Gene Action and Heterotic Groups of Early White Quality Protein Maize Inbreds under Multiple Stress Environments

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ABSTRACT

Food insecurity and malnutrition are major challenges facing rural populations in sub-Saharan Africa. A total of 150 quality protein maize (*Zea mays* L.) (QPM) hybrids generated from 30 early-maturing QPM inbreds plus six checks were evaluated under drought, low soil N, and *Striga* [*Striga hermonthica* (Delile) Benth.]-infested environments in Nigeria for 2 yr. The objectives were to (i) examine the gene action conditioning the traits in the inbreds, (ii) classify them into heterotic groups using two methods, (iii) identify the best QPM inbred testers across environments, and (iv) identify stable and high-yielding hybrids. General and specific combining ability (GCA and SCA, respectively) mean squares were significant ($P < 0.01$) for grain yield and other traits across environments, indicating that additive and nonadditive gene actions were important in the inheritance of most traits of the inbreds. Preponderance of SCA sum of squares over GCA for most measured traits across environments indicated that nonadditive gene action largely modulated inbred trait inheritance. The GCA effects of multiple traits (HGCAMT) method classified the inbreds into three heterotic groups each under drought and across environments and four groups under low N and *Striga*-infested environments. Single nucleotide polymorphism (SNP)-based method placed the inbreds into three groups across environments and was more efficient. TZEQI 6 and TZEQI 55 were identified as testers across environments. TZEQI 44 × TZEQI 4, TZEQI 35 × TZEQI 39, TZEQI 35 × TZEQI 59, TZEQI 6 × TZEQI 35, and TZEQI 45 × TZEQI 33 were the most stable and highest-yielding hybrids across environments and should be commercialized for improved nutrition and food security in sub-Saharan Africa.

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Abbreviations: AMMI, additive main effects and multiplicative interactions; ASI, anthesis–silking interval; EPP, ears per plant; $G \times E$, genotype × environment interaction; GCA, general combining ability; GD, genetic distance; HGCAMT, general combining ability effects of multiple traits; IITA, International Institute of Tropical Agriculture; IPCA, interaction principal component axes; MI, multiple-trait-base index; NCD II, North Carolina Design II; OPV, open-pollinated variety; PCA, principal component analysis; PIC, polymorphic information content; QPM, quality protein maize; SCA, specific combining ability; SNP, single nucleotide polymorphism; WAP, weeks after planting; WCA, West and Central Africa.

During the past two decades, many countries of West and Central Africa (WCA) have experienced deterioration in their standards of living, resulting in increased levels of poverty, food insecurity and malnutrition. The major factors that have contributed to the present situation include incidence of drought, infestation by *Striga*, and poor soil fertility, especially in the savannas, which are the maize belts of the subregion. Inadequate diets in the subregion have also resulted from both calorie insufficiency and protein inadequacy.

Maize, which was introduced into WCA during the sixteenth century, has rapidly gained popularity as a major food crop and a trade commodity in this region. The crop is widely grown in many agroecological zones in the subregion, but it is well adapted

to the savannas because of high solar radiation, low night temperatures, and lower incidence of diseases that characterize this region. However, many researchable issues such as development of QPM varieties that are resistant to *Striga* and tolerant to drought and low soil N need to be addressed urgently if maize is to contribute its expected share to poverty alleviation and provision of nutritionally balanced diets in WCA. Development of stress resistant and tolerant QPM varieties is likely to improve the income-generating capabilities and nutritional status of farmers. This is because maize production in the savannas is severely constrained by recurrent drought, reduced soil fertility, especially low soil N and water-holding capacity, and *Striga* parasitism (Badu-Apraku et al., 2015a).

Production worth billions of US dollars is lost annually because of these constraints. For example, annual yield loss as a result of drought was estimated to be ~24 million tons, which represents ~17% of a normal year's production in the developing world (Edmeades et al., 1992). The loss could be much higher if it occurs at the flowering and grain filling periods (Nesmith and Ritchie, 1992). *Striga* infestation was estimated to cause losses of about US $7 billion in WCA (M'Boob, 1986). In addition, increased population pressure on the available land has resulted in an intensification of crop production, reduced fallow periods, and, consequently, low soil fertility (Vogt et al., 1991), all of which together have aggravated the *Striga* problem. Annual loss of maize yield as a result of low soil N varies from 10 to 50% (Wolfe et al., 1988) in WCA and is caused by several factors, including little or lack of application of inorganic fertilizer by farmers and rapid mineralization of organic matter in the soil (Banziger and Lafitte, 1997). Under field conditions, drought, *Striga*, and soil nutrient deficiencies can occur simultaneously and the combined effect can be devastating. Drought and low soil N aggravate *Striga* parasitism on maize (Kim and Adetimirin, 1997; Badu-Apraku et al., 2004). Studies conducted in WCA by Badu-Apraku et al. (2004, 2010) on the combined effects of these stress factors showed 44 to 53% grain yield reduction because of drought, 42 to 65% from *Striga* infestation, and 40% from low soil N. Host-plant resistance is considered the most economically feasible and sustainable approach for reducing the effects of the three stress factors (DeVries, 2000; Badu-Apraku and Akinwale, 2011).

Maize is widely fed as porridge to weaning children, although often without a protein supplement such as milk, meat, or beans in many African countries. However, maize is deficient in two essential amino acids: lysine and tryptophan. Therefore infants fed on normal maize without protein supplements suffer from diseases such as kwashiorkor caused by protein deficiency. This has prompted the development, dissemination, and adoption of several QPM varieties in WCA since 1990, an initiative that has contributed to reduction in malnutrition from protein deficiency in the subregion (Badu-Apraku et al., 2013) and making significant contributions to the food and livestock industries.

Adoption and use of superior maize hybrids that have been selected for high levels of tryptophan and lysine, N-use efficiency, resistance to *Striga*, and tolerance to drought will revolutionize agriculture and contribute to increased maize production and faster reduction in protein deficiency among the rapidly growing population of WCA. In an effort to mitigate the problem of malnutrition in WCA, an early-maturing QPM inbred line development program was initiated at International Institute of Tropical Agriculture (IITA) in 2003. By 2011, 71 drought-, low-N-, and *Striga*-tolerant or resistant early QPM white inbred lines had been developed. Information on the combining ability, heterotic patterns, and the extent of genetic diversity in these QPM inbreds, which is crucial to the development of an efficient breeding strategy for the QPM hybrid program at IITA, is presently lacking. In addition, there is an urgent need to determine the impacts of *Striga* infestation, drought, and low-N stresses on the performance and combining ability of QPM germplasm for grain yield and other traits. Results of most studies conducted so far to determine the inheritance of quantitative traits in QPM germplasm have revealed significant GCA effects for grain yield and other agronomic traits, while SCA mean squares were not significant indicating the preponderance of additive over nonadditive gene action (Vasal et al., 1993; Fan et al., 2004; Wegary et al., 2013; Musila et al., 2010). In contrast, Bhatnagar et al. (2004) and Machida et al. (2010) reported the preponderance of nonadditive gene action for grain yield and additive gene action for days to silking, anthesis, and plant height in a diallel study involving selected QPM inbred lines. Furthermore, there are no early-maturing QPM inbreds and testers identified in our program to facilitate the design of efficient breeding schemes for hybrid development. Knowledge and understanding of the breeding values of IITA QPM inbreds under multiple stress environments would be very helpful in devising a viable breeding strategy to develop QPM hybrids adapted to the relevant multiple stresses in WCA. The objectives of the present study were to (i) determine the gene action conditioning grain yield and other agronomic traits in the QPM inbreds under *Striga*-infested, drought, and low-N environments; (ii) classify the inbreds into heterotic groups by two methods and compare the efficiency of the grouping methods; (iii) identify the best QPM inbred testers across research environments; and (iv) identify high-yielding and most stable hybrids across multiple stresses for commercialization.

MATERIALS AND METHODS
Development of Early-Maturing Quality Protein Maize Inbreds and Generation of Crosses

In 2003, 22 early white normal–endosperm elite *Striga*-resistant inbred lines were crossed to a QPM donor source, Pool 15 SR, in an effort to convert them to QPM. Between 2003 and 2008, the materials were taken through various stages of backcrossing and self-pollination with selection for high lysine and tryptophan and the desirable agronomic traits, including drought tolerance. The best 10 lines selected at the S_2 stage were used to develop a white QPM synthetic variety, while inbreeding and selection continued within the best 30 lines. By 2011, 71 S_6 QPM inbred lines had been developed. The lines were analyzed for lysine and tryptophan contents at the IITA nutrition laboratory and the best 30 (Supplemental Table S1) were selected for the present study.

The selected 30 QPM inbreds were divided into six sets each consisting of five inbreds. Crosses were made between the groups such that the five inbreds in one set were used as females and crossed with the five inbreds in another set (males) using the North Carolina Design II (NCD II) mating scheme of Comstock and Robinson (1948) to generate 150 single-cross hybrids, which were evaluated along with six checks comprising three each of drought-tolerant normal-endosperm open-pollinated varieties (OPVs) (EV DT-Y 2000 STR, EV DT-W 2008 STR, and 2008 DTMA-W STR) and hybrids (TZEI 5 × TZEI 98, TZEI 1 × TZEI 5, and TZEI 2 × TZEI 87) in field experiments. Early-maturing normal OPVs and hybrids were used as checks in the present study because there were no early-maturing QPM OPVs and hybrids that combined resistance to *Striga* and tolerance to drought and low-N in the IITA maize improvement program at the time of this research.

Cultural Practices, Field Evaluations, and Stress Management

Three field experiments were conducted in 2011 and 2012 in Nigeria. In the first experiment, the 150 hybrids plus six checks were evaluated at Ikenne (6°53′ N, 3°42′ E, 60 m asl, 1200 mm annual rainfall), in Nigeria under managed drought during the dry seasons of 2011 and 2012 and under terminal drought at Bagauda (12°00′ N, 8°22′ E, 580 m asl, 800 mm annual rainfall) during the 2012 growing season. Soil type at Ikenne is Eutric nitrisol, while that of Bagauda is clay loam (Soil Survey Staff, 1999). A randomized incomplete block design (12 by 13 α-lattice) with two replications was used for all evaluation trials. Each experimental unit was a single-row plot, 5 m long with row spacing of 0.75 m and hill spacing of 0.4 m within the row. Three seeds were planted per hill and the seedlings were thinned to two ~2 wk after emergence to give a final population density of about 66,000 plants ha^{-1}. The managed drought at Ikenne was achieved through an irrigation system that provided 17 mm of water per week up to 28 d after planting. Thereafter, the irrigation water was withdrawn until maturity so that the maize plants relied on stored water in the soil for growth and development.

In the second experiment, the single-cross hybrids were evaluated at Ile-Ife (lat. 7° 18′ N, long. 4° 33′ E, 244 m asl, 1100 mm annual rainfall) and Mokwa (9°18′ N, 5°4′ E, 457 m asl, 1100 mm annual rainfall), Nigeria, under low N (30 kg N ha^{-1})

in 2011 and 2012 at each location. The soil at Mokwa is a luvisol (Soil Survey Staff, 1999) with 0.27, 0.035, and 0.48% organic C, organic N, and P content. On the other hand, the soil at Ile-Ife is characterized as Alfisol (Soil Survey Staff, 1999) with 0.084% organic N. The experimental fields were depleted of N by continuously planting maize for several years and removing the biomass after each harvest. Soil samples were taken each year before planting for all the test environments and N content was determined at the IITA soil laboratory at Ibadan. The total N in the soils was determined by Kjeldahl digestion and colorimetric determination on Technicon AAII Autoanalyser (Bremner and Mulvaney, 1982). Fertilizer was applied to bring the total available N to 30 kg ha^{-1} for the low-N fields when the soil N was below 30 kg ha^{-1}. The N fertilizer was applied 2 wk after planting (WAP). Also, single superphosphate (P_2O_5) and muriate of potash (K_2O) were applied to the low-N blocks at the rate of 60 kg ha^{-1}. Each trial was kept weed free with the application of herbicides and by hand weeding.

