear and non-linear components, Singh *et al*. (2009) found that both were responsible for expression of the traits. However, the linear component was larger in magnitude than the non-linear component suggesting that variation in the performance of different cultivars could be predicted. The evaluation of $G \times E$ interaction gives an idea of stability of the population (Nath *et al*., 2013). Significant achievement in crop production may be possible by breeding varieties for their yield and yield components stability (Singh *et al*., 2009; Akhtar *et al*., 2010). Varietal mean yield over all environments and regression coefficients have been used to classify the cultivars specially adopted at poor and better yielding environments and for their general adaptability. Average phenotypic stability has been denoted by a regression coefficient of unit bi $= 1$ (Finlay and Wilkinson, 1963). A cultivar with bi $\langle 1 \rangle$ has above average stability, bi > 1 has below average stability and bi $= 0$ has absolute phenotypic stability which means a constant gain in all environments (Finlay and Wilkinson, 1963). It has also been found that the variety with the smallest mean value would

be the one that contributes the least to variety x location interactions and thus would be considered as the most stable genotype in the tests (Nath *et al*., 2013).

Additive Main Effects and Multiplicative Interaction (AMMI) analysis is one of the popular parametric but multivariate methods to predict adaptation and stability of cultivars. The usefulness of the method to be applied to some different crops has been noted by many researchers (Gauch and Zobel, 1996; Asfaw *et al*., 2009; Bose *et al*., 2014; Jorge de Oliveira *et al*., 2014).

The GGE biplot has been recognized as an innovative methodology in biplot graphic analysis in plant breeding. Fan *et al*. (2007) showed that the GGE biplot was a useful tool for identifying locations that optimized hybrid performance and for making better use of limited resources available for maize testing programs (Fan *et al*., 2007). The GGE biplot graphically displays genotype main effect plus G×E of multi-environment trials in a way that facilitates visual evaluation of cultivars and mega-environment identification (Yan *et al*., 2007).

1.4 Research Hypothesis

The following hypotheses were tested in this study:

1.4.1 Principal hypothesis

Similar mode of gene action controls agronomic traits in maize and heterotic response exists for the varietal parents under contrasting environments.

1.4.2 Secondary hypotheses

- 1. There is no genetic variability among the 14 elite open-pollinated maize varieties used
- 2. Similar mode of gene action controls grain yield and other agronomic traits in the genetic materials studied under the research conditions
- 3. Distinct heterotic groups exist for the maize varietal parents
- 4. Yield stability vary among the parents and their hybrids across contrasting environments.

1.5 OBJECTIVES

1.5.1 Overall objective

The general objective of this study was to determine the gene action and the heterotic response of 14 maize varieties under contrasting environments.

1.5.2 Specific objectives

The specific objectives of the study were to

- 1. assess genetic variability among 14 late-maturing maize varieties using genetic method;
- 2. determine the mode of gene action controlling grain yield and other agronomic traits;
- 3. classify the maize varietal parents into distinct heterotic groups; and
- 4. analyse yield stability of the parents and their hybrids across contrasting environments.

CHAPTER II

MATERIALS AND METHODS

2.1 Study areas

Field trials were conducted in 2017 and 2018 at the Teaching and Research Farms of Obafemi Awolowo University (OAU), Ile-Ife (7°31' N, 4°31' E, 256 m asl, and 1000-1250 mm annual rainfall) and Michael Okpara University of Agriculture, Umudike (05º29' N, 07º33' E; 122 m asl, and 2177 mm annual rainfall) in Nigeria (Figure 4).

Figure 4: Map of the study areas

2.2 Climatic data of the study locations

The climatic data (rainfall and temperature) of the study locations were obtained for the period, 1981 to 2017 from the National Root Crops Research Institute agrometeorological unit (https://nrcri.gov.ng/index.php/agro-meteorology/) for the location at Umudike, and the Micrometeorology Unit, Physics Department, OAU, for the Ile-Ife location being the closest weather stations to the experimental sites. The climate diagram showing the distribution of rainfall and temperature in the study locations is presented in Figure 5.

Figure 5: Climate diagram of the study locations. A= Umudike, B= Ile-Ife (from data collected at metrological stations for the period 1981-2017)

2.3 Genetic materials

Fourteen (14) elite open-pollinated maize varieties derived from late-maturing maize germplasm sources were drawn from the drought-tolerant and pro-vitamin A breeding populations of the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria (Table 1). There are no known ethical issues associated with these varieties.

S/N	Parent	Characteristics
	DT - STR - Y - SYN 2	Tolerant to drought and striga
2	DT - STR - Y - SYN 14	Tolerant to drought and striga
3	IWD C2 SYN F2	Tolerant to drought
4	STR SYN - Y2	Tolerant to striga
5	TZL Comp - 1 - WC6/DT SYN - 1W	Tolerant to drought
6	TZL Comp - 3 C3 DT	Tolerant to drought
	TZL Comp - 3 C3 DT C2	Tolerant to drought
8	TZL Comp - 4 C3 DT C2	Tolerant to drought
9	White DT STR SYN/IWD C3 SYN F2	Tolerant to drought and striga
10	White DT STR SYN/TZL Comp - 1 - W F2	Tolerant to drought and striga
11	PVA SYN 2	High in Pro-Vitamin A
12	PVA SYN 3	High in Pro-Vitamin A
13	PVA SYN 4	High in Pro-Vitamin A
14	PVA SYN 7	High in Pro-Vitamin A
Check 1	DT STR SYN $2-7$	Tolerant to drought and striga
Check 2	White DT STR SYN/IWD C3 SYN	Tolerant to drought and striga
Check 3	Local check	Unknown

Table 1: The parents used for the diallel crosses and the check varieties

2.4 Generation of crosses

All possible crosses were made in a diallel fashion without reciprocal among the 14 varieties to produce 91 variety hybrids during the growing season of 2017. The crosses were made with reciprocals using bulked pollen of each parent variety. Seeds from each cross and its reciprocals were bulked to represent a particular varietal hybrid.

2.5 Field evaluations and stress management

The 14 parental varieties, the 91 hybrids, and 3 checks were evaluated for their agronomic performance in six environments under marginal rainfall, drought and optimal growing conditions in 2018 (Table 3.2). The checks were made up of two improved OPVs obtained from IITA and a local variety commonly grown by rural farmers in the locations. The growing conditions, which constituted six environments, were based on the total amount of rainfall and time of planting. Under the optimal growing conditions, the trials were established during the main planting season of maize with optimum amount of rainfall. Under the marginal rainfall condition, the trials were planted at the onset of rainfall when the frequency of rain is erratic and soil moisture is sub-optimal for maize cultivation and towards the end of the rainy season, when flowering was targeted to coincide with drought spell. The National Root Crops Research Institute agrometeorological unit (https://nrcri.gov.ng/index.php/agro-meteorology/) provided meteorological data for the location at Umudike, while that of the Ile-Ife location was provided by the Micrometeorology Unit, Physics Department, OAU, being the closest weather stations to the experimental sites.

The experiment was laid out in a randomized incomplete block design (9 x 12 alpha lattice) with three replications in each environment. Experimental units consisted of two-row plots, each 5 m in length with a spacing of 0.75 m. The distance between two adjacent plants within a row was 0.50 m in all trials. Three seeds were planted, and the seedlings later thinned to two per hill approximately 2 weeks after emergence to achieve a final plant population density of about 53,333 plants ha^{-1} .

Environment	Location	Altitude (masl)	Rainfall (mm)	Average temperature	Soil texture	Nitrogen $(\%)$	Date established	Date harvested
Marginal	Ile-Ife	256	452.63	$^{\circ}$ C) 25.5	Loamy sand	1.5	9th April, 2018	23rd July, 2018
Optimal	Ile-Ife	256	533.75	24.4	Loamy sand	1.5	22th May, 2018	25th Sept., 2018
Drought	Ile-Ife	256	336.66	29.6	Loamy sand	1.5	14th Sept., 2018	4th Jan., 2019
Marginal	Umudike	122	1147.7	27.5	Sandy loam	0.3	14th April, 2018	6th Aug., 2018
Optimal	Umudike	122	1071.6	27.5	Sandy loam	0.3	6th June, 2018	10th Oct., 2018
Drought	Umudike	122	617.9	28.3	Sandy loam	0.3	19th Sept., 2018	$21st$ Dec., 2018

Table 2: Characteristics of the test environments used for the evaluation of the genotypes

2.6 Field Measurements

Data were recorded under all the growing conditions on days to 50% silking (DS) and days to anthesis (DA) as the number of days from planting to when 50% of the plants had emerged silks and had shed pollen, respectively. The anthesis-silking interval (ASI) was calculated as the difference between days to 50% silking and 50% anthesis. Plant (PHT) and ear heights (EHT) were measured as the distance from the base of the plant to the height of the first tassel branch and the node bearing the upper ear, respectively. Root lodging (the percentage of plants leaning more than 30° from the vertical) and stalk lodging (the percentage of plants broken at or below the highest ear node) were also recorded. Plant aspect (PASP) was an assessment of overall plant type (plant and ear heights, uniformity of plants, cob size, disease and insect damage and lodging) and was recorded on a scale of 1 to 5 where $1 =$ excellent plant architecture: uniform medium-height plants standing erect with strong stalk, uniformly big ears, well covered with husk and uniformly placed at the middle of the plant, no visible symptoms of any common tropical diseases on leaves, stems, and ears; $2 =$ very good plant architecture: uniform medium-height plants standing erect with strong stalk, uniformly moderate size ears well covered with husk and placed at the middle of the plant, no visible symptoms of any common tropical diseases on leaves, stems, and ears; $3 =$ satisfactory plant architecture: less uniform plant height, plants standing erect with strong stalk, uniformly moderate size ears well covered with husk and placed at the middle of the plant, slight symptoms of diseases on leaves and stems; $4 =$ poor plant architecture; non-uniform plant height, plants having weak stalk, uniformly small ears poorly covered with husk and ears placed far above the middle of the plant, symptoms of common tropical diseases on leaves and stems; and $5 = \text{very poor plant architecture: non-uniform plants with stalk loading, very small}$ ears poorly covered with husk and ear placement high above the middle of the plant; presence of barren plants in a plot, severe symptoms of diseases on leaves and stems (Akinwale and Adewopo, 2016). Ear aspect (EASP) was based on freedom from disease and insect damage, ear size, uniformity of ears and was recorded on a scale of 1 to 5, where $1 =$ excellent ears: uniformly big ears, well filled with grains, no ear rot or other ear disease symptoms, such as smut (*Ustilago maydis*); 2 = very good ears: uniform moderate-sized ears, well filled with grains, no ear rot or other ear disease symptom; $3 =$ satisfactory ears: less uniform moderatesized ears, well filled with grains, no ear rot or other ear disease symptom; 4 = poor ears: small sized ears, poorly filled with grains, slight symptoms of ear rot and other diseases; and $5 = \text{very}$ poor ears: very small-sized ears, ears poorly filled with grains and severe symptoms of ear rot and other ear diseases (Akinwale and Adewopo, 2016). Ear number per plant (EPP) was computed by dividing the total number of ears harvested per plot by the number of plants in a plot. Grain yield was computed from the ear weight and converted to kg ha⁻¹. A shelling percentage of 80% was assumed for all cultivars and the grain yield was adjusted to 15% moisture using the following formula:

$$
\gamma = \varepsilon \ge \frac{(100 - n)}{85} \ge \frac{(10000)}{\varphi} \ge 0.80
$$

where γ = grain yield (kg ha⁻¹), ϵ = ear weight (kg m⁻²), n = moisture at harvest, φ = plot area $(m²)$.

2.7 Statistical Analysis

Separate ANOVAs were performed on data collected across years and locations for each research condition (marginal, drought and optimal growing conditions) with PROC GLM in SAS using a RANDOM statement with the TEST option (SAS Institute, 2012). Subsequently, combined ANOVA was performed across the test environments depending on the kind of data collected in each of the environments. Means were separated using the LSD. The relationship between grain yield and other agronomic traits under marginal, drought, and optimal environments were examined by estimating the genetic correlation coefficients for the traits using the meta menus program in SAS version 9.4 (SAS Institute, 2012). Furthermore, stepwise multiple regression and sequential path diagrams were used to explain the causal relationships among traits under marginal rainfall, drought, optimal, and across environments using the procedure described by Mohammadi *et al*. (2003). The stepwise multiple regression analysis was performed using the Statistical Package for the Social Sciences, SPSS version 17.0 (SPSS Inc, 2007) to determine the first, second, and third order predictor traits on the basis of their contributions to the total variation in grain yield with minimized multicolinearity (Badu-Apraku *et al*., 2017). Firstly, all other traits were regressed on grain yield to identify those with significant contributions to grain yield at $P < 0.05$ as first order traits. The rest of the traits were regressed on each of the first order traits and those with significant contributions to grain yield through the first-order trait were classified as second-order traits. The procedure was repeated and the remaining traits were categorized into subsequent orders. The standardized b values generated by the stepwise regression analysis were the path coefficients (Mohammadi *et al*., 2003; Badu-Apraku *et al*., 2017). The significance of the path coefficients was determined in the stepwise multiple regression analysis using t-test at 5% probability level and the traits with significant path coefficients were retained. In addition, the relationships among traits within an order of traits were determined using the spearman correlation analysis implemented in SAS version 9.4 (SAS Institute, 2012). The GCA effects of the parents and SCA effects of the crosses as well as their mean squares in each environment and across environments were estimated and compared following Griffing's methods 2 and 4 (using the two models for each method); and Gardener and Eberhart Analyses II and III. The DIALLEL-SAS program developed by Zhang *et al*. (2005) and adapted to SAS software version 9.4 was utilized. The GCA and SCA effects were tested for significance using *t*-test. The standard errors of the GCA and SCA effects were estimated as the square root of the GCA and SCA variances (Griffing, 1956a).

To assign the OPVs into heterotic groups, the HSGCA method proposed by Fan *et al*. (2008) was used as follows:

 $HSGCA = Cross mean X_{ij} + Tester mean (X_i) = GCA + SCA$

where X_{ij} is the mean yield of the cross between the ith tester and the jth parent, X_i is the mean yield of the ith tester across jth parents. HSGCA estimates were subjected to Ward's minimum variance cluster analysis using the software JMP version 14 (SAS Institute Inc., Cary, NC, USA).

Heterotic grouping by the HGCAMT was achieved by standardizing the GCA effects (mean of zero and standard deviation of 1) of 10 considered, to minimize the effects of different scales of the traits. The standardized GCA effects were subsequently subjected to Ward's minimum variance cluster analysis using the software JMP version 14 (SAS Institute Inc., Cary, NC, USA). Dendrograms were constructed for the groupings based on HGCAMT and HSGCA.

The best linear unbiased prediction (BLUP) values were estimated for parents and their crosses with the experimental data. The BLUP, GCA, and SCA estimates of the genotypes were correlated. The BLUP and correlation coefficients were provided by the PROC MIXED and PROC COR function, respectively, of SAS version 9.4 (SAS Institute, 2012)

The phenotypic data of each individual environment were analysed by a linear mixed model of the form:

$$
y_{jkl} = \mu + \alpha \cdot x_{jkl} + g_j + r_k + b_{kl} + e_{jkl}
$$
 [2.1]

where y_{ikl} are the phenotypic observations of grain yield, μ is the grand mean, r_k the fixed effect of the kth replicate, b_{kl} the random effect of the *l*th block nested within the kth replicate, and e_{jkl} the residual effect. The effect g_j of the *j*th genotype was firstly modelled as random to estimate the genotypic variance σ_g^2 and subsequently fixed to derive Best Linear Unbiased Estimates (BLUEs). When considered as fixed, the genotypic effect was further partitioned into parent, hybrid, check and their orthogonal contrasts in order to explain the proportion and significance of variation of each components of the genotype. The number of ears per plant x_{ikl} and the corresponding regression coefficient α served as a covariate in order to compensate for an unequal plant stand between plots. Broad-sense heritability of an individual environment, henceforth denoted as repeatability, was calculated with the following formula (Piepho and Möhring, 2007):

$$
h^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_e^2}{r}}
$$
 [2.2]

where σ_e^2 is the residual variance and r is the number of replications. An across environment analysis was subsequently conducted by employing a mixed model of the form:

$$
y_{ijkl} = \mu + \alpha_i \bullet x_{ijkl} + u_i + g_j + gu_{ij} + r_{ik} + b_{ikl} + e_{ijkl}
$$
 (2.3)

where y_{ijkl} are the phenotypic observations of grain yield, μ the grand mean, and g_j the effect of the jth genotype that was modelled as fixed to derive BLUEs and subsequently as random to estimate variance components. The fixed effect u_i designated as the ith environment and gu_{ii} the random genotype-by-environment interaction effect. The number of ears per plant x_{iik} served again as a covariate, though this time with an environment specific regression coefficient α_i . The residual effect e_{ijkl} followed a normal distribution with $e \sim N(0, \sigma_e^2)$. The genotypes were subsequently divided into three genotypic groups comprising the parents, hybrids and checks for assessing the stability variance. The statistical model for the analysis can be described with the following mixed model (Mühleisen *et al*., 2014b):

$$
y_{hijkl} = \mu + \alpha_i \bullet x_{hijkl} + q_h + u_i + g_{hj} + q u_{hi} + f_{hij} + r_{ik} + b_{ikl} + e_{hijkl} \tag{2.4}
$$

where μ is the grand mean, q_h is the fixed effect of the hth group, and g_{hj} the fixed effect of jth genotype within the hth group. The effect qu_{hi} of the group-by-environment interaction as well as the group-by-genotype-by-environment interaction f_{hij} were modelled as random. Group specific estimates of the stability variance were obtained modelling heterogeneous residual variances for each group following the suggestion by Mühleisen *et al*. (2014b) with a variancecovariance matrix of the form:

$$
\begin{pmatrix}\n\sigma_{f_{g(1)}}^2 & 0 & 0 \\
0 & \sigma_{f_{g(2)}}^2 & 0 \\
0 & 0 & \sigma_{f_{g(3)}}^2\n\end{pmatrix}
$$
\n[2.5]

where $\sigma_{fg(1)}^2$, $\sigma_{fg(2)}^2$, and $\sigma_{fg(3)}^2$ designate the residual variance, henceforth called the stability variance, of the three groups with $f_i \sim N(0, \sigma_{f_{g(i)}}^2)$. The stability variance of a group was thus defined as its genotype-by-environment interaction analogue to the stability variance of individual genotypes described by Shukla (1972). Heterosis was finally computed with BLUEs derived from the single-step model [2.3] as:

$$
Het_{MP} = 100 \bullet (\hat{H} - \overline{MP})/\overline{MP}
$$
 [2.6]

and

$$
Het_{C}=100\bullet (\widehat{H}-max[\widehat{C}])/max[\widehat{C}]
$$
\n
$$
[2.7]
$$

Where the mid-parent heterosis, Het_{MP} was expressed as the relative difference between the estimated hybrid performance \hat{H} and the mid-parent value, \overline{MP} , whereas the commercial heterosis Het_{C} was computed as the difference between the hybrid performance and the estimated performance of the best check variety max[Ĉ]. The statistical analyses were performed using the statistical package Sommer 3.8 for the R programming environment (R Development Core Team 2016). Lastly, a GGE biplot analysis of the selected genotypes was conducted using the GGEBiplotGUI (Frutos *et al.*, 2014) package for R.

CHAPTER III

RESULTS

3.1 Genetic variability and performance of late maturing elite cultivars of maize under marginal rainfall, drought and optimal conditions in Nigeria

The combined ANOVA across six environments involving marginal rainfall, drought, and optimal conditions showed significant $(P < 0.01)$ environments (E) , genotypes (G) and genotype x environment interaction (GEI) effects for all the measured traits (Table 3). The variation due to the genotype was further partitioned into its orthogonal components. There were significant parent (P) effects for percentage emergence (EMERG), days to silking (DS), plant height (PHT) and plant aspect (PASP). The effects due to hybrid (H) were highly significant for all the traits while that due to parent (P) versus H were significant for grain yield (GY), EMERG, Anthesis-silking interval (ASI) and PASP. Broad sense heritability $(H²)$ estimates on plot mean basis ranged from 14% for both DS and ASI to 61% for EMERG. Grain yield had a heritability estimate of 45%.

Table 4 shows the average performances of the parents, hybrid and checks across the six environments. The variety hybrids out-yielded the parents by 9% and out-yielded the lowest performing check by 33%. However, Check 2 (White DT STR SYN/IWD C3 SYN) out-yielded the hybrids by 4% on average basis. The average values of the hybrids for flowering traits were similar to that of the parents. The individual performance of each genotype can be found in Appendix I. Grain yield ranged from 1.5 t ha⁻¹ for entry H35 (a cross between parent 3 and parent 13) to 3.4 t ha⁻¹ for entry H38 (a cross between parent 4 and parent 6) with a mean of 2.31 t ha⁻¹ (Appendix I).

The combined ANOVA across the marginal rainfall conditions revealed significant ($P < 0.01$) differences among environments (E) and genotypes (G) for all the measured traits (Table 5). Significant ($P < 0.05$ or $P < 0.01$) genotype x environment interaction (GEI) effects were detected for all the traits except EMERG and PASP. There was no significant parent effect under this growing condition; however, the effect due to hybrid was highly significant for all the traits considered in the study. The P vs H effect was significant for EMERG, PHT and PASP. The H vs check (C) effect was highly significant for GY, DS and ASI. H² estimates ranged from 5% for ASI to 62% for EMERG. Grain yield had a heritability estimate of 22% while that of days to anthesis (DA), DS, ear aspect (EASP) and ear rots (EROT) could not be estimated because of zero genotypic variance recorded for the traits. With respect to grain yield, the repeatability estimates of locations Ile-Ife and Umudike under marginal rainfall condition were 43% and 48% respectively (Table 5).

The average yield and other agronomic traits of the parents, hybrids and checks evaluated under marginal rainfall condition are presented in Table 6. The variety hybrids had an average yield of 2.4 t ha⁻¹. This was 9% higher than the average yield of the parents and 60% higher than the lowest yielding check variety (Check 1). Check 2 (White DT STR SYN/IWD C3 SYN) outperformed the hybrids by 8%. The hybrids had higher emergence and taller plants than their parents. There was 16% GY reduction each of the parents and the hybrids under marginal rainfall when compared to the parents and the hybrids under optimal condition respectively.

Individual performances of the genotypes under marginal rainfall are shown in Appendix II. Individual grain yield of the genotypes under this condition when compared to the corresponding yield performance of the genotypes under optimal environments revealed varying yield reductions from -95% for H41 (a cross between parent 4 and parent 9) to 59% for parent 10 (P10) with a mean of 16%. Thirty percent of the genotypes had negative percentage yield reductions. Generally, the genotypes that recorded more DA, had relatively higher percentage GY reduction with low GY. Grain yield ranged from 1.2 t ha⁻¹ for entry H65 (a cross between parent 7 and parent 9) to 4.1 t ha⁻¹ for entry H58 (a cross between parent 6 and parent 9) with a mean of 2.40 t ha⁻¹ (Appendix II).

The combined ANOVA under optimal condition revealed significant ($P < 0.05$ or $P < 0.01$) variation among E, G and GEI mean squares for all measured traits except GEI effect for grain yield (Table 7). The partitioning of the variation due to genotype revealed that the parental effect was significant for PHT, PASP and EASP while the hybrid effect was highly significant for all the measured traits. The P vs H effect was significant for only the GY. The effect due to P vs C was only significant for PHT. The H vs C and the H, P vs C effects were significant for both DS and PHT. H² estimates ranged from 9% for DS to 62% for GY. Under optimal environments, the heritability estimates of ASI, PHT, PASP, EASP, EROT and number of ears per plant (EPP) could not be estimated because of zero genotypic variance recorded for the traits. The H^2 estimates of grain yield in each of the locations, Ile-Ife and Umudike were 40% and 78% respectively (Table 7).

