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Gene action controlling grain yield and other agronomic traits of extra-early quality protein maize under stress and non-stress conditions

B. Annor · B. Badu-Apraku

Abstract Extra-early quality protein maize (QPM) hybrids with combined tolerance to drought and low soil nitrogen (N) are crucial for reduced food insecurity and malnutrition in sub-Saharan Africa (SSA). Ninety six extra-early QPM single-crosses derived from 24 extra-early QPM inbreds using the North Carolina Design II plus four checks were evaluated under stress (drought and low-N) and non-stress environments in Nigeria, 2012 and 2013. The objectives were to (i) determine the gene action for grain yield and other agronomic traits in the QPM inbreds (ii) identify the best inbred testers across environments (iii) classify the inbreds into heterotic groups and (iv) evaluate the performance and stability of the hybrids. General combining ability (GCA) effects contributed more to the total variation among the hybrids for grain yield and most measured traits under each and across environments suggesting that additive gene effects were more important in the inheritance of the traits.

The inbreds were classified into three heterotic groups. Inbreds TZEEQI 7 and TZEEQI 134 were the best testers while TZEEQI 7, TZEEQI 60, TZEEQI 61, TZEEQI 8, TZEEQI 11, TZEEQI 137, TZEEQI 63, TZEEQI 66, TZEEQI 44, and TZEEQI 157 possessed favorable alleles for stress tolerance and could be used for population improvement and development of stress tolerant hybrids. The hybrids TZEEQI 183 × TZEEQI 7, TZEEQI 181 × TZEEQI 7 and TZEEQI 144 × TZEEQI 183 were high yielding and the most stable across environments and should be tested extensively in on-farm trials and commercialized in the sub-region.

Keywords Heterotic grouping · Drought tolerance · Low-soil nitrogen · Quality protein maize · *Zea mays* L.

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Introduction

Maize (*Zea mays* L.) is a major staple food crop for rural and urban consumers in sub-Saharan Africa (SSA). Its importance as food and industrial crop in SSA has been increasing steadily over the last few decades (Fakorede et al. 2003). Maize provides about 20 % of the world's food calories and 15 % of all food proteins, and has potential for reducing the food security challenges posed by the increasing levels of urbanization in SSA countries (Byerlee and Eicher

1997). However, during the last two decades, production and productivity have not matched population growth due to a number factors including poor availability of improved seeds, herbicides, and fertilizers, inadequate agronomic management practices, labour shortage, rising cost of inputs and increased levels of biotic and abiotic constraints. Presently, *Striga hermonthica* (Del.) Benth parasitism, drought, and low soil nitrogen (low-N) constitute the most important stress factors limiting maize production in SSA (Badu-Apraku et al. 2011a). Of these stress factors, recurrent drought and low-N are the most important.

Considering the ongoing climatic changes caused principally by global warming, the pressure on food production in drought-prone environments will increase in the near future (Curry et al. 1995). Global warming and its associated effects have also changed weather patterns leading to erratic and unreliable amounts and distribution of rainfall which are resulting in several billions of U.S dollars lost annually to drought (Badu-Apraku et al. 2011a). According to Edmeades et al. (1995), 15 % average annual grain yield loss is caused by recurrent drought in SSA. This yield loss may even be as high as 40–90 % when the drought coincides with the flowering and grain filling periods (NeSmith and Ritchie 1992).

Soil nitrogen is important for increased maize production as it promotes vegetative growth, maximizes both kernel initiation and kernel set, and plays a key role in filling the kernel sink (Below et al. 1997). Its deficiency interferes with protein synthesis, induces leaf senescence and therefore reduces the general growth of the plant (Bruns and Abel 2003) thereby limiting yield. In most developing countries, maize production is carried out under low-N conditions (McCown et al. 1992) due to limited use of N fertilizers, reduced N-uptake in drought prone environments, high price ratios between fertilizer and grain yield, non-availability of fertilizer or lack of credit for farmers (Banziger and Lafitte 1997). Annual maize yield losses resulting from low-N varies from 10 to 50 % (Wolfe et al. 1988). Under farmer's field conditions, drought and soil nutrient deficiencies do occur simultaneously, and the combined effects may be total crop failure (Cechin and Press 1993; Kim and Adetimirin 1997; Badu-Apraku et al. 2011a). Therefore, maize varieties and hybrids targeted to drought prone areas of the sub-region must be tolerant to drought and low-N for increased productivity. The development of the extra-early (80–85 days to physiological maturity) quality protein maize (QPM) germplasm with combined tolerance to drought and low-N is therefore crucial for increased maize productivity in SSA and offers an effective partial solution to enhance maize production and food security among resource poor farmers.

Normal maize has a major nutritional constraint as human food due to its deficiency in two essential amino acids: lysine and tryptophan, even though it contains about 10 % protein. Therefore infants fed on it without balanced protein supplements suffer from malnutrition and develop diseases such as kwashiorkor or pellagra (Badu-Apraku and Lum 2010). QPM has about twice the normal levels of lysine and tryptophan and may supply about 70–73 % of human protein requirements, compared to 46 % from normal maize. The biological value of the protein is 80 % for QPM compared to 40–57 % for normal maize and 86 % for eggs (Bressani 1992). Also, QPM has 90 % relative value (RV) of milk compared to 40 % RV for normal maize. Extra-early QPM cultivars can therefore, be important source of nutrients for the malnourished populations in rural as well as urban areas of SSA.

Combining ability is the ability of genotypes to combine during hybridization such that favourable genes/characters are transmitted to their progenies (Panhwar et al. 2008). Combining ability studies are important in designing plant breeding programs especially in testing procedures when studying and comparing the performance of inbred lines in hybrid combinations. Combining ability can be classified as (i) general combining ability (GCA) which is associated with genes which are additive in their effects and (ii) specific combining ability (SCA) which is attributed to the non-additive gene effects (Rojas and Sprague 1952). The additive gene effects are the predictable portion of the genetic effects and are therefore more useful to plant breeders. In biometrical genetics, North Carolina Design II (Comstock and Robinson 1948) is frequently used by plant breeders to assess the nature of the genetic action influencing quantitative traits. One of the features of this design is that the variation due to hybrids is partitioned into components due to GCA-female and GCA-male (i.e. female, male main effects) and to SCA in terms of male × female interactions (Pixley and Frey 1991).