In the third experiment, the single-cross hybrids were evaluated in 2012 for yield potential and tolerance or resistance to *Striga* under artificial infestation with *Striga* at Mokwa and Abuja (9°16′ N, 7°20′ E, 300 m asl, 1500 mm annual rainfall), both in the Southern Guinea Savanna agroecological zone of Nigeria where *Striga* is endemic. The soil type at Abuja is ferric luvisol (Soil Survey Staff, 1999). The fields were fumigated with ethylene gas at ~7 d before planting to induce suicidal germination of *Striga* seeds in the soil. The *Striga* seeds used for infestation were mixed with finely sieved sand in the ratio of 1:99 by weight and about 5000 germinable seeds were placed in each planting hole on the ridges, as described by Kim (1991). Fertilizer application was delayed until about 30 d after planting when 30 kg N ha^{-1}, 30 kg P ha^{-1}, and 30 kg K ha^{-1} were applied as 15-15-15 N–P–K. The reduced rate and delay in application of fertilizer were necessary to ensure good germination of *Striga* seeds and attachment of *Striga* plants to the roots of host plants in *Striga*-infested plots (Kim 1991). Weeds other than *Striga* were controlled manually.

Collection of Agronomic Data

Data were recorded on drought-stressed, *Striga*-infested, and low-N plots. Days to 50% silking was recorded as the number of days from planting to when 50% of the plants had emerged silks, and days to anthesis when 50% of the plants had shed pollen. The anthesis–silking interval (ASI) was calculated as the difference between days to 50% silking and 50% anthesis. Plant height was measured as the distance from the base of the plant to the height of the first tassel branch and ear height as the distance to the node bearing the upper ear. Root lodging (percentage of plants leaning more than 30° from the vertical) and stalk lodging (percentage broken at or below the highest ear node) were measured. Number of ears per plant (EPP) was obtained by dividing the total number of ears per plot by the number of plants harvested. Plant aspect was recorded on a scale of 1 to 9 based on plant type, where 1 was excellent and 9 was poor. Husk cover was rated on a scale of 1 to 5, where 1 indicated husks tightly arranged and extended beyond the ear tip and 5 indicated ear tips exposed. Ear aspect was recorded based on a scale of 1 to 9, where 1 was clean, uniform, large, and well-filled ears and 9 indicated ears with undesirable features. In addition, stay-green characteristic was recorded for the drought-stressed and low-N

plots at 70 d after planting on a scale of 1 to 9, where 1 was almost all leaves green and 9 was virtually all leaves dead. Host plant-damage-syndrome rating (Kim, 1991) and emerged *Striga* plants were recorded at 8 and 10 WAP in the *Striga*-infested plots. *Striga* damage syndrome was scored per plot on a scale of 1 to 9 where 1 was no damage, indicating normal plant growth and high resistance, and 9 indicated complete collapse or death of the maize plant, that is, highly susceptible (Kim, 1991). In the managed-drought and low-N experiments, harvested ears from each plot were shelled to determine the percentage grain moisture. Grain yield was adjusted to 15% moisture and computed from the shelled-grain weight. On the other hand, in the *Striga*-infested experiment, grain yield was computed based on 80% (800 g grain kg⁻¹ ear weight) shelling percentage and adjusted to 150 g kg⁻¹ moisture content.

Single Nucleotide Polymorphism Marker Assays

DNA Extraction

Young leaf samples were collected from 8 to 10 seedlings in the field at 2 WAP. The leaves were bulked and lyophilized before DNA extraction. Genomic DNA was isolated from the collected samples using a modified CTAB protocol of Saghai-Maroof et al. (1984). The restriction enzyme *Hin*dIII was used to digest the DNA to determine the quality of the DNA samples. The digested DNA was transferred into an optical plate containing 96 wells, fitly sealed with rubber plate covers, and shipped to the Institute for Genomic Diversity, Cornell University, Ithaca, NY, for genotyping by sequencing. The SNP genotyping was performed as described by Badu-Apraku et al. (2015b).

Statistical Analyses

Separate analyses of variance (ANOVA) were performed on data collected under each research condition (drought, low-N, and *Striga*-infested environments) with PROC GLM in SAS (SAS Institute, 2011). Subsequently, combined ANOVA across research environments was performed for grain yield and other measured traits with PROC GLM in SAS using a RANDOM statement with the TEST option (SAS Institute, 2011). The main effects of males-within-sets and females-within-sets mean squares estimated the variance due to the GCA while the female × male-within-set interaction mean squares estimated the SCA variance (Hallauer and Filho, 1988). The proportion of GCA-male, GCA-female, and SCA for each trait was computed as percentage of the sum of squares for the crosses across research environments. The GCA-males and GCA-females effects for each trait were computed from the adjusted means (Singh and Chaudhary, 1985).

To assign inbred lines into heterotic groups under *Striga* infestation, drought, low-N, and across environments the HGCAMT method proposed by Badu-Apraku et al. (2013) and genetic distance (GD) estimated from SNP markers were adopted. Ward's minimum variance cluster analysis based on the Euclidean distance generated from HGCAMT and GD-based data were used to assign the 30 inbred lines into heterotic groups under each contrasting environments and across environments using SAS (SAS Institute, 2011). The grouping by the HGCAMT was achieved by standardizing the GCA effects (mean of zero and standard deviation of 1) of the traits that had

significant mean squares for genotype to minimize the effects of different scales of the traits. The efficiency of the two heterotic grouping methods were compared by arranging the 150 hybrids from the highest to the lowest based on grain yield under drought, low-N, *Striga* infestation, and across research environments. The procedure involved dividing the total number of hybrids for each method into two major groups: intergroup and intragroup crosses. These two groups were subsequently divided into high-yielding hybrids (Yield Group 1 with a mean grain yield ranking among the top 50 lines), intermediate hybrids (Yield Group 2 with a grain yield between the 51st and 100th line), and low-yielding hybrids (Yield Group 3 with a mean grain yield between 101st and 150th line). The better classification method was considered as the one in which classified heterotic groups allowed interheterotic group crosses to produce more superior hybrids than the intragroup crosses (Fan et al., 2009). The implication was that a more efficient grouping method should place more of intergroup crosses in the higher yielding hybrid class and more of the intragroup crosses in the low-yielding hybrid category. Furthermore, Fan et al. (2009) defined the breeding efficiency as the percentage of high-yielding hybrids across the total number of interheterotic crosses, that is, the best heterotic grouping method is the one that allows more interheterotic group crosses to produce more superior hybrids than the intragroup crosses. In the present study, we defined the breeding efficiency as the average of the proportion of total interheterotic group hybrids that is due to superior high-yielding interheterotic group hybrids plus the proportion of total low-yielding intraheterotic group hybrids that is due to the low-yielding intraheterotic group hybrids. For this purpose, Groups 1 and 3 were considered the high-yielding and low-yielding group, respectively. The equation for estimating the breeding efficiency is as follows:

$$\text{BE} = \frac{\left[\dfrac{\text{HYINTERGH}}{\text{TNINTERGH}} \times 100\right] + \left[\dfrac{\text{LYINTRAGH}}{\text{TNINTRAGH}} \times 100\right]}{2},$$

where BE = breeding efficiency, HYINTERGH is the number of high-yielding interheterotic group hybrids, TNINTERGH is the total number of interheterotic group hybrids, LYINTRAGH is the number of low-yielding intraheterotic group hybrids, and TNINTRAGH is the total number of intraheterotic group hybrids.

An inbred was considered a tester based on three criteria. It must (i) belong to a known heterotic group, (ii) have a high significant positive GCA across the test environments, and (iii) have high yield per se (Badu-Apraku et al., 2013).

The additive main effects and multiplicative interactions (AMMI) model (Zobel et al., 1988; Gauch and Zobel, 1988; Crossa, 1990) was adopted to assess the relationships among the single crosses, environments, genotype × environment interactions (G × E), and obtain information on the performance and yield stability of the single-cross hybrids across the three stress environments. The AMMI uses principal component analysis (PCA) to decompose the multiplicative effects (G × E) into a number of interaction principal component axes (IPCA). The GGE biplot software, a Windows application that fully automates biplot analysis (Yan, 2001) was used for the AMMI analysis.

A total of 30 genotypes (top 19 tolerant and the five most susceptible QPM hybrids plus three each of OPV and normal-endosperm hybrid checks) evaluated across eight environments were selected and subjected to AMMI analysis. A multiple-trait-base index (MI) that integrated grain yield, EPP, plant and ear aspects, stay-green characteristic, *Striga* damage rating, and number of emerged *Striga* plants was used to select the entries for the AMMI analysis. Each trait was standardized to minimize the effect of the different scales. A positive MI value was considered an indication of tolerance or resistance to the multiple stresses, while negative values indicated susceptibility. The multiple trait base index was computed as follows:

$$MI = (2 \times YLD) + EPP - EASP - PASP$$
$$- SGR - SD8 - SD10 - (0.5 \times ESP8)$$
$$- (0.5 \times ESP10),$$

where YLD is grain yield across environments, EPP is number of ears per plant across environments, EASP is ear aspect across environments, PASP is plant aspect across environments, SGR is stay-green characteristic across drought and low-N environments, SD8 and SD10 are *Striga* damage rating at 8 and 10 WAP across *Striga* environments, and ESP8 and ESP10 are number of emerged *Striga* plants at 8 and 10 WAP across *Striga* environments.

Single nucleotide polymorphisms (1,151 out of 143,415) covering the whole maize genome with 0.05 allele frequency and no missing data were used to explore the genetic diversity of the inbred lines using TASSEL version 4.1.12 (Bradbury et al., 2007). In this study, filtering criteria, which allowed some percentage of missing data, were used. This resulted in additional SNPs, but the phylogeny of the lines was not affected when larger numbers of SNPs were used (data not shown). The allocation of the SNP loci on the 10 maize chromosomes was 232 in chromosome 1, 172 in chromosome 2, 177 in chromosome 3, 169 in chromosome 4, 167 in chromosome 5, 95 in chromosome 6, 143 in chromosome 7, 133 in chromosome 8, 81 in chromosome 9, and 82 in chromosome 10. The allele frequency, gene diversity, heterozygosity, polymorphic information content (PIC), and pair-wise Roger's genetic distance estimates (Rogers, 1972) among the inbred lines were calculated using PowerMarker version 3.25 (Liu and Muse, 2005).

RESULTS
Analysis of Variance of Grain Yield and Other Traits under Contrasting Environments
Analysis of variance showed significant ($P < 0.05$) differences in mean squares of environment (E), hybrids, GCA-male (set) (GCAm), GCA-female (set) (GCAf), and SCA (set) for grain yield and most measured traits under drought, low-N, *Striga* infestation and across environments (Tables 1, 2). The few exceptions were ear aspect for GCAm (set) and SCA (set) under drought (Table 1), ASI for hybrids, GCAm (set), and GCAf (set) and husk cover for GCAm (set) and SCA (set) under *Striga*-infested environments (Table 2). Most measured traits had significant ($P < 0.05$) mean squares for the hybrids × E, GCAm

(set) × E, GCAf (set) × E, and SCA (set) × E interactions under drought, low-N, and across environments. The hybrids × E mean squares were significant ($P < 0.05$) for all measured traits except days to anthesis and *Striga* damage at 8 WAP under *Striga* infestation (Table 2). In contrast, the GCAm (set) × E was significant for grain yield, days to silking, plant height, husk cover, ear aspect, ears per plant, and number of emerged *Striga* plants at 10 WAP, while significant mean squares were obtained for the GCAf (set) × E for grain yield, ear height, husk cover, EPP, *Striga* damage rating at 10 WAP and the number of emerged *Striga* plants at 10 WAP under *Striga*-infested environments. Similarly, significant ($P < 0.05$) SCA (set) × E interaction mean squares were detected for grain yield, ASI, ear aspect, EPP, *Striga* damage at 10 WAP and the number of emerged *Striga* plants at 8 WAP under *Striga*-infested environments (Table 2).

Relative Importance of General and Specific Combining Ability
Partitioning the hybrid sum of squares into its components showed that GCA (GCAm plus GCAf) accounted for 50.1 to 71.6% of the total variation among hybrids for days to anthesis and silking, ASI, and husk cover under drought; grain yield, days to anthesis and silking, ear height, and stay-green characteristic under low N; and days to anthesis and EPP under *Striga* infestation and days to anthesis and silking and stay-green trait across test environments (Table 3). Similar magnitudes of GCA and SCA sum of squares were obtained for grain yield under low N (50.1 vs. 49.9%) and across environments (49.5 vs. 50.5%) as well as for days to silking (49.7 vs. 50.3%) under *Striga* infestation. It is striking to note that the *Striga* traits (number of emerged *Striga* plants and the *Striga* damage syndrome rating) had larger SCA sum of squares than GCA sum of squares under *Striga* infestation. Across research environments, eight traits (grain yield, ASI, plant and ear heights, husk cover, plant and ear aspects, and EPP) of the 11 measured traits had greater SCA sum of squares than GCA sums of squares.