The average yield of the hybrids was 2.9 t ha⁻¹, which was 7% higher than that of the parents and the best performing check variety respectively. Both the parents and their hybrids had similar values for the flowering traits, EASP, EROT and EPP. The hybrids were taller and had better scores for PASP (Table 8).

The highest GY $(4.5 \text{ t} \text{ ha}^{-1})$ on genotype basis was recorded by entry H38 (a cross between P4 and P6) while the lowest grain yield (1.4 tha^{-1}) was recorded by H41 (a cross between P4 and P9). The average GY across the optimal environments was 2.86 t ha⁻¹ (Appendix III). Entry H38, with the highest GY, gave the tallest plants (166 cm). It had 2.3 and 1.9 as its PASP and EASP scores respectively, and these values were among the lowest five scores across all the cultivars. It also showed superiority in terms of EPP and EROT. It had an ASI of 2 days, which was second to the lowest under optimal condition (Appendix III).

The combined ANOVA under drought indicated significant (P< 0.05 or P< 0.01) differences between E and G for all the measured traits except G effect for EASP (Table 9). Significant (P < 0.05 or P < 0.01) GEI effects were detected for all the traits except ASI, EASP and EPP. The effect due to the parents was significant for GY, EMERG, DA, DS, and PHT. That of the hybrid was significant for all the traits except EASP and EPP. H^2 estimates ranged from 17% for ear aspect to 69% for percentage emergence at 9 days after planting. Grain yield had a heritability estimate of 21% while that of ear rots could not be estimated because of zero genotypic variance recorded for the traits. The effects due to H vs C and P, H vs C were each significant for GY, EMERG and DA. The H^2 estimates of GY under drought in both Ile-Ife and Umudike were 70% and 27% respectively.

Presented in Table 10 are the average performances for yield and other agronomic traits for the parents, their hybrids and the check varieties under drought. The hybrids slightly out-performed the parents, in terms of GY, by 6%. The best yielding check under drought condition, a local variety commonly grown by the farmers, out-yielded the hybrids by 47%. Similar values of other agronomic traits were observed for both parents and hybrids except in the case of PHT and PASP. There were 40% and 43% GY reduction of the parents and the hybrids under drought when compared to the parents and the hybrids under optimal condition respectively. The local check variety maintained the same average yield under both drought and optimal condition (Table 10).

Grain yield on individual genotype basis under drought ranged from 0.5 t ha⁻¹ for entry H35 (a cross between parent 3 and parent 13) to 3.3 t ha⁻¹ for entry H38 (a cross between parent 4 and parent 6) with a mean of 2.40 t ha⁻¹. Grain yield under drought when compared to the corresponding yield performance of the genotypes under optimal environments revealed varying yield reductions from -34% for H48 (a cross between parent 5 and parent 7) to 82% for entry H89 (a cross between parent 12 and parent 13) with a mean of 42% (Appendix IV). Out of the 108 genotypes, four (entries H48, P7, H64, and H41) had negative percentage yield reduction. Most of the genotypes that recorded more DA, DS and ASI with lower plant heights had relatively higher GY reduction with lower GY.

SOV	DF	GY	EMERG	DA	DS	ASI	PHT	PASP	EASP	EROT	EPP
Environment (E)	5	841.42**	80742.34**	3434.23**	6872.97**	1430.23**	270697.94**	82.48**	38.46**	504.29**	$11.04**$
$\bf Rep/E$	12	$3.70**$	1766.94**	28.02**	$25.31**$	$8.65***$	1519.90**	$2.25**$	$3.23**$	1.62	$0.13**$
Block/E*Rep	144	$1.26**$	329.82**	$9.28**$	$10.12**$	1.87	513.49**	$0.60**$	$0.70**$	1.34	$0.04**$
Genotype (G) Parent (P)	107 13	$2.10**$ 0.66	525.28** $170.06**$	$10.15**$ 6.49	$15.64**$ 9.48*	$26.11**$ 3.61	757.62** $602.88**$	$0.57**$ $0.48*$	$1.04**$ 0.76	$2.15**$ 0.79	$0.06**$ 0.031
Hybrid (H)	90	$2.14**$	550.31**	$10.65**$	$17.42**$	$4.79**$	673.54**	$0.53**$	$1.02**$	$2.23**$	$0.054**$
P vs H		$6.97**$	800.13*	1.14	25.84	$9.85*$	898.49	$1.58*$	0.49	0.42	0.005
P vs Check (C)	$\mathbf{1}$	0.06	1856.62**	7.37	17.18	0.16	968.44	0.12	$3.07*$	0.39	0.005
H vs C		1.64	1448.20**	17.18	0.47	11.84*	677.78	0.01	$3.25*$	0.11	0.081
P , H vs C		1.43	1757.55**	16.02	1.17	9.09	566.28	0.01	$3.74*$	0.16	0.069
G^*E	535	$1.19**$	211.88**	$9.56**$	13.56**	$25.27**$	412.35**	$0.40**$	$0.76**$	1.89**	$0.04**$
Error	1139	0.69	97.29	5.73	6.65	1.59	239.54	0.25	0.48	1.21	0.03
Heritability		0.45	0.61	0.14	0.14	0.16	0.49	0.35	0.29	0.15	0.23

Table 3: Mean squares and heritability estimates of 108 maize genotypes evaluated across six environments in Nigeria, 2017-2018

 $**$ = Significant at 0.01 probability levels; Env = environment; Rep=replication; GY = Grain yield (tha⁻¹); EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height (cm); PASP = plant aspect (1 – 5 scale); EASP = ear aspect (1 – 5 scale); EROT $=$ ear rot; EPP $=$ ears per plant.

Group		GY EMERG DA DS ASI PHT PASP EASP							EROT	EPP
Parent	2.2	68	62	65	$\overline{3}$	124.73 3.4		3.3	12	0.7
Hybrid 2.4 70			62	65	$\overline{3}$	127.36 3.3		3.3	$1\,3$	0.7
Check1 1.8 76			62	66 4		124.14	3.5	3.8		0.7
Check2 2.5		82	61	65	\overline{A}	134.37 3.1		3.6	19	0.7
Check3	γ	69	62	66 4		129.79 3.1		3.3	0.8	0.7

Table 4: The average yield and other agronomic traits of the parents, hybrids and checks across six environments in Nigeria, 2017-2018

 $GY =$ Grain yield (t ha⁻¹); EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; $DS =$ days to 50% silking; ASI = anthesis-silking interval; PHT = plant height (cm); PASP = plant aspect (1 – 5) scale); EASP = ear aspect $(1 – 5 scale)$; EROT = ear rot; EPP = ears per plant.

**,* = Significant at 0.01 and 0.05 probability levels respectively; Env = environment; Rep=replication; GY = Grain yield (tha⁻¹); EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP = ears per plant. Env1_GY = location Ile-Ife; Env2_GY = location Umudike.

	Group GY EMERG DA DS ASI PHT PASP EASP EROT EPP YR (%)					
Parent 2.2 68			61 65 4 111.33 3.7 3.3 1.9		0.6 16.4	
	Hybrid 2.4 75 62 67 5 114.23 3.6 3.3 2.0				0.6 15.5	
Check1 1.5 67			65 72 7 100.06 4.3 4.3 1.3		0.7	34.8
Check2 2.6 85			62 67 5 111.76 3.3 3.4 2.7		0.8 3.7	
Check3 1.7 61			63 71 8 117.75 3.5 3.3 1.2		0.5	32.0

Table 6: The average yield and other agronomic traits of the parents, hybrids and checks evaluated under marginal rainfall condition in Nigeria, 2017-2018

 $GY =$ Grain yield (t ha⁻¹); EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; $DS = days$ to 50% silking; ASI = anthesis-silking interval; PHT = plant height (cm); PASP = plant aspect (1 – 5) scale); $EASP = ear$ aspect (1 – 5 scale); $EROT = ear$ rot; $EPP = ear$ per plant; $YR = yield$ reduction.

Table 7: Mean squares and heritability estimates of 108 maize genotypes evaluated under optimal growing condition in Nigeria, 2017- 2018

SOV	DF	GY	EMERG	DA	DS	ASI	PHT	PASP	EASP	EROT	EPP	Env3_GY	Env4_GY
Environment (E) Rep/E	4	1002.93** $6.58**$	22128.73** 2702.40**	6500.23** 16.69	10300.94** 8.87	435.90** $6.37**$	325487.97** 614.55	26.05** $3.29**$	27.48** $3.27**$	357.75** 2.66	$0.41**$ $0.27**$		
Block/E*Rep	48	$1.09*$	$152.57**$	11.51	11.91	1.46	270.08	$0.50**$	0.29	$2.04*$	0.02		
Genotype (G)	107	$2.04**$	157.72**	$19.52**$	22.78**	$3.91**$	719.55**	$0.57**$	$0.65**$	1.87*	$0.04**$		
Parent (P)	13	0.85	97.81	5.73	5.02	4.25	449.79*	$0.50**$	$0.62*$	1.09	0.03		
Hybrid (H)	90	1.98**	172.41**	20.31**	23.86**	$3.89**$	627.40**	$0.51**$	$0.63**$	$2.13**$	$0.04**$		
P vs H		$5.01*$	0.69	14.99	15.55	0.00	530.71	0.87	0.08	0.49	0.00		
P vs Check (C)		0.02	0.19	17.81	47.35	7.08	4483.23*	0.57	0.27	0.82	0.01		
H vs C		3.02	14.54	35.30	$65.27*$	4.59	3038.09**	0.01	0.52	2.20	0.01		
P , H vs C		2.84	12.28	36.49	68.96*	5.15	3142.02**	0.02	0.68	2.26	0.01		
$G*E$	107	0.80	128.52**	$17.26**$	$20.63**$	$4.14**$	713.14**	$0.61**$	$0.64**$	$2.15**$	$0.04**$		
Error	380	0.78	70.39	11.25	12.06	1.55	269.43	0.28	0.28	1.33	0.02		
Heritability		0.62	0.20	0.14	0.09	0.00	0.00	0.00	$\mathbf{0}$	$\boldsymbol{0}$	0.00	0.40	0.78

**,* = Significant at 0.01 and 0.05 probability levels respectively; Env = environment; Rep=replication; GY = Grain yield (tha-1); EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP = ears per plant. Env3_GY = location Ile-Ife; Env4_GY = location Umudike.

Table 8: The average yield and other agronomic traits of the parents, hybrids and checks evaluated under optimal growing condition in Nigeria, 2017-2018

	Group GY EMERG DA DS ASI PHT PASP EASP EROT EPP							
Parent 2.7 85					64 67 3 135.53 3.1	3.1 1.7		0.8
Hybrid 2.9 84			64 67 3		139.37 3.0	3.1	1.7	0.8
Check1 2.3 81			63 65 2		140.28 3.0	3.1	2.0	0.8
Check2 2.7 85		63.	65 2		158.00 3.0	3.8	2.5	0.7
Check 3 2.5 83		63		65 2	145.83 3.2	3.1	12	0.8

 $GY =$ Grain yield (t ha⁻¹); EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; $DS = days$ to 50% silking; ASI = anthesis-silking interval; PHT = plant height (cm); PASP = plant aspect (1 – 5) scale); EASP = ear aspect (1 – 5 scale); EROT = ear rot; EPP = ears per plant.

SOV	DF	GY	EMERG	DA	DS	ASI	PHT	PASP	EASP	EROT	EPP	Env5 GY	$Env6_GY$
Environment (E)		355.32**	16790.13**	$207.05**$	76.40**	$31.74**$	83156.56**	$11.68**$	85.16**	0.08	19.08**		
$\bf Rep/E$	4	$2.70**$	714.49**	39.51**	28.54**	1.83	1424.21**	2.85**	$1.63**$	$0.93**$	0.08		
Block/E*Rep	48	$0.86**$	266.65**	$4.72**$	$4.61**$	$1.29*$	779.19**	$0.58**$	$0.58**$	0.31	$0.06*$		
Genotype (G)	107	1.49**	597.98**	$4.43**$	5.98**	$1.30*$	505.81**	$0.47**$	0.41	$0.39**$	$0.06**$		
Parent (P)	13	$0.81*$	220.54**	$5.14*$	$8.31*$	1.35	592.49**	0.43	0.29	0.12	0.02		
Hybrid (H)	90	1.38**	554.91**	$4.00**$	$5.51**$	$1.24*$	448.89**	$0.45**$	0.43	$0.42**$	0.05		
P vs H		0.24	0.05	0.03	1.63	1.20	1.74	0.00	0.31	0.11	0.02		
P vs Check (C)		0.90	4315.11**	4.30	1.77	0.55	153.04	0.04	1.09	0.54	0.07		
H vs C		$4.49*$	5945.00**	13.93*	3.61	3.38	279.17	0.58	0.28	0.05	0.01		
P , H vs C		$4.25*$	6137.62**	$11.15*$	2.61	2.98	94.14	0.40	0.35	0.10	0.00		
G^*E	107	$1.17**$	187.75**	$3.40**$	$4.73**$	1.00	375.07*	$0.34*$	0.34	$0.43**$	0.04		
Error	380	0.51	93.00	2.30	2.76	0.92	281.21	0.25	0.35	0.25	0.04		
Heritability		0.21	0.69	0.25	0.24	0.24	0.26	0.32	0.17	$\boldsymbol{0}$	0.21	0.70	0.27

Table 9: Mean squares and heritability estimates of 108 maize genotypes evaluated under drought in Nigeria, 2017-2018

**,* = Significant at 0.01 and 0.05 probability levels respectively; Env = environment; Rep=replication; GY = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP =ears per plant. Env5_GY = location Ile-Ife; Env6_GY = location Umudike.

	Group GY EMERG DA DS ASI PHT PASP EASP EROT EPP YR(%)							
Parent 1.6 52				60 62 3 127.17 3.3	$3.4\qquad 0.2$		0.7	40.3
Hybrid 1.7 52				60 62 3 128.34 3.2	3.4 0.2		0.7	42.8
Check1 1.6 81				59 61 2 132.08 3.3	3.8	0.0^-	0.6	30.4
Check2 2.3 74				59 63 4 133.36 3.2	$3.5\qquad 0.5$			0.6 14.8
Check3 2.5 64		60.	62 3	125.79 2.6	3.4	0.2°	0.7	(0.0)

Table 10: The average yield and other agronomic traits of the parents, hybrids and checks evaluated under drought in Nigeria, 2017-2018

 $GY =$ Grain yield (t ha⁻¹); EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; $DS = days$ to 50% silking; ASI = anthesis-silking interval; PHT = plant height (cm); PASP = plant aspect (1 – 5) scale); $EASP = ear$ aspect (1 – 5 scale); $EROT = ear$ rot; $EPP = ear$ per plant; $YR = yield$ reduction.

3.1.1 Genetic correlation between grain yield and other agronomic traits

Most of the measured traits exhibited significant ($P < 0.01$ or < 0.05) genetic correlation coefficients with grain yield (GY) under different research conditions (Table 11). Grain yield showed highly significant ($P < 0.01$) negative genetic correlations with days to anthesis (DA), plant aspect (PASP) and ear aspect (EASP) under all the research conditions and across environments, and also with days to silking (DS) under all the research conditions. It also showed significant and negative correlation with ear rot (EROT) under all the test environments and across. Grain yield had highly significant $(P< 0.01)$ negative correlation with anthesissilking interval (ASI) under optimal environment but significant positive correlations under marginal rainfall condition and across the environments. Under marginal rainfall and drought conditions, the correlation between GY and PHT was significant and positive.

Table 11: Genetic correlation between grain yield and other agronomic traits of 108 genotypes of maize evaluated under marginal rainfall, drought, optimal conditions and across environments in Nigeria, 2017-2018

			Genetic Correlation Coefficients	
Traits	Marginal	Optimal	Drought	Across Environments
GY x DA	$-0.98**$	$-0.30**$	$-0.99**$	$-0.30**$
$GY \times DS$	$-0.98**$	$-0.27**$	$-0.83**$	-0.17
GY x ASI	$0.38**$	$-0.98**$	0.02	$0.21*$
GY x PHT	$0.23*$	$-0.98**$	$0.91**$	$0.20*$
GY x PASP	$-0.78**$	$-0.98**$	$-0.98**$	$-0.64**$
GY x EASP	$-0.98**$	$-0.98**$	$-0.39**$	$-0.82**$
GY x EPP	$0.85**$	$-0.98**$	-0.10	0.15
GY x EMERG	0.13	$0.33**$	$0.99**$	$0.48**$
GY x EROT	$-0.98**$	$-0.98**$	$-0.98**$	$-0.19*$

 \overline{GY} = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; $PHT = plant$ height; $PASP = plant$ aspect; $EASP = ear$ aspect; $EROT = ear rot$; $EPP = ear$ plant.

3.1.2 Path relationship between grain yield and other agronomic traits

Path diagrams of the causal relationships among traits under each research condition are shown in Figures 6, 7, 8 and 9 for the marginal rainfall, drought, optimal conditions and across environments, respectively. The pattern and structure of the path coefficients were different under the different research conditions. Under both marginal rainfall and optimal conditions, the independent traits were separated into two groups containing four traits each under marginal rainfall (Figure 6) and three and five traits under optimal condition (Figure 7). The independent traits were divided into three groups of 4, 2, and 3 traits under drought (Figure 8) and 4, 3, and 2 traits across environments (Figure 9). Under marginal rainfall condition, EASP (*P* = −0.32), PASP ($P = -0.34$), EPP ($P = 0.23$), and AD ($P = -0.29$) had direct effects on grain yield and accounted for 60% of its total variation (Figure 6). The other four traits influenced grain yield indirectly through one (EROT, PLHT and ASI) or three (DS) of the primary traits but none through all four primary traits. The path coefficients of the second group to the first group traits were 50% positive and relatively low (*<*0.4 also for 50% of the cases). However, the coefficients for PLHT on PASP ($P = -0.71$), DS on AD ($P = 1.29$) and ASI on AD ($P = -0.89$) were large.

Under optimal condition, only EASP, PASP and AD had direct effects on grain yield, all of which were negative ($P = -0.47$, -0.20 and -0.16 , respectively); accounting for 38% of the total variation in grain yield (Figure 7). Only two of the second order traits (PLHT and EROT) affected grain yield indirectly through more than one first order traits. Here, five out of the eight path coefficients for the second order traits were relatively low and three of them were negative. Exceptions to this trend were PLHT through PASP ($P = -0.63$) and DS through AD $(P = 1.07)$. Anthesis-silking interval (ASI) had a modest effect through AD ($P = -0.43$) in the first order trait.

Ear aspect ($P = -0.23$), PASP ($P = -0.38$), EPP ($P = -0.17$) and E9 ($P = 0.43$) had direct effects on grain yield under drought and accounted for 68% of the total variation in grain yield (Figure 8). Plant height (PLHT) and AD made up the second order traits and indirectly affected the grain yield through two of the first order traits each. Of the four coefficients for the second order traits, three were negative and relatively moderate. In the third order were DS, EROT and ASI. Days to silking (DS) and ASI affected grain yield indirectly through the two second order traits each. The effects of the coefficients for most of the third order traits on the second order traits were relatively high. Ear rot (EROT) had a relatively low indirect effect on yield through a second order trait, AD.

Across the test environments, EASP ($P = -0.39$), PASP ($P = -0.27$), EPP ($P = 0.20$), and E9 $(P = 0.31)$ had direct effects on grain yield which accounted for 54% of its total variation (Figure 9). The three traits that made up the second order traits influenced grain yield indirectly through two (EROT and PLHT) or one (AD) of the primary traits. Days to silking (DS) and ASI formed the third order traits with relatively high coefficients ($P = 1.16$, and $P = -0.63$, respectively) to the second order trait, AD.

Figure 6: Path analysis model diagram showing causal relationships of measured traits of modern open pollinated maize cultivars, their hybrids and check varieties evaluated under marginal rainfall condition in Nigeria. Bold value is the residual effect; values in parenthesis are direct effects while other values are correlation coefficients. R^2 = co-efficient of determination; $R\hat{1}$ = residual effects; YIELD= grain yield; EASP= ear aspect; EPP= ears per plant; PASP= plant aspect; PLHT= plant height; AD= days to anthesis; EROT= ear rot; DS= days to silking; ASI= anthesis–silking interval; E9= germination percentage at 9 days after planting.

Figure 7: Path analysis model diagram showing causal relationships of measured traits of modern open pollinated maize cultivars, their hybrids and check varieties evaluated under optimal growing condition in Nigeria. Bold value is the residual effect; values in parenthesis are direct path coefficients while other values are correlation coefficients. R^2 = co-efficient of determination; R1= residual effects; YIELD= grain yield; EASP= ear aspect; EPP= ears per plant; PASP= plant aspect; PLHT= plant height; AD= days to anthesis; EROT= ear rot; DS= days to silking; ASI= anthesis–silking interval; E9= germination percentage at 9 days after planting.

Figure 8: Path analysis model diagram showing causal relationships of measured traits of modern open pollinated maize cultivars, their hybrids and check varieties evaluated under drought in Nigeria. Bold value is the residual effect; values in parenthesis are direct path coefficients while other values are correlation coefficients. R^2 = co-efficient of determination; R1= residual effects; YIELD= grain yield; EASP= ear aspect; EPP= ears per plant; PASP= plant aspect; PLHT= plant height; AD= days to anthesis; EROT= ear rot; DS= days to silking; ASI= anthesis–silking interval; E9= germination percentage at 9 days after planting.

Figure 9: Path analysis model diagram showing causal relationships of measured traits of modern open pollinated maize cultivars, their hybrids and check varieties evaluated across contrasting environments in Nigeria. Bold value is the residual effect; values in parenthesis are direct path coefficients while other values are correlation coefficients. $R^2 =$ co-efficient of determination; $R1 =$ residual effects; YIELD= grain yield; EASP= ear aspect; EPP= ears per plant; PASP= plant aspect; PLHT= plant height; AD= days to anthesis; EROT= ear rot; DS= days to silking; ASI= anthesis–silking interval; E9= germination percentage at 9 days after planting.

3.2 Mode of gene action controlling grain yield and other agronomic traits

Results from the combined analyses of variances (ANOVA) of the genotypes evaluated under marginal rainfall condition showed highly significant environment (E) effects for all the measured traits. Significant genotype (G) effect was observed only for plant aspect (PASP), percentage emergence (EMERG) and plant height (PHT). Under drought environments, the ANOVA also revealed that mean squares due to E were significant for all traits except ear rot (EROT). Mean squares due to G were significant for ear aspect (EASP) and EMERG (Table 12). Under optimal growing conditions, high significant mean squares were detected for E for all the measured traits. Significant G effect $(P < 0.01)$ was only observed for grain yield (GY) . Across all the six research environments, significant mean squares were detected for G and E for all measured traits except G for flowering traits and EROT.