The International Institute of Tropical Agriculture (IITA) maize improvement program has during the past few years intensified efforts at developing and promoting the adoption of extra-early and early maturing QPM varieties with tolerance/resistance to *Striga*, drought as well as low soil N. This has resulted in the conversion of several elite normal endosperm extra-early and early cultivars to QPM. Also, extra-early maturing QPM inbreds with increased levels of lysine and tryptophan have been developed. The extra-early QPM inbred lines should be heterotic in hybrid combinations so that they could be successfully utilized for population improvement and for the development of extra-early QPM hybrids which are presently lacking in the sub-region. However, the combining ability and heterotic groups of the extra-early QPM inbreds have not been determined. Furthermore, no extra-early QPM inbred testers are available in SSA to facilitate the development of stress-tolerant hybrids. The identification of extra-early QPM inbred testers and determination of the heterotic groups of the inbreds is crucial for successful extra-early QPM breeding programs in the SSA. The objectives of the present study were to (i) determine the gene action controlling grain yield and other agronomic traits of the inbreds (ii) identify the best QPM inbred testers across stress and non-stress environments (iii) classify the QPM inbreds into heterotic groups and (iv) evaluate the performance and stability of the QPM hybrids across stress and non-stress environments.

Materials and methods

Genetic materials

The extra-early white QPM inbred lines were developed in the IITA Maize Improvement Program from a cross between two extra-early white normal endosperm elite *Striga* resistant inbred lines and QPM donor source (Pool 15 SR) in an effort to convert them to QPM. The F_1 crosses were backcrossed to the recurrent parents to obtain BC_1 and BC_2. The BC_2 was selfed for four cycles to develop 245 S_6 inbreds. Based on the results of screening of the 245 inbreds under drought and the analysis of the tryptophan contents, the most promising 18 drought tolerant and six susceptible inbreds with high tryptophan content

were selected for the present study (Supplementary Table 1).

Generation of North Carolina Design II crosses

The twenty four drought tolerant and susceptible extra-early white QPM inbred lines were crossed using the North Carolina Design II (NCD II) mating design (Comstock and Robinson 1948) with six sets each consisting of four inbreds. The four inbreds in one set were used as females and crossed with four inbreds in another set used as males. Each inbred line was used as a female parent in one set and as a male parent in another set. The 96 extra-early NCD II crosses plus four checks (two QPM single crosses, one three-way normal endosperm and one commercial normal endosperm hybrid) were evaluated under stress (drought and low-N) and non-stress (well-watered, rainfed and high-N) environments in Nigeria.

Field studies

Two set of trials, inbred trial (24 extra-early white QPM inbred lines used in the NCD II) and hybrid trial (96 extra-early white QPM hybrids plus four checks) were evaluated under drought, low-N, well-watered, rainfed and high-N environments in 2012 and 2013. The inbreds trial was evaluated under terminal drought at Bagauda (lat. 12°00′N, long. 8°22′E, 580 m and 800 mm annual rainfall), a natural drought-prone site during the 2012 rainy season. The inbreds were also evaluated under induced drought stress and well-watered conditions during the dry season of 2012/2013 as well as under rainfed conditions at Ikenne (lat. 3°7′E, long. 6°87′N, elevation 30 m, 1200 mm annual rainfall) during the rainy season of 2013. A randomized complete block design with two replications was used for all the inbred trials at all locations. The experimental units were single-row plots, each 4 m long with inter-row spacing of 0.75 m. Plant spacing within rows was 0.40 m. Three seeds were planted per hill and seedlings later thinned to two per hill at 2 weeks after planting (WAP) to give a final population density of about 66,666 plants ha^{-1}. For the induced drought stress experiment at Ikenne, the plants were irrigated only during the first 3 weeks of growth, using a sprinkler irrigation system which provided 17 mm of water weekly as described by Badu-Apraku and Akinwale (2011) and Badu-Apraku

et al. (2011b). The plants were thus subjected to induced drought at the flowering and grain filling periods and relied on the stored moisture in the soil from 21 days after planting (DAP) until maturity. The soil in the experiment station at Ikenne is eutric nitrosol and the experimental area is flat with high water-holding capacity (Soil Survey Staff 1999). The well-watered environment at Ikenne was obtained by supplying irrigation water throughout the growing period. Except for the well-watered treatments, all management practices were the same for both well-watered and drought experiments. Fertilizer was applied at the rate of 60 kg ha^{-1} each of N, phosphorus and potassium to the well-watered and induced drought experiments at planting. An additional 30 kg ha^{-1} N was top-dressed at three WAP. However, under terminal drought and rainfed conditions, the fertilizer was applied at 2 and 4 WAP. The trials were kept weed-free with the application of atrazine and gramoxone as pre- and post-emergence herbicides at 5 l/ha each of primextra and paraquat and subsequently, by hand weeding.

The inbred lines were also evaluated under low-N (30 kg ha^{-1}) and high-N (90 kg ha^{-1}) conditions at Mokwa (9°18′N, 5°4′E, 457 m altitude, 1100 mm annual rainfall) and Ile-Ife (7°28′ N, 4°33′ E, and 244 m above sea level, 1200 mm annual rainfall) during the 2012 rainy season. The experimental fields were depleted of nitrogen by continuously planting maize and removing the plant residue after each harvest. Soil samples were taken from 0 to 15 cm depth before planting. The nitrogen content was determined at the IITA soil laboratory at Ibadan, Nigeria according to AOAC (1984) method. The results of the soil analysis revealed that the soil at Mokwa contained 0.085 % of nitrogen, 0.20 % potassium and 6.32 % phosphorus while the soil at Ife contained 0.084 % of nitrogen, 0.358 % of potassium and 2.05 % of phosphorus. Nitrogen fertilizer (Urea) was applied to bring the total available nitrogen to 30 kg ha^{-1} for the low-N and 90 kg ha^{-1} for the high-N fields, respectively as revealed by the soil tests. The N fertilizer was applied at two WAP. Single superphosphate and muriate of potash fertilizers were applied to both the low- and high-N blocks to supply 60 kg P$_2$O$_5$ ha^{-1} and 60 kg K$_2$O ha^{-1}, respectively. The low- and high-N trials were in adjacent blocks, separated by about 10 m alley to minimize the movement of N across blocks. All other crop management practices were the same as described above for the drought and well-watered experiments.

The hybrid trial was evaluated under terminal drought at Bagauda during the 2012 rainy season. The hybrids were also evaluated under induced drought stress during the dry season of 2012/2013 and rainfed conditions during the rainy season of 2013 at Ikenne. In addition, the hybrids were evaluated under low- and high-N conditions at Mokwa and Ile-Ife during the rainy seasons of 2012 and 2013. A 10 × 10 lattice design with two replications was used in all hybrid trials at all locations. The number of rows, planting distance and all other management practices were the same as described for the inbred trials.

Data collection

Data were recorded on drought-stressed, low-N and non-stress (well-watered, rainfed and high-N environments) plots for number of days to 50 % anthesis and silking, plant and ear heights, root and stalk lodging, plant and ear aspects and husk cover. Anthesis-silking interval (ASI) was computed as the difference between number of days to 50 % silking and 50 % anthesis while the number of ears per plant was calculated as the number of harvested ears divided by the number of plants in a plot. In addition, the stay-green characteristic was scored for the drought stressed and low-N experiments at 70 DAP on a scale of 1–9, where 1 represented plants with almost all leaves green and 9, plants with virtually all leaves dead. Shelled grains from cobs harvested from each plot under drought and low-N were weighed. Grain moisture of the shelled grains was measured using Dickey-John moisture meter. Grain yield, adjusted to 15 % moisture content was computed from the shelled grain weight. Under non-stress conditions, cobs harvested from each plot were weighed and representative samples were shelled to determine percent grain moisture content. Grain yield adjusted to 15 % moisture content was computed from cob weight and grain moisture using 80 % shelling percentage.