Relative Importance of Female and Male General Combining Ability Effects under Contrasting Environments
Variations were observed in the contributions of the GCAf and GCAm effects to the total sum of squares for grain yield and other traits under the three stress environments. However, variance ratio (F-test) of the mean squares of GCAm to the GCAf and GCAf to GCAm were not statistically significant ($P = 0.05$) for any of the traits based on the method of Kearsey and Pooni (1996). For example, GCAf effect was 1.3 times the GCAm effect with the GCAf sum of squares contributing 24% and the GCAm sum of squares 19% of the total variance for grain yield under drought but the two effects were not statistically different (Table 3).

Table 1. Mean squares derived from the combined analysis of variance for grain yield and other traits of 150 hybrids evaluated under drought stress at Ikenne in 2011 and Bagauda in 2012 and under low soil N at Ile-Ife and Mokwa during the 2011 and 2012 growing seasons in Nigeria.

Source[†]	df	YIELD[‡]	DA[‡]	DS[‡]	ASI[‡]	PHT[‡]	EHT[‡]	HC[‡]	PASP[‡]	EASP[‡]	EPP[‡]	STGR[‡]
		kg ha^{-1}	—— d ——			—— cm ——						
Drought												
Environment (E)	1	3,814,201.10**	255.88**	354.63**	1207.35**	91369.94**	4760.28**	128.97**	16.27**	9.06*	3.23**	29.85**
Set	5	1,334,122.30**	25.21**	38.60**	8.82ns	442.30*	186.73*	1.21**	0.43*	1.80ns[§]	0.09**	0.35ns
E × set	5	697,987.50ns	2.56ns	7.15ns	8.40ns	617.58**	278.24**	0.23ns	0.21ns	1.24ns	0.04ns	1.77**
Rep (E × set)	10	322,504.60ns	3.18ns	9.08ns	4.47ns	331.31*	172.53**	0.08ns	0.19ns	1.90ns	0.02ns	0.44ns
Block (E × Rep)	48	869,137.10**	8.98**	22.77**	7.10*	827.14**	364.74**	0.27**	0.53**	1.78ns	0.03**	0.76**
Hybrids	155	1,833,204.10**	18.30**	44.07**	10.07**	617.25**	242.31**	0.43**	0.66**	2.29**	0.13**	0.59**
GCA-male (set)	24	1,964,313.20**	29.17**	78.36**	18.36**	747.18**	344.07**	0.79**	0.86**	2.30ns	0.17**	0.91**
GCA-female (set)	24	2,459,006.60**	35.57**	78.86**	14.13**	741.74**	271.28**	0.48**	1.04**	3.00*	0.17**	0.56*
SCA (set)	96	1,459,915.00**	10.35**	25.27**	6.39*	528.11**	188.54**	0.26**	0.51**	2.10ns	0.10**	0.51**
Hybrid × E	155	1,010,516.20**	8.89**	20.00**	6.00*	435.61**	157.80**	0.35**	0.34**	1.68ns	0.05**	0.63**
E × GCA-male (set)	24	1,456,663.30**	8.35**	24.14**	7.92*	484.96**	198.84**	0.52**	0.41**	1.65ns	0.07**	0.85**
E × GCA-female (set)	24	1,082,257.50**	10.93**	19.86**	5.95ns	538.63**	124.61*	0.63**	0.47**	2.00ns	0.06**	0.60*
E × SCA (set)	96	987,358.40**	9.22**	20.50**	5.93ns	403.88**	152.64**	0.24**	0.32**	1.68ns	0.05**	0.52**
Error	240	433,012.80	2.88	7.26	4.76	168.69	75.98	0.13	0.17	1.72	0.02	0.35
Low N												
Environment (E)	3	25,959,025.60**	1090.98**	1233.67**	19.57**	37370.69**	13541.19**	77.38**	24.17**	8.30**	0.34**	19.22**
Set	5	318,142.40ns	26.26**	26.59**	0.41ns	733.95**	823.85**	1.09**	0.34**	0.14ns	0.01ns	0.54ns
E × set	15	868,304.50ns	7.03**	7.34**	0.62ns	199.70ns	219.88**	0.63**	0.34**	0.11ns	0.01ns	0.64*
Rep (E × set)	20	665,726.30ns	1.68ns	2.22ns	1.10ns	105.24ns	64.02ns	0.12ns	0.14ns	0.10ns	0.01ns	0.22ns
Block (E × Rep)	96	1,570,526.40**	4.58**	6.89**	0.95*	958.98**	687.26**	0.33**	0.32**	0.17**	0.01ns	0.85**
Hybrids	155	6,375,708.10**	22.00**	27.18**	1.45**	406.99**	292.60**	0.38**	0.86**	0.66**	0.04**	1.51**
GCA-male (set)	24	8,604,695.00**	45.18**	50.44**	1.31*	569.08**	459.57**	0.32**	0.85**	0.77**	0.05**	2.79**
GCA-female (set)	24	10,924,213.20**	46.09**	58.35**	1.77**	448.61**	387.51**	0.37**	1.46**	1.15**	0.06**	2.56**
SCA (set)	96	4,855,118.00**	9.05**	12.15**	1.42**	274.47**	163.41**	0.32**	0.70**	0.53**	0.03**	0.93**
Hybrid × E	465	1,396,772.60**	3.45**	4.64**	0.78ns	188.58**	132.71**	0.27**	0.22**	0.16**	0.01**	0.47**
E × GCA-male (set)	72	1,594,658.00**	3.46**	5.02**	0.89ns	144.08ns	149.69**	0.30**	0.20**	0.16**	0.01**	0.44ns
E × GCA-female (set)	72	1,708,931.10**	4.43**	5.62**	0.84ns	199.61*	165.72**	0.33**	0.29**	0.17**	0.02**	0.47*
E × SCA (set)	288	1,268,871.00**	3.01**	4.08**	0.76ns	205.45**	120.56**	0.24**	0.19**	0.15**	0.01ns	0.46**
Error	480	689,555.00	1.66	2.35	0.86	142.47	85.42	0.16	0.11	0.09	0.01	0.35

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

[†] GCA, general combining ability; SCA, specific combining ability.

[‡] YIELD, grain yield; DA, days to anthesis; DS, days to silking; ASI, anthesis–silking interval; PHT, plant height; EHT, ear height; HC, husk cover; EASP, ear aspect; PASP, plant aspect; EPP, ears per plant; STGR, stay-green characteristic.

[§] ns, not significant.

Presented in Table 4 are the GCA effects of the inbred lines under drought, low–N, *Striga*, and across environments. Under drought, the inbreds TZEQI 34 and TZEQI 39 showed significant positive GCAm effects for grain yield, while TZEQI 24, TZEQI 44, and TZEQI 56 had significant positive GCAf effects for grain yield. The inbreds TZEQI 4, TZEQI 6, TZEQI 12, TZEQI 24, TZEQI 25, TZEQI 34, TZEQI 35, TZEQI 49, TZEQI 55, and TZEQI 59 displayed significant positive GCAm effects for grain yield under low N, while TZEQI 6, TZEQI 34, TZEQI 45, TZEQI 49, and TZEQI 56 showed significant positive GCAf effects for grain yield. Under *Striga* infestation, significant positive GCAm effects for grain yield were detected for the inbreds TZEQI 12 and TZEQI 55, while TZEQI 44 and TZEQI 55 had

significant positive GCAf effects for grain yield. Only two inbreds (TZEQI 29 and TZEQI 49) showed significant negative GCAm effects for *Striga* damage at 10 WAP, while all the 30 early white QPM inbreds used in this study had significant negative GCAf effects for *Striga* damage at 10 WAP, except TZEQI 35, TZEQI 44, and TZEQI 55. In contrast, all inbreds exhibited significant negative GCAf effects for the number of emerged *Striga* plants at 10 WAP, except TZEQI 44 and TZEQI 55. It is striking to note that TZEQI 56 was the only inbred that displayed significant negative GCAm and GCAf effects for number of emerged *Striga* plants at 10 WAP. Across the multiple stress environments (*Striga*, drought, and low–N environments), five inbreds (TZEQI 6, TZEQI 34, TZEQI 44, TZEQI 49, and TZEQI 55) exhibited significant positive GCA effects

Table 2. Mean squares derived from the combined analysis of variance for grain yield and other traits of 150 hybrids evaluated under artificial *Striga* infestation at Abuja and Mokwa during the 2012 growing season and across eight stress (drought, low-N, and *Striga*-infested) environments in Nigeria, 2011–2012.

Striga infestation

Source[†]	df[‡]	YIELD[‡] (kg ha^{-1})	DA[‡] (d)	DS[‡] (d)	ASI[‡] (d)	PHT[‡] (cm)	EHT[‡] (cm)	HC[‡]	EASP[‡]	EPP[‡]	SDR1[‡]	SDR2[‡]	ESP1[‡]	ESP2[‡]
Environment (E)	1	890,889,027.70**	1018.68**	191.85**	330.89**	185119.51**	42540.04**	63.05**	3.80**	6.72**	910.97**	236.43**	534.51**	401.87**
Set	5	3,536,815.20**	39.12**	32.69**	1.67ns	268.70*	320.10**	0.38ns	2.20**	0.09**	3.29**	5.05**	1.69**	1.04**
E × set	5	449,322.20ns§	2.71ns	7.49ns	1.48ns	225.73ns	150.53ns	0.30ns	0.31ns	0.06*	1.10ns	1.10ns	0.19ns	0.15ns
Rep (E × set)	10	357,358.60ns	4.34ns	7.79ns	2.36ns	123.14ns	34.77ns	0.18ns	0.89**	0.05*	0.70ns	0.39ns	0.19ns	0.18ns
Block (E × Rep)	48	1,151,806.60**	4.71**	10.18**	3.89**	449.17**	206.09**	0.19ns	1.02**	0.04*	1.60**	1.40**	0.86**	0.51**
Hybrids	155	1,809,118.40**	15.90**	16.90**	3.04ns	320.47**	171.32**	0.29*	1.01**	0.06**	1.81**	1.94**	0.72**	0.45**
GCA-male (set)	24	2,568,871.80**	27.17**	24.74**	3.32ns	265.64**	173.53**	0.25ns	1.24**	0.09**	2.69**	3.25**	0.84**	0.52**
GCA-female (set)	24	2,355,120.20**	20.83**	21.85**	2.46ns	276.32**	162.65**	0.35*	0.98**	0.06**	1.89**	1.83**	0.99**	0.46**
SCA (set)	96	1,308,446.30**	10.61**	11.79**	3.14*	307.83**	152.47**	0.27ns	0.83**	0.03**	1.45**	1.40**	0.58**	0.40**
Hybrid × E	155	1,087,211.50**	3.16ns	7.43*	3.25*	164.77*	97.57**	0.33*	0.71**	0.04**	0.96ns	1.28**	0.53*	0.34**
E × GCA-male (set)	24	1,594,416.70**	3.13ns	9.16*	3.60ns	197.48*	103.66ns	0.47**	0.86**	0.07**	0.97ns	1.00ns	0.43ns	0.56**
E × GCA-female (set)	24	1,050,522.60**	2.84ns	6.21ns	1.89ns	181.29ns	156.93*	0.37*	0.57ns	0.06**	0.92ns	1.52**	0.56ns	0.36*
E × SCA (set)	96	958,359.40**	3.22ns	6.90ns	3.45**	151.50ns	74.80ns	0.27ns	0.69**	0.03*	0.93ns	1.25**	0.58*	0.29ns
Error	240	554,167.00	2.78	5.59	2.40	119.70	69.74	0.22	0.38	0.02	0.77	0.74	0.41	0.23

Across research environments

Source[†]	df[‡]	YIELD[‡] (kg ha^{-1})	DA[‡] (d)	DS[‡] (d)	ASI[‡] (d)	PHT[‡] (cm)	EHT[‡] (cm)	HC[‡]	EASP[‡]	EPP[‡]	df	PASP	STGR
Environment (E)	7	33,8426,135.00**	808.50**	1653.75**	750.13**	96677.77**	41010.09**	496.66**	410.32**	5.76**	5	32.29**	117.22**
Set	5	2,288,939.00**	76.50**	76.80**	4.50ns	740.24**	1154.23**	0.35ns	1.36*	0.06**	5	0.55**	0.48ns
E × set	35	950,338.00**	5.78**	8.25**	2.59ns	306.73**	180.70**	0.68**	0.67ns	0.04**	25	0.29**	0.82**
Rep (E × set)	40	502,829.00ns	2.72ns	5.32ns	2.26ns	166.23ns	83.83ns	0.13ns	0.75ns	0.02ns	30	0.16ns	0.29ns
Block (E × Rep)	192	1,290,499.00**	5.71**	11.68**	3.22**	798.57**	486.34**	0.28**	0.78**	0.02**	144	0.39**	0.82**
Hybrids	155	7,390,426.00**	47.42**	66.97**	4.60**	762.50**	466.13**	0.47**	1.86**	0.11**	155	1.29**	1.45**
GCA-male (set)	24	8947140.00**	90.71**	118.66**	6.31**	828.37**	619.86**	0.53**	1.64**	0.15**	24	1.35**	2.89**
GCA-female (set)	24	12,767,962.00**	90.44**	129.38**	6.35**	753.26**	512.96**	0.56**	3.08**	0.17**	24	2.27**	2.52**
SCA (set)	96	5,539,267.00**	22.35**	33.52**	3.45**	615.74**	307.18**	0.42**	1.59**	0.08**	96	1.00**	0.83**
Hybrid × E	1085	1,273,664.00**	4.45**	8.93**	3.08**	249.76**	127.66**	0.31**	0.71**	0.03**	775	0.24**	0.54**
E × GCA-male (set)	168	1,717,971.00**	4.66**	11.89**	4.41**	266.89**	158.41**	0.39**	0.81**	0.05**	120	0.28**	0.59**
E × GCA-female (set)	168	1,461,422.00**	5.59**	10.37**	3.20**	290.31**	155.31**	0.38**	0.73**	0.04**	120	0.31**	0.52**
E × SCA (set)	672	1,119,506.00**	4.16**	7.90**	2.74**	238.06**	112.34**	0.23**	0.67**	0.03**	480	0.22**	0.50**
Error	960	591,573.00	2.25	4.38	2.22	143.33	79.14	0.17	0.57	0.02	720	0.13	0.35

* Significant at the 0.05 probability level.