Partitioning of the genotypic mean squares into its components revealed that GCA and SCA mean squares were significant for some of the traits under marginal rainfall condition, drought, optimal, and across test environments (Table 12). Both GCA and SCA mean squares were significant for PASP, EMERG, days to anthesis (DA), and days to silking (DS) under marginal rainfall condition. However, GCA mean square for plant height was significant but not SCA under this research condition. Under drought, GCA effect was significant for all the traits except ears per plant (EPP), PHT and EROT. The mean squares for SCA were only significant for EPP and EMERG under this growing condition. Under optimal conditiont, both GCA and SCA mean squares were significant for GY. However, non-significant GCA and SCA effects were recorded for most of the remaining agronomic traits under optimal condition except GCA effect for EASP and SCA effect for EMERG. Across the environments, GCA mean squares were significant for GY, EMERG, DA, and PHT while SCA effects were significant for all the measured traits except EROT (Table 12). The GCA \times E interaction effect was significant for EASP, DA, DS, and PHT under marginal rainfall condition. However, no significant SCA x E effect was recorded for all the traits under this condition. Furthermore, no significant GCA x E and SCA x E interaction effects were observed for all the traits under both drought and optimal growing conditions. However, GCA x E interaction effects were significant for EASP, EMERG, anthesis-silking interval (ASI), and EROT across the test environments. For all the traits measured across the test environments, no significant SCA x E interaction effects were recorded.

The observed relative importance of GCA over SCA under marginal rainfall condition, as given by the GCA/SCA ratio, was low for EMERG (0.16), GY (0.17) and ASI (0.18) and moderate for traits such as DS (0.35), DA (0.42), and PHT (0.42). In addition, Baker ratio for these latter traits were close to 1 with values of 0.81, 0.83, and 0.83 respectively (Table 12). Under drought condition, moderate GCA/SCA and high Baker ratios were recorded for GY (0.35 and 0.80), PASP (0.40 and 0.83), DS (0.42 and 0.83), DA (0.51 and 0.86), and EMERG (0.69 and 0.89) respectively, while similar ratios were recorded only for GY and PHT under optimal condition. Across the research conditions, the GCA/SCA ratio for GY was 0.38 with a Baker ratio of 0.82. The proportions of SCA effects (non-additive genetic variance) of the crosses for grain yield and other measured traits were larger than that of the GCA effects (additive genetic variance) under all contrasting environments (Table 12). Under marginal rainfall condition, the contributions of the GCA effects ranged from 13.9% for EMERG to 29.4% for PHT. Here, GCA effect contributed only 14.9% of the total genotypic variation for GY. The proportion of the GCA effects of the open pollinated maize parents under drought conditions ranged from 11.6% for EPP to 40.7% for EMERG. That of the GY was higher (25.7%) than the value recorded under marginal rainfall condition. Under optimal condition, the highest contribution of GCA effect (26.3%) was recorded for PHT while the lowest GCA effect contribution (7.3%) was recorded for EPP. Across the test environments, the proportion of GCA effects for GY was 27.6%. The lowest contribution of GCA effect (10.3%) was recorded for ASI.

Source of variation	DF	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
Marginal rainfall											
Environment (E)	$\mathbf{1}$	683.23**	66.84**	13.81**	$8.23**$	7017.04**	1396.37**	4704.46**	1002.60*	212868.68**	292.11**
ENTRY (G)	90	0.53	$0.14*$	0.54	0.02	130.26**	2.04	5.16	2.78	121.90*	1.34
GCA	13	0.55	$0.20*$	0.81	0.02	125.51*	$11.83**$	$27.41**$	4.58	247.93**	2.15
SCA	77	0.53	$0.13*$	0.49	0.02	131.07**	$4.72*$	$13.21**$	4.34	100.62	1.20
$GCA*E$	13	0.32	0.09	$0.79*$	0.01	45.53	$" -9.47**$	$" -23.23**$	-2.17	129.90*	2.18
$SCA*E$	77	0.41	0.09	0.47	0.01	51.64	-2.48	-9.68	-3.35	69.21	1.19
ERROR	90	0.40	0.09	0.52	0.01	52.29	2.66	7.57	3.69	79.97	1.36
Baker ratio		0.67	0.76	0.77	0.73	0.66	0.83	0.81	0.68	0.83	0.78
GCA/SCA		0.17	0.26	0.28	0.23	0.16	0.42	0.35	0.18	0.42	0.30
GCA effect (%)		14.88	20.82	21.79	18.68	13.92	29.71	25.95	15.13	29.38	23.17
SCA effect (%)		85.12	79.18	78.21	81.32	86.08	70.29	74.05	84.87	70.62	76.83
Drought											
Environment (E)	$\mathbf{1}$	94.44**	$3.02**$	25.30**	5.258**	5783.22	54.46**	18.43**	9.42**	24426.97**	0.05
ENTRY (G)	90	0.50	0.17	$0.15*$	0.02	204.74**	1.47	2.04	0.46	164.83	0.16
GCA	13	$0.89*$	$0.33*$	$0.23*$	0.02	577.51**	$3.43*$	$4.21*$	$0.76*$	271.68	0.22
SCA	77	0.44	0.14	0.14	$0.019*$	141.81**	1.14	1.68	0.41	146.79	0.15
GCA*ENV	13	0.46	0.17	0.10	0.02	82.82	0.65	1.24	0.30	78.03	0.08
SCA*ENV	77	0.38	0.12	0.10	0.01	52.80	1.31	1.81	0.35	129.20	0.20
ERROR	90	0.40	0.13	0.11	0.01	58.42	1.23	1.79	0.38	128.47	0.18
Baker ratio		0.80	0.83	0.77	0.61	0.89	0.86	0.83	0.79	0.79	0.75
GCA/SCA		0.35	0.40	0.28	0.13	0.69	0.51	0.42	0.31	0.31	0.25
GCA effect (%)		25.66	28.74	22.09	11.60	40.74	33.68	29.76	23.95	23.81	20.19
SCA effect (%)		74.34	71.26	77.91	88.40	59.26	66.32	70.24	76.05	76.19	79.81

Table 12: Mean squares and combining ability ratios for grain yield and other agronomic traits of 91 late maturing varietal hybrids of maize evaluated under marginal rainfall, drought, and optimal conditions and across test environments between 2017 and 2018 in Nigeria

 $GY =$ Grain yield; EMERG = percentage emergence at 9 days after planting; $DA =$ days to 50% anthesis; $DS =$ days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP =ears per plant. * P<0.05; **P<0.01
Positive GCA effects for grain yield were observed for parents: P4, P5 and P6 under marginal rainfall, drought, and optimal conditions, P2 and P8 under drought and optimal conditions, P1 under optimal condition, P11, P12 and P14 under marginal rainfall and P4, P5, P6, P2, P1 and P10 across research environments (Table 13). Significant negative GCA effect for plant aspect was detected for P4 under drought environment. Other OPVs with negative GCA effects for PASP under drought are P5, P6, P9, P10, and P11. Under marginal rainfall condition, negative GCA effects for plant aspect were detected for P3, P5, P8, P11, P12, P13, P14 and for P2, P6, P8, P9, P10, P11, and P14 under optimal condition. Under marginal rainfall condition and across test environments, significant negative GCA effects for ear aspect were observed for P2. Parent 4 had negative GCA effect for ear aspect under all the research conditions and across test environments (Table 13).

Table 13: General combining ability (GCA) effects for grain yield and other agronomic traits of the 14 late maturing open pollinated maize evaluated in diallel crosses under marginal rainfall (MR), drought (DT), optimal (OPT) conditions and across (ACR) test environments between 2017 and 2018 in Nigeria

Parent	Grain yield (t ha-1)				Plant Aspect				Ear aspect				Ears per plant			
	MR	DT	OPT	ACR	MR	DT	OPT	ACR	MR	DT	OPT	ACR	MR	DT	OPT	ACR
P ₁	-0.08	-0.04	0.22	0.03	0.11	0.09	0.12	0.11	-0.02	0.02	-0.04	-0.01	-0.02	0.02	0.02	0.01
P ₂	-0.01	0.02	0.25	0.09	0.13	0.05	-0.10	0.03	$-0.49**$	0.00	$-0.15*$	$-0.21**$	-0.01	0.00	-0.01	-0.01
P ₃	0.02	-0.23	-0.30	-0.17	-0.03	$0.12*$	0.11	0.07	0.04	0.06	$0.29**$	0.13	0.07	0.03	0.02	0.04
P ₄	0.04	$0.36*$	0.22	0.21	0.02	$-0.25**$	0.03	-0.07	-0.09	$-0.13*$	-0.08	-0.10	-0.02	-0.01	0.01	-0.01
P ₅	0.17	0.19	0.01	0.12	-0.12	$-0.10*$	0.09	-0.05	0.03	$-0.13*$	0.10	0.00	0.04	0.00	-0.01	0.01
P ₆	0.13	$0.31*$	$0.57*$	$0.34*$	0.08	-0.09	-0.06	-0.02	0.10	$-0.12*$	-0.10	-0.04	0.02	0.03	0.00	0.02
P7	-0.06	-0.11	-0.18	-0.12	0.00	$0.10*$	0.06	0.05	0.06	$0.25**$	0.08	0.13	-0.02	-0.05	0.00	-0.02
P ₈	-0.34	0.02	0.08	-0.08	-0.01	0.05	-0.07	-0.01	0.15	0.01	-0.09	0.02	-0.05	-0.01	0.02	-0.01
P ₉	-0.07	-0.04	-0.16	-0.09	0.10	$-0.12*$	-0.03	-0.02	0.28	0.07	$0.17**$	$0.17*$	-0.01	0.03	-0.02	0.00
P10	-0.02	0.17	-0.09	0.02	0.04	$-0.12*$	-0.10	-0.06	0.07	-0.03	-0.09	-0.01	-0.01	0.00	-0.02	-0.01
P11	0.00	-0.08	-0.06	-0.05	-0.11	-0.01	-0.11	-0.08	0.05	-0.05	$-0.13*$	-0.04	0.01	-0.02	-0.02	-0.01
P12	0.22	-0.22	-0.41	-0.13	-0.03	$0.12*$	0.05	0.05	-0.22	0.02	0.06	-0.05	-0.01	-0.04	-0.02	-0.03
P13	-0.18	-0.22	-0.07	-0.16	-0.01	$0.12*$	0.01	0.04	0.11	-0.02	-0.08	0.00	-0.01	0.02	0.03	0.01
P ₁₄	0.18	-0.13	-0.09	-0.01	$-0.18*$	0.05	-0.01	-0.05	-0.07	0.05	0.06	0.01	0.03	-0.01	0.00	0.01
SE	0.55	0.24	0.37	0.20	0.18	0.08	0.10	0.07	0.16	0.12	0.11	0.07	0.06	0.05	0.03	0.03
LSD0.05	1.09	0.47	0.73	0.39	0.35	0.16	0.21	0.14	0.32	0.24	0.21	0.14	0.13	0.10	0.05	0.05

The SCA effects of the diallel crosses for grain yield are presented in Table 14 (that of the entire traits are presented in Table 29). The SCA effects ranged from -1.06 for P4 x P10 to 1.36 for P6 x P9 under marginal rainfall condition, -1.09 for P12 x P13 to 1.04 for P3 x P6 under drought, and -1.34 for P4 x P9 to 1.09 for P4 x P6 under optimal conditions. When data were combined across the three research conditions, the SCA effects ranged from -0.70 for P4 x P9 to 0.89 for P3 x P6. It was observed that all the crosses with the highest positive SCA effect in each of the research conditions and across had P6 as one of its parents and those with the lowest SCA effect (negative) had P4 except under drought condition. Among the 91 crosses, 47 crosses under marginal rainfall, 40 crosses under drought and 49 crosses under optimal conditions showed positive SCA effects for GY. Out of 91 crosses, 40 crosses exhibited positive SCA effects across the test environments for GY. Under optimal condition, P4 x P6 had significant ($P < 0.05$) positive SCA effect for GY while P4 x P9 had significant negative SCA effect. Across the test environments, P3 x P6, P5 x P8 and P4 x P6 had significant positive SCA effects while P4 x P9 had significant negative SCA effects.

The best performing parents and hybrids based on *per se* performance and their combining abilities for the measured traits are presented in Table 15. The result showed that the best hybrids in SCA effects did not always involve the best general combiners. Hybrids with high SCA effects for grain yield and ears per plant involved the best general combiners as one of their parents. The result showed a better general parallelism between SCA effects and the *per se* performance of the hybrids than that between GCA effects and *per se* performance of parents for most of the traits.

Traits	GY	PASP	EASP	EPP	EMERG	DA	DS	$\boldsymbol{\mathrm{ASI}}$	PHT	EROT
Parents (per se)	P1	P ₁₀	P ₁₀	P4	P7	P ₁₂	P13	P ₁₄	P11	P ₂
General combiners	P6	P1 ₁	P2	P ₃	P ₂	P6	P6	P11		P ₂
Speciefic combiners	P3xP6	P ₄ xP ₆	P10xP13	P3xP9	P9xP12	P5xP12	P5xP12	P2xP3	P10xP13	P4xP5
Crosses (per se)	P4xP6	P4xP6	P10xP13	P3xP9	P2xP9	P5xP12	P5xP12	P2xP14	P4xP5	P1xP2

Table 15: Best performing parents and crosses based on *per se* **performance and combining abilities for grain yield and other traits in a diallel cross across test environments**

 \overline{GY} = grain yield; PASP = plant aspect; EASP = ear aspect; EPP = ears per plant; EMERG = percentage emergence; DA = days to anthesis; DS = days to silking; ASI = anthesissilking interval; $PHT =$ plant height; $EROT = ear$ rot.

3.2.1 Determination of the GCA effects of parents and SCA effects of the hybrids across stress and non-stress environments: comparison of results from Gardener & Eberhert and Griffing's methods of diallel

Results of the diallel analyses using Griffing's methods 2 and 4, model 1 (fixed model) revealed that both general combining ability (GCA) and specific combining ability (SCA) effects were significant ($P < 0.05$ or $P < 0.01$) for grain yield (GY), percentage emergence (EMERG) and plant height (PHT) across the research conditions (Tables 16 and 17). There were high significant GCA and SCA effects for GY using the two methods. GCA x environment interaction effects were not significant for all the traits except for EMERG using Griffing's method 4 model 1 where the effect was highly significant ($P < 0.01$). However, no significant SCA x environment interaction effects were observed for all the traits under both methods. Generally, the contributions of GCA variance to the overall genotypic variance were low compared to that of SCA variance for the reported traits. Using Griffing's method 2 model 1, GCA variance contribution ranged from 8.44% for ASI to 26.10% for PHT. The proportion of GCA (additive effect) in the overall genotypic variance for GY across stress and non-stress environments was 26%. Similar trend was observed with Griffing's method 4 model 1, however, the proportion of GCA for GY increased to 28% while it ranged from 10.25% for ASI to 29.84% for PHT. The observed relative importance of GCA over SCA, as given by the GCA/SCA ratio, was very low for traits such as ASI (0.09), PASP (0.13) and EPP (0.14) and moderate for traits such GY (0.35), PHT (0.35), and EROT (0.34). In addition, Baker ratio for these latter traits as well as EMERG were close to 1 with values of 0.83, 0.83, 0.82 and 0.80 respectively. Similar trend existed for Griffing's method 4 model 1 but with relatively higher GCA/SCA ratios.

Using Griffing's methods 2 and 4, model 2 (random model), the diallel ANOVA revealed that both GCA and SCA effects were consistently significant ($P < 0.05$ or $P < 0.01$) for GY, days to anthesis (DA) and PHT across the varying environments (Tables 18 and 19). There were high significant ($P < 0.01$) SCA effects for GY using the two methods. GCA x environment interaction effects were only significant for GY, PASP, EMERG, ASI (Method 2); ear aspect (EASP), EMERG, ASI and ear rot (Method 4). Similar to Model 1, no significant SCA x environment interaction effects were recorded for all the traits under both methods. Generally, the contributions of GCA effect to the overall genotypic variance were low compared to that of SCA effects for the measured traits. These results (for the Methods 2 and 4) approximately corroborated with the results obtained for the two methods in model 1. Relatively higher values for the contribution of GCA were observed in Method 4 of the two models. The trend for the relative importance of GCA over SCA, as given by the GCA/SCA ratio, was similar with that of the fixed model. The same was applicable with the trend observed in the Baker ratio.

Gardener and Eberhart analysis II (GEANII) revealed significant variety effect across the environments for GY, EASP, EMERG, DA, days to silking (DS) and PHT. However, SCA effects were significant for all the traits except ear rot (EROT) (Table 20). Variety x environment interaction effect was significant only for GY, EMERG and ASI while there were no significant SCA x environment effects for all the traits. Similar to Griffing's methods, the contributions of GCA effect to the overall genotypic variation were low compared to that of SCA effects for the traits. The proportion of GCA effect in the total genotypic variation ranged from 11.4% for ASI to 35.1% for PHT. The proportion of GCA (additive effect) in the overall genotypic variance for GY across stress and non-stress environments was 26.6%. Table 4.18 indicated that SCA was predominant for most of the traits indicating that non-additive gene effects were the primary type of gene action for these traits. The relative importance of GCA over SCA was 0.13 for ASI, 0.36 for GY and 0.54 for PHT. The Baker ratios were 0.60, 0.81 and 0.86 respectively.

Table 21 shows the mean squares and the combining ability ratios for GY and other traits from the Gardener and Eberhart Analysis III (GEAN III). The result indicated that the effect of GCA was significant for traits such as GY, EASP, EMERG, DA, DS and PHT. This was in tandem with the result generated by GEANII for the variety effect. Similar to GEANII, SCA effects were significant for all the traits except EROT. There were highly significant GCA and SCA effects for GY. GEANIII showed neither significant GCA x environment interaction effect nor SCA x environment interaction effect. Similar situation was observed for Griffing's method 2 model 1. The contributions of GCA and SCA effects to the total genotypic variance were identical to what was observed from the method 4 of Griffing. In addition, the trends for GCA/SCA and Baker ratios were identical with that of Griffing's method 4.

Table 16: Mean squares and combining ability ratios for grain yield and other traits of diallel crosses among 14 selected late maturing open pollinated varieties of maize under four stress and two non-stress environments in Nigeria (2017-2018) using Griffing's method 2 model 1

SOV	DF	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
ENV	5.	275.92**	$26.74**$	$12.58**$	$3.66**$	27042.16**	1182.66**	2464.88**	390.57**	89393.73**	170.33**
ENTRY	104	$0.78**$	$0.22**$	$0.39*$	$0.02*$	192.45**	3.99	6.18	1.81	288.41**	0.81
GCA	13	$.55**$	0.18	$0.66**$	0.018	303.98**	$6.69*$	9.00	1.27	516.28**	$1.50*$
SCA	91	$0.64**$	$0.20*$	0.34	0.019	155.64**	4.11	6.87	1.97*	208.89*	0.64
GCA*ENV	65	0.49	0.18	0.26	0.014	90.53	1.64	1.83	0.94	152.66	0.75
SCA*ENV	455	0.35	0.13	0.27	0.014	60.01	2.75	3.21	0.49	131.24	0.65
ERROR	520	0.42	0.15	0.29	0.02	70.52	3.66	5.36	1.49	151.13	0.74
Baker ratio		0.83	0.64	0.79	0.66	0.80	0.77	0.72	0.56	0.83	0.82
GCA/SCA		0.35	0.13	0.27	0.14	0.28	0.23	0.19	0.09	0.35	0.34
GCA/Genotypic SS (%)		25.71	11.39	21.54	12.07	21.81	18.87	15.77	8.44	26.10	25.18
SCA/Genotypic SS (%)		74.29	88.61	78.46	87.93	78.19	81.13	84.23	91.56	73.90	74.82

 \overline{GY} = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; $PASP = plant$ aspect; $EASP = ear$ aspect; $EROT = ear$ rot; $EPP = ear$ plant. *P<0.05; **P<0.01

Table 17: Mean squares and combining ability ratios for grain yield and other traits of diallel crosses among 14 selected late maturing open pollinated varieties of maize under four stress and two non-stress environments in Nigeria (2017-2018) using Griffing's method 4 model 1

SOV	DF	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
ENV	5.	242.81**	21.92**	$11.60**$	$3.15**$	23571.30**	1035.29**	2201.49**	355.44**	76941.05**	145.35**
ENTRY	90	$0.82**$	$0.21**$	$0.40**$	$0.02*$	213.14**	4.13	6.69	1.90	257.64**	0.86
GCA	13	$.56**$	0.24	$0.69**$	0.02	425.98**	$7.92*$	$10.69*$	1.52	532.33**	$1.70**$
SCA	77	$0.69**$	$0.20*$	0.36	$0.02*$	$177.21**$	4.26	7.92**	$2.25**$	$211.27**$	0.72
GCA*ENV	65	0.50	0.18	0.35	0.01	$106.15**$	2.25	2.41	1.06	166.43	0.97
SCA*ENV	385	0.39	0.14	0.26	0.01	60.55	3.07	3.49	0.50	130.99	0.72
ERROR	450	0.41	0.14	0.27	0.01	68.36	3.65	5.31	1.51	138.15	0.76
Baker ratio		0.82	0.71	0.80	0.66	0.83	0.79	0.73	0.57	0.83	0.83
GCA/SCA		0.38	0.20	0.33	0.16	0.41	0.31	0.23	0.11	0.43	0.40
GCA/Genotypic SS (%)		27.63	16.79	24.69	13.96	28.87	23.88	18.56	10.25	29.84	28.62
SCA/Genotypic SS (%)		72.37	83.21	75.31	86.04	71.13	76.12	81.44	89.75	70.16	71.38

 \overline{GY} = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP = ears per plant. *P<0.05; **P<0.01

Table 18: Mean squares and combining ability ratios for grain yield and other traits of diallel crosses among 14 selected late maturing open pollinated varieties of maize under four stress and two non-stress environments in Nigeria (2017-2018) using Griffing's method 2 model 2

SOV	DF	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
ENV	5	275.92**	$26.74**$	12.58**	$3.66***$	27042.16**	1182.66**	2464.88**	390.57**	89393.73**	170.33**
ENTRY	104	$0.78**$	$0.22**$	$0.39*$	$0.02*$	192.45**	3.99	6.18	1.81	288.41**	0.81
GCA	13	$1.55*$	0.18	$0.66*$	0.018	303.98	$6.69*$	9.00	1.27	516.28*	$1.50*$
SCA	91	$0.64**$	$0.20**$	0.34	$0.019*$	155.64**	$4.11**$	$6.87**$	$1.97**$	208.89**	0.64
GCA*ENV	65	$0.49*$	$0.18*$	0.26	0.014	$90.53**$	1.64	1.83	$0.94**$	152.66	0.75
SCA*ENV	455	0.35	0.13	0.27	0.014	60.01	2.75	3.21	0.49	131.24	0.65
ERROR	520	0.42	0.15	0.29	0.02	70.52	3.66	5.36	1.49	151.13	0.74
Baker ratio		0.83	0.64	0.79	0.66	0.80	0.77	0.72	0.56	0.83	0.82
GCA/SCA		0.35	0.13	0.27	0.14	0.28	0.23	0.19	0.09	0.35	0.34
GCA/Genotypic SS (%)		25.70	11.34	21.54	12.16	21.81	18.87	15.76	8.44	26.09	25.18
$SCA/Genotypic SS$ (%)		74.30	88.66	78.46	87.84	78.19	81.13	84.24	91.56	73.91	74.82

 \overline{GY} = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; $PASP = plant$ aspect; $EASP = ear$ aspect; $EROT = ear$ rot; $EPP = ear$ plant. *P<0.05; **P<0.01

Table 19: Mean squares and combining ability ratios for grain yield and other traits of diallel crosses among 14 selected late maturing open pollinated varieties of maize under four stress and two non-stress environments in Nigeria (2017-2018) using Griffing's method 4 model 2