Statistical analysis

Analysis of variance (ANOVA) were conducted separately for inbred and hybrid experiments on data collected across stress (drought and low-N), non-stress and across stress and the non-stress environments with

general linear model (GLM) procedure of statistical analysis system (SAS) software, version 9.3 using a RANDOM statement with the TEST option (SAS Institute Inc 2011). The location-year combinations under each research condition were considered as environments in the combined analysis for each field experiment. In the ANOVA for the hybrid trials, locations, replicates, blocks and hybrids were regarded as random factors under stress, non-stress and across environments. On the other hand, in the ANOVA for the inbred trials, locations, replicates and blocks were considered as random factors while the inbreds were considered as a fixed factor under the contrasting environments. The variation due to hybrids was divided into variation due to male (sets), female (sets), and female × male (sets) interaction. The main effects of male (sets) and female (sets) represented the general combining ability (GCA) while the female × male (sets) interaction represented specific combining ability (SCA) effect (Hallauer and Miranda Filho 1988). The F tests for male (sets), female (sets) and female × male (sets) mean squares were calculated using the mean squares for their respective interaction with environment.

The proportion of GCA-male, GCA-female and SCA for each trait was calculated as the percentage of the sum of squares for the crosses under stress, non-stress and across environments. The GCA-males and GCA-female effects for grain yield and the other traits were computed from the adjusted means using the line × tester approach (Singh and Chaudhary 1985). Standard errors for GCA effects were estimated according to Cox and Frey (1984). Two tailed t tests were used to test the significance of the GCA and SCA effects. In addition, the F test or variance ratio was used to compare the mean squares of the GCA male and female as suggested by Kearsey and Pooni (1996).

To identify the inbred lines or hybrids for combined tolerance to drought and low-N, a base index (I) that integrated increased grain yield across drought and low-N with good plant and ear aspects, delayed leaf senescence, short ASI and increased number of ears per plant was used. The best performing genotypes under stress conditions were identified based on the index values estimated as follows:

$$I = [(2 \times yield) + EPP - ASI - PASP \\ - EASP - STGR]$$

where PASP is the plant aspect, EASP the ear aspect, EPP the ears per plant, ASI the anthesis-silking interval and STGR the stay-green characteristic. Each parameter was standardized with a mean of zero and a standard deviation of 1 to minimize the effect different scales. A positive value of I was an indicator of tolerance of the lines or hybrid to stress, while a negative value was an indicator of susceptibility of a line or hybrid (Badu-Apraku et al. 2011a).

Heterotic grouping based on GCA of multiple traits (HGCAMT) proposed by Badu-Apraku et al. (2013, 2015a) was used to group the 24 inbred lines. The grouping was achieved by standardizing the GCA effects (mean of zero and standard deviation of 1) of the traits that had significant means squares for G under each study conditions using the following statistical model:

$$Y = \sum_{i=1}^{n} ((Y_i - \bar{Y}_i)/s) + \varepsilon ij$$

where Y is HGCAMT, which is the genetic value measuring relationship among genotypes based on the GCA of multiple traits i to n; Yi is the individual GCA effect of genotypes for trait i, Y is the mean of GCA effects across genotypes for trait i, s is the standard deviation of the GCA effects of trait i and εij is the residual of the model associated with the combination of inbred i and trait j.

The traits included grain yield, days to silking and anthesis, ASI, plant and ear heights, ear aspect, plant aspect, ears per plant and the stay-green characteristic. The standardised GCA effects were subsequently subjected to Ward's minimum variance cluster analysis to construct the dendrogram for grouping of the inbreds using SAS software version 9.3 (SAS Institute Inc 2011).

The means of the grain yield data for the single cross hybrids (best 15 and worst 10) selected using the base index plus the four checks were subjected to the additive main effects and multiplicative interaction (AMMI) analysis to examine the relationships among hybrids (G), environments (E) and G × E Interaction (GEI) and to identify the high yielding and stable hybrids across environments as well as the hybrids adapted to specific environments. The AMMI model used was described in detail by Zobel et al. (1988), Gauch and Zobel (1988) and Crossa (1990).

Results

Significant (P < 0.05) differences were observed among inbreds for grain yield under stress and non-stress environments (Supplementary Table 1). Furthermore, significant (P < 0.05) effects were observed for the G and E mean squares for all measured traits under stress, non-stress and across environments except mean squares of G for plant height and husk cover under stress, ASI, husk cover and EPP under non-stress as well as EPP across environments. The GEI was significant for all measured traits under each and across environments except ASI, plant height and husk cover under stress, days to silking, ASI and ear height under non-stress as well as plant and ear heights across environments (Tables 1, 2). The general combining ability of male (GCAm) and female (GCAf) were significant (P < 0.01) for all measured traits under stress except GCAm for plant height and husk cover. Under non-stress conditions, GCAf and GCAm were significant for all traits except husk cover and EPP for GCAm and ASI for GCAf (Table 1). Across environments, GCAf and GCAm were significant for all traits except GCAm for husk cover (Table 2). The specific combining ability (SCA) was only significant for days to silking and anthesis under stress, grain yield under non-stress conditions (Table 1) and grain yield, days to silking and anthesis and ear aspect across environments (Table 2). Under stress conditions, the GCAm × E interaction were significant for only yield, days to anthesis, ear height and plant aspect while GCAf × E interactions were significant for all measured traits except ASI, plant height and husk cover. The SCA × E interactions were significant for grain yield, days to silking and plant aspect. Under non-stress conditions, GCAm × E interaction effects were significant for days to anthesis, ASI, plant aspect and EPP while the GCAf × E interaction effects were significant for grain yield, husk cover and plant aspect. The SCA × E interaction effect was significant only for plant aspect (Table 1). Across environments, the GCAf × E interaction effects were significant for all traits except days to silking, ASI, husk cover and EPP while GCAm × E interaction mean squares were significant for all traits except ASI, plant height, ear height and husk cover. The SCA × E interaction effects were significant for grain yield, days to silking and plant aspect (Table 2).

Partitioning of hybrid sums of squares into GCA (GCAf + GCAm) and SCA revealed that GCA accounted for more than 50 % (55–87 %) of the total variation among the hybrids for all the measured traits under stress, non-stress and across environments except for plant height under stress environments. There were slight variations in the contributions of the GCAf and GCAm effects to the total sum of squares for all traits under stress and non-stress environments. However, the 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 the measured traits except ASI with GCAm 3.2 times larger than the GCAf under non-stress environment (Table 3).