** Significant at the 0.01 probability level.

[†] GCA, general combining ability; SCA, specific combining ability.

[‡] YIELD, grain yield; DA, days to anthesis; DS, days to silking; ASI, anthesis–silking interval; PHT, plant height; EHT, ear height; HC, husk cover; EASP, ear aspect; PASP, plant aspect; EPP, ears per plant; SDR1, *Striga* damage rating at 8 wk after planting (WAP); SDR2, *Striga* damage rating at 10 WAP; ESP1, emerged *Striga* plants at 8 WAP; ESP2, emerged *Striga* plants at 10 WAP; STGR, stay-green characteristic.

§ ns, not significant.

Table 3. Proportion of the sum of squares for crosses attributable to general combining ability and specific combining ability (SCA) for grain yield and other agronomic traits of early-maturing quality protein maize inbred lines under drought, low-N, *Striga* and across research environments in Nigeria, 2011–2012.

Traits	Drought[†]			Low N			*Striga*			Across all environments		
	GCAm[†]	GCAf	SCA	GCAm	GCAf	SCA	GCAm	GCAf	SCA	GCAm	GCAf	SCA
Grain yield (kg ha⁻¹)	0.191	0.240	0.569	0.221	0.280	0.499	0.253	0.232	0.515	0.204	0.291	0.505
Days to anthesis	0.275	0.335	0.390	0.354	0.362	0.284	0.300	0.230	0.469	0.335	0.334	0.330
Days to silking	0.303	0.305	0.391	0.320	0.371	0.309	0.264	0.233	0.503	0.311	0.339	0.351
Anthesis–silking interval	0.316	0.243	0.440	0.149	0.202	0.649	0.181	0.134	0.685	0.238	0.240	0.522
Plant height (cm)	0.207	0.206	0.587	0.269	0.212	0.519	0.150	0.156	0.694	0.205	0.186	0.609
Ear height (cm)	0.251	0.198	0.551	0.306	0.258	0.436	0.183	0.172	0.645	0.262	0.217	0.520
Husk cover	0.342	0.209	0.449	0.165	0.190	0.645	0.152	0.209	0.639	0.190	0.202	0.608
Plant aspect	0.218	0.263	0.519	0.165	0.190	0.645	–	–	–	0.177	0.299	0.525
Ear aspect	0.168	0.219	0.613	0.190	0.284	0.525	0.224	0.177	0.600	0.148	0.278	0.574
Ears per plant	0.237	0.237	0.527	0.210	0.262	0.527	0.317	0.222	0.461	0.230	0.263	0.507
Stay-green characteristic	0.260	0.161	0.580	0.308	0.282	0.410	–	–	–	0.332	0.289	0.380
Striga damage rating at 8 WAP[‡]	–	–	–	–	–	–	0.259	0.182	0.559	–	–	–
Striga damage rating at 10 WAP	–	–	–	–	–	–	0.305	0.171	0.524	–	–	–
Emerged *Striga* plants at 8 WAP	–	–	–	–	–	–	0.216	0.200	0.584	–	–	–
Emerged *Striga* plants at 10 WAP	–	–	–	–	–	–	0.222	0.209	0.569	–	–	–

[†] GCAm, general combining ability, male; GCAf, general combining ability, female; SCA, specific combining ability.

[‡] WAP, weeks after planting.

(GCAm plus GCAf effects) for grain yield. In contrast, the GCA effect of the stay-green characteristic was negative and significant for the inbreds TZEQI 34, TZEQI 35, TZEQI 39, and TZEQI 55 across drought and low-N environments. Similarly, TZEQI 23 and TZEQI 45 displayed negative and significant GCAm effects for the stay-green characteristic, while the GCAf effects for this trait were negative and significant for the inbreds TZEQI 22, TZEQI 44, and TZEQI 56.

Heterotic Groupings Under Contrasting Environments

Summary of the different heterotic groups for the 30 early-maturing QPM inbreds based on dendograms (Supplemental Fig. S1–S4) constructed from HGCAMT under drought, low-N, *Striga* infestation, and across test environments as well as Roger's distance estimates of SNP-based markers using Ward's minimum variance cluster analysis are presented in Table 5. On the one hand, the HGCAMT method classified the inbreds into three groups each under drought and across test locations, while four groups were identified under low-N and *Striga*-infested conditions. On the other hand, the SNP-based method identified three groups for the set of inbreds used in the present study. The classification of inbreds into groups by the HGCAMT under drought, low-N, *Striga*, and across test environments was in close correspondence with the SNP-based approach in terms of the placement of the inbreds into similar groups. For example, the classification of the inbreds into heterotic Groups 1, 2, and 3 by the HGCAMT across test environments and the SNP-based methods followed similar trends with lines such as

TZEQI 4, TZEQI 5, TZEQI 12, TZEQI 13, TZEQI 22, TZEQI 33, and TZEQI 35 being placed in Group 1 by the two methods, while lines such as TZEQI 34, TZEQI 44, TZEQI 45, TZEQI 49, and TZEQI 56 were placed in Group 2. Similarly, the two methods placed the inbreds TZEQI 14, TZEQI 16, TZEQI 17, TZEQI 18, TZEQI 26, TZEQI 28, and TZEQI 30 in Group 3.

Comparison of General Combining Ability Effects of Multiple Traits and Single-Nucleotide-Polymorphism-based Genetic Distance Methods and Identification of Testers

The HGCAMT method identified 36, 37, and 30 as high-yielding hybrids and 16, 17, 11, and 21 as the low-yielding hybrids under drought, low-N, *Striga*, and across research environments, respectively. On the other hand, the SNP-based method identified 39, 43, 36, and 43 as high-yielding hybrids and 27, 27, 21, and 26 as the low-yielding hybrids under drought, low-N, *Striga*, and across research environments, respectively (Table 6). Thus the breeding efficiency of the SNP-based method was the highest under low N (49.5%), across research environments (48.5%), drought (47.5%), and *Striga*-infested environments (40%). The SNP-based method indicated a breeding efficiency that was greater than that of the HGCAMT method by 40% under drought, 27% under low N, 48% under *Striga*, and 43% across research environments (Table 6). The SNP-based grouping method, being the most efficient in this study, was used to identify inbreds TZEQI 6 and TZEQI 55 as the best testers across the research environments.

Table 4. Estimates of general combining ability (GCA) effects of 30 early white quality protein maize inbred lines for grain yield, *Striga* damage rating, emerged *Striga* plants, and stay-green characteristic under contrasting environments in Nigeria, 2011–2012.

Inbreds	Drought†		Low N		Striga		Across all environments		Striga damage at 10 WAP‡‡		Emerged *Striga* plants at 10 WAP		Stay-green characteristic‡	
	YGCAm	YGCAf	YGCAm	YGCAf	YGCAm	YGCAf	YGCAm	YGCAf	R2GCAm	R2GCAf	C2GCAm	C2GCAf	SGGCAm	SGGCAf
TZEQI 4	381.32 ns§	−322.76 ns	371.47*	−268.85 ns	156.76 ns	42.5 ns	320.25*	−204.49 ns	−0.11 ns	−314.87*	−1.89 ns	−383.83*	−0.13 ns	−0.08 ns
TZEQI 5	−16.55 ns	89.35 ns	−394.48*	−231.75*	−534.91*	−31.66 ns	−335.11*	−101.45 ns	0.61*	−397.94*	−2.83 ns	−462.43*	−0.01 ns	−0.10 ns
TZEQI 6	222.38 ns	177.06 ns	385.99*	734.19*	64.33 ns	161.2 ns	264.67*	451.66*	−0.16	−207.08*	6.61 ns	−261.38*	0.03 ns	0.08 ns
TZEQI 12	309.44 ns	36.52 ns	380.76*	−155.93 ns	550.45*	−721.5 ns	405.35*	−249.21*	−0.34 ns	−1082.50*	5.08 ns	−1148.23*	0.06 ns	0.21*
TZEQI 13	−327.58 ns	−247.67 ns	−1.01 ns	112.04 ns	−175.29 ns	−27.92 ns	−126.22 ns	−12.88 ns	0.23 ns	−384.33*	−5.24 ns	−456.99*	0.07 ns	0.09 ns
TZEQI 14	−347.32 ns	−210.73 ns	−583.67*	−330.76 ns	−610.08*	−503.31*	−531.18*	−343.89*	0.43*	−861.88*	−5.45 ns	−933.07*	0.22*	0.26*
TZEQI 15	175.6 ns	266.64 ns	−253.55 ns	147.69 ns	−153.57 ns	−37.03 ns	−121.27 ns	131.25 ns	−0.17 ns	−394.40*	−0.2 ns	−463.36*	0.16 ns	0.17 ns
TZEQI 16	−68.66 ns	−303.4 ns	−377.10*	−492.77*	−19.37 ns	117.65 ns	−210.56 ns	−292.82*	−0.11 ns	−248.63*	−8.58 ns	−313.12*	−0.04 ns	0.01 ns
TZEQI 17	−420.55 ns	−361.03 ns	−897.40*	−1162.92*	−394.63 ns	−845.87*	−652.50*	−883.18*	0.41*	−1214.15*	0.09 ns	−1268.45*	0.47*	0.47*
TZEQI 18	−456.47 ns	−553.46*	−479.32*	−422.04*	−485.68 ns	−142.03 ns	−475.20*	−384.89*	0.35 ns	−503.04*	0.9 ns	−568.77*	0.18 ns	0.19*
TZEQI 22	−437.07 ns	37.81 ns	−112.67 ns	99.90 ns	226.73 ns	−449.10*	−108.92 ns	−52.87 ns	−0.14 ns	−805.50*	−4.88 ns	−878.17*	0.03 ns	−0.18*
TZEQI 23	−114.07 ns	−73.78 ns	101.22 ns	319.65 ns	−158.56 ns	−326.89 ns	−17.55 ns	59.66 ns	0.38 ns	−685.46*	1.2 ns	−756.65*	−0.23*	−0.08 ns
TZEQI 24	131.58 ns	585.75*	504.05*	153.91 ns	−75.45 ns	−248.56 ns	266.06*	161.25 ns	0.25 ns	−605.94*	6.47 ns	−674.90*	−0.10 ns	−0.15 ns
TZEQI 25	98.34 ns	−150.56 ns	407.70*	−94.26 ns	277.07 ns	−263.94 ns	297.70*	−150.76 ns	−0.1 ns	−630.23*	3.57 ns	−694.72*	−0.11 ns	0.10 ns
TZEQI 26	−557.71*	−212.52 ns	−951.17*	−649.84*	−197.12 ns	346.99 ns	−664.29*	−291.31*	−0.12 ns	−21.29*	−5.03 ns	−75.59*	0.10 ns	0.21*
TZEQI 27	−44.47 ns	99.87 ns	−651.10*	−204.64 ns	−297.17 ns	225.92 ns	−410.96*	−20.87 ns	0.43*	−135.08*	8.13 ns	−200.81*	0.16 ns	0.21*
TZEQI 28	−572.22*	−432.97*	−847.48*	−234.84 ns	−386.37 ns	−26.27 ns	−663.38*	−232.23 ns	0.19 ns	−382.67*	4.98 ns	−455.34*	0.34*	0.19*
TZEQI 29	0.7 ns	−325.6 ns	81.29 ns	−58.24 ns	340.01 ns	124.55 ns	125.82 ns	−79.38 ns	−0.44*	−234.02*	4.04 ns	−305.21*	−0.07 ns	−0.05 ns
TZEQI 30	−591.03*	−461.59*	−825.91*	−623.18*	−266.14 ns	−75.41 ns	−627.24*	−445.84*	0.02 ns	−432.78*	−5.56 ns	−501.74*	0.34*	0.05 ns
TZEQI 33	−122.65 ns	32.26 ns	−73.81 ns	314.27 ns	−166.91 ns	−183.79 ns	−109.3 ns	119.25 ns	0 ns	−550.08*	−2.49 ns	−614.57*	0.13 ns	0.08 ns
TZEQI 34	492.71*	237.48 ns	792.03*	815.43*	−129.77 ns	−95.25 ns	486.75*	443.27*	0.26 ns	−463.53*	5.28 ns	−517.83*	−0.40*	−0.34*
TZEQI 35	372.88 ns	−5.61 ns	664.39*	−95.22 ns	314.64 ns	389.25 ns	504.07*	48.3 ns	−0.28 ns	28.25*	−1.7 ns	−37.48*	−0.19*	−0.21*
TZEQI 39	864.83*	385.97 ns	286.16 ns	1.58 ns	17.73 ns	203.98 ns	363.72*	148.28 ns	0.01 ns	−152.42*	−0.22 ns	−225.08*	−0.31*	−0.25*
TZEQI 44	439.78 ns	506.83*	349.75 ns	275.30 ns	471.68 ns	748.50*	402.74*	451.48*	−0.18 ns	389.93*	−1.69 ns	318.74*	0.04 ns	−0.26*
TZEQI 45	−97.46 ns	−68.04 ns	203.94 ns	590.43*	338.41 ns	318.49 ns	162.21 ns	357.83*	0.01 ns	−38.88*	1.18 ns	−107.84*	−0.27*	0.01 ns
TZEQI 49	109.52 ns	332.35 ns	437.69*	504.52*	444.12 ns	361.74 ns	357.26*	425.78*	−0.41*	−4.55 ns	10.33 ns	−69.04*	0.03 ns	−0.09 ns
TZEQI 55	263.18 ns	159.01 ns	670.55*	263.15 ns	657.19*	432.93*	565.37*	279.56*	−0.39 ns	64.65*	−6.95 ns	10.34*	−0.20*	−0.42*
TZEQI 56	−181.37 ns	422.69*	85.27 ns	877.83*	−82.25 ns	248.36 ns	−23.27 ns	606.68*	−0.17 ns	−112.65*	−12.41*	−178.38*	−0.22 ns	−0.41*
TZEQI 59	472.03 ns	256.86 ns	674.99*	21.32 ns	317.19 ns	299.3 ns	534.80*	149.7 ns	−0.3 ns	−57.10*	5.36 ns	−129.77*	−0.13 ns	0.14 ns
TZEQI 60	20.91 ns	103.29 ns	51.41 ns	−205.95 ns	−43.04 ns	−42.85 ns	20.17 ns	−87.87 ns	−0.19 ns	−401.42*	1.89 ns	−472.61*	0.04 ns	0.13 ns
LSD	477.11	411.25	352.99	365.42	499.17	405.18	259.07	238.95	0.4	0.49	10.73	9.3	0.18	0.17