SOV	DF	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
ENV	5	242.81**	$21.92**$	$11.60**$	$3.15**$	23571.30**	1035.29**	2201.49**	355.44**	76941.05**	145.35**
ENTRY	90	$0.82**$	$0.21**$	$0.40**$	$0.02*$	213.14**	4.13	6.69	1.90	257.64**	0.86
GCA	13	$1.56*$	0.24	0.69	0.019	425.98*	$7.92*$	10.69	1.52	532.33*	1.70
SCA	77	$0.69**$	$0.20**$	$0.36*$	$0.02*$	$177.21**$	$4.26*$	$7.92**$	$2.25**$	211.27**	0.72
GCA*ENV	65	0.50	0.18	$0.35*$	0.015	$106.15**$	2.25	2.41	$1.06**$	166.43	$0.97*$
SCA*ENV	385	0.39	0.14	0.26	0.014	60.55	3.07	3.49	0.50	130.99	0.72
ERROR	450	0.41	0.14	0.27	0.01	68.36	3.65	5.31	1.51	138.15	0.76
Baker ratio		0.82	0.71	0.79	0.66	0.83	0.79	0.73	0.57	0.83	0.83
GCA/SCA		0.38	0.20	0.33	0.16	0.41	0.31	0.23	0.11	0.43	0.40
GCA/Genotypic SS (%)		27.63	16.79	24.56	13.96	28.87	23.89	18.56	10.25	29.84	28.65
$SCA/Genotypic SS$ (%)		72.37	83.21	75.44	86.04	71.13	76.11	81.44	89.75	70.16	71.35

 \overline{GY} = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP = ears per plant. *P<0.05; **P<0.01

Table 20: Mean squares and combining ability ratios for grain yield and other traits of diallel crosses among 14 selected late maturing open pollinated varieties of maize under four stress and two non-stress environments in Nigeria (2017-2018) using Gardener and Eberhart Analysis II

SOV	DF	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
ENV	5	275.92**	26.74**	12.58**	$3.66**$	27042.16**	1182.66**	2464.88**	390.57**	89393.73**	170.33**
ENTRY	104	$0.78**$	$0.22**$	$0.39*$	$0.02*$	192.45**	3.99	6.18	1.81	288.41**	0.81
VARIETY	13	1.48**	0.26	$0.62*$	0.025	325.37**	$7.05**$	$11.18**$	1.72	675.52**	1.68
HETEROSIS AVERAGE	91	$0.68**$	$0.22**$	0.36	$0.020*$	173.46**	$4.57**$	7.84**	$2.10**$	233.10**	0.69
HETEROSIS VARIETY	$\mathbf{1}$	$2.60*$	0.69	0.18	0.005	226.103	2.31	8.00	1.56	753.93	0.32
HETEROSIS	13	0.48	0.26	0.39	0.024	147.192	$6.64**$	$7.46**$	$1.25*$	322.38	0.54
SCA	77	$0.69**$	$0.20**$	$0.36*$	$0.020*$	$177.21**$	$4.26*$	7.92**	$2.25**$	211.27**	0.72
VARIETY x ENV	65	$0.61*$	0.19	0.29	0.017	95.06*	2.39	4.15	$2.27**$	191.71	0.90
HETEROSIS x ENV AV. HETEROSIS x	455	0.39	0.14	0.29	0.015	67.02	3.00	3.38	0.51	145.33	0.71
ENV VAR. HETEROSIS x	5	0.22	0.23	0.15	0.008	155.95	0.97	1.79	0.26	134.86	0.58
ENV	65	0.40	0.16	$0.46**$	0.020	89.99	2.65	2.63	0.54	216.90*	0.61
SCA*ENV	385	0.39	0.14	0.26	0.015	61.98	3.08	3.53	0.51	133.38	0.73
ERROR	520	0.42	0.15	0.29	0.02	70.52	3.66	5.36	1.49	151.13	0.74
Baker ratio		0.81	0.72	0.78	0.72	0.79	0.77	0.74	0.60	0.86	0.82
GCA/SCA		0.36	0.22	0.29	0.21	0.31	0.28	0.24	0.13	0.54	0.40
GCA/Genotypic SS (%)		26.59	18.17	22.53	17.61	23.66	21.84	19.25	11.40	35.06	28.41
SCA/Genotypic SS (%)		73.41	81.83	77.47	82.39	76.34	78.16	80.75	88.60	64.94	71.59

 $GY =$ Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; $PASP = plant$ aspect; $EASP = ear$ aspect; $EROT = ear$ rot; $EPP = ear$ plant. *P<0.05; **P<0.01

Table 21: Mean squares and combining ability ratios for grain yield and other traits of diallel crosses among 14 selected late maturing open pollinated varieties of maize under four stress and two non-stress environments in Nigeria (2017-2018) using Gardener and Eberhart Analysis III

SOV	DF	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
ENV	5	275.92**	$26.74**$	12.58**	$3.66**$	27042.164**	1182.66**	2464.88**	390.57**	89393.73**	231.67**
ENTRY	104	$0.78**$	$0.22**$	$0.39*$	$0.02*$	192.45**	3.99	6.18	1.81	288.41**	1.10
VARIETY	13	0.41	0.28	0.31	0.030	46.58	5.97**	$8.40**$	$1.53*$	465.57*	0.52
VARIETY VS CROSS	1	$2.60*$	0.69	0.18	0.005	226.10	2.31	8.00	1.56	753.93	0.32
CROSSES	90	$0.82**$	$0.21**$	$0.40**$	$0.020*$	213.14**	$4.76**$	$8.26**$	$2.13**$	257.64**	0.86
GCA	13	$1.56**$	0.24	$0.69*$	0.019	425.98**	$7.92**$	$10.69**$	1.52	532.33**	1.70
SCA	77	$0.69**$	$0.20**$	$0.36*$	$0.020*$	$177.21**$	$4.26*$	7.92**	$2.25**$	211.27**	0.72
VARIETIES x ENV	65	0.51	0.17	$0.41*$	$0.022*$	78.90	2.35	2.09	0.65	242.18**	0.54
VARRIETY-CROSS x ENV	5	0.22	0.23	0.15	0.008	155.95	0.97	1.79	0.26	134.86	0.58
CROSSES x ENV	450	0.41	0.14	0.27	0.015	68.36	2.96	3.38	0.59	138.15	0.76
GCA x ENV	65	0.45	0.17	0.32	0.013	82.99	1.84	1.58	0.87	149.86	0.92
SCA x ENV	385	0.39	0.14	0.26	0.015	61.98	3.08	3.53	0.51	133.38	0.73
ERROR	520	0.42	0.15	0.29	0.02	70.52	3.66	5.36	1.49	151.13	0.74
Baker ratio		0.82	0.71	0.79	0.66	0.83	0.79	0.73	0.57	0.83	0.83
GCA/SCA		0.38	0.20	0.32	0.16	0.41	0.31	0.23	0.11	0.43	0.40
GCA/Genotypic SS (%)		27.63	16.79	24.45	13.96	28.87	23.89	18.56	10.25	29.84	28.65
SCA/Genotypic SS (%)		72.37	83.21	75.55	86.04	71.13	76.11	81.44	89.75	70.16	71.35

 $GY =$ Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP = ears per plant. *P<0.05; **P<0.01

3.2.1.1 Comparison of GCA effects from different diallel methods

Table 22 presents the GCA effects of the open pollinated parents using Griffing's Method 2 model 1. The GCA effects for grain yield ranged from -0.18 t ha⁻¹ for parent 3 (P3) to 0.29 t ha⁻¹ for parent 6 (P6). Other cultivars with positive GCA effect for grain yield across stress and non-stress environments include, in decreasing order of effect, P4, P5, P2, P10, and P1 with GCA effect of 0.20, 0.09, 0.07, 0.05, and 0.04 t ha⁻¹, respectively. Parents 6, 4, 5, and 10 had negative GCA effects for both PASP and EASP while P2 and P1 expressed positive effects for PASP. However, P2 expressed significant negative effects for EASP, in addition to positive GCA effects for grain yield. Parent 9 had significant positive GCA effect for EASP while P13 had significant negative GCA effect for EMERG.

The GCA effects of the 14-parent diallel as calculated by Method 4 model 1 are presented in Table 23. The result showed that the direction (positive or negative) of the GCA effects for all 14 parental lines in terms of GY was same with Method 2. The GCA effects ranged from -0.17 t ha⁻¹ for P3 to 0.34 t ha⁻¹ for P6. Other cultivars with positive GCA effects for grain yield include P4, P5, P2, P1, and P10 with GCA effects of 0.21, 0.12, 0.09, 0.03, and 0.02 t ha⁻¹, respectively. Among the parents with positive GCA effects for GY, P6, P4, P5, and P10 had negative GCA effects for PASP while all except P5 had negative GCA effects for EASP. Similar to Method 2 model 1, P9 had significant positive GCA effect for EASP while P13 had significant negative GCA effect for EMERG.

The GCA effects as calculated by GEANIII are identical with that of Griffing's Method 4 (Table 24). Therefore, they share similar results.

Parent	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
P ₆	0.292	-0.017	-0.021	0.016	2.225	-0.456	-0.658	-0.200	-0.320	-0.096
P4	0.202	-0.065	-0.092	0.004	0.178	0.428	0.533	0.076	4.040	0.061
P ₅	0.088	-0.029	-0.003	0.008	2.024	-0.215	-0.178	0.046	-0.159	0.132
P2	0.071	0.029	$-0.17**$	-0.010	2.492	-0.084	0.020	0.106	-1.191	-0.272
P10	0.045	-0.087	-0.050	-0.009	1.521	0.167	-0.091	-0.174	3.273	-0.017
P ₁	0.042	0.085	-0.013	0.008	0.134	0.221	0.320	0.061	-5.121	-0.167
P11	-0.026	-0.076	-0.056	-0.005	-0.955	0.173	-0.083	-0.196	3.057	-0.061
P ₁₄	-0.037	-0.024	0.026	0.008	0.838	0.105	-0.129	-0.157	-1.592	0.172
P ₉	-0.058	0.002	$0.159*$	0.004	-0.276	-0.137	-0.057	0.061	-1.811	0.124
P ₈	-0.079	0.000	0.048	-0.017	0.292	-0.615	-0.583	-0.004	0.526	-0.147
P7	-0.102	0.050	0.111	-0.027	0.513	-0.068	0.142	0.180	3.534	-0.027
P12	-0.112	0.035	-0.044	-0.022	-1.379	-0.105	-0.213	-0.130	-1.054	-0.011
P13	-0.148	0.059	0.000	0.011	$-5.538**$	0.414	0.585	0.143	-2.299	0.207
P ₃	-0.176	0.038	0.105	0.030	-2.068	0.172	0.391	0.190	-0.883	0.100
SE	0.177	0.064	0.064	0.023	1.833	0.418	0.579	0.252	3.206	0.155
Min	-0.176	-0.087	-0.170	-0.027	-5.538	-0.615	-0.658	-0.200	-5.121	-0.272
Max	0.292	0.085	0.159	0.030	2.492	0.428	0.585	0.190	4.040	0.207
Range	0.468	0.172	0.329	0.057	8.030	1.043	1.242	0.390	9.161	0.479
LSD0.05	0.349	0.126	0.127	0.045	3.611	0.824	1.140	0.496	6.315	0.306

Table 22: General combining ability effects of open pollinated parents for grain yield and other traits across stress and non-stress environments in Nigeria (2017-2018) generated from Griffing's Method 2 Model 1

 \overline{GY} = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; $PASP = plant$ aspect; $EASP = ear$ aspect; $EROT = ear$ rot; $EPP = ear$ plant.

Parent	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
P ₆	0.336	-0.024	-0.041	0.016	2.651	-0.623	-0.818	-0.190	0.201	-0.084
P4	0.207	-0.068	-0.102	-0.008	0.325	0.390	0.449	0.028	3.878	0.031
P ₅	0.124	-0.046	0.001	0.007	2.120	-0.310	-0.172	0.109	0.232	0.150
P ₂	0.087	0.028	$-0.213**$	-0.006	3.067	-0.087	0.051	0.142	-1.158	-0.269
P ₁	0.031	0.109	-0.012	0.008	0.261	0.220	0.255	-0.009	-5.794	-0.213
P10	0.020	-0.061	-0.014	-0.008	1.852	0.235	-0.040	-0.176	3.068	-0.025
P ₁₄	-0.013	-0.046	0.013	0.008	1.347	-0.012	-0.253	-0.147	-0.862	0.175
P11	-0.045	-0.076	-0.043	-0.010	-1.261	0.283	0.001	-0.209	2.285	-0.067
P ₈	-0.079	-0.010	0.024	-0.010	0.156	-0.597	-0.544	0.013	1.249	-0.170
P ₉	-0.092	-0.016	$0.171*$	0.000	-0.564	-0.109	-0.066	0.022	-1.018	0.151
P7	-0.117	0.054	0.130	-0.021	0.151	-0.109	0.106	0.187	3.945	-0.016
P12	-0.134	0.049	-0.046	-0.026	-1.580	0.017	-0.120	-0.161	-1.635	-0.033
P13	-0.155	0.040	0.003	0.015	$-6.474**$	0.567	0.806	0.212	-2.524	0.219
P ₃	-0.170	0.065	0.128	0.037	-2.050	0.135	0.345	0.179	-1.868	0.149
SE	0.199	0.070	0.071	0.025	2.052	0.459	0.666	0.284	3.559	0.174
Min	-0.170	-0.076	-0.213	-0.026	-6.474	-0.623	-0.818	-0.209	-5.794	-0.269
Max	0.336	0.109	0.171	0.037	3.067	0.567	0.806	0.212	3.945	0.219
Range	0.506	0.186	0.385	0.063	9.541	1.190	1.624	0.421	9.739	0.488
LSD0.05	0.392	0.138	0.141	0.050	4.043	0.903	1.313	0.560	7.011	0.343

Table 23: General combining ability effects of open pollinated parents for grain yield and other traits across stress and non-stress environments in Nigeria (2017-2018) generated from Griffing's Method 4 Model 1

 \overline{GY} = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; $PASP = plant$ aspect; $EASP = ear$ aspect; $EROT = ear$ rot; $EPP = ear$ plant.

Parent	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
P6	0.336	-0.024	-0.041	0.016	2.651	-0.623	-0.818	-0.190	0.201	-0.084
P4	0.207	-0.068	-0.102	-0.008	0.325	0.390	0.449	0.028	3.878	0.031
P ₅	0.124	-0.046	0.001	0.007	2.120	-0.310	-0.172	0.109	0.232	0.150
P ₂	0.087	0.028	$-0.213**$	-0.006	3.067	-0.087	0.051	0.142	-1.158	-0.269
P1	0.031	0.109	-0.012	0.008	0.261	0.220	0.255	-0.009	-5.794	-0.213
P10	0.020	-0.061	-0.014	-0.008	1.852	0.235	-0.040	-0.176	3.068	-0.025
P14	-0.013	-0.046	0.013	0.008	1.347	-0.012	-0.253	-0.147	-0.862	0.175
P11	-0.045	-0.076	-0.043	-0.010	-1.261	0.283	0.001	-0.209	2.285	-0.067
P ₈	-0.079	-0.010	0.024	-0.010	0.156	-0.597	-0.544	0.013	1.249	-0.170
P ₉	-0.092	-0.016	$0.171*$	0.000	-0.564	-0.109	-0.066	0.022	-1.018	0.151
P7	-0.117	0.054	0.130	-0.021	0.151	-0.109	0.106	0.187	3.945	-0.016
P12	-0.134	0.049	-0.046	-0.026	-1.580	0.017	-0.120	-0.161	-1.635	-0.033
P13	-0.155	0.040	0.003	0.015	$-6.474**$	0.567	0.806	0.212	-2.524	0.219
P ₃	-0.170	0.065	0.128	0.037	-2.050	0.135	0.345	0.179	-1.868	0.149
$\rm SE$	0.198	0.072	0.072	0.025	2.055	0.469	0.658	0.279	3.593	0.174
Min	-0.170	-0.076	-0.213	-0.026	-6.474	-0.623	-0.818	-0.209	-5.794	-0.269
Max	0.336	0.109	0.171	0.037	3.067	0.567	0.806	0.212	3.945	0.219
Range	0.506	0.186	0.385	0.063	9.541	1.190	1.624	0.421	9.739	0.488
LSD0.05	0.390	0.141	0.142	0.050	4.048	0.924	1.296	0.550	7.078	0.343

Table 24: General combining ability effects of open pollinated parents for grain yield and other traits across stress and non-stress environments in Nigeria (2017-2018) generated from Gardener and Eberhart Analysis III

 \overline{GY} = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; $PASP = plant$ aspect; $EASP = ear$ aspect; $EROT = ear$ rot; $EPP = ear$ plant.

Presented in Table 25 are the GCA effects for grain yield from a 14-parent diallel calculated according to Methods 2 and 4 (Model 1) of Griffing, and Gardener and Eberhart Analysis III (GEANIII). The results showed that the direction (i.e., positive or negative) of the GCA effects for all the 14 parents was the same across all the three methods. The GCA effects for method 4 and GEANIII were the same.

Parent	$M_{2,1}$	$M_{4,1}$	GEANIII
P ₆	0.292	0.336	0.336
P4	0.202	0.207	0.207
P ₅	0.088	0.124	0.124
P2	0.071	0.087	0.087
P ₁₀	0.045	0.020	0.020
P ₁	0.042	0.031	0.031
P11	-0.026	-0.045	-0.045
P14	-0.037	-0.013	-0.013
P ₉	-0.058	-0.092	-0.092
P ₈	-0.079	-0.079	-0.079
P7	-0.102	-0.117	-0.117
P12	-0.112	-0.134	-0.134
P13	-0.148	-0.155	-0.155
P ₃	-0.176	-0.170	-0.170
SE	0.177	0.199	0.198
Min	-0.176	-0.170	-0.170
Max	0.292	0.336	0.336
Range	0.468	0.506	0.506
LSD0.05	0.349	0.392	0.390

Table 25: General combining ability for grain yield (t ha-1) of 14 parental open pollinated maize varieties according to the models for Griffing's methods 2 and 4 and Gardner and Eberhart analysis III (GEANIII)

 $M_{2,1}$ = Griffing's method 2 model 1; $M_{4,1}$ = Griffing's method 2 model 1; GEANIII = Gardener and Eberhart Analysis III

Correlation analysis result (Table 26) for the GCA effects of 14 parental cultivars from Methods 2 and 4 and GEANIII showed that correlation coefficients (r) among GCA effects from the three methods were highly significant ($P < 0.01$). The correlation coefficients between Griffing's method 4 and GEANIII is unity indicating no difference in the values of the GCA effects calculated from these models.

Table 26: Correlation coefficients among GCA effects (grain yield) for Griffing's methods 2 and 4 (model 1) and Gardener and Eberhart Analysis III

$M_{2,1}$ $0.991**$ $0.991**$		$M_{4,1}$	GEANIII					
	$M_{4,1}$		$1.000**$					

** = significant at 1% probability; $M_{2,1}$ = Griffing's method 2 model 1; $M_{4,1}$ = Griffing's method 2 model 1; GEANIII = Gardener and Eberhart Analysis III

3.2.1.2 Comparison of SCA effects from different diallel methods

The SCA effects across the environments for Methods 2 and 4, GEANII, and GEANIII involving14 parents, analysed according to their corresponding models for grain yield are presented in Appendix V. The results showed that the SCA effects from the two methods of Griffing differed in both magnitude and direction. The SCA effects as calculated by Method 4 was similar to those of GEANII and GEANIII. The only differences lied with crosses P12 x P13 and P13 x P14. Under Method 4, the SCA effect of P12 x P13 was -0.317 while it was 0.064 under GEAN. The cross between P13 and P14 had a SCA effect of -0.035 under Method 4 but had -0.073 under GEAN. The SCA effects from GEANII and GEANIII were identical. These exactitudes and similarities were also corroborated by the high significant correlation coefficients associated with the different diallel methods (Table 27). Therefore, to avoid redundancy, we will present and discuss the SCA effects of grain yield and other traits as calculated by Griffing's methods 2, 4 and GEANII.

		GEANII	GEANIII	
$M_{2,1}$	$0.988**$	$0.995**$	$0.995**$	
$M_{4,1}$		$0.992**$	$0.992**$	
GEANII			$1.000**$	

Table 27: Correlation coefficients among SCA effects (grain yield) for Griffing's methods 2 and 4, and Gardener and Eberhart Analyses II and III

**. Correlation is significant at the 0.01 level; $M_{2,1}$ = Griffing's method 2 model 1; $M_{4,1}$ = Griffing's method 2 model 1; GEANII = Gardener and Eberhart Analysis II; GEANIII = Gardener and Eberhart Analysis III

Across the environments, the SCA effects for grain yield as calculated by Griffing's Method 2 model 1 $(M_{2,1})$ ranged from -0.716 for P4 x P9 to 0.948 for P3 x P6 (Table 28). Of the 91 hybrids evaluated, 43 hybrids had positive SCA effects for grain yield. Of these 43, 32 had negative SCA effects for PASP while 26 had negative SCA effects for EASP. The SCA effects for PASP ranged from -0.464 for P4 x P6 to 0.332 for P7 x P9. For EASP, the SCA effects ranged from -0.713 for P10 x P13 to 0.462 for P4 x P10. The cross between P4 and P6 had the second highest SCA effect for grain yield (0.710) but the least SCA effect for PASP (-0.464) and the second least SCA effect for EASP (-0.517). It shares a common parent (P6) with the cross that had the highest SCA effect (P4 x P6). It should be noted that P6 had the highest GCA effect for grain yield (Table 22).

Table 29 contains the SCA effects for grain yield and other traits as calculated by Griffing's Method 4. The SCA effects for grain yield ranged from -0.701 for P4 x P9 to 0.885 for P3 x P6. Forty out of the 91 hybrids evaluated had positive SCA effects for grain yield. Of these 40, 29 had negative SCA effects for PASP while 27 had negative SCA effects for EASP. For PASP, the SCA effects ranged from -0.449 for P4 x P6 to 0.369 for P13 x P14. For EASP, the SCA effects ranged from -0.756 for P10 x P13 to 0.502 for P2 x P6. The cross between P4 and P6 had the third highest SCA effect for grain yield (0.647) but the least SCA effect for PASP (- 0.449) and the second least SCA effect for EASP (-0.490). The cross between P5 and P8 had the second largest SCA effect according to Method 4 with SCA effects of -0.376 for PASP and -0.355 for EASP. However, these crosses (P3 x P6, P5 x P8, and P4 x P6) with outstanding SCA effects for grain yield had positive SCA effects for flowering traits. The same situation was also obtained for Method 2.

The SCA effects, across the environments, for grain yield and other traits as calculated by Gardener and Eberhart II (GEANII) are presented in Table 30. The SCA effects for grain yield ranged from -0.701 for P4 x P9 to 0.885 for P3 x P6. Of the 91 hybrids evaluated, 41 hybrids had positive SCA effects for grain yield. Of these 41, 29 had negative SCA effects for PASP while 27 had negative SCA effects for EASP. The SCA effects for PASP ranged from -0.449 for P4 x P6 to 0.353 for P7 x P9. For EASP, the SCA effects ranged from -0.756 for P10 x P13 to 0.502 for P2 x P6. The cross between P4 and P6 had the third highest SCA effect for grain yield (0.647) but the least SCA effect for PASP (-0.449) and the second least SCA effect for EASP (-0.490). The cross between P5 and P8 had the second largest SCA effect according to GEANII with SCA effects of -0.376 for PASP and -0.355 for EASP. Similar to Methods 2 and 4, these crosses (P3 x P6, P5 x P8, and P4 x P6) with outstanding SCA effects for grain yield had positive SCA effects for flowering traits.