The GCA effects of the inbred lines under stress, non-stress and across environments are shown in Table 4. Under stress environments, inbred TZEEQI 183 showed significant and positive GCA effects for grain yield when used as either male or female parent whereas TZEEQI 1 had significant and positive GCA effects for grain yield when used as a male parent while TZEEQI 7, TZEEQI 60 and TZEEQI 134 had significant and positive GCA effects for grain yield when used as female parents. Inbred TZEEQI 109 had significant and negative GCA effects (GCAm and GCAf) for the stay-green characteristic while inbred TZEEQI 102 had significant and negative GCAf for stay-green characteristic. Positive and significant GCAf effects for plant aspect were recorded for inbreds TZEEQI 61 and TZEEQI 145, GCAm for TZEEQI 66 and both GCAm and GCAf for TZEEQI 157. Ear aspect showed significant and positive GCAm for TZEEQI 66 and TZEEQI 157 as well as positive and significant GCAf for TZEEQI 38, TZEEQI 96 and TZEEQI 145. EPP had significant and positive GCAm for inbreds TZEEQI 1, TZEEQI 66 as well as the GCAf for TZEQI 7. Under non-stressconditions, inbreds TZEEQI 7 and TZEEQI 134 had positive and significant (P ≤ 0.5) GCAm for grain yield. TZEEQI 1 and TZEEQI 60 had significant and positive GCA for grain yield only when used as male while TZEEQI 109 and TZEEQI 137 had significant and positive GCA for grain yield when used as female parents. Across stress and non-stressenvironments, inbreds TZEEQI 7, TZEEQI 60, TZEEQI 109, TZEEQI 134 and TZEEQI 183 had significant and positive GCA for grain yield when used as male as well as female parent. However, TZEEQI 1 had significant and positive GCA for grain yield when used as only a male parent.

Table 1 Mean squares from analysis of variance for grain yield and other agronomic traits of 96 extra-early QPM single crosses and checks evaluated under stress and non-stress environments in Nigeria, 2012 and 2013

Source	DF	Grain yield (kg ha^{-1})	Days to silking	Days to anthesis	ASI	Plant height (cm)	Ear height (cm)	Husk cover	Plant aspect	Ear aspect	Ears plant^{-1}	STGR
Stress environments												
Env	5	192,628,588.20**	1231.37**	848.28**	530.81**	101,305.36**	24,337.82**	86.32**	28.41**	15.79**	7.30**	82.42**
Set	5	4,026,810.10***	70.83***	33.75***	16.73***	2617.15	2156.09***	0.15	0.59***	2.18***	0.17***	4.36***
Env*Set	25	596,071.60***	10.83***	6.71***	4.98	2764.95*	173.90**	0.27	0.29***	0.33***	0.07***	1.41***
Rep(Env*Set)	30	221,956.50	3.97	3.74	2.62	2218.58	75.09	0.18	0.21*	0.14	0.02	0.41
Block(Env*Rep)	108	795,695.30***	10.58***	7.70***	4.96	2413.26**	302.92**	0.34*	0.53***	0.25**	0.03	0.89**
Hybrid	99	1,253,384.00***	18.17***	15.78***	7.99***	5294.23	458.24***	0.33	0.40***	0.51***	0.05***	1.03***
GCA-male	18	963,296.70***	24.10***	28.26***	8.55***	1751.24	692.66***	0.29	0.40***	0.33***	0.06***	0.63*
GCA-female	18	1,616,768.00***	17.10***	25.34***	9.63***	2794.89*	687.09***	0.45*	0.39***	0.60***	0.05***	1.25***
SCA	54	300,358.40	5.69*	5.00*	4.99	1602.43	70.28	0.24	0.14	0.17	0.03	0.29
Env* Hybrid	495	480,228.00***	5.59***	4.08***	4.30	4600.51	105.18**	0.29	0.19***	0.19**	0.03*	0.50***
Env × GCA-male	90	491,031.90***	4.76	4.36*	3.99	1590.66	120.24**	0.26	0.19*	0.16	0.03	0.44
Env × GCA-female	90	619,612.40***	5.89***	4.66*	4.28	1829.88	137.45**	0.27	0.21**	0.21**	0.04*	0.57***
Env × SCA	270	310,988.40***	5.05*	3.47	4.40	1705.04	81.93	0.31	0.18***	0.15	0.02	0.37
Error	432	238,462	4.02	3.31	4.06	1602.52	76.39	0.26	0.14	0.13	0.03	0.38
Non-stress environments												
Env	4	135,763,750.00***	194.21**	169.06**	29.84**	45,398.33**	42,886.33**	38.41**	8.01**	4.04**	5.49**	
Set	5	5,631,037.50***	31.40***	22.55***	12.20**	2399.41**	1404.54	0.16	0.72***	1.50**	0.16	
Env*Set	20	2,542,654.60***	10.32***	3.19*	9.36***	234.51*	579.76	0.15	0.27	0.37***	0.18	
Rep(Env*Set)	25	1,530,761.50***	2.25	1.90	3.27	178.35	464.73	0.13	0.08	0.15	0.21	
Block(Env*Rep)	90	699,031.80	8.74***	3.59***	7.18***	233.49***	685.55	0.14	0.13	0.15	0.2	
Hybrid	99	2,481,922.00***	12.75***	10.14***	5.88	731.07***	989.89***	0.19	0.37***	0.38***	0.21	
GCA-male	18	2,243,789.10***	17.95***	17.43***	12.38***	1253.07***	1163.32*	0.16	0.58***	0.43***	0.23	
GCA-female	18	3,158,722.90***	17.33***	18.92***	3.90	1117.52***	1857.00***	0.31**	0.51***	0.43***	0.37*	
SCA	54	1,243,436.50***	5.21	2.34	4.06	148.53	585.30	0.16	0.11	0.12	0.15	
Env* Hybrid	396	888,221.00*	5.63	2.23*	4.84	167.53*	692.90	0.15**	0.16**	0.15**	0.21*	
Env × GCA-male	72	699,637.80	6.22	2.53*	6.52*	179.65	741.32	0.15	0.15*	0.15	0.27*	
Env. × GCA-female	72	1,072,111.00***	4.82	1.89	4.36	158.04	870.58	0.21**	0.20***	0.16	0.17	
Env × SCA	216	685,610.00	5.41	2.01	4.35	149.71	672.91	0.13	0.15*	0.13	0.23	
Error	360	627,139.00	5.02	1.78	4.44	138.22	702.52	0.12	0.11	0.13	0.19	

Env. environment; *Rep* replication; *GCA* general combining ability; *SCA* specific combining ability; *ASI* anthesis-silking interval; *STGR* stay-green characteristic

*, ** = Significant at 0.05 and 0.01 probability levels, respectively

Table 2 Mean squares from analysis of variance for grain yield and other agronomic traits of 96 extra-early QPM single crosses and checks across eleven stress and non-stress environments in Nigeria, 2012 and 2013