* Significant at the 0.05 probability level.

† YGCAm and YGCAf, general combining ability (male and female) for grain yield; R2GCAm and R2GCAf, general combining ability (male and female) for *Striga* damage rating; C2GCAm and C2GCAf, general combining ability (male and female) for emerged *Striga* plants; SGGCAm and SGGCAf, general combining ability (male and female) stay-green characteristic.

‡ WAP, weeks after planting.

§ ns, not significant.

Table 5. Summary of the heterotic groups of 30 early-maturing quality protein maize inbred lines identified by the general combining ability effects of multiple traits (HGCAMT) method under contrasting environments and the single nucleotide polymorphism (SNP)-based method.

Method	Group 1	Group 2	Group 3	Group 4
HGCAMT-drought	TZEQI 4,TZEQI 5, TZEQI 12, TZEQI 13, TZEQI 14, TZEQI 16, TZEQI 22, TZEQI 23, TZEQI 25, TZEQI 27, TZEQI 29, TZEQI 33, TZEQI 35, TZEQI 45, TZEQI 55, and TZEQI 60	TZEQI 6, TZEQI 15, TZEQI 24, TZEQI 34, TZEQI 39, TZEQI 44, TZEQI 49, TZEQI 56, and TZEQI 59,	TZEQI 17, TZEQI 18, TZEQI 26, TZEQI 28, and TZEQI 30	
HGCAMT-Low-N	TZEQI 6, TZEQI 12, TZEQI 22, TZEQI 23, TZEQI 33, TZEQI 34, TZEQI 44, TZEQI 45, TZEQI 49, and TZEQI 56	TZEQI 4, TZEQI 5, TZEQI 24, TZEQI 35, TZEQI 39, TZEQI 55, and TZEQI 59	TZEQI 13, TZEQI 14, TZEQI 16, TZEQI 17, TZEQI 18, TZEQI 26, TZEQI 27, TZEQI 28, and TZEQI 30	TZEQI 15, TZEQI 25, TZEQI 29, and TZEQI 60
HGCAMT-*Striga*	TZEQI 13, TZEQI 15, TZEQI 16, TZEQI 26, TZEQI 29, TZEQI 30, TZEQI 33, TZEQI 56, and TZEQI 60	TZEQI 4, TZEQI 6, TZEQI 27, TZEQI 35, TZEQI 39, TZEQI 44, TZEQI 45, TZEQI 49, TZEQI 55, and TZEQI 59	TZEQI 5, TZEQI 18, TZEQI 23, TZEQI 24, TZEQI 25, TZEQI 28, and TZEQI 34	TZEQI 12, TZEQI 14, TZEQI 17, and TZEQI 22
HGCAMT-across	TZEQI 4, TZEQI 5, TZEQI 12, TZEQI 13, TZEQI 15, TZEQI 22, TZEQI 23, TZEQI 24, TZEQI 25, TZEQI 27, TZEQI 29, TZEQI 33, TZEQI 35, TZEQI 39, TZEQI 55, TZEQI 59, and TZEQI 60	TZEQI 6, TZEQI 34, TZEQI 44, TZEQI 45, TZEQI 49, and TZEQI 56	TZEQI 14, TZEQI 16, TZEQI 17, TZEQI 18, TZEQI 26, TZEQI 28, and TZEQI 30	
SNP-based	TZEQI 4, TZEQI 5, TZEQI 6, TZEQI 12, TZEQI 13, TZEQI 22, TZEQI 33, and TZEQI 35	TZEQI 15, TZEQI 24, TZEQI 34, TZEQI 39, TZEQI 44, TZEQI 45, TZEQI 49, TZEQI 55, TZEQI 56, TZEQI 59, and TZEQI 60	TZEQI 14, TZEQI 16, TZEQI 17, TZEQI 18, TZEQI 23, TZEQI 25, TZEQI 26, TZEQI 27, TZEQI 28, TZEQI 29, and TZEQI 30	

Performance and Stability of White Quality Protein Maize Single-cross Hybrids Across Environments

Grain yield ranged from 77 kg ha^{-1} for TZEQI 14 × TZEQI 30 to 4025 kg ha^{-1} for TZEQI 27 × TZEQI 39 across drought environments (data not shown). The QPM hybrid TZEQI 27 × TZEQI 39 out yielded the best normal-endosperm drought-tolerant hybrid check, TZEI 5 × TZEI 98, and the OPV check, EV DT-Y 2000 STR, by 29 and 61%, respectively, across drought environments. Under low-N environments, yield ranged from 1015 kg ha^{-1} for TZEQI 28 × TZEQI 14 to 5732 kg ha^{-1} for TZEQI 25 × TZEQI 34 (data not shown). The most outstanding low-N-tolerant QPM hybrid, TZEQI 25 × TZEQI 34, out yielded the low-N-tolerant normal hybrid check, TZEI 5 × TZEI 98, by 27% and the low-N-tolerant normal-endosperm OPV check, EV DT-Y 2000 STR, by 14%. Across *Striga*-infested environments, yield ranged from 910 kg ha^{-1} for TZEQI 14 × TZEQI 30 to 4294 kg ha^{-1} for TZEQI 27 × TZEQI 59 (data not shown). The best *Striga*-resistant QPM hybrid, TZEQI 27 × TZEQI 59, out-yielded the best *Striga*-resistant normal-endosperm hybrid check, TZEI 2 × TZEI 87, by 30% and the most *Striga*-resistant normal-endosperm OPV check, EV DT-Y 2000 STR, by 43% (data not shown). Across test environments, grain yields ranged from 962 kg ha^{-1} for TZEQI 28 × TZEQI 14 to 4096 kg ha^{-1} for TZEQI 25 × TZEQI 34. The QPM hybrid TZEQI 25 × TZEQI 34 out yielded the best normal-endosperm hybrid check, TZEI 5 × TZEI 98, by 10% and the top-yielding normal-endosperm OPV check, EV DT-Y 2000 STR, by 5%. It is striking that the QPM hybrid TZEQI 25 × TZEQI 34

was the most outstanding hybrid under both low-N and across test environments (data not shown).

The significant G, E, and $G \times E$ mean squares for grain yield under drought, low-N, *Striga*, and across environments prompted the use of the AMMI biplot to explain the main effects and provide insight into the $G \times E$. The AMMI biplot with the G and E main effects for grain yield and the IPCA1 scores is presented in Fig. 1. The vertical line represents the grand mean for grain yield while the horizontal line (y-ordinate) is the IPCA1 value of zero. Genotypes close to the horizontal line have small interactions and are considered to be more stable than those farther from it. The results of the AMMI biplot analysis showed that E accounted for 40% of the total variation in the sum of squares for grain yield, while the G and IPCA1 sources of variation accounted for 40 and 6% of the total variation, respectively. A total of 86% of the treatment sum of squares were captured by the AMMI biplot, thus making it effective in explaining both the main effects and providing insight into the $G \times E$.

The AMMI biplot showed large variability among the eight environments and wide yield range among the 30 genotypes. Hybrid 21 (TZEQI 45 × TZEQI 33) was characterized by IPCA1 score of zero, indicating that it had no interaction with the environments and was therefore the most stable hybrid across environments. The hybrids 20 (TZEQI 6 × TZEQI 35), 15 (TZEQI 35 × TZEQI 59), 9 (TZEQI 35 × TZEQI 39), and 4 (TZEQI 44 × TZEQI 4) were also relatively stable across environments as a result of their small interaction with the environments as indicated by their near zero IPCA1 scores. They also displayed grain yield greater than the mean grain yield and therefore were considered as stable and

Drought			
Yield group	Hybrid type	HGCAMT	SNP-based
1	Intergroup	36	39
1	Intragroup	14	11
2	Intergroup	28	41
2	Intragroup	22	9
3	Intergroup	34	23
3	Intragroup	16	27
BE		34	48

Low N			
Yield group	Cross type	HGCAMT	SNP-based
1	Intergroup	37	43
1	Intragroup	13	7
2	Intergroup	42	37
2	Intragroup	8	13
3	Intergroup	33	23
3	Intragroup	17	27
BE		39	50

Striga infested			
Yield group	Cross type	HGCAMT	SNP-based
1	Intergroup	30	36
1	Intragroup	20	14
2	Intergroup	39	37
2	Intragroup	11	13
3	Intergroup	39	30
3	Intragroup	11	21
BE		27	40

Across environments			
Yield group	Cross type	HGCAMT	SNP-based
1	Intergroup	30	43
1	Intragroup	20	7
2	Intergroup	29	36
2	Intragroup	21	14
3	Intergroup	29	24
3	Intragroup	21	26
BE		34	48.5

high-yielding hybrids across environments. Hybrids 16 (TZEQI 27 × TZEQI 59) and 7 (TZEQI 55 × TZEQI 12) had mean grain yield greater than the grand mean but a strong positive interaction with IPCA1, implying that they were probably adapted to favorable environments. In contrast, hybrid 3 (TZEQI 56 × TZEQI 59) had grain yield above the grand mean but negative interaction with IPCA1 score, suggesting that the hybrid was probably adapted to low-yield environments. The worst five hybrids, 26 (TZEQI 26 × TZEQI 18), 27 (TZEQI 23 × TZEQI 30), 28 (TZEQI 17 × TZEQI 18), 29 (TZEQI 25

× TZEQI 17), and 30 (TZEQI 17 × TZEQI 27), selected based on their negative base indices, were also identified as the lowest yielding by the AMMI analysis.