Crosses	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
P3xP6	0.948	-0.037	-0.401	0.005	5.531	0.014	0.723	0.729	-7.561	-0.361
P _{4xP6}	0.710	-0.464	$" -0.517*$	0.072	4.544	0.503	0.854	0.368	7.873	0.072
P5xP8	0.703	-0.410	-0.372	0.045	3.472	0.014	1.044	1.032	10.177	-0.186
P5xP13	0.601	-0.109	-0.232	0.076	7.937	-1.160	-1.568	-0.412	1.284	0.550
P _{2xP14}	0.548	-0.237	-0.253	0.035	-4.423	0.090	-0.876	-1.193	0.848	-0.283
P6xP9	0.488	-0.281	-0.203	0.052	-5.430	-0.708	-1.519	-0.800	6.764	-0.075
P10xP13	0.469	-0.424	$-0.713**$	0.090	-9.587	0.745	0.304	-0.511	10.940	-0.750
P9xP12	0.467	-0.168	-0.168	-0.038	9.052	0.083	0.354	0.283	7.255	-0.222
P3xP11	0.466	-0.073	0.017	-0.017	9.153	-0.569	0.329	0.813	3.131	-0.165
P1xP9	0.449	-0.099	-0.147	0.004	1.989	-0.364	-0.657	-0.257	-0.088	-0.243
P2xP11	0.424	-0.301	-0.131	0.022	7.642	-0.594	0.148	0.663	3.996	0.010
P10xP14	0.376	-0.271	0.033	0.122	7.684	-0.474	-1.647	-0.375	7.585	0.679
P4xP14	0.336	-0.053	-0.252	0.042	2.237	0.028	0.160	0.047	-0.903	0.683
P _{4xP7}	0.334	-0.104	-0.141	-0.018	0.902	-0.024	0.393	0.441	-3.182	-0.124
P9xP13	0.318	-0.184	-0.311	-0.025	-10.929	0.148	-0.161	-0.287	7.283	-0.324
P7xP12	0.295	0.070	-0.171	0.062	-3.064	-1.043	-2.115	-1.048	4.925	-0.120
P1xP7	0.280	-0.032	0.103	0.091	3.767	0.064	-0.254	-0.272	-2.427	0.783
P6xP11	0.266	0.025	0.037	0.014	-2.713	-1.192	-1.701	-0.597	1.386	0.213
P1xP12	0.261	-0.010	-0.462	-0.095	4.196	-0.029	0.231	0.286	0.646	-0.169
P1xP13	0.244	-0.144	0.126	-0.021	3.131	-0.111	-0.041	0.083	5.539	0.192
P5xP14	0.231	-0.166	-0.247	-0.031	1.182	-0.568	-0.697	-0.239	0.554	-0.399
P2xP10	0.228	0.088	-0.228	-0.015	5.432	-0.113	0.608	0.606	-1.476	-0.048
P7xP10	0.224	-0.020	0.086	0.021	-0.535	-0.912	-1.136	-0.306	1.709	-0.112
P _{2xP8}	0.213	-0.016	-0.424	-0.045	0.239	-0.176	0.221	0.406	-5.367	-0.044
P7xP8	0.213	-0.392	-0.046	0.089	4.311	0.946	2.154	1.189	8.291	-0.070
P8xP12	0.209	0.025	-0.031	0.001	1.285	-1.046	-1.480	-0.403	0.310	0.023

Table 28: Specific Combining Ability (SCA) effects for grain yield and other traits from diallel crosses of 14 open pollinated maize varieties evaluated across sub optimal and optimal environments as calculated by Griffing's Method 2 model 1

GY = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP =ears per plant.

Crosses	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
P3xP6	0.885	-0.050	-0.407	-0.003	4.960	0.205	0.904	0.719	-7.327	-0.426
P5xP8	0.652	-0.376	-0.355	0.040	3.387	0.078	0.975	0.940	8.832	-0.186
P _{4xP6}	0.647	-0.449	$-0.490*$	0.084	3.844	0.695	1.073	0.395	7.284	0.086
P5xP13	0.558	-0.067	-0.244	0.073	8.651	-1.232	-1.819	-0.555	0.889	0.514
P9xP12	0.509	-0.158	-0.182	-0.031	9.414	-0.081	0.245	0.342	6.813	-0.232
P _{2xP14}	0.495	-0.207	-0.200	0.031	-5.632	0.196	-0.807	-1.250	-0.144	-0.293
P10xP13	0.487	-0.425	$-0.756**$	0.085	-9.108	0.511	0.006	-0.590	11.140	-0.759
P1xP9	0.480	-0.099	-0.164	0.008	2.024	-0.405	-0.609	-0.159	-0.438	-0.229
P3xP11	0.465	-0.092	-0.023	-0.020	9.315	-0.656	0.266	0.826	4.657	-0.213
P6xP9	0.464	-0.249	-0.199	0.057	-5.694	-0.582	-1.376	-0.781	5.220	-0.118
P _{2xP11}	0.413	-0.292	-0.104	0.023	7.247	-0.714	0.008	0.630	4.504	0.009
P10xP14	0.363	-0.268	0.006	0.121	6.719	-0.439	-1.599	-0.395	6.830	0.679
P9xP13	0.345	-0.141	-0.330	-0.026	-9.831	-0.046	-0.399	-0.328	6.486	-0.368
P _{4xP7}	0.330	-0.098	-0.154	-0.012	0.991	0.042	0.487	0.470	-3.660	-0.109
P7xP12	0.318	0.059	-0.192	0.060	-2.628	-1.138	-2.197	-1.035	4.865	-0.114
P4xP14	0.294	-0.022	-0.233	0.054	1.455	0.169	0.343	0.073	-1.699	0.705
P1xP7	0.292	-0.053	0.079	0.085	3.876	0.092	-0.179	-0.220	-2.395	0.814
P1xP12	0.281	-0.042	$-0.464*$	-0.091	4.143	-0.163	0.179	0.375	1.669	-0.107
P7xP10	0.250	-0.043	0.026	0.014	-0.629	-0.952	-1.176	-0.322	1.273	-0.119
P1xP13	0.249	-0.143	0.118	-0.025	3.814	-0.277	-0.222	0.072	6.207	0.221
P6xP11	0.227	0.039	0.039	0.018	-2.959	-1.149	-1.650	-0.604	1.406	0.203
P2xP10	0.222	0.071	-0.225	-0.019	4.400	-0.191	0.502	0.560	-1.535	-0.047
P8xP12	0.218	0.027	-0.009	-0.002	1.496	-1.200	-1.636	-0.401	-0.062	0.062
P7xP8	0.214	-0.379	-0.045	0.076	4.684	0.956	2.126	1.153	6.927	-0.062
P10xP12	0.198	0.077	0.065	0.012	-4.731	0.489	0.971	0.383	-0.173	0.118
P3xP12	0.183	-0.240	-0.131	0.042	0.503	1.182	1.601	0.449	-0.589	-0.231

Table 29: Specific Combining Ability (SCA) effects for grain yield and other traits from diallel crosses of 14 open pollinated maize varieties evaluated under sub optimal and optimal environments as calculated by Griffing's Method 4 model 1

GY = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP =ears per plant.

Crosses	GY	PASP	EASP	EPP	EMERG	DA	DS	ASI	PHT	EROT
P3xP6	0.885	-0.050	-0.407	-0.003	4.960	0.205	0.904	0.719	-7.327	-0.426
P5xP8	0.652	-0.376	-0.355	0.040	3.387	0.078	0.975	0.940	8.832	-0.186
P _{4xP6}	0.647	-0.449	$-0.490*$	0.084	3.844	0.695	1.073	0.395	7.284	0.086
P5xP13	0.558	-0.067	-0.244	0.073	8.651	-1.232	-1.819	-0.555	0.889	0.514
P9xP12	0.509	-0.158	-0.182	-0.031	9.414	-0.081	0.245	0.342	6.813	-0.232
P _{2xP14}	0.495	-0.207	-0.200	0.031	-5.632	0.196	-0.807	-1.250	-0.144	-0.293
P10xP13	0.487	-0.425	$-0.756**$	0.085	-9.108	0.511	0.006	-0.590	11.140	-0.759
P1xP9	0.480	-0.099	-0.164	0.008	2.024	-0.405	-0.609	-0.159	-0.438	-0.229
P3xP11	0.465	-0.092	-0.023	-0.020	9.315	-0.656	0.266	0.826	4.657	-0.213
P6xP9	0.464	-0.249	-0.199	0.057	-5.694	-0.582	-1.376	-0.781	5.220	-0.118
P2xP11	0.413	-0.292	-0.104	0.023	7.247	-0.714	0.008	0.630	4.504	0.009
P10xP14	0.363	-0.268	0.006	0.121	6.719	-0.439	-1.599	-0.395	6.830	0.679
P9xP13	0.345	-0.141	-0.330	-0.026	-9.831	-0.046	-0.399	-0.328	6.486	-0.368
P _{4xP7}	0.330	-0.098	-0.154	-0.012	0.991	0.042	0.487	0.470	-3.660	-0.109
P7xP12	0.318	0.059	-0.192	0.060	-2.628	-1.138	-2.197	-1.035	4.865	-0.114
P4xP14	0.294	-0.022	-0.233	0.054	1.455	0.169	0.343	0.073	-1.699	0.705
P1xP7	0.292	-0.053	0.079	0.085	3.876	0.092	-0.179	-0.220	-2.395	0.814
P1xP12	0.281	-0.042	-0.464	-0.091	4.143	-0.163	0.179	0.375	1.669	-0.107
P7xP10	0.250	-0.043	0.026	0.014	-0.629	-0.952	-1.176	-0.322	1.273	-0.119
P1xP13	0.249	-0.143	0.118	-0.025	3.814	-0.277	-0.222	0.072	6.207	0.221
P6xP11	0.227	0.039	0.039	0.018	-2.959	-1.149	-1.650	-0.604	1.406	0.203
P2xP10	0.222	0.071	-0.225	-0.019	4.400	-0.191	0.502	0.560	-1.535	-0.047
P8xP12	0.218	0.027	-0.009	-0.002	1.496	-1.200	-1.636	-0.401	-0.062	0.062
P7xP8	0.214	-0.379	-0.045	0.076	4.684	0.956	2.126	1.153	6.927	-0.062
P10xP12	0.198	0.077	0.065	0.012	-4.731	0.489	0.971	0.383	-0.173	0.118
P3xP12	0.183	-0.240	-0.131	0.042	0.503	1.182	1.601	0.449	-0.589	-0.231
P _{2xP8}	0.183	0.002	-0.359	-0.055	-0.325	-0.203	0.127	0.341	-6.354	-0.028

Table 30: Specific Combining Ability (SCA) effects for grain yield and other traits from diallel crosses of 14 open pollinated maize varieties evaluated under sub optimal and optimal environments as calculated by Gardener and Eberhart Analysis II

GY = Grain yield; EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP =ears per plant.

3.3 Classification of the maize varietal parents into distinct heterotic groups

The results of the dendrogram constructed based on the HSGCA (Figures 10, 12, 14 and 16) and HGCAMT (Figs. 11, 13, 15 and 17) at R-square of approximately 0.4, revealed four and three heterotic groups for the two methods respectively in all the test environments and across. Under marginal rainfall condition and using the HSGCA method, the first group comprised four OPVs, the second group contained four OPVs also, the third group consisted of only one OPV while the fourth group was made up of 5 OPVs (Figure 10). Using HGCAMT method, the first group had two OPVs (DT - STR - Y - SYN 2 [P1] and DT - STR - Y - SYN 14 [P2]), all from the same drought and striga tolerant population. The second group consisted of three OPVs while the third group was made up of nine OPVs among which were all the OPVs considered from the Pro Vitamin A (PVA) population (Figure 11). From the dendrogram of the multiple traits, it was observed that the flowering traits were grouped in a cluster while the grain yield was grouped alongside EPP and EMERG. The heat map showed the varied performances of the OPVs with respect to the multiple traits considered. The values increase as one moves towards the red colour while the values decrease as one moves towards the blue colour (Figure 11).

Four heterotic groups were identified from the result of the cluster analysis of the grain yield data based on HSGCA under drought condition (Figure 12). The first group was made up of 7 OPVs consisting of white- and yellow-grained OP maize varieties all from various germplasm sources. The second group comprised of four drough tolerant OPVs. The third group was made up of only PVA SYN 3 (P12). TZL Comp - 4 C3 DT C2 (P8) and PVA SYN 2 (P11) made up group 4. Under drought condition, three heterotic groups were identified based on HGCAMT (Figure 13). Three of the four PVA OPVs were classified into the same heterotic group with other four OPVs, of which two were from yellow-grained, drought and striga tolerant population (DT - STR - Y - SYN 2 [P1] and DT - STR - Y - SYN 14 [P2]). Group two had three whitegrained drought tolerant OPVs in addition to PVA SYN 7 (P14). The third group consisted of three OP maize. Three groups could be identified from the clustering of the multiple traits. PASP, EASP, DS and DA were clustered together while grain yield was clustered with PHT and EMERG (Figure 13).

Under optimal condition while using the HSGCA method, the first group comprised six OPVs, the second group contained three OPVs, the third group also consisted of three OPVs while the fourth group was made up of two (Figure 14). Using HGCAMT method (Figure 15), the first group had six OPVs (three from drought tolerant population, two from PVA enriched population), the second group consisted of five OPVs (three from drought tolerant population
and two from PVA enriched population) while the third group was made up of three OPVs all of which are from a drought tolerant population. From the dendrogram of the multiple traits, it was observed that grain yield was clustered with EPP and PHT while PASP, EASP and EROT were in the same group (Figure 15).

Four heterotic groups were identified from the result of the cluster analysis of the grain yield data based on HSGCA across the test environments (Figure 16). The first group was made up of mostly drought tolerant OPVs consisting of white and yellow grains from various germplasm sources. The second group contained all the PVA OPVs except PVA SYN 2 (P11), which was classified into group three. IWD C2 SYN F2 (P3) and White DT STR SYN/IWD C3 SYN F2 (P9) made up group 4 which are white-grained and drought tolerant materials. Across the environments, three heterotic groups were identified based on HGCAMT (Figure 17). The OPVs, DT - STR - Y - SYN 2 (P1) and DT - STR - Y - SYN 14 (P2) occupied the first group, IWD C-2 SYN F2 (P3) and PVA SYN 4 (P13) occupied group three while the rest of the parental OPVs considered were classified into group two. In clustering of the multiple traits, the grain yield was clustered along with EMERG and PHT while EASP, EROT and EPP formed a different cluster (Figure 17).

In summary, the heterotic groups by the different grouping methods are presented in Table 31. Under marginal rainfall, drought and across test environments, DT - STR - Y - SYN 2 (P1) and DT - STR - Y - SYN 14 (P2) were always grouped together by HGCAMT. The case was different with HSGCA method. In addition, the HGCAMT method grouped White DT STR SYN/IWD C3 SYN F2 (P9) and White DT STR SYN/TZL Comp - 1 - W F2 (P10) together in each and across test environments. However, they were grouped in different clusters by HSGCA method.

Figure 10: Dendrogram of 14 late maturing OP maize constructed from HSGCA effects method using Ward's minimum variance cluster analysis under marginal rainfall condition. DTSY2 = DT - STR - Y - SYN 2 ; DTSY14 = DT - STR - Y - SYN 14 ; IWD = IWD C-2 SYN F2; $STRY2 = STR SYN - Y2$; TZLC1 = TZL Comp - 1 - WC6/DT SYN - 1W; TZC3 = TZL Comp - 3 C3 DT; TZC3C2 $=$ TZL Comp - 3 C3 DT C2; TZC4C2 = TZL Comp - 4 C3 DT C2; WDTS1 = White DT STR SYN/IWD C3 SYN F2; WDTS2 = White DT STR SYN/TZL Comp - $1 - W$ F2; PVA2 = PVA SYN 2; PVA3 = PVA SYN 3; PVA4 = PVA SYN 4; PVA7 = PVA SYN 7. (Order: P1 to P14)

Figure 11: Dendrogram of 14 late maturing OP maize constructed from GCA effects of grain yield and other traits (HGCAMT) using Ward's minimum variance cluster analysis under marginal rainfall condition. DTSY2 = DT - STR - Y - SYN 2 ; DTSY14 = DT - STR - Y - SYN 14 ; IWD = IWD C-2 SYN F2; STRY2 = STR SYN - Y2; TZLC1 = TZL Comp - 1 - WC6/DT SYN - 1W; TZC3 = TZL Comp - 3 C3 DT; TZC3C2 = TZL Comp - 3 C3 DT C2; TZC4C2 = TZL Comp - 4 C3 DT C2; WDTS1 = White DT STR SYN/IWD C3 SYN F2; WDTS2 = White DT STR SYN/TZL Comp - $1 - W$ F2; PVA2 = PVA SYN 2; PVA3 = PVA SYN 3 ; PVA4 = PVA SYN 4; PVA7 = PVA SYN 7. (Order: P1 to P14)

Figure 12: Dendrogram of 14 late maturing OP maize constructed from HSGCA effects method using Ward's minimum variance cluster analysis under drought condition. DTSY2 $= DT - STR - Y - SYN$ 2 ; DTSY14 = DT - STR - Y - SYN 14 ; IWD = IWD C-2 SYN $P2$; STRY2 = STR SYN -Y2; TZLC1 = TZL Comp - 1 - WC6/DT SYN - 1W; TZC3 = TZL Comp - 3 C3 DT; TZC3C2 = TZL Comp - 3 C3 DT C2; TZC4C2 = TZL Comp - 4 C3 DT C2; WDTS1 = White DT STR SYN/IWD C3 SYN F2; WDTS2 = White DT STR SYN/TZL Comp - 1 - W F2; PVA2 = PVA SYN 2; PVA3 = PVA SYN 3 ; PVA4 = PVA SYN 4; PVA7 $=$ PVA SYN 7. (Order: P1 to P14)

Figure 13: Dendrogram of 14 late maturing OP maize constructed from GCA effects of grain yield and other traits (HGCAMT) using Ward's minimum variance cluster analysis under drought condition. DTSY2 = $DT - STR - Y - SYN$ 2 ; DTSY14 = $DT - STR - Y - SYN$ 14 ; IWD = IWD C-2 SYN F2; STRY2 = STR SYN - Y2; TZLC1 = TZL Comp - 1 - WC6/DT SYN - 1W; TZC3 = TZL Comp -3 C3 DT; TZC3C2 = TZL Comp -3 C3 DT C2; TZC4C2 = TZL Comp -4 C3 DT C2; WDTS1 = White DT STR SYN/IWD C3 SYN F2; WDTS2 = White DT STR SYN/TZL Comp - $1 - W$ F2; PVA2 = PVA SYN 2; PVA3 = PVA SYN 3 ; PVA4 = PVA SYN 4; PVA7 = PVA SYN 7. (Order: P1 to P14)

Figure 14: Dendrogram of 14 late maturing OP maize constructed from HSGCA effects method using Ward's minimum variance cluster analysis under optimal growing condition. DTSY2 = DT - STR - Y - SYN 2 ; DTSY14 = DT - STR - Y - SYN 14 ; IWD = IWD C-2 SYN F2; $STRY2 = STR SYN - Y2$; TZLC1 = TZL Comp - 1 - WC6/DT SYN - 1W; TZC3 = TZL Comp - 3 C3 DT; TZC3C2 $=$ TZL Comp - 3 C3 DT C2; TZC4C2 = TZL Comp - 4 C3 DT C2; WDTS1 = White DT STR SYN/IWD C3 SYN F2; WDTS2 = White DT STR SYN/TZL Comp - 1 - W F2; PVA2 = PVA SYN 2; PVA3 = PVA SYN 3 ; PVA4 = PVA SYN 4; PVA7 = PVA SYN 7. (Order: P1 to P14)

Figure 15: Dendrogram of 14 late maturing OP maize constructed from GCA effects of grain yield and other traits (HGCAMT) using Ward's minimum variance cluster analysis under optimal growing condition. DTSY2 = DT - STR - Y - SYN 2 ; DTSY14 = DT - STR - Y - SYN 14 ; $IWD = IWD C-2 SYN F2$; $STRY2 = STR SYN - Y2$; $TZLC1 = TZL Comp - 1 - WC6/DT SYN - 1W$; $TZC3 = TZL$ Comp - 3 C3 DT; TZC3C2 = TZL Comp - 3 C3 DT C2; TZC4C2 = TZL Comp - 4 C3 DT C2; WDTS1 = White DT STR SYN/IWD C3 SYN F2; WDTS2 = White DT STR SYN/TZL Comp - 1 - W F2; PVA2 = PVA SYN 2; $PVA3 = PVA SYN3$; $PVA4 = PVA SYN4$; $PVA7 = PVA SYN7$. (Order: P1 to P14)

Figure 16: Dendrogram of 14 late maturing OP maize constructed from HSGCA effects method using Ward's minimum variance cluster analysis across test environments. DTSY2 $= DT - STR - Y - SYN$ 2 ; DTSY14 = DT - STR - Y - SYN 14 ; IWD = IWD C-2 SYN F2; STRY2 = STR SYN -Y2; TZLC1 = TZL Comp - 1 - WC6/DT SYN - 1W; TZC3 = TZL Comp - 3 C3 DT; TZC3C2 = TZL Comp - 3 C3 DT C2; TZC4C2 = TZL Comp - 4 C3 DT C2; WDTS1 = White DT STR SYN/IWD C3 SYN F2; WDTS2 = White DT STR SYN/TZL Comp - 1 - W F2; PVA2 = PVA SYN 2; PVA3 = PVA SYN 3 ; PVA4 = PVA SYN 4; PVA7 $=$ PVA SYN 7. (Order: P1 to P14)

Figure 17: Dendrogram of 14 late maturing OP maize constructed from GCA effects of grain yield and other traits (HGCAMT) using Ward's minimum variance cluster analysis across test environments. DTSY2 = $DT - STR - Y - SYN$ 2 ; DTSY14 = $DT - STR - Y - SYN$ 14 ; IWD = IWD C-2 SYN F2; STRY2 = STR SYN - Y2; TZLC1 = TZL Comp - 1 - WC6/DT SYN - 1W; TZC3 = TZL Comp -3 C3 DT; TZC3C2 = TZL Comp -3 C3 DT C2; TZC4C2 = TZL Comp -4 C3 DT C2; WDTS1 = White DT STR SYN/IWD C3 SYN F2; WDTS2 = White DT STR SYN/TZL Comp - $1 - W$ F2; PVA2 = PVA SYN 2; PVA3 = PVA SYN 3; PVA4 = PVA SYN 4; PVA7 = PVA SYN 7. (Order: P1 to P14)

Method	RCOND	No. of clusters	Cluster 1		Cluster 2			Cluster 3	Cluster 4
HSGCA	Marginal 4		DTSY2, PVA7, PVA4	TZC3C2,	IWD, TZC4C2	PVA3,	PVA ₂	WDTS1	DTSY14, TZC3, WDTS2, STRY2, TZLC1
	Optimal	$\overline{4}$	DTSY2, WDTS1, PVA4, PVA3	TZC3C2,		TZC4C2, DTSY14, TZLC1, TZC3		IWD, PVA7, PVA2	STRY2, WDTS2
	Drought	$\overline{4}$	DTSY2, PVA4, STRY2, TZC3	TZLC1,	PVA7, TZC3C2,	WDTS2, DTSY14, WDTS1, IWD, PVA3			TZC4C2, PVA2
	Across	$\overline{4}$	DTSY2, TZC4C2, STRY2			PVA3, PVA4, PVA7		WDTS2, DTSY14, TZLC1, TZC3C2, TZC3, PVA2	IWD, WDTS1
HGCAMT Marginal 3			DTSY2, DTSY14			IWD, TZLC1, STRY2		TZC3, WDTS1, WDTS2, TZC3C2, PVA2, PVA3, PVA7, TZC4C2, PVA4	
	Optimal	3	DTSY2, IWD, TZLC1, PVA3, WDTS2, PVA2 PVA7					STRY2, TZC3C2, WDTS1, PVA4, DTSY14, TZC4C2, TZC3	
	Drought	3	DTSY2, $DTSY14$, PVA2, PVA3, PVA4	TZC4C2,	WDTS2,			IWD, TZC3C2, PVA7, WDTS1, STRY2, TZLC1, TZC3	
	Across	3	DTSY2, DTSY14		TZC3	TZLC1, PVA7, WDTS1, TZC3C2, TZC4C2, PVA3,		STRY2, WDTS2, PVA2, IWD, PVA4 DTCV2 – DT - CTD - V - CVN12 - DTCV14 – DT - CTD - V - CVN14 - IWD – IWD C-2 CVNLE2 - CTDV2 – CTD CVN - V2 -TZL C1 – TZL Comp. -1 - WC4 DT CVN - 1W.	