Source	DF	Grain yield (kg ha^{-1})	Days to silking	Days to anthesis	ASI	Plant height	Ear height	Husk cover	Plant aspect	Ear aspect	Ears plant^{-1}
Env	10	203,619,157**	1410.75***	747.98***	393.49***	94,641.56***	33,211.59***	59.77***	26.54***	13.52**	6.11**
Set	5	8,784,269***	87.38***	53.30***	11.35*	3847.90***	3110.48***	0.16	1.10***	3.59***	0.16
Env*Set	50	1,405,999***	10.97***	4.94***	7.87***	1591.71***	366.46	0.21	0.27***	0.32***	0.12
Rep(Env*Set)	55	816,868***	3.19	2.90	2.91	1291.20*	252.20	0.16	0.15	0.14	0.11
Block(Env*Rep)	198	751,757***	9.75***	5.83***	5.97***	1422.45***	476.84***	0.25*	0.35***	0.20***	0.11
Hybrid	99	3,064,736***	25.52***	22.77***	9.24***	3997.64***	1050.81***	0.38***	0.65***	0.80***	0.14
GCA-male	18	2,660,787***	35.88***	43.31***	17.51***	2343.92***	1470.27***	0.31	0.86***	0.62***	0.20**
GCA-female	18	4,203,657***	30.17***	38.92***	10.94***	3193.85***	1999.26***	0.57***	0.75***	0.93***	0.21**
SCA	54	896,291***	6.49***	4.66***	4.92	1037.70	285.21	0.26	0.15	0.20***	0.08
Env* Hybrid	990	662,508***	5.60***	3.26**	4.55*	2566.50	369.73	0.22*	0.17***	0.16***	0.11**
Env × GCA-male	180	580,646***	5.52*	3.43***	4.96	932.65	395.77	0.20	0.16***	0.16*	0.13**
Env × GCA-female	180	794,761***	5.35	3.63**	4.16	1047.84	469.57***	0.23	0.20***	0.18***	0.11
Env × SCA	540	496,080*	5.14*	2.81	4.37	982.68	348.03	0.22	0.16***	0.13	0.11
Error	792	415,133	4.47	2.61	4.23	936.93	361.00	0.19	0.13	0.13	0.10

Env environment; *Rep* replication; *GCA* general combining ability; *SCA* specific combining ability; *ASI* anthesis-silking interval

*, ** = significant at 0.05 and 0.01 probability levels, respectively

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Table 4 Estimates of general combining ability (GCA) effects of extra early white QPM inbreds for grain yield and other agronomic traits under stress, non-stress and across environments

| Inbred | Grain yield | | | | | | Stress | | | | | | | |
| | Across | | Non-stress | | Stress | | Plant aspect | | Ear aspect | | Ears plant^{-1} | | STGR | |
	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm	GCAf	GCAm
TZEEQI 1	83.87	355.94**	−34.59	357.90**	182.59	354.31**	0.00	−0.16*	−0.08	−0.22*	0.01	0.08**	0.08	0.03
TZEEQI 3	−73.02	−95.43	−95.70	−182.92	−54.12	−22.51	0.06	0.05	0.07	0.03	−0.01	−0.06*	−0.18	−0.01
TZEEQI 7	509.25**	293.72**	634.29**	454.23**	405.05**	159.96	−0.08	0.07	−0.20*	−0.09	0.06*	0.03	−0.17	−0.07
TZEEQI 8	−62.83	−66.22	−27.19	−167.65	−92.53	18.30	0.06	0.06	0.00	−0.02	−0.01	−0.02	0.18	0.04
TZEEQI 11	−21.03	−22.92	−59.24	−19.41	10.80	−25.83	0.02	−0.08	−0.05	0.06	−0.01	0.04	−0.04	−0.09
TZEEQI 38	−425.38**	−204.58*	−547.86**	−267.17*	−323.32**	−152.42	0.00	−0.04	0.24**	0.05	−0.04	−0.05*	0.03	0.12
TZEEQI 44	−51.26	7.12	−52.38	−34.81	−50.33	42.07	−0.01	−0.08	0.05	0.01	−0.04	0.03	−0.12	−0.11
TZEEQI 52	−142.01	−211.01*	−202.06	−294.82*	−91.96	−141.17	−0.04	0.07	0.07	0.00	0.00	−0.05*	0.06	0.17*
TZEEQI 60	253.48**	170.35*	211.45	328.32**	288.51*	38.70	−0.08	0.02	−0.19	0.02	0.05	−0.03	−0.03	0.02
TZEEQI 61	−60.21	33.54	42.99	1.31	−146.21	60.40	0.13*	0.00	0.07	−0.03	−0.02	0.05*	0.10	−0.07
TZEEQI 63	−24.08	−150.26*	−32.6	−50.63	−16.98	−233.28*	−0.08	−0.04	−0.07	0.02	0.02	−0.03	−0.08	−0.07
TZEEQI 66	13.23	−110.26	162.89	−124.36	−111.49	−98.51	0.02	0.15*	0.08	0.17*	−0.03	0.02	0.18	0.05
TZEEQI 96	−157.85	25.98	−187.37	−9.42	−133.26	55.48	0.04	0.01	0.13*	0.01	−0.01	0.01	0.21*	0.31**
TZEEQI 101	−61.68	−45.29	−128.57	−75.46	−5.94	−20.15	0.01	0.00	−0.05	−0.08	−0.03	0.00	0.21*	0.00
TZEEQI 102	−31.55	−142.65*	−29.76	−120.22	−33.04	−161.34	0.09	0.07	0.06	0.03	0.03	0.02	−0.24*	−0.12
TZEEQI 109	251.08**	161.96*	345.70*	205.10	172.24	126.01	−0.14*	−0.08	−0.13*	0.04	0.00	−0.04	−0.19*	−0.19*
TZEEQI 134	297.98**	231.61**	283.20*	359.05*	310.29**	125.41	−0.18*	−0.06	−0.11	−0.05	0.05	0.02	−0.17	0.04
TZEEQI 137	133.74	110.52	292.95*	164.55	1.07	65.50	0.01	0.00	−0.02	−0.09	0.00	0.01	0.03	0.03
TZEEQI 144	−85.64	−154.17*	−68.68	−271.65*	−99.77	−56.28	0.01	−0.02	0.00	0.05	−0.01	0.02	−0.06	−0.11
TZEEQI 145	−346.08**	−187.96*	−507.47**	−251.95*	−211.60*	−134.64	0.16*	0.08	0.13*	0.09	−0.04	−0.05*	0.20	0.03
TZEEQI 157	−183.26*	−245.63**	−165.85	−360.99**	−197.78*	−149.49	0.13*	0.24*	0.11	0.15*	−0.04	−0.02	−0.24	0.02
TZEEQI 181	−125.68	130.64	−149.81	199.07	−105.57	73.62	0.00	−0.13*	0.05	−0.06	−0.04	0.01	−0.07	−0.03
TZEEQI 183	214.12*	170.40*	200.82*	145.42	225.21*	191.21*	−0.16*	−0.10	−0.14*	−0.09	0.03	0.01	0.13	−0.08
TZEEQI 190	94.82	−55.42	114.84	16.49	78.14	−115.34	0.02	0.00	−0.02	0.00	0.04	0.00	0.18	0.10
Sed	82.3	70.35	141.78	114.53	98.39	87.59	0.06	0.05	0.06	0.05	0.02	0.02	0.09	0.08