DISCUSSION

The significant variation observed among the single-cross hybrids for grain yield under drought, low–N, and *Striga*-infested environments indicated that adequate genetic variability existed among the early-maturing maize hybrids to allow good progress from selection under the multiple stress environments. The implication of the presence of large genetic variation among the inbreds is that there was adequate genetic variability among the hybrids to permit good progress from selection for improvements in most measured traits. Bhatnagar et al. (2004) reported significant variation in performance among and between seven white and nine yellow QPM inbred lines in grain yield, root lodging, and stalk lodging in five southern US environments. This result is also in agreement with the findings of Badu-Apraku et al. (2011a) and Badu-Apraku and Oyekunle (2012) for normal-endosperm, early-maturing maize. The presence of significant environmental variation for all measured traits under drought, low–N, and *Striga*-infested environments was a demonstration of the uniqueness and variability of the environments and emphasized the need for multilocation testing for several years for each of the contrasting environments. This finding is consistent with the results obtained with normal–endosperm, early-maturing maize by Badu-Apraku et al. (2007) and Ifie et al. (2015). The significant GCA and SCA for grain yield and most traits across environments suggested that both additive and nonadditive gene actions were important in the inheritance of grain yield and other traits across the multiple stress environments. This result implied that selection or systematic hybridization among the best combining QPM inbred lines could be adopted to improve the lines for the measured traits. This result is consistent with the findings of Pixley and Bjarnason (1993) for grain yield of QPM inbred lines under optimal growing environments. Similar results were also reported by Wegary et al. (2013) for 15 QPM inbred lines evaluated under drought and low-N stresses and optimal conditions in 17 environments in eastern and southern Africa. Furthermore, similar results were reported for 21 diallel crosses derived from seven extra-early yellow normal–endosperm maize inbreds evaluated under contrasting environments (Badu-Apraku and Oyekunle, 2012). In the present study there was preponderance of SCA sums of squares over those of GCA for grain yield, plant and ear heights, plant and ear aspects, EPP, and the stay-green characteristic under drought. Similarly, the SCA sum of squares was higher than those of GCA for ASI, plant height, husk cover, plant aspect, ear aspect, and EPP under low N. Furthermore, the SCA sum of squares was greater than those of GCA for
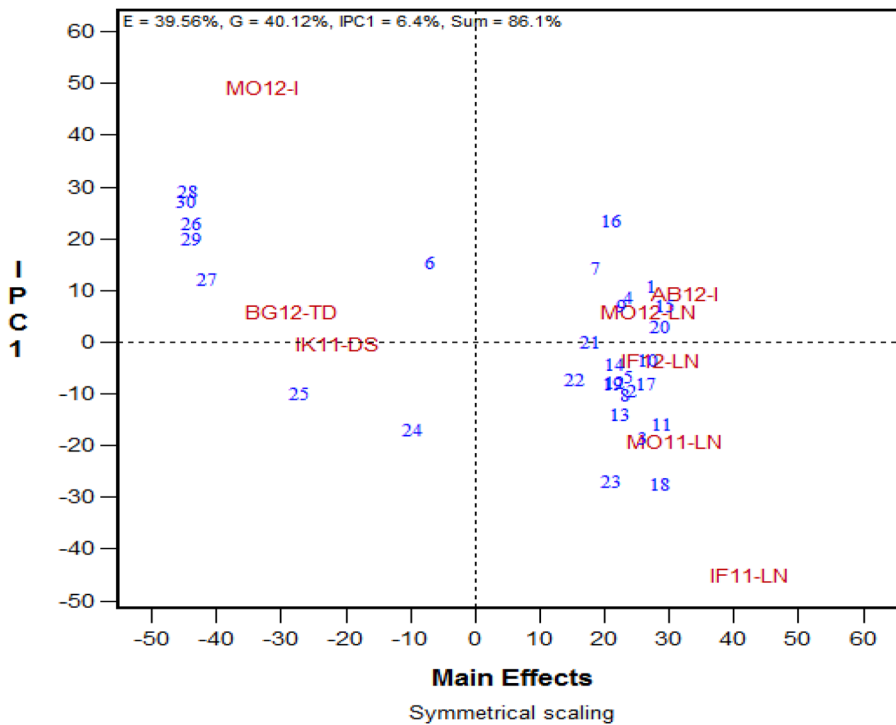
Code	Hybrid
1	TZEQI 16 X TZEQI 55
2	TZEQI 26 X TZEQI 56
3	TZEQI 56 X TZEQI 59
4	TZEQI 44 X TZEQI 4
5	TZEQI 56 X TZEQI 39
6	TZEQI 4 X TZEQI 16
7	TZEQI 55 X TZEQI 12
8	TZEQI 27 X TZEQI 39
9	TZEQI 35 X TZEQI 39
10	TZEQI 28 X TZEQI 60
11	Check 1 - TZEI 5 X TZEI 98
12	Check 3 - TZEI 2 X TZEI 87
13	TZEQI 34 X TZEQI 35
14	TZEQI 60 X TZEQI 30
15	TZEQI 35 X TZEQI 59
16	TZEQI 27 X TZEQI 59
17	TZEQI 55 X TZEQI 35
18	Check 6 - EV DT -Y 2000 STR
19	TZEQI 13 X TZEQI 44
20	TZEQI 6 X TZEQI 35
21	TZEQI 45 X TZEQI 33
22	TZEQI 56 X TZEQI 22
23	Check 4 - EV DT -W 2008 STR
24	Check 2 - TZEI 1 X TZEI 5
25	Check 5 - 2008 DTMA -W STR
26	TZEQI 26 X TZEQI 18
27	TZEQI 23 X TZEQI 30
28	TZEQI 17 X TZEQI 18
29	TZEQI 25 X TZEQI 17
30	TZEQI 17 X TZEQI 27

Figure 1. Additive main effects and multiplicative interactions biplot of grain yield and the first interaction principal component axis (IPCA 1) of best 19 and worst five white quality protein maize hybrids plus three open-pollinated varieties and three normal-endosperm hybrid checks evaluated under managed drought at Ikenne during the 2011–2012 dry season (IK11-DS), terminal drought stress at Bagauda in 2012 (BG12-TD), low N at Makwa in 2011 (MO11-LN) and 2012 (MO12-LN), low N at Ile-Ife in 2011 (IF11-LN) and 2012 (IF12-LN), and *Striga* infestation at Abuja in 2012 (AB12-I) and Mokwa in 2012 (MO12-I) in Nigeria.

all measured traits except for the days to anthesis and EPP under *Striga* infestation. Also, across research environments, grain yield, ASI, plant and ear heights, husk cover, plant and ear aspects, and EPP had greater SCA sums of squares than GCA sums of squares. In contrast, there was greater contribution of GCA sum of squares than SCA to the stay-green characteristic under low N and across drought and low-N environments. These results implied that nonadditive gene action largely modulated the inheritance of most measured traits in the set of QPM inbreds under the multiple stress environments. This result is consistent with the findings of Bhatnagar et al. (2004) and Machida et al. (2010), who reported SCA effects of QPM inbreds to be more important than GCA effects for grain yield, while GCA effects for plant height and days to anthesis and silking were more important than SCA under optimal management. This result also corroborates the findings of Betrán et al. (2003), Meseka et al. (2006), and Makumbi et al. (2011), who reported nonadditive gene action to be more important in the inheritance of grain yield of normal-endosperm maize under low N. Similarly, in a study involving 36 diallel crosses derived from nine normal-endosperm early yellow maize inbreds evaluated under drought and *Striga* environments, no inbreds with significantly higher GCA than others could be identified, and there were no inbreds that could be considered as

ideal testers in this study because of the minor importance of GCA and the preponderance of SCA over GCA (Badu-Apraku et al., 2011b). Furthermore, Guei and Wassom (1992) reported that nonadditive genetic effects control grain yield and EPP, while additive genetic effects condition flowering traits in two normal-endosperm tropical maize populations (Pool 26 Sequia and La Posta Sequia) under drought. However, this result is in disagreement with the findings of Musila et al. (2010), who reported the preponderance of additive gene action for grain yield, days to anthesis, ASI, and EPP in early-maturing QPM inbred lines under low-N, drought, and optimal environments. This result also appears to be in disagreement with the findings of Wegary et al. (2013), who showed GCA effects of grain yield of 15 QPM inbreds to be more important under drought stress, while SCA effects of grain yield were more important under low-N and optimal conditions. The authors showed preponderance of GCA effects for most agronomic traits evaluated in the test environments. Similarly, Badu-Apraku et al. (2011a) showed that the GCA sums of squares for grain yield and other traits of nine normal-endosperm, early-maturing inbreds were larger than those of SCA under drought, well-watered, *Striga*-infested, and *Striga*-free conditions, indicating that additive gene action was more important than the nonadditive component in the inheritance of drought tolerance

and *Striga* resistance. The preponderance of the SCA sum of squares over GCA for grain yield under *Striga* infestation in the present study indicated the importance of nonadditive genetic effects over additive genetic effects. The larger proportion of SCA sum of squares over GCA for *Striga* damage and number of emerged *Striga* plants at 8 and 10 WAP indicated that nonadditive gene action played a major role in the inheritance of *Striga* resistance. This is contrary to the results of Gethi and Smith (2004), Yallou et al. (2009), Badu-Apraku and Oyekunle (2012), and Ifie et al. (2015), who reported larger proportion of GCA sum of squares over SCA for *Striga* damage and number of emerged *Striga* plants at 8 and 10 WAP for early-maturing, normal–endosperm maize inbreds. Furthermore, Kim (1994), Akanvou et al. (1997), and Badu-Apraku (2007) reported that additive gene action was more important in normal–endosperm maize inbreds for *Striga* damage, while nonadditive gene action was more important for *Striga* emergence. The differences in the findings of earlier workers and the results of the present study may be attributed to the differences in the genetic materials (QPM vs. normal–endosperm maize) used in the different studies.

The significant mean squares observed for most measured traits for the hybrid × E, GCAm (set) × E, GCAf (set) × E, and SCA (set) × E interactions under drought, low-N, and across environments and the significant SCA (set) × E interaction mean squares detected for grain yield, EPP, ASI, ear aspect, *Striga* damage at 10 WAP, and the number of emerged *Striga* plants at 8 WAP under *Striga*-infested environments indicated that the ranking of hybrids was different in the contrasting research environments. This result implied that hybrid performance would be different in varying research environments. This finding is in agreement with that of Derera et al. (2008), who reported significant G × E effects for grain yield and other secondary traits of normal–endosperm maize under drought stress. However, this is contrary to the findings of Badu-Apraku and Oyekunle (2012), who reported that under drought stress, environment × male within set, environment × female within set, and environment × male × female within set were not significant for grain yield and associated traits and attributed this to the uniform drought stress management practices. The significant GCAm × E and GCAf × E effects observed for some traits under drought, *Striga*, and low-N environments indicated that the combining ability of the parental inbred lines was not consistent in the different environments. This result is in agreement with the findings of Makumbi et al. (2011) and Badu-Apraku et al. (2013). In this study, more traits showed significant SCA × E than GCA × E interactions across stress environments suggesting that SCA was less influenced by environment than GCA.