Table 31: Summary of the heterotic groups of 14 late-maturing OP maize identified by different heterotic grouping methods under marginal rainfall, drought, optimal conditions, and across the three research environments

DTSY2 = DT - STR - Y - SYN 2 ; DTSY14 = DT - STR - Y - SYN 14 ; IWD = IWD C-2 SYN F2; STRY2 = STR SYN - Y2; TZLC1 = TZL Comp - 1 - WC6/DT SYN - 1W; TZC3 = TZL Comp - 3 C3 DT; TZC3C2 = TZL Comp - 3 C3 DT C2; TZC4C2 = TZL Comp - 4 C3 DT C2; WDTS1 = White DT STR SYN/IWD C3 SYN F2; WDTS2 = White DT STR SYN/TZL Comp - 1 - W F2; PVA2 = PVA SYN 2; PVA3 = PVA SYN 3; PVA4 = PVA SYN 4; PVA7 = PVA SYN 7.

3.3.1 Prediction of hybrid performance using Best Linear Unbiased Predictor (BLUP)

Presented in Table 32 are the predicted breeding values (BLUP) alongside the combining abilities values for grain yield of maize in each and across environments. For the parental varieties under marginal rainfall condition, the prediction ranged from -0.338 t ha⁻¹ for Parent 7 to 0.222 t ha⁻¹ for Parent 9. Under optimal condition, the prediction ranged from -0.752 t ha⁻¹ for P3 to 0.666 t ha⁻¹ for P10. The predicted value was highest $(0.631 \text{ t} \text{ ha}^{-1})$ for P7 and lowest $(-$ 0.517 t ha⁻¹) for P14 under drought. Across the test environment, prediction for grain yield among the OP parents ranged from -0.387 t ha⁻¹ (P3) to 0.126 t ha⁻¹ (P4). The direction of the prediction was not consistent with that of the GCA for some of the parents in all the test environments. The correlations between the GCA of the parents and the predicted values for grain yield were not significant and generally low, ranging from 15% under marginal rainfall condition to 34% under optimal growing condition (Table 32).

The best linear unbiased predictions for the hybrid performance were also generated (Table 32). The highest significant prediction was recorded for the cross between P6 and P9 $(0.552 \text{ t} \text{ ha}^{-1})$ under marginal rainfall condition. However, the cross between P4 and P6 had the highest and significant ($P < 0.01$) prediction of 1.139 t ha⁻¹, 0.922 t ha⁻¹ and 0.783 t ha⁻¹ under optimal, drought conditions and across test environments respectively. The direction of the prediction was inconsistent with that of the SCA for few of the hybrids in all the test environments. High and significant correlations ($P < 0.01$) were recorded for grain yield between the SCA values and the predicted values. The correlations ranged from 83% under optimal conditions to 91% under marginal rainfall condition (Table 32).

		MARGINAL RAINFALL	OPTIMAL		DROUGHT		ACROSS	
Parent	GCA	BLUP	GCA	BLUP	GCA	BLUP	GCA	BLUP
P1	-0.085	0.043	0.222	0.271	-0.045	-0.0383	0.031	0.111
P ₂	-0.010	-0.176	0.252	0.060	0.021	-0.2381	0.087	-0.164
P ₃	0.022	-0.191	-0.300	$-0.752*$	-0.232	-0.0358	-0.170	$-0.387*$
P4	0.038	-0.179	0.223	0.020	$0.359*$	$0.608*$	0.207	0.126
P ₅	0.167	0.015	0.012	-0.465	0.194	-0.3029	0.124	-0.254
P6	0.132	0.121	$0.567*$	-0.172	$0.309*$	-0.2926	$0.336*$	-0.106
P7	-0.059	-0.338	-0.183	-0.461	-0.108	$0.631*$	-0.117	-0.122
P ₈	-0.345	-0.227	0.085	-0.221	0.022	0.0744	-0.079	-0.156
P ₉	-0.071	0.222	-0.163	-0.284	-0.041	0.1615	-0.092	0.062
P10	-0.020	-0.254	-0.087	$0.666*$	0.169	0.0637	0.020	0.124
P11	0.002	-0.141	-0.059	-0.064	-0.079	0.1878	-0.045	-0.033
P12	0.225	0.152	-0.410	-0.166	-0.217	-0.2760	-0.134	-0.063
P13	-0.178	0.119	-0.070	-0.349	-0.218	-0.4383	-0.155	-0.252
P ₁₄	0.182	-0.273	-0.088	0.079	-0.135	$-0.517*$	-0.013	-0.297
Correlation	0.154ns			0.341ns	0.200ns			0.332ns
Hybrid	SCA	BLUP	SCA	BLUP	SCA	BLUP	SCA	BLUP
P1xP2	0.007	-0.044	-0.422	0.115	-0.126	-0.102	-0.180	-0.013
P1xP3	-0.688	-0.248	0.522	0.262	-0.033	-0.154	-0.067	-0.107
P1xP4	0.046	0.045	-0.434	0.069	0.338	0.406	-0.017	0.179
P1xP5	-0.187	-0.051	0.561	$0.634*$	-0.328	-0.103	0.015	0.149
P1xP6	-0.302	-0.108	-0.292	0.322	-0.131	0.004	-0.242	0.054
P1xP7	0.679	0.220	0.316	0.244	-0.119	-0.191	0.292	0.117
P1xP8	-0.737	-0.420	0.238	0.388	-0.956	$-0.580*$	-0.485	-0.296
P1xP9	0.218	0.071	0.647	0.550	0.575	0.352	0.480	0.344
P1xP10	0.196	0.019	-0.380	-0.144	0.017	0.044	-0.056	-0.054
P1xP11	0.075	0.056	-0.764	-0.286	-0.466	-0.333	-0.385	-0.199

Table 32: Correlation between predicted breeding values (BLUPs), general combining ability (GCA) for parental varieties and specific combining ability (SCA) for their hybrids on grain yield

3.4 Grain yield and stability of tropical maize hybrids developed from elite cultivars in contrasting environments under rainforest agro-ecology

Results of the combined analysis of variance revealed significant mean squares (*P<*0.01) for environment, genotype and GEI effects for grain yield (Table 33). The test environments contributed 68.2% of the total variation in the sum of squares; genotypes accounted for 3.6% and the GEI source for 10.3% of the total variation. When genotype is partitioned into its components, hybrid accounted for the largest proportion of variation (91.78%), followed by parent (4.29%) and hybrid vs parent (3.03%). Although hybrid vs check and check vs hybrid and parent had significant contributions to genotype, their percentage contribution to variation is considerably small $\left(\langle 1\% \right)$.

Table 34 illustrates the summary statistics obtained from the testing environments. The repeatability of the grain yield trials ranged from 35% for marginal rainfall condition at Ile-Ife to 80% for optimal condition at Umudike, and the broad sense heritability across environments was estimated as 51% underlying the high quality of the assessed phenotypic data for all subsequent analysis. Grain yield was on average 188% higher in Ile-Ife than the location Umudike. At location Ile-Ife, the average yield during the optimal growing condition was slightly lower than that under marginal rainfall condition but 83% higher in comparison to that of drought condition. The average yield during the optimal growing condition was on the other hand higher in Umudike than that of the two marginal growing conditions. The correlations among and across the environments are shown in Table 35. Among the environments, there were generally weak associations, which depicted independencies and distinctiveness of these environments with respect to the yield potential of the tested genotypes. The variation in environmental conditions was reflected by large differences in the average grain yield observed across the growing conditions. The difference between the lowest and the highest yielding environment was 3.2 t ha^{-1} .

Source of variation	Degree of freedom	% variation
Environment (E)	5	68.2**
Genotype (G)	107	$3.6**$
Parent (P)	13	4.29
Hybrid (H)	90	91.78**
P vs H	1	$3.03**$
P vs C	1	0.01
H vs C	1	$0.45*$
C vs P , H	$\mathbf{1}$	$0.44*$
GxE	535	$10.3**$
Error	1140	12.8

Table 33: Percentage sum of squares from the combined ANOVA of grain yield (t ha -1) of 108 maize genotypes evaluated at 6 environments in Nigeria

** indicate significance at the *P*< 0.01

Table 34: Summary statistics for the tested check varieties, open-pollinated parental varieties and population hybrids

Location	Growing condition	Yield range (t ha $\mathbf{1}$	Mean yield (t) ha^{-1})	$\sigma_{\rm g}^2$	σ_{gu}^2	$\sigma_{\rm e}^2$	h ²
Ile-Ife	Marginal	1.90-6.16	4.09	0.18		1.03	0.35
Ile-Ife	Optimal	$1.90 - 6.07$	4.00	0.23		0.86	0.44
Ile-Ife	Drought	$0.32 - 4.28$	2.19	0.42		0.52	0.71
Umudike	Marginal	$0.24 - 2.01$	0.90	0.03		0.13	0.45
Umudike	Optimal	$0.59 - 2.79$	1.42	0.14		0.10	0.80
Umudike	Drought	$0.39 - 2.29$	1.24	0.05		0.18	0.45
Across		$1.55 - 3.38$	2.31	0.05	0.13	0.47	0.51

Genotypic variance (σ_g^2) , genotypic-by-environment interaction variance (σ_{gu}^2) , residual variance (σ_e^2) , repeatability/heritability (h^2) .

Table 35: Pearson phenotypic correlation coefficients among the different environments and across environment for the average grain yield performance

	I-OPT	I-DT	U-MR	U-OPT	U-DT	Across
I-MR	0.06	0.08	0.15	-0.05	0.10	$0.51**$
I-OPT		0.16	0.08	$0.56**$	0.04	$0.65**$
I-DT			0.17	$0.25**$	$0.19*$	$0.62**$
U-MR				0.00	$0.24*$	$0.37**$
U-OPT					$0.36**$	$0.60**$
U-DT						$0.43**$

* and ** indicate significance at the *P*< 0.05 and 0.01, respectively.

I-MR = marginal rainfall condition at Ile-Ife; I-OPT= optimal growing condition at Ile-Ife; I-DT=drought condition at Ile-Ife; U-MR = marginal rainfall condition at Umudike; U-OPT= optimal growing condition at Umudike; U-DT=drought condition at Umudike.

The stability variances and the average grain yield of the different genotype groups are presented in Figure 18. The average grain yield of the hybrids (2.36 t ha^{-1}) was higher than that of the parents as well as the checks i.e. the hybrids out-yielded the parents by 7% and the checks by 10% (Figure 18 B). The stability analysis of the individual genotype groups revealed furthermore that the grain yield performance of the hybrids was much more stable than both the parents and the check varieties, while the checks were the least stable according to their estimated stability variance (Figure 18 A).

Figure 18: Stability variances and average grain yield (t ha−1) of parents, hybrids and checks tested on six environments with their corresponding standard errors

Presented in figure 19 is a violin plot of the yield response of individual genotypes across the varying environments, the mid-parent heterosis (%) and the commercial heterosis (%). Several hybrids out-yielded the parental populations and the check varieties. Approximately 54% of the hybrids yielded above average, in contrast to 36% of the parental populations and the average grain yield across the environments was 2.21 t ha⁻¹ and 2.33 t ha⁻¹ for the parental populations and their hybrids, respectively (Figure 19A). The violin plot for the mid-parent heterosis is presented in Figure 19B. It ranged from -29.31% for entry H65 (a cross between parent 7 and parent 9) to 72.69% for entry H28 (a cross between parent 3 and parent 6). The commercial heterosis varied from -35.43% for the cross between parent 3 and parent 13 to 53.38% for the cross between parent 4 and parent 6 (Figure 19C). Out of the 91 hybrids, 48 showed positive commercial heterosis.

Figure 19: Violin plot of the average grain yield distribution of the population hybrids (blue), the performance of the 14 parental populations (red horizontal bars), and the three check varieties (green horizontal bars) (A) as well as the relative mid-parent (B) and commercial heterosis (C) of the 91 population hybrids

Details of the individual grain yield of all the genotypes in each environment and their average performance across the environments can be found in Appendices I, II, III and IV. In summary, hybrid H38 (STR SYN - Y2 x TZL Comp - 3 C3 DT) had the highest average grain yield across the environments (3.38 t ha⁻¹), while check 1 (DT STR SYN 2 – 7) showed the lowest grain yield with

 1.55 t ha⁻¹ (Table 36). Approximately 10% of the best yielding parental populations and the hybrids were plotted alongside the three check varieties to show their "mean vs stability" estimates (Figure 20). The GGE biplot analysis indicated furthermore that entry H38 i.e. the highest yielding genotype was also relatively more stable than most of the entries as well as all the check varieties. The check 3 (entry C108) was the least stable genotype and second to the lowest yielding material.

Entry	Genotype	I MR	I OPT	I DT	U MR	U OPT	U DT	Mean
H38	P _{4xP6}	4.09	5.89	4.00	1.34	2.79	2.18	3.38
H ₂₈	P3xP6	5.47	5.68	4.28	1.14	2.13	1.18	3.31
H49	P5xP8	5.64	5.28	2.65	1.12	1.81	1.45	2.99
H ₅₈	P _{6x} P ₉	6.16	4.36	2.48	1.13	1.93	1.41	2.91
H ₂₅	P2xP14	5.10	5.70	1.96	1.43	1.65	1.13	2.83
H ₃₉	P4xP7	5.06	4.44	2.91	1.44	1.78	1.32	2.83
H ₆₀	P6xP11	5.09	6.07	1.29	0.83	2.04	1.65	2.83
H22	P2xP11	4.97	4.18	2.29	1.28	2.26	1.70	2.78
H37	P _{4xP5}	4.79	4.06	3.18	0.89	2.19	1.47	2.76
H46	P4xP14	4.07	4.65	2.88	1.35	1.95	1.52	2.74
P10	P ₁₀	3.13	5.61	2.74	1.06	2.13	0.84	2.59
P ₁	P1	4.91	4.44	1.92	0.25	1.66	1.10	2.38
C ₁₀₇	Check 2	4.51	3.62	4.05	0.26	1.37	1.14	2.49
C ₁₀₈	Check 3	3.06	3.48	4.05	0.88	1.12	0.68	2.21
C ₁₀₆	Check 1	1.90	2.85	2.00	0.43	0.93	1.21	1.55

Table 36: The yield of 10% best performing maize varieties and the checks across the environments

I-MR = marginal rainfall condition at Ile-Ife; I-OPT= optimal growing condition at Ile-Ife; I-DT=drought condition at Ile-Ife; U-MR = marginal rainfall condition at Umudike; U-OPT= optimal growing condition at Umudike; U-DT=drought condition at Umudike.

AXIS1 48.15 %

Figure 20: Mean vs stability view of the GGE biplot showing the performance and stability of 10% best yielding population hybrids and parents, alongside the three check varieties across the test environments

CHAPTER IV

DISCUSSION

4.1 Genetic variability and performance of late maturing elite cultivars of maize under marginal rainfall, drought and optimal conditions in Nigeria

The presence of genetic variability is of prime importance in making progress from selection for improved grain yield under stress conditions (Badu-Apraku *et al*., 2015a). The observed significant differences $(P< 0.01)$ among genotypes (G) , environment (E) , and genotype x environment interactions (GEI) for grain yield and most of the measured traits under sub optimal, optimal and across test environments indicated the existence of genetic variability in the latematuring maize germplasm to allow good progress from selection for high grain yield. It also showed that the research environments in Nigeria varied in terms of climatic and edaphic conditions. The result also implied that the research environments were discriminating enough for the identification of outstanding genotype (Badu-Apraku *et al*., 2011a; 2016b). The presence of significant mean squares for the hybrids under the different research conditions indicates the differential responses of the variety hybrids to both stressed and non-stressed conditions. From the combined analyses of variance for each of the research conditions, environment accounted for the largest proportion of the sum of squares for grain yield and other traits, followed by the genotype and then GEI. The large environmental effects indicate that the test locations were highly variable and suggest the need for the testing of the genotypes in a wide array of environments to identify outstanding genotypes as reported by Badu-Apraku *et al*. (2011a), Edmeades (2013), and Badu-Apraku and Fakorede (2017).

The relatively higher broad sense heritability recorded for plant height, plant aspect and ears per plant compared to grain yield under marginal rainfall condition (associated with the onset of rainfall when the frequency of rain is erratic and soil moisture is sub-optimal for maize cultivation) indicated that the heritability of grain yield under this growing condition could be low and suggest the possibility of using these traits to complement grain yield in the identification of high yielding cultivars (Bänziger *et al*., 2000; Badu-Apraku *et al*., 2011a). These results were correspondingly supported by the significant positive genetic correlations observed between grain yield and ears per plant and plant height, and the highly significant negative correlation between grain yield and plant aspect. These results suggested that heritability estimates of the secondary adaptive traits such as plant aspect and ears per plant and their genetic correlations with grain yield are important genetic components, which should be considered

together and not separately in the selection of reliable secondary traits to complement yield under this growing condition and under stress in general.

Under drought (towards the end of the rainy season, when flowering was targeted to coincide with drought spell), the relatively higher broad sense heritability recorded for percentage emergence and plant aspect compared to grain yield indicated that initial selection for these traits under this condition would be effective as reported by Badu-Apraku *et al*. (2011a and 2013). Furthermore, percentage emergence and plant aspect recorded highly significant positive and negative genetic correlations respectively with grain yield, indicating that they were most reliable traits to complement grain yield under drought conditions. The low $H²$ estimates recorded for flowering traits, plant height, ear aspect and ears per plant implied that early generation selection for these traits to improve drought tolerance in this germplasm might be ineffective. However, the highly significant negative genetic correlations of plant and ear aspects with grain yield under this stress condition suggested the high possibility of these secondary traits being reliable under water stress. These results agreed with the report by Badu-Apraku *et al*. (2012a), who identified plant and ear aspects as reliable traits for the selection of improved grain yield under stress using the extra-early maize cultivars.

Under optimal environments, the high H^2 estimate recorded for grain yield suggested that initial selection for high grain yield would be effective (Badu-Apraku *et al*., 2011a and 2013c).

The moderate heritability estimates recorded for percentage emergence, plant height, plant aspect, and ear aspect as well as their significant genetic correlations with grain yield across the environments confirmed the importance of these traits in the selection of high yielding and drought tolerant open pollinated maize cultivar.

Out of the 108 entries tested across the environments, 42% yielded above average $(2.31 \text{ t} \text{ ha}^{-1})$ These genotypes were made up of 41 population hybrids, 3 parental varieties and a check variety (White DT STR SYN/IWD C3 SYN). Based on the threshold score of 3 for ear aspect, 24% of these above-average genotypes could be selected, having scored 3 or less. However, considering a threshold score of 3 for plant aspect, only 18% could be selected, all of which are hybrids except parent 10 (White DT STR SYN/TZL Comp - 1 - W F2). The high performance of these population hybrids underlines their improved genetic constitution, potentially making them a highly useful and promising cultivar type for small-scale farmers in SSA. Developing variety types with high degrees of heterozygosity and genetic heterogeneity for adaptation traits can additionally help in achieving better individual and population buffering capacity (Haussmann *et al.,* 2012).

Information such as causal-and-effect relationships among several traits, including the primary trait, which is grain yield in maize, are need by breeder in crop improvement. Consequently, breeders use multivariate statistics to minimize the chances of misleading interpretations based on correlation coefficients alone (Badu-Apraku *et al*., 2017). According to Eze and Nwofia (2016), path coefficient analysis is used to untangle cause and effect relationship that is confounded by correlation coefficients. Using sequential path coefficient analysis effectively led to clearer knowledge and understanding of the interrelationships among the traits evaluated in the study. The same traits were determined under all the environments, however, E9 was stepwise-excluded from the models under marginal rainfall and optimal conditions as it lacked any significant direct or indirect effect on grain yield under these conditions. The environment influenced the structures of the path diagrams of the traits with grain yield. Whereas under marginal rainfall and optimal conditions, the secondary traits were only in two groups, they were in three groups under drought and across environments. However, two traits – PASP and EASP were common to all the environmental conditions in the first group of secondary traits having direct effect on grain yield. Badu-Apraku *et al*. (2013c) had earlier reported that the plant and ear aspects among few other secondary traits were the most reliable traits for selecting for improved grain yield under drought. Results of this present study justify the use of some of these traits as both the genetic correlations and the sequential path coefficient analysis suggested the importance of PASP and EASP in determining grain yield of OP maize.

4.2 Mode of gene action controlling grain yield and other agronomic traits

The presence of significant GCA and SCA mean squares for some of the traits under the three research conditions and across test environments indicated that additive and non-additive genetic effects were important in this set of genotypes under all test environments. The results of the present study suggested that there was scope for the improvement of some of the measured traits using hybridization, backcrossing, and recurrent selection methods to develop varietal hybrids and synthetics as well as population development. The results also implied that there was a chance to identify a potentially discriminating tester under the contrasting environments as well as superior OPVs with good combining abilities. Furthermore, the results implied that the OPVs could be classified into distinct heterotic groups under each research environment, and that those that could serve as ideal testers could be identified under the contrasting environments. The results of the present study indicated that both additive and non-additive gene actions were involved in the inheritance of all the measured traits. However, there was the preponderance of SCA over GCA mean squares for grain yield and other measured traits under all the contrasting environments with the relative importance of GCA to SCA effects for grain yield and ear aspect increasing from stress to non-stress environments while most of the other traits decreased from stress to non-stress environments. The implication of this result is that non-additive gene action was more important than additive gene action for these traits (Badu-Apraku *et al*., 2015a) and that SCA was the major component accounting for the differences among the OPVs evaluated in the present study. The present results are in agreement with the findings of several other authors (Amiruzzaman *et al*., 2013; Krupakar *et al*., 2013; Rajitha *et al*., 2014; Synrem *et al*., 2017) who reported the preponderance of non-additive gene action for the expression and inheritance of yield and other traits measured in maize. The results of this study is in partial agreement with the findings of Wegary *et al*. (2013) who reported GCA effects to be more important under drought, while SCA effects were more important under optimal conditions for grain yield. The differences in the results reported in the studies may be due to the different backgrounds of the materials used and might have had some genes with different modes of action (Badu-Apraku *et al*., 2013b). The results of the present study suggest that the gene actions controlling grain yield and most measured traits under drought were similar in this set of late maturing elite OPVs. The implication is that the presence of drought in either of the parental OPVs would be sufficient to obtain hybrids with an acceptable performance under drought (Badu-Apraku *et al*., 2015a).