STGR stay−green characteristic; GCAf GCA of female parent; GCAm GCA of male parents

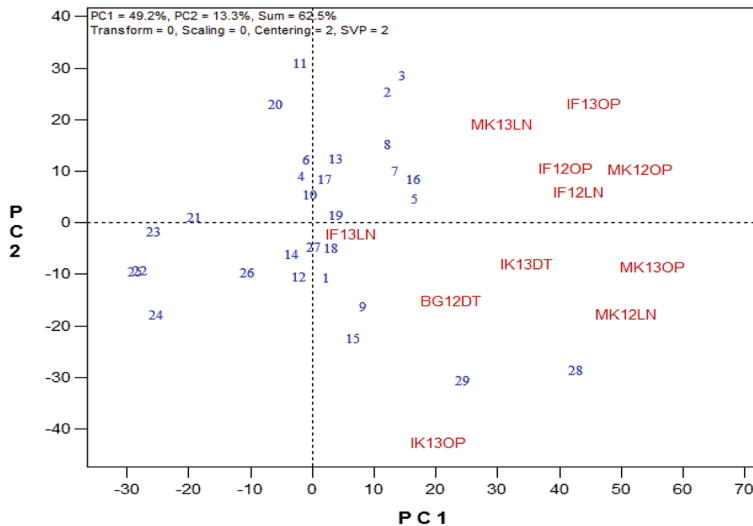*, ** = significant at 0.05 and 0.01 probability levels, respectively

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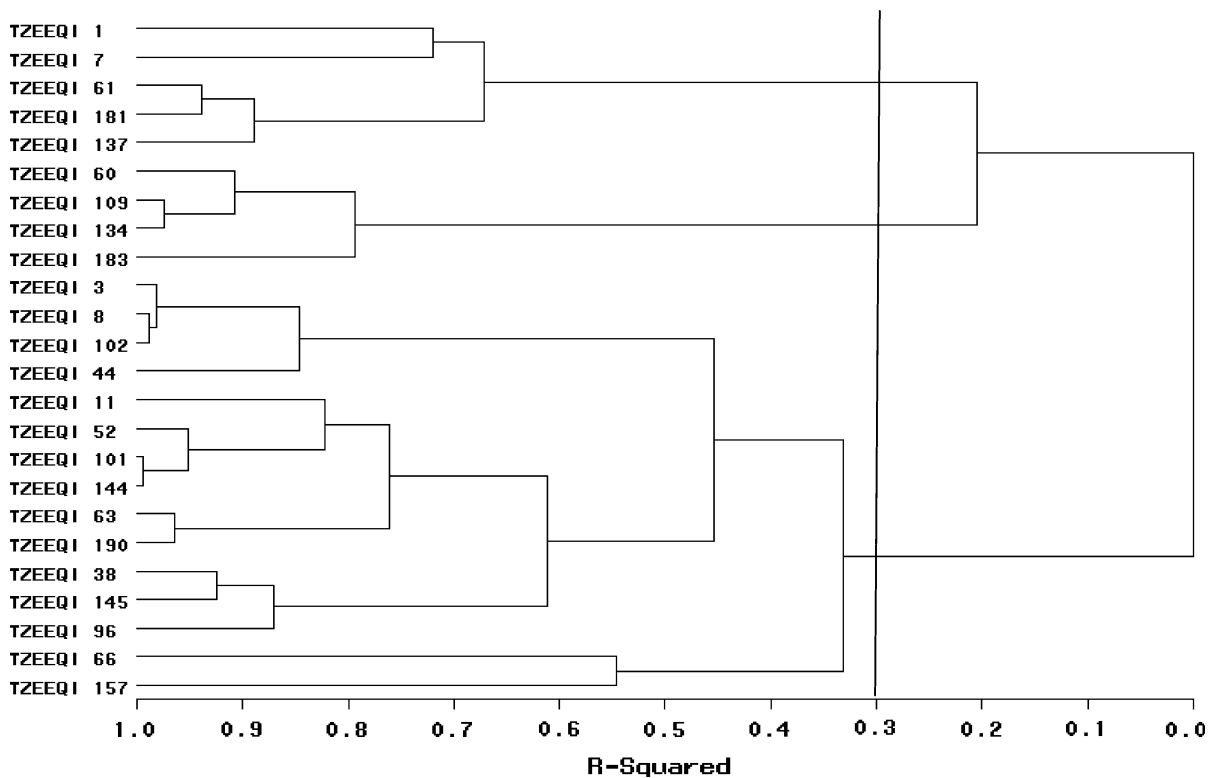
Fig. 1 Dendrogram of 24 extra-early white QPM inbreds constructed from GCA effects of grain yield and multiple traits (HGCAMT) using Ward's minimum variance cluster analysis across environments

21 × TZEEI 29 with an overall mean of 2047 kg ha^{-1}. Under non-stress environments the mean grain yield varied from 1806 kg ha^{-1} for TZEEQI 52 × TZEEQI 3 to 4580 kg ha^{-1} for the commercial hybrid check (TZEEI 21 × TZEEI 29) with a mean of 3024 kg ha^{-1}. The highest yielding extra-early normal endosperm hybrid check, TZEEI 21 × TZEEI 29 out-yielded the best QPM hybrid by 25 % under stress and 19 % under non-stress environments. The grain yield reduction ranged from 4–52 % for the hybrids under stress environments. The yield loss was generally associated with increased days to anthesis and ASI, poor ear and plant aspects and fewer ears per plant (Supplementary Table 2).