The GCA and SCA effects of inbred lines ultimately determine the potential value of inbred lines in hybrid

combinations. The nonsignificant variance ratio between the GCAm and GCAf for grain yield and all other measured traits under drought, low-N, *Striga* infestation, and across environments indicated that both maternal and paternal effects played similar roles in the inheritance of the traits in the set of QPM inbreds. This result is consistent with the findings of Ifie et al. (2015) who reported similarity in the magnitude of the GCAf and GCAm sum of squares for grain yield and most traits of normal–endosperm maize across research environments. In contrast, Derera et al. (2008) reported that maternal effects modified grain yield of normal–endosperm maize under drought as well as ASI, prolificacy, and ear aspect under drought and well-watered environments. Similarly, Oyekunle and Badu-Apraku (2014) demonstrated the importance of maternal effects in the inheritance of grain yield under well-watered conditions. Also, Jumbo and Carena (2012) found maternal effects for ear height in normal–endosperm, early-maturing maize hybrids under optimal growing conditions while Adebayo et al. (2014) reported paternal effects for ear aspect in late- and intermediate-maturing normal–endosperm single-cross hybrids under drought. The differences in the results of the present study and those of other workers may be attributed to the differences in the genetic materials used in this study. The significant positive GCAm effects displayed for grain yield by the inbreds TZEQI 34 and TZEQI 39 and GCAf effects revealed by TZEQI 24, TZEQI 44, and TZEQI 56 under drought indicated that the inbreds would contribute favorable alleles for grain yield under drought when used as males and females, respectively. The GCA (GCAm plus GCAf) effects of the stay-green characteristic were negative and significant for the inbreds TZEQI 34, TZEQI 35, TZEQI 39, and TZEQI 55 across drought and low-N environments. Furthermore, negative and significant GCAm effects were displayed by the inbreds TZEQI 23 and TZEQI 45 across drought and low-N environments, while the inbreds TZEQI 22, TZEQI 44, and TZEQI 56 exhibited negative and significant GCAf effects. The implication is that inbreds with negative and significant GCA effects for the stay-green characteristic will contribute alleles that will delay leaf senescence in the progenies. Similar results were reported in early-maturing maize inbreds by Ifie et al. (2015) under low N. On the other hand, the inbreds with negative and positive GCAm or GCAf effects will delay leaf senescence in their progenies across drought and low-N environments when used as male or female, respectively. Under *Striga* infestation, the inbreds TZEQI 12 and TZEQI 55 had positive and significant GCAm effects for grain yield, while inbreds TZEQI 44 and TZEQI 55 had positive and significant GCAf effects for grain yield, indicating that they will contribute favorable alleles for grain yield under *Striga* infestation. Two inbreds (TZEQI 49 and TZEQI 29) showed significant and negative GCAm

effects for *Striga* damage at 10 WAP, while 27 of the 30 early white QPM inbreds used in the study showed negative and significant GCAf effects for *Striga* damage at 10, indicating that the inbreds will contribute to reduced *Striga* damage. On the other hand, 28 inbreds exhibited significant and negative GCAm effects for the number of emerged *Striga* plants at 10 WAP when used as the female parents. It is striking to note that TZEQI 56 was the only inbred that displayed negative and significant GCAm and GCAf effects for number of emerged *Striga* plants at 10 WAP. This inbred is expected to contribute *Striga* resistance or tolerance to the progeny. Resistance genes from this inbred and the others identified in this study should be introgressed into breeding populations for improvement of the levels of *Striga* resistance and tolerance. The expression of positive and significant GCA effects for grain yield by the five inbreds (TZEQI 6, TZEQI 34, TZEQI 44, TZEQI 49, and TZEQI 55) across the stress environments suggested that they will contribute high grain yield in their crosses across multiple stress environments.

Classification of inbreds into appropriate heterotic groups is essential to maximize their potential usefulness for the development of productive hybrids and synthetics and also to create new heterotic groups. Therefore, the HGCAMT and SNP-based marker methods were used for the classification of the inbreds. Results showed that the HGCAMT method classified the inbreds into three groups each under drought, low N, and across test locations, while four groups were identified under *Striga*-infested conditions. In contrast, the SNP-based marker method identified three groups for the set of inbreds in the present study. The close correspondence in the classification of the inbreds into heterotic groups by the HGCAMT and the SNP-based approach in terms of the placement of the inbreds into similar groups implied that both methods were efficient. However, the SNP-based method had a breeding efficiency that exceeded that of the HGCAMT method by 40% under drought, 26% under low N, 48% under *Striga*, and 43% across research environments, indicating that it was more efficient than the HGCAMT. This implies that the SNP-based marker method could be used for grouping the numerous IITA QPM inbreds that are yet to be field tested. This result suggests that SNP-based GD method may be used in assessing diversity among tropical early maize inbreds and subsequently assigning them into distinct heterotic groups. This result is consistent with the findings of other earlier workers (Lanza et al., 1997; Balestre et al., 2008; Badu-Apraku et al., 2013, 2015a; Akinwale et al., 2014) who reported successful heterotic grouping of maize inbreds using molecular markers. However, the result is in disagreement with the findings of several workers (Semagn et al., 2012; Menkir et al., 2010; Benchimol et al., 2008; Shieh and Thseng, 2006) who reported that grouping of inbreds with molecular markers

is not effective. The inbreds TZEQI 6 and TZEQI 55 were identified as the best testers across research environments. The inbred testers offer a unique opportunity for grouping the numerous IITA maize inbreds that are yet to be field tested using SNP-marker based GD.

It must be pointed out that, traditionally, in studies involving the NCD II, no attempts are made to group genotypes because all the possible crosses are not involved in such studies. Under such circumstances, it is not possible to obtain information on all possible SCA effects of the inbreds for heterotic grouping. Another major limitation of the NCD II, as well as the diallel and the line × tester mating designs, is that when the SCA effects of grain yield is declared nonsignificant by the ANOVA as a result of the overdominating effects of the GCA, it is not possible to classify the genotypes into heterotic groups. A major advantage of the HGCAMT and SNP-based methods is that under such circumstances, it is possible to group the genotypes using the GCA effects of multiple traits and the genetic distances. It is interesting to note that the SNP-based and HGCAMT methods made it possible for the 30 inbred lines used in the present NCD II study to be classified into heterotic groups. This is a major advantage of the SNP-based and the HGCAMT methods.

Combining the results of the present study with those obtained by Badu-Apraku et al. (2015a) reveals some interesting trends in the genetics of inheritance of grain yield and other traits under drought, low N, and across environments as exemplified by the white-grain QPM vs. yellow-grain QPM inbred lines. The GCA and SCA mean squares were significant for grain yield and most other traits under drought, low N, and across research environments in both the white and yellow QPM inbreds, indicating that additive and nonadditive gene actions were both important in the inheritance of grain yield and most other traits of the inbreds. The implications of these results is that a breeding scheme that capitalizes largely on both additive and dominance variance, such as inbreeding and hybridization, recurrent selection involving testcrosses should be adopted in the breeding program. Since the gene action in the yellow QPM inbreds is predominantly additive, the inbreds in each heterotic group should be recombined to form a population, and the frequency of favorable alleles could be increased using recurrent selection methods. In contrast, there was preponderance of SCA sum of squares over GCA for most measured traits across contrasting environments for the white QPM inbreds, indicating that nonadditive gene action largely modulated the inheritance of the traits in the set of QPM white inbreds. In contrast, GCA was more important than SCA under each contrasting environment and across environments in the yellow QPM inbreds, suggesting that the additive gene action was more important than the nonadditive in this set

of inbreds. Therefore hybrid development should be the focus of the program for the white QPM inbreds.

The outstanding yield performance of the QPM hybrids over the drought-tolerant, normal-endosperm hybrid and OPV checks under each and across environments in this study suggests that significant progress has been made in developing multiple stress-tolerant QPM hybrids for increased maize production and food security as well as reduced malnutrition in WCA.

A prime objective of the present study was to identify the most stable and high-yielding hybrids for commercialization. The AMMI biplot identified hybrids 4 (TZEQI 44 × TZEQI 4), 9 (TZEQI 35 × TZEQI 39), 15 (TZEQI 35 × TZEQI 59), 20 (TZEQI 6 × TZEQI 35), and 21 (TZEQI 45 × TZEQI 33) as the highest yielding and most stable across environments. The high grain yield and significant positive interactions of TZEQI 27 × TZEQI 59 and TZEQI 55 × TZEQI 12 with IPCA1 implied that they were adapted to favorable environments. These hybrids should be tested in high-yield environments to ensure the consistency in yield performance for consideration for commercialization. In contrast, hybrid 3 (TZEQI 56 × TZEQI 59) had grain yield above the grand mean but negative interaction with IPCA1 score, suggesting that the hybrid was adapted to low-yield environments. It is striking to note that the worst five hybrids selected, based on their negative base indices, were also identified as the lowest yielding by the AMMI analysis, confirming the effectiveness of the base index used in the IITA breeding program.

In conclusion, nonadditive gene action modulated the inheritance of grain yield and most other traits in the set of the white QPM inbreds across multiple stress environments, suggesting that hybrid development should be the focus of the program for the white QPM inbreds. The inbred testers TZEQI 6 and TZEQI 55 identified in this study should be used for grouping of other QPM inbreds in tropical maize hybrid breeding programs. The hybrids TZEQI 6 × TZEQI 35, TZEQI 6 × TZEQI 35, TZEQI 35 × TZEQI 59, TZEQI 35 × TZEQI 39, and TZEQI 44 × TZEQI 4 were outstanding in yield and stability and should be commercialized to contribute to sustainable maize production and improved nutrition and food security in the subregion.

Acknowledgments

References

Adebayo, M.A., A. Menkir, E. Blay, V. Gracen, and E.Y. Danquaha. 2014. Performance-based grouping of adapted and exotic drought tolerant maize (*Zea mays* L) inbred lines under stressed and non-stressed conditions. Maydica 59:115–123.

Akanvou, L., E.V. Doku, and J. Kling. 1997. Estimates of genetic variances and interrelationships of traits associated with *Striga* resistance in maize. Africa Crop Sci. J. 5:1–8. doi:10.4314/acsj.v5i1.27864

Akinwale, R.O., B. Badu-Apraku, M.A.B. Fakorede, and I. Vroh-Bi. 2014. Heterotic grouping of tropical early-maturing maize inbred lines based on combining ability in *Striga*-infested and *Striga*-free environments and the use of SSR markers for genotyping. Field Crops Res. 156:48–62. doi:10.1016/j.fcr.2013.10.015

Badu-Apraku, B. 2007. Genetic variances and correlations in an early tropical white maize population after three cycles of recurrent selection for *Striga* resistance. Maydica 52:205–217.

Badu-Apraku, B., and R.O. Akinwale. 2011. Cultivar evaluation and trait analysis of tropical early maturing maize under *Striga*-infested and *Striga*-free environments. Field Crops Res. 121:186–194. doi:10.1016/j.fcr.2010.12.011

Badu-Apraku, B., R.O. Akinwale, and M.A.B. Fakorede. 2010. Selection of early maturing maize inbred lines for hybrid production using multiple traits under *Striga*-infested and *Striga* free environments. Maydica 55:261–274.

Badu-Apraku, B., B. Annor, M. Oyekunle, R.O. Akinwale, M.A.B. Fakorede, A.O. Talabi, I.C. Akaogu, G. Melaku, and Y. Fasanmade. 2015a. Grouping of early maturing quality protein maize inbreds based on SNP markers and combining ability under multiple environments. Field Crops Res. 183:169–183. doi:10.1016/j.fcr.2015.07.015

Badu-Apraku, B., M.A.B. Fakorede, M. Gedil, A.O. Talabi, B. Annor, M. Oyekunle, R.O. Akinwale, Y. Fasanmade, I.C. Akaogu, and M. Aderounmu. 2015b. heterotic responses among crosses of IITA and CIMMYT early white maize inbred lines under multiple stress environments. Euphytica 206:245–262. doi:10.1007/s10681-015-1506-0

Badu-Apraku, B., M.A.B. Fakorede, and A.F. Lum. 2007. Evaluation of experimental varieties from recurrent selection for *Striga* resistance in two extra-early maize populations in the savannas of West and Central Africa. Exp. Agric. 43:183–200. doi:10.1017/S0014479706004601

Badu-Apraku, B., A.F. Lum, R.O. Akinwale, and M. Oyekunle. 2011a. Biplot analysis of diallel crosses of early maturing tropical yellow maize inbreds in stress and nonstress environments. Crop Sci. 51:173–188. doi:10.2135/cropsci2010.06.0366

Badu-Apraku, B., and M. Oyekunle. 2012. Genetic analysis of grain yield and other traits of extra-early yellow maize inbreds and hybrid performance under contrasting environments. Field Crops Res. 129:99–110. doi:10.1016/j.fcr.2012.01.018

Badu-Apraku, B., M. Oyekunle, R.O. Akinwale, and A.F. Lum. 2011b. Combining ability of early-maturing white maize inbreds under stress and non-stress environments. Agron. J. 103:544–557. doi:10.2134/agronj2010.0345

Badu-Apraku, B., M. Oyekunle, M.A.B. Fakorede, I. Vroh, R.O. Akinwale, and M. Aderounmu. 2013. Combining ability, heterotic patterns and genetic diversity of extra-early yellow inbreds under contrasting environments. Euphytica 189:413–433. doi:10.1007/s10681-013-0876-4