As indicated by the significant GCA x environment interaction mean squares for some traits under marginal rainfall condition and across test environments, the parents exhibited differential performance in hybrid combinations under the different environmental factors in the study. Badu-Apraku *et al*. (2011a,b; 2015a) reported similar results and this emphasizes the need for testing OPVs in contrasting environments to identify those with stable performance for the development of stress tolerant hybrids and synthetics. This further underscores the earlier view of Kang (1996) and Akinwale *et al*. (2014) who stated that the environment plays prominent role in the phenotypic expression of agronomic characters, thereby suggesting that ignoring environmental component in the field would impede progress and advances in selection. The significant GCA x environment interaction provides vital information on the efficient use of an OPV parent as a tester in the different environments and suggests the need to select different parental lines for hybrid development under the research condition and at individual locations.

The GCA effect of an elite OPV is a function of its relative importance as a tester for the improvement of a target trait in a population and as a parent for the development of synthetic varieties and varietal hybrids. Genotypes that are outstanding in terms of GCA and SCA for grain yield and other agronomic traits could be employed for the development of heterotic populations that can serve as an initial gene pool for further improvement and development of high yielding synthetic varieties and hybrids for the SSA region (Akinwale *et al*., 2014). The significant and positive GCA effects observed for grain yield of the OPVs P4 and P6 under drought, P6 under optimal environments, and P6 across research environments indicated that these OPVs possess favourable alleles for grain yield and would contribute high yields to their progenies (Badu-Apraku *et al*., 2015a). The combining ability estimate of a genotype across research environments is a measure of the performance stability of that genotype in a hybrid combination or in a population development. Genotypes with outstanding GCA and SCA across research environments are suitable for hybrid and population development for the region of SSA (Akinwale *et al*., 2014). Parent 4, 5, 9 and 10 had good general combining ability for plant aspect under drought condition. Parent 2 under marginal rainfall, optimal and across research conditions, P4 and P6 under drought condition, P5 under drought, and P11 under optimal condition all had significant negative GCA effects for ear aspect. This is an indication that these parents would contribute favourable alleles to plant aspect and ear aspect in their progenies. Parents 5 and 6 showed significant negative GCA effects for days to anthesis under drought and across research conditions and for days to silking under drought. Significant negative GCA effects for Parent 6 and 8 under marginal rainfall and P8 across research conditions for days to anthesis were also recorded. Parent 4 had a good general combining ability for anthesis-silking interval under drought. These results suggest that these OPVs will contribute favourable alleles to their progenies for earliness under contrasting environments. Mhike *et al*. (2010) and Halilu *et al*. (2012) reported similar significant GCA estimates for these traits and other agronomic traits. Across test environments, significant positive GCA effects for plant height were observed for P4, P5, P7, P8, P10, and P11 while significant negative GCA effects were observed in P1, P3, P12, and P13.

The SCA effect of a particular cross determines its usefulness in exploiting heterosis. Across the test environments, only P3 x P6, P5 x P8 and P4 x P6 showed significant positive SCA effects for grain yield while under optimal condition; P4 x P6 also had significant positive SCA effect for grain yield. The cross, P4 x P6, involved two parents with positive GCA effects, suggesting an additive x additive type of gene action that can be fixed in subsequent generations if no repulsion phase linkages are involved (Meseka and Ishaaq, 2012). On the other hand, P3 x P6 and P5 x P8 involved crosses between parental lines, P6 and P5 with positive GCA effects and P3 and P8 with negative GCA effects indicating involvement of additive x dominant gene interactions in the two crosses. The high yield potential expressed by P3 x P6 and P5 x P8 across

test environments could be attributed to the contribution of favourable alleles from both poor and good combiners. This suggests the exploitation of heterosis in F1 generation as high yield potential might not easily be fixed in the subsequent generation. This finding is in line with the result of Meseka and Ishaaq (2012) in maize, meanwhile, Peng and Virmani (1999) had earlier reported the interaction between positive alleles from good combiners and negative alleles from poor combiners in rice hybrids.

The different methods of the diallel considered in this study all indicated that the contributions of SCA effect were greater than GCA effect for grain yield and all other measured agronomic traits with slight differences in numerical strength. The results of the 14-parent diallel calculated according to the different methods of Griffing and the Gardener and Eberhart Analysis III (GEANIII) showed that the direction (either positive or negative) of the GCA effects for all the 14 parents was the same across all the methods. This confirms the work of Yao *et al*. (2013) who demonstrated same using different number of lines. The current study also affirms the results of Singh and Paroda (1984) where it was proved that the GCA effects for Griffing's Method 4 and GEANIII were identical. Correlation analysis results showed that the correlation coefficients among the GCA effects of the parents were highly significant. Resampling analyses carried out by Yao *et al*. (2013) showed that the mean correlation coefficients ranged from 0.925 to 0.994. The correlation results of the current study fell within the same range. The result is also in accordance with the comparison of diallel methods carried out by El-Hosary (2014) in Egypt. These results suggest that the GCA effects obtained from all these methods were similar and can be transferred or interchanged. Therefore, any of these methods could be utilized to calculate the GCA effects without introducing much bias or having much loss of valuable information.

The SCA effects from the two methods (2 and 4) of Griffing differed. However, the SCA effects as calculated by Method 4 and GEAN were similar. This implies that SCA effects from Method 4 and that from either GEANII or GEANIII were mutually transferable. The identicalness of GEANII and GEANIII in this study corroborated the findings of Yao *et al*. (2013). The correlation coefficients among SCA effects from all the four methods were highly significant (P < 0.01). Therefore, SCA effects generated from all these methods are equally interchangeable when equal number of parents are involved. Nevertheless, it is worthy to note the upward biasedness in the SCA effects as calculated by Griffing's method 2. This may be because of the inclusion of the parents in the computation of the SCA effects. Yao *et al*. (2013) also suggested the same reason. Against this backdrop, we recommend Griffing's Method 4, GEANII or GEANIII for such evaluations.

4.3 Classification of the maize varietal parents into heterotic groups

Information on heterotic groupings of maize germplasm is vital for hybrid breeding programme. Assignment of germplasms into different heterotic groups is fundamental for the maximum exploitation of heterosis for hybrid cultivar development (Gurung *et al*., 2009). The choice of heterotic groups is fundamental because groups and heterotic patterns are important tools for exploiting heterosis of the trait of interest.

Classification by the two methods in this study did not show similar and identical trends. The HSGCA and HGCAMT methods gave 4 and 3 groups respectively. In the grouping of early maturing quality protein maize inbreds by Badu-Apraku *et al*. (2015b) using HSGCA and HGCAMT methods, HSGCA method also had one group more than HGCAMT method. The grouping was not related to the endosperm colour of the OPVs as the groups were consistently composed of OPVs from both endosperm colour types. Similar result was reported for 28 early maturing inbreds classified into heterotic groups based on combining ability by Akinwale *et al*. (2014). The classification of DT - STR - Y - SYN 2 and DT - STR - Y - SYN 14, White DT STR SYN/IWD C3 SYN F2 and White DT STR SYN/TZL Comp - 1 - W F2 together in the same group in each and across test environments indicated that the grouping of the OPVs was based largely on their pedigree and to a small extent on the reaction of the OPVs to the stress environments. This result is in line with the findings by several authors (Akaogu *et al*., 2012; Badu-Apraku *et al*., 2013b and Akinwale *et al*., 2014).

Best linear unbiased prediction (BLUP) is a standard method for estimating random effects of a mixed model, which was originally developed in animal breeding for estimation of breeding values but widely used in many areas of research today (Piepho *et al*., 2008). Several authors (Bernardo, 1996; Piepho *et al*., 2008; Balestre *et al*., 2011; Kleinknecht *et al*., 2013; Oliveira *et al*., 2016; and Carvalho *et al*., 2017) have demonstrated that BLUP has good predictive accuracy when compared to other procedures. By employing variance component estimates by REML and predicting breeding values by BLUP, breeders could efficiently predict progeny values by focusing only on the most promising combinations (Resende and Sturion, 2001).

In this study, correlations between estimated GCA and BLUP values were low suggesting that one might not use BLUP to select the best parents for grain yield. Cruz Baldissera *et al*. (2012) has noted that care should be taken in selecting and interpreting results when comparing combining ability estimates and BLUP. However, the case for SCA was different as it had very high and significant correlations with BLUP for grain yield. This shows that BLUP can be used to select the best performing hybrid for grain yield (Oliveira *et al*., 2016).

As suggested by BLUP, the best combinations were P6xP9 under marginal rainfall condition and P4xP6 for other research conditions and these were coincident with the superior observed hybrids. These combinations can be selected to increase grain yield as they revealed the crosses that complemented mean grain yield the most and showed the importance of divergence and complementarity between parents to exploit heterotic and genetic gains under various growing conditions (Gowda *et al*., 2013).

4.4 Grain yield and stability of tropical maize hybrids developed from elite cultivars in contrasting environments under rainforest agro-ecology

As in other SSA countries, the average grain yield of maize in Nigeria is with approximately 1.7 t ha⁻¹ generally low when e.g. compared to the average yield in United States (9.3 t ha⁻¹) over the same time period (1986-2011) (Olaniyan, 2015). In recent years, this has culminated into breeding for high-yielding cultivars, as maize is a major staple food for about 50% of the sub-Sahara African population (IITA, 2009), and the vast majority of maize is grown on small-scale rural farms. The current study aimed therefore to evaluate the genetic potential of maize population hybrids, which are a promising alternative for low priced and more accessible improved seed for small-scale subsistence farmers.

The vulnerability of agroecosystems in which small scale-famers in SSA cultivate maize to variations in weather is currently of increasing concern, as optimal production scenarios associated with unpredictable changes in climate may become more common (Gaudin *et al*., 2015). The environments used in this study were diverse with respect to the growing conditions and geographic locations. Mühleisen *et al*. (2014a) emphasized the importance of diverse agroecosystems for assessing yield stability of crops with high accuracy in such scenarios. Result from correlation revealed that there was no significant relationship among the three growing conditions at Ile-Ife, indicating that the growing conditions are unique and distinct. It may also imply that different cultivar must be recommended for under the different growing conditions. For Umudike, the significant relationship between late planting and early $(r=0.24**)$ and late planting and optimal growing conditions $(r=0.36**)$ suggest that there can be common cultivars that will perform well under all growing conditions at Umudike. However, caution must be exercised because the correlation coefficients are small and the coefficient of determination $(R^2=5.8\%$ and $R^2=12.96\%$, respectively) indicate that the relationships are not reliable.

From the result of correlation analysis of the data of individual environments with data combined across environments, it is observed that although all the individual environments had significant correlation with across environments, optimal growing conditions at Ile-Ife had the highest correlation coefficient and by implication highest R^2 followed by late season at Ile-Ife and optimal growing conditions at Umudike. This implies that optimal condition at Ile-Ife is most representative of all environments for evaluating the maize genotypes.

Different maize genotypes typically display differential responses to varying environmental conditions. As a result, the major challenge for maize breeders has always been the selection of superior genotypes for narrow or wide adaptation and the identification of the best testing sites that could be used to identify superior and stable genotypes (Badu-Apraku *et al*., 2015b). The significant mean squares detected in the present study for the 108 genotypes indicated accordingly differential responses of the genotypes to environments and the need to identify high-yielding and stable genotypes across different test environments (Badu-Apraku *et al.*, 2013c). The presence of a highly significant GEI for grain yield of the cultivars is accordingly a confirmation of the need for the extensive testing of these cultivars in multiple environments and/or over several years before a particular cultivar can be recommended to farmers. This also confirms the need for breeders in the region to take GEI into serious consideration in evaluating cultivars, and to estimate its magnitude, relative to the magnitude of the G and E main effects affecting grain yield. Assessment of the total sum of squares revealed that the environmental sums of squares accounted for 68.2% of the variation for grain yield with the genotype contributing only 3.6%, reflecting a much wider range of environmental main effects over genotypic main effects. This finding is in agreement with the results of several multienvironment trials already conducted in SSA (Haussmann *et al*., [2001;](javascript:void(0);) Badu-Apraku *et al*., 2011c; Badu-Apraku *et al*., 2013c; Sserumaga *et al*., 2018).

The result of partitioning the variation in the genotypic effect revealed that hybrid accounted for over 90% of the variation among the 108 genotypes evaluated. Although parent accounted for 4% of the variation in genotype, the variation was not significant. It is therefore striking to note that even though there is no significant variation among the 14 parents used, their hybrids exhibited wide variability. The significant difference in the hybrid vs parent orthogonal contrast is a strong indication of heterosis in the maize germplasm evaluated. It further implies that the varieties used as parents can classified into heterotic groups and through reciprocal recurrent selection, inbred lines can be extracted from each heterotic group and better hybrids can be developed from such inbreds.

Yield stability was compared for different genotype groups rather than individual genotypes using diverse environments in order to obtain more precise estimates of the stability variance in comparison to the latter approach. It was evident in the study that the population-hybrids exhibited the highest level of stability followed by the parental populations. At the same time, the hybrids gave the highest average grain yield across all test environments. The high and stable performance of these population hybrids underlines their improved genetic constitution, potentially making them a highly useful and promising cultivar type for small-scale farmers in SSA.

Some previous studies also reported higher yield stability for hybrids than that of their parents when measuring the yield stability based on the stability variance (Oury *et al*., 2000; Gowda *et al*., 2010; Mühleisen *et al*., 2014a). However, a study by Koemel *et al*. (2004) using the regression approach as suggested by Eberhart and Russell (1966) observed no differences between hybrids and lines for wheat. In a similar work on sorghum by Haussmann *et al*. (2000), the hybrids out-yielded their parent lines with an average relative hybrid superiority of 54%. Wide ranges of stability variance were recorded within the genotype groups, with hybrids as well as line blends having slightly higher stability than pure stands of inbred lines. The authors speculated that improvements in yield stability might have been associated with an increase in heterozygosity and heterogeneity. According to Léon (1994), this effect of heterozygosity on grain yield stability varies among crop species depending on their reproductive system suggesting that in an outcrossing species like maize, heterozygosity has a strong positive effect on grain yield stability. Developing variety types with high degrees of heterozygosity and genetic heterogeneity for adaptation traits can additionally help in achieving better individual and population buffering capacity (Haussmann *et al.,* 2012). This point was further buttressed in a study carried out in winter wheat by Döring *et al*. (2015), where the stability also increased with an increase in the heterogeneity of the studied wheat cultivar groups.

CONCLUSION AND OUTLOOK

It is concluded from this study that there is wide genetic variability among the 108 genotypes evaluated. The variety hybrids showed high potential to deliver better yield than their parental variety and checks. Inconsistencies in broad-sense heritability values across environments for most of these traits are generally expected because heritability is not constant and can be affected by variations due to environmental factors and interaction between the environment and the genotypes. From the sequential path coefficient analysis, plant aspect and ear aspect should be considered as important selection indices for improvement aimed at developing high yielding open pollinated maize varieties in the sub-Saharan region.

The different methods of the diallel considered in this study all indicated that the contributions of SCA effect were greater than GCA effect for grain yield and all other measured agronomic traits. The correlation among the GCA effects obtained from the different methods of diallel suggested that these methods were similar and their GCA effects could be transferred or interchanged. The SCA effects from the two methods (2 and 4) of Griffing differed. However, the SCA effects as calculated by Method 4 and Gardener & Eberhart Analyses (GEAN) II and III were similar indicating their mutual transferability.

The OPV, P6 (TZL Comp - 3 C3 DT) had significant and positive GCA effects for grain yield across research environments. The favourable alleles from this parent should be harnessed for the development of high yielding and drought tolerant open pollinated varieties that can serve the rural maize farmers of the sub region in the face of climate change. This study has demonstrated that non-additive gene action was more important than additive gene action for the measured traits, indicating that SCA was the major component accounting for the differences among the OPVs evaluated in the study.

Four and three heterotic groups were identified by the HSGCA and HGCAMT methods respectively. The classification of some of the parents with similar genetic backgrounds together in the same group in each and across test environments indicated that the grouping of the OPVs was based largely on their pedigree and to a small extent on the reaction of the OPVs to the stress environments. Using HSGCA method, TZL Comp - 3 C3 DT and White DT STR SYN/IWD C3 SYN F2 was consistently grouped differently under all the test environments suggesting their heterotic potential when used in a cross. The parental varieties were classified into distinct heterotic groups from which contrasting heterotic populations could be formed that will serve as base population from where superior inbreds could be extracted.

For the BLUP, it was possible to identify the cross between P4 (STR SYN - Y2) and P6 (TZL Comp - 3 C3 DT) as the best hybrid combination, originating from completely contrasting parents. There was a difference between diallel analysis and best linear unbiased prediction (BLUP) method in terms of predicting efficiency under drought and across test environments. The ideal situation for breeders is the use of combining ability analysis together with BLUP method for efficient identification of promising genotypes and for the promotion of rapid development of new cultivars. However, if a breeder's choice were to use only one methodology, BLUP would be more efficient in determining hybrids with the best performance.

The variety hybrids showed high potential to deliver better yield and higher stability than their parental variety and checks. There is evidence of significant heterosis indicating that superior variety hybrids (P4 x P6 and P3 x P6) from this study can be recommended for further testing and ultimate release for resource-poor farmers in the rainforest agro-ecological zones of Nigeria since their development and production are easier and cheaper than the conventional hybrids.

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APPENDICES

Entry	Genotype	GY	EMERG	DA	ASI	DS	PHT	PASP	EASP	EPP	EROT
P ₁	P ₁	2.6	66	62	$\overline{4}$	66	123.60	3.3	3.2	0.7	1.4
P ₂	P ₂	2.0	66	63	$\overline{4}$	67	119.95	3.5	3.5	0.6	0.8
P ₃	P ₃	1.8	65	62	$\overline{4}$	66	136.03	3.1	3.2	0.7	0.8
P ₄	P4	2.3	67	63	$\overline{4}$	67	132.37	3.3	3.3	0.8	1.7
P ₅	P ₅	1.9	71	63	3	67	119.24	3.5	3.2	0.7	1.4
P ₆	P ₆	2.1	67	64	$\overline{4}$	68	117.37	3.4	3.4	0.7	1.1
P7	P7	2.2	75	63	$\overline{4}$	67	125.79	3.5	3.2	0.6	1.1
P ₈	P ₈	2.1	71	62	$\overline{4}$	66	119.66	3.5	3.5	0.6	1.2
P ₉	P ₉	2.4	70	62	5	67	110.91	3.6	3.5	0.7	1.3
P10	P10	2.5	66	62	$\overline{4}$	66	133.54	2.9	2.7	0.6	1.1
P11	P11	2.3	70	62	$\overline{4}$	66	138.82	3.3	3.0	0.7	1.2
P12	P12	$2.2\,$	68	61	$\overline{4}$	65	130.37	3.3	3.3	0.7	1.4
P13	P13	2.0	71	61	$\overline{4}$	65	122.92	3.7	3.1	0.6	1.4
P ₁₄	P ₁₄	1.9	63	64	3	67	112.94	3.5	3.4	0.7	1.4
H1	P1xP2	2.3	75	62	\mathfrak{S}	66	122.18	3.4	3.0	0.7	0.5
H2	P1xP3	2.0	61	63	3	67	115.33	3.6	3.7	0.7	1.0
H ₃	P1xP4	2.6	77	62	$\overline{4}$	66	131.61	3.3	3.1	0.7	0.8
H ₄	P1xP5	2.5	71	62	3	65	126.86	3.3	3.3	0.8	1.2
H ₅	P1xP6	2.5	76	62	$\overline{4}$	66	120.34	3.4	3.1	0.6	1.6
H ₆	P1xP7	2.5	75	62	3	65	125.55	3.3	3.4	0.7	1.6
H ₇	P1xP8	1.8	61	62	$\overline{4}$	66	117.56	3.6	3.4	0.7	0.8
H8	P1xP9	2.7	70	62	3	65	114.60	3.4	3.3	0.7	0.9
H ₉	P1xP10	2.2	70	62	3	66	123.35	3.2	3.2	0.7	1.0
H10	P1xP11	2.0	63	64	$\overline{\mathcal{A}}$	67	117.60	3.5	3.1	0.6	0.9
H11	P1xP12	2.5	73	62	$\overline{4}$	66	119.69	3.4	2.8	0.6	0.9
H12	P1xP13	2.5	69	63	3	66	126.24	3.3	3.3	0.7	1.5
H13	P1xP14	2.4	78	62	$\overline{4}$	66	122.13	3.3	3.3	0.7	0.8
H14	P _{2xP3}	2.0	68	62	$\mathbf{2}$	64	133.55	3.5	3.2	0.8	1.4
H15	P2xP4	3.0	65	63	$\overline{4}$	66	121.71	3.2	2.8	0.7	0.8
H ₁₆	P2xP5	2.1	73	63	3	65	126.61	3.4	3.4	0.7	1.1
H17	P _{2xP6}	2.5	76	62	$\overline{4}$	65	127.53	3.5	3.6	0.7	1.0
H18	P2xP7	2.2	74	62	5	67	132.75	3.2	3.2	0.6	1.0
H ₁₉	P _{2xP8}	2.5	73	61	$\overline{4}$	65	122.45	3.3	2.8	0.6	1.0
H20	P _{2xP9}	2.2	82	62	$\overline{\mathcal{A}}$	65	118.07	3.5	3.7	0.6	1.2
H21	P2xP10	2.7	79	62	$\overline{\mathcal{L}}$	66	127.66	3.3	2.8	0.6	0.9
H22	P2xP11	2.8	80	61	$\overline{\mathcal{A}}$	65	134.76	2.9	2.9	0.7	0.9
H23	P2xP12	2.0	70	62	\overline{c}	64	131.23	3.2	3.0	0.6	1.4
H24	P2xP13	2.2	70	62	$\overline{\mathcal{L}}$	67	124.04	3.3	2.9	0.7	1.1
H25	P _{2xP14}	2.8	69	63	\overline{c}	65	122.46	3.1	3.0	0.7	1.1
H ₂₆	P3xP4	2.5	68	62	$\overline{\mathcal{A}}$	66	134.51	3.2	3.3	0.7	2.3
H27	P3xP5	2.3	77	61	$\overline{\mathcal{A}}$	65	129.72	3.3	3.4	0.6	1.3

Appendix I: Performance of 108 maize genotypes evaluated across six environments in Nigeria, 2017-2018

 $P1-P14 = 14$ open pollinated parents, $H1-H91 =$ the corresponding hybrids; C106, C107 andC108 = Check 1, Check 2 and Check 3 respectively; $GY =$ Grain yield (tha⁻¹); EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PLHT = plant height (cm); PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP = ears per plant