The AMMI biplot of the grain yield and stability of the 29 extra-early maturing QPM hybrids (top 15, worst 10 plus four checks) selected using the base index under stress environments is presented in Fig. 2. The vertical dotted line of the biplot depicts the grand mean for grain yield, while the horizontal dotted line (*y*-ordinate) represents the interaction principal component axes 1 (IPCA1) value of zero. Genotypes located close to the horizontal line have small interactions with the environments and are therefore considered to be more stable than those farther away from it while the farther a cultivar is to the right side of the grand mean line, the higher the grain yield. Therefore, extra-early QPM hybrids 5 (TZEEQI 183 × TZEEQI 7), 18 (TZEEQI 181 × TZEEQI 7) and 19 (TZEEQI 144 × TZEEQI 183) were the most stable and relatively high yielding across environments due to their closeness to the zero IPCA1 score and display of grain yield greater than the mean grain yield. Hybrids 2 (TZEEQI 7 × TZEEQI 60), 3 (TZEEQI 7 × TZEEQI 44), 7 (TZEEQI 109 × TZEEQI 134), 8 (TZEEQI 134 × TZEEQI 183) and 16 (TZEEQI 109 × TZEEQI 137) had grain yields greater than the mean grain yield across environments but had a strong positive interaction with the IPCA1 suggesting that they were adapted to high-yield environments (IK13DT, IF12LN, MK13LN, IF12OP and IF13OP). On the contrary, the normal endosperm commercial hybrid check, 28 (TZEEI 21 × TZEEI 29) and the three-way hybrid check 29 ((TZEE

Entry	Pedigree
1	TZEEQI 134 x TZEEQI 181
2	TZEEQI 7 x TZEEQI 60
3	TZEEQI 7 x TZEEQI 44
4	TZEEQI 52 x TZEEQI 1
5	TZEEQI 183 x TZEEQI 7
6	TZEEQI 183 x TZEEQI 8
7	TZEEQI 109 x TZEEQI 134
8	TZEEQI 134 x TZEEQI 183
9	TZEEQI 134 x TZEEQI 190
10	TZEEQI 144 x TZEEQI 181
11	TZEEQI 63 x TZEEQI 109
12	TZEEQI 63 x TZEEQI 101
13	TZEEQI 1 x TZEEQI 102
14	TZEEQI 60 x TZEEQI 1
15	TZEEQI 183 x TZEEQI 11
16	TZEEQI 109 x TZEEQI 137
17	TZEEQI 7 x TZEEQI 61
18	TZEEQI 181 x TZEEQI 7
19	TZEEQI 144 x TZEEQI 183
20	TZEEQI 101 x TZEEQI 137
21	TZEEQI 38 x TZEEQI 60
22	TZEEQI 44 x TZEEQI 3
23	TZEEQI 52 x TZEEQI 63
24	TZEEQI 8 x TZEEQI 52
25	TZEEQI 52 x TZEEQI 3
26	TZEEQI 2 x TZEEQI 12 (C)
27	TZEEQI 11 x TZEEQI 5 (C)
28	TZEEI 21 x TZEEI 29 (C)
29	(TZEEI 21 x TZEEI 14) x TZEEI 29 (C)

Fig. 2 AMMI biplot of grain yield and the first interaction principal component axis (IPCA 1) of 25 extra-early white QPM hybrids (best 15 and worst 10 based on the base index) and four checks evaluated across 11 environments between 2012 and 2013 in Nigeria. C = check; BG12DT = Bagauda under drought stress, 2012; IK13DT = Ikenne under drought stress, 2012/2013; IF12LN and IF13LN = Ile-Ife under low-N, 2012 and 2013; MK12LN and MO13LN = Mokwa under low-N, 2012 and 2013; IF12HN and IF13HN = Ile-Ife under high-N, 2012 and 2013; K12HN and MO13HN = Mokwa under high-N, 2012 and 2013

21 × TZEEI 14) × TZEEI 29) were identified as the highest yielding across environments but had a very strong negative interaction with IPCA1 scores indicating that they were adapted to low-yield environments (IK13DT, BG12DT, IF13LN, MK12LN, IK13OP and MK13OP). Of the 100 extra-early hybrids evaluated across drought and low nitrogen, 52 % exhibited varying levels of tolerance to stress (Table not shown).

Discussion

The significant differences detected among the inbreds and hybrids for grain yield and most measured traits under stress, non-stress and across environments indicated that there was adequate genetic variability among the inbreds and hybrids to allow good progress from selection for improvements of the traits. This result is consistent with the findings of Rosielle and Hamblin (1981), Badu-Apraku et al. (2011b) and Badu-Apraku and Oyekunle (2012). The significant

environment and GEI detected for grain yield and most measured traits under stress, non-stress and across environments indicated that the expression of the traits would differ under contrasting environments. This result corroborates the findings of Badu-Apraku et al. (2011a, b) and confirms the important role that environment plays in indentifying tolerant genotypes with favourable response to stress and non-stress conditions.

The significant GCA observed for grain yield and most measured traits under each and across environments indicated that additive gene action was important in the inheritance of grain yield and the other traits. The significant SCA effect detected for grain yield only under non-stress and across environments revealed that non-additive gene action was also important in the inheritance of grain yield under non-stress environments. The preponderance of GCA effects over SCA for grain yield and most measured traits under stress, non-stress and across environments indicated that additive gene action was more important than non-additive gene action for the traits and that

GCA was the major contributor to the heritable variation in grain yield and most of the measured traits of the QPM hybrids. The predominance of GCA over SCA effects, indicated that early generation testing may be more effective and that promising hybrids could be identified and selected mainly based on the prediction from GCA effects and that the best hybrids could be obtained by crossing the parents with the highest GCA (Baker 1978; Badu-Apraku et al. 2013). Furthermore, the preponderance of additive gene action in the present study indicated that a great potential existed for the improvement of the traits of interest through recurrent selection methods (Badu-Apraku et al. 2011b) and the identification of suitable parents for direct use or for further breeding (Simmonds 1979). This observation corroborates the findings of other studies on the inheritance of quantitative traits in QPM (Vasal et al. 1993; Bhatnagar et al. 2004). On the other hand, the result disagrees with the findings of Katsantonis et al. (1988) and Betrán et al. (2003) who reported that gene action controlling grain yield varied with the type of stress, with additive gene action more important than non-additive gene action under drought stress while non-additive gene action was more important under low-N. The non-significant SCA mean squares observed for the stay-green characteristic under stress environments indicated that non-additive gene action was not important in the inheritance of stay-green characteristic in this study. This result corroborates the findings of Badu-Apraku et al. (2013) and Ifie et al. (2015). This result however is in disagreement with the findings of Badu-Apraku et al. (2015b) who reported significant GCA and SCA effects for the stay-green characteristic under low-N. The differences in the results of the different studies could be due to the use of different genetic materials. The significant GCAm x environment and GCAf x environment effects obtained for grain yield and most measured traits under stress, non-stress and across environments indicated that the GCA of the parental inbred lines varied in the different environments. This result is consistent with the findings of Badu-Apraku et al. (2013). The authors found significant GCA × E interaction mean squares for most measured traits under different environments. The non-significant SCA for grain yield under non-stress environments and most measured traits under stress, non-stress and across environments revealed that the SCA was consistent in the different environments unlike the GCA. Similar results were reported by Ifie et al. (2015). The larger sum of squares of the GCAm compared to the GCAf for ASI under non-stress environments indicated that paternal inheritance played an important role in the inheritance of ASI under non-stress environments. However, the non-significant differences in the contributions of the GCAf and GCAm sum of squares for grain yield and most measured traits under each and across environments indicated that maternal and paternal effects played similar roles in the inheritance of the traits. Contrary to the results of this study, Derera et al. (2008) reported that maternal effects modified grain yield, ASI and ear aspect under drought as well as ASI and ear aspect under well-watered environments in maize hybrids. Similarly, Oyekunle and Badu-Apraku (2014) showed the importance of maternal effects in the inheritance of grain yield under only well-watered conditions. Also, Adebayo et al. (2014) found paternal effects for ear aspect in late and intermediate maturing single cross hybrids under drought.