Balestre, M., R.G. Von Pinho, J.C. Souza, and J.L. Lima. 2008. Comparison of maize similarity and dissimilarity genetic coefficients based on microsatellite markers. Genet. Mol. Res. 7:695–705. doi:10.4238/vol7-3gmr458

Banziger, M., and H.R. Lafitte. 1997. Efficiency of secondary traits for improving maize for low-nitrogen target environments. Crop Sci. 37:1110–1117. doi:10.2135/cropsci1997.0011183X003700040013x

Benchimol, L.L., C.L. De Souza, A.A.F. Garcia, P.M.S. Kono, C.A. Mangolin, A.M.M. Barbosa, A.S.G. Coelho, and A.P. De Souza. 2008. Genetic diversity in tropical maize inbred lines: Heterotic group assignment and hybrid performance determined by RFLP markers. Plant Breed. 119:491–496. doi:10.1046/j.1439-0523.2000.00539.x

Betrán, J.F., J.M. Ribaut, D.L. Beck, and D. Gonzalez De Leon. 2003. Genetic analysis of inbred and hybrid grain yield under stress and non-stress environments in tropical maize. Crop Sci. 43:807–817. doi:10.2135/cropsci2003.8070

Bhatnagar, S., F.J. Betran, and L.W. Rooney. 2004. Combining ability of quality protein maize inbreds. Crop Sci. 44:1997–2005. doi:10.2135/cropsci2004.1997

Bradbury, P.J., Z. Zhang, D.E. Kroon, T.M. Casstevens, Y. Ramdoss, and E.S. Buckler. 2007. TASSEL: Software for association mapping of complex traits in diverse samples. Bioinformatics 23:2633–2635. doi:10.1093/bioinformatics/btm308

Bremner, J.M., and C.S. Mulvaney. 1982. Nitrogen: Total. In: A.L. Page and R.H. Miller, editors, Methods of soil analysis. Part 2. 2nd ed. Agronomy Monography 9. Madison, WI: ASA and SSA. p. 595–624.

Comstock, R.E., and H.F. Robinson. 1948. The components of genetic variance in population of biparental progenies and their use in estimating the average degree of dominance. Biometrics 4:254–266. doi:10.2307/3001412

Crossa, J. 1990. Statistical analysis of multi-location trials. Adv. Agron. 44:55–85. doi:10.1016/S0065-2113(08)60818-4

Derera, J., P. Tongoona, S.V. Bindiganavile, and M.D. Laing. 2008. Genetic action controlling grain yield in Southern Africa hybrids under drought and non-drought environments. Euphytica 162:411–422. doi:10.1007/s10681-007-9582-4

DeVries, J. 2000. The inheritance of Striga reactions in maize. In: B.J.G. Haussmann, D.E. Hess, M.L. Koyama, L. Grivet, H.F.W. Rattunde and H.H. Geiger, editors, Breeding for Striga resistance in cereals: Proceedings of the International Workshop Organized by IITA, 18–20 Aug. 1999, Ibadan, Nigeria. Magraf Verlag, Weikersheim, Germany. p. 73–84.

Edmeades, G.O., J. Bolanos, and H.R. Lafitte. 1992. Progress in breeding for drought tolerance in maize. In: D. Wilkinson, editor, Proceedings of the 47th Annual Corn and Sorghum Industrial Research Conference, Washington, DC. 8–10 Dec. 1992. ASTA, Washington, DC. p. 93–111.

Fan, X.M., J. Tan, J.Y. Yang, and H.M. Chen. 2004. Combining ability and heterotic grouping of ten temperate, subtropical and tropical quality protein maize inbreds. Maydica 49:267–272.

Fan, X.M., Y.M. Zhang, W.H. Yao, H.M. Chen, J. Tan, C.X. Xu, X.L. Han, L.M. Luo, and M.S. Kang. 2009. Classifying maize inbred lines into heterotic groups using a factorial mating design. Agron. J. 101:106–112. doi:10.2134/agronj2008.0217

Gauch, H.G., and R.W. Zobel. 1988. Predictive and postdictive success of statistical analyses of yield trials. Theor. Appl. Genet. 76:1–10. doi:10.1007/BF00288824

Gethi, J.G., and M.E. Smith. 2004. Genetic responses of single crosses of maize to Striga hermonthica (Del.) Benth. and Striga asiatica (L.). Kuntze. Crop Sci. 44:2068–2077. doi:10.2135/cropsci2004.2068

Guei, R.G., and C.E. Wassom. 1992. Inheritance of some drought adaptive traits in maize. Interrelationships between yield, flowering, and ears per plant. Maydica 37:157–164.

Hallauer, A.R., and J.B.M. Filho. 1988. Quantitative genetics in maize breeding. 2nd ed. Iowa State Univ. Press, Ames.

Ifie, B.E., B. Badu-Apraku, V. Gracen, and E.Y. Danquah. 2015. Genetic analysis of grain yield of IITA and CIMMYT early-maturing maize inbreds under Striga-infested and low-soil nitrogen environments. Crop Sci. 55:610–623. doi:10.2135/cropsci2014.07.0470

Jumbo, M.B., and M.J. Carena. 2012. Combining ability, maternal, and reciprocal effects of elite early-maturing maize population hybrids. Euphytica 162:325–333. doi:10.1007/s10681-007-9618-9

Kearsey, M.J., and H.S. Pooni. 1996. The genetical analysis of quantitative traits. Chapman and Hall, London.

Kim, S.K. 1991. Breeding maize for Striga tolerance and the development of a field infestation technique. In: S.K. Kim, editor, Combating Striga in Africa: Proceedings of an International Workshop organized by IITA, ICRISAT and IDRC, 22–24 Aug. 1988. Ibadan, Nigeria: IITA. p. 96–108.

Kim, S.K. 1994. Genetics of maize tolerance to Striga hermonthica. Crop Sci. 34:900–907. doi:10.2135/cropsci1994.0011183X003400040012x

Kim, S.K., and V.O. Adetimirin. 1997. Responses of tolerant and susceptible maize varieties to timing and rate of nitrogen under Striga hermonthica infestation. Agron. J. 89:38–44. doi:10.2134/agronj1997.00021962008900010006x

Lanza, L.L.B., C.L. De Souza, Jr., L.M.M. Ottoboni, M.L.C. Vieira, and A.P. De Souza. 1997. Genetic distance of inbred lines and prediction of maize single cross performance using RAPD markers. Theor. Appl. Genet. 94:1023–1030. doi:10.1007/s001220050510

Liu, K.J., and S.V. Muse. 2005. PowerMarker: An integrated analysis environment for genetic marker analysis. Bioinformatics 21:2128–2129. doi:10.1093/bioinformatics/bti282

M'Boob, S.S. 1986. A regional program for West and Central Africa. In: Proceedings of FAO/OAU All-African Government Consultation on Striga Control, 20–24 Oct. 1986, Maroua, Cameroon. p. 190–194.

Machida, L., J. Derera, P. Tongoona, and J. Macrobert. 2010. Combining ability and reciprocal cross effects of elite quality protein maize inbred lines in subtropical environments. Crop Sci. 50:1708–1717. doi:10.2135/cropsci2009.09.0538

Makumbi, D., F.J. Betrán, M. Bänziger, and J. Ribaut. 2011. Combining ability, heterosis and genetic diversity in tropical maize (Zea mays L.) under stress and non-stress conditions. Euphytica 180:143–162. doi:10.1007/s10681-010-0334-5

Menkir, A., V.O. Adetimirin, C.G. Yallou, and M. Gedil. 2010. Relationship of genetic diversity of inbred lines with different reactions to Striga hermonthica (Del.) Benth and the performance of their crosses. Crop Sci. 50:602–611. doi:10.2135/cropsci2009.05.0247

Meseka, S.K., A. Menkir, A.E.S. Ibrahim, and S.O. Ajala. 2006. Genetic analysis of performance of maize inbred lines selected for tolerance to drought under low nitrogen. Maydica 51:487–495.

Musila, R.N., O.A. Diallo, D. Makumbi, and K. Njoroge. 2010. Combining ability of early-maturing quality protein maize inbred lines adapted to Eastern Africa. Field Crops Res. 119:231–237. doi:10.1016/j.fcr.2010.07.009

Nesmith, D.S., and J.T. Ritchie. 1992. Effects of water-deficits during tassel emergence on development and yield components of maize (*Zea mays* L.). Field Crops Res. 28:251–256. doi:10.1016/0378-4290(92)90044-A

Oyekunle, M., and B. Badu-Apraku. 2014. Genetic Analysis of Grain Yield and Other Traits of Early-Maturing Maize Inbreds under Drought and Well-Watered Conditions. J. Agron. Crop Sci. 200:92–107. doi:10.1111/jac.12049

Pixley, K.V., and M.S. Bjarnason. 1993. Combining ability for yield and protein quality among modified-endosperm opaque-2 tropical maize inbreds. Crop Sci. 33:1229–1234. doi:10.2135/cropsci1993.0011183X003300060023x

Rogers, J.S. 1972. Measures of genetic similarity and genetic distance. Studies in Genetics VII. Univ. of Texas Publ., 7213:145–153.

Saghai-Maroof, M.A., K.M. Soliman, R. Jorgenson, and R.W. Allard. 1984. Ribosomal DNA spacer length polymorphisms in barley: Mendelian inheritance, chromosomal location and population dynamics. Proc. Natl. Acad. Sci. USA 81:8014–8018. doi:10.1073/pnas.81.24.8014

SAS Institute. 2011. Base SAS 9.3 procedures guide. SAS Institute Inc., Cary, NC.

Semagn, K., C. Magorokosho, B.S. Vivek, D. Makumbi, Y. Beyene, S. Mugo, B.M. Prasanna, and M.L. Warburton. 2012. Molecular characterization of diverse CIMMYT maize inbred lines from eastern and southern Africa using single nucleotide polymorphic markers. BMC Genomics 13:113. doi:10.1186/1471-2164-13-113

Shieh, G.J., and F.S. Thseng. 2006. Genetic diversity of Tainan white maize inbred lines and prediction of single cross hybrid performance using RAPD markers. Euphytica 124:307–313. doi:10.1023/A:1015753820623

Singh, R.K., and B.D. Chaudhary. 1985. Biometrical methods in quantitative genetic analysis. Kalyani Publisher, New Delhi, India.

Soil Survey Staff. 1999. Soil taxonomy: A basic system of soil classification for making and interpreting soil surveys. 2nd ed. USDA–NRCS Agriculture Handbook No. 436. U.S. Gov. Print. Office, Washington, DC. p. 869.

Vasal, S.K., G. Srinivasan, S. Pandey, F. González, J. Crossa, and D.L. Beck. 1993. Heterosis and combining ability of CIMMYT's quality protein maize germplasm: I. Lowland tropical. Crop Sci. 33:46–51. doi:10.2135/cropsci1993.0011183X003300010006x

Vogt, W., J. Sauerborn, and M. Honisch. 1991. *Striga hermonthica* distribution and infestation in Ghana and Togo on grain crops. In: J.K. Ransom, L.J. Musselman, A.D. Worsham and C. Parker, editors, 5th International Symposium Parasitic Weeds, 24–30 June 1991. CIMMYT, Nairobi, Kenya. p. 372–377.

Wegary, D., S.B. Vivek, and M.T. Labuschagne. 2013. Combining ability of certain agronomic traits in quality protein maize under stress and non-stress environments in eastern and southern Africa. Crop Sci. 54:1004–1014. doi:10.2135/cropsci2013.09.0585

Wolfe, D.W., D.W. Henderson, T.C. Hsiao, and A. Alvio. 1988. Interactive water and nitrogen effects on maize. II. Photosynthetic decline and longevity of individual leaves. Agron. J. 80:865–870. doi:10.2134/agronj1988.00021962008000060005x

Yallou, C.G., A. Menkir, V.O. Adetimirin, and J.G. Kling. 2009. Combining ability of maize inbred lines containing genes from *Zea diploperennis* for resistance to *Striga hermonthica* in maize. Euphytica 115:149–158.

Yan, W. 2001. GGE biplot: A Windows application for graphical analysis of multi-environment trial data and other types of two-way data. Agron. J. 93:1111–1118. doi:10.2134/agronj2001.9351111x

Zobel, R.W., M.J. Wright, and H.G. Gauch. 1988. Statistical analysis of a yield trial. Agron. J. 80:388–393. doi:10.2134/agronj1988.00021962008000030002x