Entry	Genotype	GY	EMERG	DA	ASI	DS	PHT	PASP	EASP	EPP	EROT	YR (%)
P ₁	P ₁	2.9	68	63	$\overline{7}$	70	110.14	3.5	3.3	0.7	1.8	11.4
$\mathbf{P}2$	P2	1.9	58	64	τ	71	106.67	3.8	4.1	0.5	0.5	36.8
P ₃	P ₃	2.1	59	64	5	69	123.17	3.5	3.5	0.5	0.8	-23.1
P ₄	P ₄	1.9	61	66	7	73	107.81	4.1	3.4	0.6	$\ensuremath{\mathfrak{Z}}$	27
P ₅	P ₅	2.3	70	63	5	68	110.94	3.8	3.2	0.7	$\boldsymbol{2}$	-15.2
P ₆	P ₆	2.6	76	64	5	70	107.67	3.9	3.6	0.7	$\mathbf{1}$	$1.7\,$
${\bf P}7$	${\bf P}7$	1.6	67	64	8	$72\,$	110.61	3.8	3.1	0.4	1.7	25.9
P8	P ₈	1.8	65	62	τ	69	114.94	3.5	3.4	0.5	2.2	31.5
P ₉	P ₉	2.7	72	61	$\overline{7}$	69	107.69	3.8	2.8	0.7	2.2	-10.6
P10	P10	1.7	69	65	6	71	108.31	3.9	2.9	0.5	$\mathbf{1}$	59.4
P11	P11	$\sqrt{2}$	70	62	6	68	111.47	3.8	3	0.7	2.3	30.3
P12	P12	2.8	77	62	6	68	107.29	3.6	\mathfrak{Z}	0.7	2.1	-5.7
P13	P13	2.8	71	61	5	66	110.61	3.9	2.8	0.6	2.7	-22.1
P14	P14	1.9	70	63	3	66	115.47	3.6	3.8	0.7	2.2	36.2
H1	P1xP2	2.3	70	63	8	71	97.18	3.8	3.2	0.6	0.5	23.1
H2	P1xP3	1.5	68	66	6	73	96.58	4.3	$\overline{4}$	0.7	$\boldsymbol{2}$	54.7
H ₃	P1xP4	$2.5\,$	82	66	5	71	110.67	3.6	3.5	0.6	1.8	18
H ₄	P1xP5	2.4	71	63	3	66	115.82	3.3	3.5	0.6	1.4	34.5
H ₅	P1xP6	2.2	83	65	6	71	109.46	3.8	3.6	0.6	2.2	39.1
H ₆	P1xP7	\mathfrak{Z}	81	62	6	67	114.92	3.5	3.5	0.8	1.8	2.4
H7	P1xP8	1.5	71	64	6	69	106.31	4.1	3.9	0.5	0.8	56.4
H8	P1xP9	2.4	70	64	$\overline{4}$	68	97.28	4.2	3.2	0.5	1.2	33.9
H9	P1xP10	$2.5\,$	75	62	$\overline{4}$	66	116.33	3.4	2.7	0.6	1.7	-6.7
H10	P1xP11	2.7	74	63	6	69	105.91	3.7	2.2	0.5	1.3	-21.8
H11	P1xP12	2.5	83	63	5	68	114.83	3.8	$\mathbf{2}$	0.4	1.8	11.2
H12	P1xP13	2.8	79	64	5	70	107.75	3.7	3.5	0.6	2.5	-0.7
H13	P1xP14	2.4	81	64	6	70	117.04	3.4	3.2	0.5	$\mathbf{1}$	26.8
H14	P _{2xP3}	2.8	79	64	3	67	124.75	3.2	2.9	0.8	2.3	-54
H15	P _{2xP4}	3	74	63	3	66	108.25	3.6	2.1	0.5	1.3	23.6
H16	P _{2xP5}	1.8	78	65	$\sqrt{2}$	67	114.31	3.8	3.6	0.8	2.7	40.6
H17	P _{2xP6}	2.1	$77 \,$	62	τ	68	107.25	$\overline{4}$	3.8	$0.8\,$	1.7	37.8
H18	P _{2xP7}	2.9	74	62	$\boldsymbol{7}$	69	118.64	3.3	3	0.7	1.4	-9.4
H19	P _{2xP8}	1.9	80	63	τ	69	111.38	3.8	2.5	0.5	1.8	52.1
H20	P _{2xP9}	1.7	83	64	6	70	102.39	4.2	3.7	0.6	\overline{c}	36.9
H21	P2xP10	2.6	80	64	6	70	100.45	4.1	2.2	0.5	0.8	30.7
H ₂₂	P _{2xP11}	3.1	87	62	τ	69	113.92	3.6	3.2	0.7	1.2	8.1
H ₂₃	P _{2xP12}	2.3	76	63	$\mathbf{2}$	64	116.58	3.6	2.7	0.5	2.7	-5.4
H ₂₄	P _{2xP13}	$\boldsymbol{2}$	78	64	$\boldsymbol{7}$	71	100.52	4.1	2.3	0.5	1.3	34
H25	P _{2xP14}	3.2	73	64	$\mathfrak 2$	66	115.6	3.5	2.7	0.8	1.5	17.7
H ₂₆	P3xP4	2.7	69	62	$\boldsymbol{7}$	69	124.14	3.3	3.3	0.7	3.3	$\sqrt{6}$
H ₂₇	P3xP5	2.7	85	62	τ	69	112.51	3.5	3.4	0.6	$\mathbf{1}$	-3.9
H ₂₈	P3xP6	3.3	83	63	τ	70	114.71	3.8	2.5	0.7	1.8	17.4
H ₂₉	P3xP7	2.2	72	62	$\overline{\mathcal{A}}$	66	124.72	3.5	3.3	0.8	2.5	21.8
H30	P3xP8	2.5	76	61	$\overline{\mathcal{A}}$	65	105.69	3.5	3.5	0.7	1.3	0.4

Appendix II: Performance of 108 maize genotypes evaluated under marginal rainfall condition in Nigeria, 2017-2018

P1-P14 = 14 open pollinated parents, H1-H91 = the corresponding hybrids; C106, C107 andC108 = Check 1, Check 2 and Check 3 respectively. $GY =$ Grain yield (tha⁻¹); EMERG = percentage emergence at 9 days after planting; DA = days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP = ears per plant; YR = yield reduction.

Entry	Genotype	GY	EMERG	DA	ASI	DS	PHT	PASP	EASP	EPP	EROT
P ₁	P ₁	3.3	79.2	64	3	66	138.54	3.0	2.9	0.7	2.0
P2	P2	3.0	83.7	64	3	67	131.31	3.5	3.1	0.7	1.1
P ₃	P ₃	1.7	78.5	63	3	66	143.97	2.9	2.8	0.9	1.3
P ₄	P ₄	2.7	83.3	63	$\mathbf{2}$	65	146.61	2.9	3.3	0.8	1.8
P ₅	P ₅	2.0	88.0	67	3	70	128.92	3.5	3.1	0.9	2.1
P ₆	P ₆	2.7	85.6	67	\mathfrak{Z}	70	127.83	3.0	3.0	0.9	$2.0\,$
P7	P7	2.2	88.3	67	3	70	134.08	3.3	3.1	0.6	1.5
P ₈	P ₈	2.6	85.1	63	3	66	124.36	3.4	3.5	0.7	1.3
P ₉	P ₉	$2.5\,$	89.4	64	5	69	107.53	3.6	3.7	0.8	1.6
P10	P10	4.1	81.1	63	\mathfrak{Z}	67	148.29	2.1	2.1	0.8	$2.0\,$
P11	P11	2.9	87.0	64	\mathfrak{Z}	67	164.31	3.0	3.0	$0.8\,$	1.3
P12	P12	2.6	85.1	62	5	67	146.61	3.1	3.2	0.7	2.1
P13	P13	2.3	79.0	63	3	66	135.81	3.8	3.2	0.9	1.6
P14	P14	3.1	89.9	66	$\mathbf{2}$	67	119.22	3.1	2.9	0.8	1.9
H1	P1xP2	3.0	90.2	63	3	67	142.36	2.9	2.8	$0.8\,$	1.1
H2	P1xP3	3.2	79.2	64	\overline{c}	67	130.54	3.0	3.3	0.8	$1.0\,$
H ₃	P1xP4	3.0	87.4	62	\mathfrak{Z}	65	150.11	3.3	2.7	0.8	0.5
H4	P1xP5	3.7	87.8	63	\mathfrak{Z}	67	144.39	3.2	2.9	0.9	2.1
H ₅	P1xP6	3.6	84.7	63	\mathfrak{Z}	65	129.08	3.3	2.7	0.6	1.8
H ₆	P1xP7	3.1	86.7	64	$\mathbf{2}$	66	139.28	3.1	3.1	0.8	2.8
H7	P1xP8	3.4	80.1	62	3	65	135.31	3.1	2.8	0.9	1.5
H8	P1xP9	3.6	86.4	62	\mathfrak{Z}	65	124.39	3.0	3.1	0.8	1.5
H9	P1xP10	2.4	82.4	65	\mathfrak{Z}	68	126.94	3.2	3.4	0.7	1.2
H10	P1xP11	2.2	73.5	67	3	70	123.39	3.4	3.3	0.9	1.3
H11	P1xP12	2.9	87.9	63	3	66	125.83	3.1	3.1	0.7	0.9
H12	P1xP13	2.8	80.7	64	\mathfrak{Z}	66	140.89	3.0	3.0	0.7	1.8
H13	P1xP14	3.2	87.1	63	\overline{c}	65	130.03	3.1	3.3	0.9	1.5
H14	P _{2xP3}	1.8	78.5	63	$\overline{3}$	66	135.22	3.8	3.6	0.8	1.8
H15	P _{2xP4}	3.9	77.3	64	$\overline{4}$	68	134.28	3.1	2.8	0.9	0.9
H16	P2xP5	3.0	88.3	64	$\overline{4}$	67	137.58	3.0	3.0	0.8	0.8
H17	P2xP6	3.5	90.9	64	3	67	153.67	2.9	3.0	0.8	1.3
H18	P2xP7	2.6	86.6	63	$\boldsymbol{7}$	70	142.50	2.8	3.0	0.6	1.2
H ₁₉	P2xP8	3.9	84.2	61	\mathfrak{Z}	64	137.61	3.0	2.6	0.8	1.1
H20	P2xP9	2.7	88.4	61	3	64	130.42	3.2	3.6	0.6	1.5
H21	P2xP10	3.7	87.2	62	3	65	161.33	2.6	2.6	0.8	1.7
H ₂₂	P2xP11	3.3	88.1	63	$\overline{2}$	65	159.14	2.3	2.7	0.7	1.3
H23	P2xP12	2.2	85.1	65	\mathfrak{Z}	68	144.83	3.0	3.1	0.7	1.2
H ₂₄	P2xP13	3.1	86.9	64	3	67	142.64	2.7	3.0	0.8	1.8
H25	P2xP14	3.8	81.8	65	$\mathbf{1}$	66	128.08	2.9	2.8	0.8	1.8
H ₂₆	P3xP4	2.9	81.8	65	\mathfrak{Z}	68	139.21	3.1	3.1	0.8	3.5
H27	P3xP5	2.6	85.7	63	$\overline{2}$	65	137.19	3.1	3.5	0.8	2.8
H ₂₈	P3xP6	4.0	89.8	65	3	68	116.92	3.3	3.3	0.8	0.9
H ₂₉	P3xP7	2.8	83.8	66	$\overline{2}$	68	142.61	3.1	3.1	0.8	1.6

Appendix III: Performance of 108 maize genotypes evaluated under optimal growing condition in Nigeria, 2017-2018

P1-P14 = 14 open pollinated parents, H1-H91 = the corresponding hybrids; C106, C107 andC108 = Check 1, Check 2 and Check 3 respectively. $GY =$ Grain yield (tha⁻¹); EMERG = percentage emergence at 9 days after planting; DA $=$ days to 50% anthesis; DS = days to 50% silking; ASI = anthesis-silking interval; PHT = plant height; PASP = plant aspect (1-5); EASP = ear aspect (1-5); EROT = ear rot; EPP = ears per plant.

Entry	Genotype	${\rm GY}$	EMERG	DA	ASI	DS	PHT	PASP	EASP	EPP	EROT	YR
P ₁		1.5	52.0	59	$\overline{2}$	62	122.13	3.3	3.3	0.7	0.3	$(\%)$ 53.4
$\mathbf{P}2$	P ₁ P2	$1.2\,$	57.6	60	3	63	121.89	3.3	3.4	0.6	0.7	59.0
P ₃	P ₃	1.7	58.1	61	3	63	140.94	3.0	3.2	0.7	0.3	1.9
$\mathbf{P}4$	P ₄	2.3	56.1	60	3	62	142.68	3.0	3.1	1.1	0.2	14.2
P ₅	P ₅	1.3	54.8	59	$\sqrt{2}$	62	117.86	3.3	3.3	0.6	$0.0\,$	36.5
P ₆	P ₆	$1.1\,$	39.1	61	3	64	116.61	3.3	3.7	0.7	0.2	57.7
P7	${\bf P}7$	2.6	68.6	59	3	61	132.68	3.5	3.4	0.7	0.0	-20.0
${\bf P8}$	P8	1.9	62.6	59	3	63	119.67	3.5	3.6	0.6	0.2	25.9
P ₉	P ₉	$2.0\,$	48.1	60	$\sqrt{2}$	62	117.50	3.5	3.9	0.7	0.0	21.0
P10	P10	1.8	49.2	60	$\sqrt{2}$	62	144.03	2.7	3.2	0.6	0.3	55.3
P11	P11	$2.0\,$	52.5	59	3	62	140.67	3.0	3.1	0.7	0.0	30.5
P12	P12	$1.2\,$	42.4	59	$\sqrt{2}$	61	137.19	3.1	3.7	0.6	0.0	54.8
P13	P13	0.9	61.6	60	3	62	122.43	3.3	3.5	0.4	0.0	60.9
P14	P14	$0.7\,$	29.5	63	$\overline{4}$	66	104.11	3.9	3.5	0.6	0.0	76.4
H1	P1xP2	1.7	66.4	59	3	62	127.01	3.5	3.2	0.7	0.0	44.3
H2	P1xP3	1.2	37.1	61	$\sqrt{2}$	63	118.88	3.5	3.7	0.6	0.0	62.7
H ₃	P1xP4	2.4	62.8	59	3	62	134.04	3.0	3.1	0.7	0.0	21.1
$\rm H4$	P1xP5	1.4	53.8	59	\overline{c}	61	120.36	3.3	3.4	0.9	0.0	63.1
H ₅	P1xP6	1.8	60.4	59	3	63	122.47	$3.2\,$	3.1	0.5	0.8	48.7
H ₆	P1xP7	$1.5\,$	56.1	59	$\sqrt{2}$	62	122.44	3.2	3.7	0.7	0.2	51.3
H7	P1xP8	$0.7\,$	32.6	61	3	64	111.08	3.7	3.6	0.6	0.0	79.7
$\rm H8$	P1xP9	$2.0\,$	53.3	60	$\sqrt{2}$	62	122.14	3.1	3.6	0.7	0.0	43.4
H ₉	P1xP10	1.8	52.5	60	3	63	126.76	3.0	3.5	0.6	0.2	25.0
H10	P1xP11	1.1	40.4	61	3	63	123.50	3.4	3.8	0.6	0.2	50.2
H11	P1xP12	2.0	47.5	61	\overline{c}	63	118.40	3.3	3.4	0.6	0.0	29.4
H12	P1xP13	1.9	47.2	60	$\sqrt{2}$	62	130.08	3.3	3.3	0.7	0.2	31.1
H13	P1xP14	1.6	66.7	60	3	63	119.33	3.4	$3.5\,$	0.7	0.0	51.0
H14	P _{2xP3}	1.4	46.6	59	$\sqrt{2}$	61	140.69	3.5	3.1	0.7	0.0	19.9
H15	P _{2xP4}	2.1	42.9	62	3	65	122.61	3.0	3.4	0.7	0.2	46.9
H16	P _{2xP5}	1.7	52.3	59	$\boldsymbol{2}$	62	127.94	3.4	3.5	0.5	0.0	44.6
H17	P _{2xP6}	1.8	60.6	60	$\boldsymbol{2}$	62	121.68	3.6	3.9	0.7	$0.0\,$	47.4
H18	P _{2xP7}	1.1	60.1	60	$\sqrt{2}$	63	137.11	3.6	3.7	0.5	0.3	58.8
H19	P _{2xP8}	1.8	53.5	60	$\boldsymbol{2}$	61	118.36	3.3	3.3	0.6	0.0	54.6
H20	P _{2xP9}	$2.0\,$	75.3	60	$\boldsymbol{2}$	62	121.41	3.2	3.8	0.6	0.2	25.4
H21	P2xP10	1.9	71.0	60	\mathfrak{Z}	63	121.19	3.3	3.6	0.6	0.2	47.4
H22	P _{2xP11}	$2.0\,$	64.9	59	$\boldsymbol{2}$	61	131.21	2.8	2.9	0.7	0.0	38.7
H ₂₃	P2xP12	1.5	49.2	59	$\boldsymbol{2}$	61	132.28	3.1	3.3	0.5	0.3	31.1
H ₂₄	P _{2xP13}	1.3	45.5	60	$\boldsymbol{2}$	62	128.97	3.2	3.5	$0.8\,$	0.2	56.7
H25	P _{2xP14}	1.3	50.5	60	3	62	123.71	3.1	3.5	0.6	0.2	65.0
H ₂₆	P3xP4	1.9	54.3	59	$\sqrt{2}$	61	140.17	3.1	3.5	0.7	0.0	35.3
H27	P3xP5	1.6	60.9	58	\mathfrak{Z}	61	139.46	3.2	3.4	0.5	0.0	39.2
H28	P3xP6	2.7	55.9	59	$\boldsymbol{2}$	61	114.49	3.1	3.3	0.7	0.0	31.9
H ₂₉	P3xP7	0.9	51.0	60	$\boldsymbol{2}$	62	126.14	3.8	3.7	0.5	0.0	67.1
H30	P3xP8	1.5	56.8	60	\mathfrak{Z}	63	120.31	3.5	4.1	0.6	0.2	41.2

Appendix IV: Performance of 108 maize genotypes evaluated under drought in Nigeria, 2017-2018

P1-P14 = 14 open pollinated parents, H1-H91 = the corresponding hybrids; C106, C107 andC108 = Check 1, Check 2 and Check 3 respectively. $GY =$ Grain yield (tha⁻¹); EMERG = percentage emergence at 9 days after planting; $DA = \text{days}$ to 50% anthesis; $DS = \text{days}$ to 50% silking; $ASI = \text{anthesis-silking interval}$; $PHT = \text{plant}$ height; PASP = plant aspect; EASP = ear aspect; EROT = ear rot; EPP = ears per plant; YR = yield reduction.

Crosses	$M_{2,1}$	$M_{4,1}$	GEANII	GEANIII
P3xP6	0.948	0.885	0.885	0.885
P _{4xP6}	0.710	0.647	0.647	0.647
P5xP8	0.703	0.652	0.652	0.652
P5xP13	0.601	0.558	0.558	0.558
P2xP14	0.548	0.495	0.495	0.495
P6xP9	0.488	0.464	0.464	0.464
P10xP13	0.469	0.487	0.487	0.487
P9xP12	0.467	0.509	0.509	0.509
P3xP11	0.466	0.465	0.465	0.465
P1xP9	0.449	0.480	0.480	0.480
P _{2xP11}	0.424	0.413	0.413	0.413
P10xP14	0.376	0.363	0.363	0.363
P4xP14	0.336	0.294	0.294	0.294
P _{4xP7}	0.334	0.330	0.330	0.330
P9xP13	0.318	0.345	0.345	0.345
P7xP12	0.295	0.318	0.318	0.318
P1xP7	0.280	0.292	0.292	0.292
P6xP11	0.266	0.227	0.227	0.227
P1xP12	0.261	0.281	0.281	0.281
P1xP13	0.244	0.249	0.249	0.249
P5xP14	0.231	0.157	0.157	0.157
P2xP10	0.228	0.222	0.222	0.222
P7xP10	0.224	0.250	0.250	0.250
P _{2xP8}	0.213	0.183	0.183	0.183
P7xP8	0.213	0.214	0.214	0.214
P8xP12	0.209	0.218	0.218	0.218
P _{2xP4}	0.200	0.165	0.165	0.165
P3xP12	0.181	0.183	0.183	0.183
P4xP11	0.169	0.170	0.170	0.170
P10xP12	0.165	0.198	0.198	0.198
P7xP11	0.161	0.181	0.181	0.181
P6xP14	0.144	0.064	0.064	0.064
PlxP14	0.140	0.114	0.114	0.114
P8xP11	0.129	0.134	0.134	0.134
P8xP13	0.124	0.117	0.117	0.117
P3xP8	0.085	0.065	0.065	0.065
P1xP5	0.055	0.015	0.015	0.015
P _{4xP5}	0.055	-0.001	-0.001	-0.001
P12xP13	0.049	-0.317	0.064	0.064
P4xP13	0.044	0.033	0.033	0.033
P5xP9	0.016	-0.001	-0.001	-0.001
P _{2xP9}	0.015	0.019	0.019	0.019

Appendix V: Specific combining ability effects of 91 crosses for grain yield (t ha-1) from Griffing's methods, and Gardener and Eberhart Analyses II and III for diallels involving 14 open pollinated parents

 $M_{2,1}$ = Griffing's method 2 model 1; $M_{4,1}$ = Griffing's method 2 model 1; GEANII = Gardener and Eberhart Analysis II; GEANIII = Gardener and Eberhart Analysis III

DEFINITION OF TERMS

Additive gene effect: It is a mechanism of quantitative inheritance such that the combined effects of genetic alleles at two or more loci are equal to the sum of their individual effects. A characteristic that governs general combining ability.

Combining ability: It is the value of a genotype based on the performance of their offspring produced in a definite mating system.

Commercial heterosis: The difference between the mean of the F1 hybrid and the mean of the highest performing reference variety.

Diallel Cross: The crossing in all possible combinations of a series of genotypes.

Dominance: Intra-allelic interaction such that one allele manifests itself more or less, when heterozygous, than its alternative allele.

Epistasis: Dominance of one gene over a non-allelic gene. The gene suppressed is said to be hypostatic. More generally, the term epistasis is used to describe all types of interallelic interaction whereby manifestation at any locus is affected by genetic phase at any or all loci**.**

General combining ability: The average performance of a line in hybrid combinations expressed as a deviation from the overall mean of all crosses made from other parental lines. Quantitatively, it measures the comparative performance of lines.

Heritability: The proportion of observed variability which is due to heredity, the remainder being due to environmental causes. In a narrow sense, the proportion of observed variability due to the additive effects of genes.

Heterosis: It is the superiority of F1 hybrids over both its parents. It is manifested as an increase in vigor, size, growth rate, yield and resistance to diseases.

Heterotic Groups: A group of related genotypes from the same population which display similar combining ability effects when crossed with genotypes from other germplasm groups.

Heterotic pattern: Heterotic groups that complement each other. They are specific crosses between genotypes which show high levels of heterosis.

Hybrid: The product of a cross between genetically unlike parents.

Mid-parent heterosis: The average heterosis observed when two random population are crossed together.

Non-additive gene effects: This is when the gene effects of the allelic pair do not sum up since members of the allelic pair are not expressed equally. It is associated with specific combining ability.

Specific combining ability: Instances where hybrid deviates from the expected value which is the sum of the general combining ability of the parent inbred lines included in the crosses.

Testers: These are genotypes of good general combining ability and well defined heterotic groups, which are used for identifying and selecting superior genotypes to be used in breeding programs.

Yield stability: This refers to a genotype's ability to perform consistently, whether at high or low yield levels, across a wide range of environments.