Inbred lines displaying significant and positive GCA effects for grain yield are most likely to contribute favorable alleles in a recurrent selection program and could be used as parents to develop synthetic population that could be improved for drought and low-N tolerance. Alternatively, such inbred lines could be used to develop outstanding hybrids for commercialization. The significant positive GCAm effects displayed for the grain yield of inbred TZEEQI 1 and GCAf effects for grain yield of TZEEQI 7, TZEEQI 60 and TZEEQI 134 under stress indicated that the inbreds would contribute favorable alleles for grain yield under stress when used as males and females, respectively. Similarly, the positive and significant GCAm and GCAf effects displayed by TZEEQI 183 suggested that the inbreds could contribute to improved grain yield in their offspring when used either as male or female parent. The negative and significant GCAm and GCAf effects of the stay-green characteristic for TZEEQI 109 suggested that the inbred would contribute alleles that would delay leaf senescence in its progenies when used either as male or female parent. In contrast, the negative and significant GCAf effects exhibited by TZEEQI 102 indicated that the inbred would contribute to delayed leaf senescence in the progeny when used only as a female parent. The significant positive GCAm effects

displayed for grain yield by the inbreds TZEEQI 1 and TZEEQI 60 and GCAf effects by TZEEQI 109 as well as TZEEQI 137 under non-stress environment revealed that the inbreds would contribute favorable alleles for grain yield when used either as males or females under non-stress environments. Similarly, the positive and significant GCAm and GCAf effects for grain yield displayed by inbreds TZEEQI 7 and TZEEQI 134 showed that the inbreds could contribute to improved grain yield in their offspring when used either as male or female parents.

Classification of the extra-early QPM inbreds into appropriate heterotic groups is essential to maximize their potential usefulness for the development of productive hybrids and synthetic varieties and for the identification of potential extra-early QPM testers which are lacking completely in SSA. The inbreds classified into the same heterotic group in the present study may be recombined to form heterotic populations that could be improved through recurrent selection. The inbreds TZEEQI 7 and TZEEQI 134 identified as the best testers in the present study could be utilized for classifying QPM inbreds into heterotic groups, to assess the combining ability and to identify superior hybrid combinations in tropical extra-early QPM.

The grain yield reductions of 9–55 % for the extra-early inbreds and 4–52 % for hybrids under stress environments revealed that the levels of stress imposed during the evaluations were severe enough to allow effective discrimination among the inbreds and hybrids. The yield reductions recorded in the present study fall within the range reported by previous workers (NeSmith and Ritchie 1992; Badu-Apraku et al. 2005; Derera et al. 2008 and Badu-Apraku et al. 2011b).

The positive base index values recorded for TZEEQI 7, TZEEQI 60, TZEEQI 61, TZEEQI 8, TZEEQI 11, TZEEQI 137, TZEEQI 63, TZEEQI 66, TZEEQI 44 and TZEEQI 157 under stress environments suggested that these inbreds possess stress tolerant genes. These inbreds may be used as germplasm sources for introgression of genes for stress tolerance into tropical extra-early QPM populations and for the development of hybrids and synthetic varieties with combined tolerance to drought and low-N. Hybrids, TZEEI 21 × TZEEI 29 (commercial check), TZEE 21 × TZEEI 14 × TZEEI 29 (check), TZEEQI-134 × TZEEQI-181 (QPM) and

TZEEQI-7 × TZEEQI-60 (QPM) identified as the most outstanding in terms of stress tolerance should be tested extensively in multi-location trials and promoted for adoption and commercialization in the stress-prone areas of SSA.

Presently, there are no adapted extra-early maturing quality protein maize hybrids with high grain yield potential which could be of great benefit to resource poor maize farmers through increased production and improved incomes and nutrition in SSA. In the present study, the highest yielding extra-early normal endosperm hybrid check, TZEEI 21 × TZEEI 29 out-yielded the best QPM hybrid by 25 % under stress and 19 % under non-stress conditions. The lower grain yield recorded for the extra-early QPM hybrids was not surprising because the inbred lines used in the present study were selected based on only their reactions to drought and tryptophan content and had not been grouped into their respective heterotic groups before the study to facilitate the exploitation of maximum heterosis through carefully planned crosses. The results of this study is a clear indication that there is a need for more efforts and resources to be devoted to breeding more yield competitive stress tolerant extra-early QPM maize inbreds and hybrids. Nevertheless, inbred lines identified with positive and significant GCA effects for grain yield (TZEEQI 7, TZEEQI 60, TZEEQI 60, TZEEQI 109, TZEEQI 134 and TZEEQI 183) across environment in the present study could be crossed with other QPM inbred lines from different genetic sources to increase the chances of identifying more productive extra-early QPM hybrids.

The QPM hybrids, TZEEQI 183 × TZEEQI 7, TZEEQI 181 × TZEEQI 7 and TZEEQI 144 × TZEEQI 183 identified by the AMMI biplot as relatively high yielding and most stable across environments should be tested extensively for consistency of their performance and commercialized in the sub-region. However, the hybrids, TZEEQI 7 × TZEEQI 60, TZEEQI 7 × TZEEQI 44, TZEEQI 109 × TZEEQI 134, TZEEQI 134 × TZEEQI 183, TZEEQI 109 × TZEEQI 137, TZEEI 21 × TZEEI 29 and (TZEE 21 × TZEEI 14) × TZEEI 29 identified to be high yielding in specific environment could also be tested extensively in those environments and commercialized.

In conclusion, the GCA effects contributed more than 50 % (55–87 %) of the total variation among the

hybrids for grain yield and most measured traits under each and across environments suggesting that additive genetic effects were more important in the control of inheritance of the traits. The inbreds were classified into three heterotic groups based on the HGCAMT. Inbreds, TZEEQI 7 and TZEEQI 134 were identified as the best testers and could be used to group tropical extra-early QPM inbreds. Inbreds TZEEQI 7, TZEEQI 60, TZEEQI 61, TZEEQI 8, TZEEQI 11, TZEEQI 137, TZEEQI 63, TZEEQI 66, TZEEQI 44 and TZEEQI 157 possess genes for stress tolerance. These inbreds may be used as germplasm sources for introgression of genes for stress tolerance into extra-early QPM populations and for the development of hybrids and synthetic varieties with combined tolerance to drought and low-N. The QPM hybrids TZEEQI 183 × TZEEQI 7, TZEEQI 181 × TZEEQI 7 and TZEEQI 144 × TZEEQI 183 were identified as high yielding and most stable across environments. These hybrids should be tested extensively in on-farm trials and commercialized in the sub-region while efforts continue to develop extra-early QPM hybrids which are competitive with the normal endosperm extra-early hybrids.

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