View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by Elsevier - Publisher Connector

Field Crops Research 183 (2015) 169–183

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Grouping of early maturing quality protein maize inbreds based on SNP markers and combining ability under multiple environments

B. Badu-Apraku[a,*], B. Annor[a], M. Oyekunle[c], R.O. Akinwale[b], M.A.B. Fakorede[b], A.O. Talabi[a], I.C. Akaogu[a], G. Melaku[a], Y. Fasanmade[a]

[a] International Institute of Tropical Agriculture (UK) Limited, 7th Floor of Grosvenor House, 125 High Street, Croydon CR0 9XP UK
[b] Department of Crop Production and Protection, Obafemi Awolowo University, Ile-Ile, Nigeria
[c] Department of Plant Science, Ahmadu Bello University, Samaru, Nigeria

ARTICLE INFO

Article history:
Received 14 April 2015
Received in revised form 14 July 2015
Accepted 14 July 2015
Available online 14 August 2015

Keywords:
Zea mays L.
Heterotic grouping
General combining ability
Specific combining ability

ABSTRACT

Food insecurity and malnutrition are two major challenges facing rural populations in sub-Saharan Africa (SSA). Hybrids of quality protein maize (QPM) have a crucial role here to play because QPM contains increased lysine and tryptophan concentrations and has a higher biological value than the normal maize. Information on the combining ability and heterotic patterns of QPM inbreds is crucial for the success of hybrid programs in the sub-region. Ninety-one diallel crosses derived from 14 early maturing yellow-endosperm QPM inbreds were evaluated from 2010 to 2012 under *Striga* infested, drought, low-N and optimal environments in Nigeria. The objectives were to (i) examine the combining ability of the set of early yellow QPM inbreds, (ii) classify the inbreds into heterotic groups and identify the best testers (iii) compare the efficiencies of the heterotic grouping methods in classifying the inbreds and (iv) determine the grain yield and stability of the inbreds in hybrid combinations under the research environments. General (GCA) and specific (SCA) combining ability effects were important in the inheritance of grain yield and other traits of the inbreds. However, GCA was more important than SCA under each contrasting environment and across environments suggesting that the additive gene action was more important than the non-additive in the set of inbreds. The SCA effects of grain yield and the heterotic group's SCA and GCA of grain yield (HSGCA) methods classified the inbreds into three groups each, while the heterotic grouping based on GCA of multiple traits (HGCAMT) and the SNP-based genetic distance (GD) methods had two groups each across research environments. There was close correspondence among the classifications of all the grouping methods in terms of placement of inbreds into the same heterotic groups. The SNP-based method was the most efficient and was used to identify TZEQI 87 and TZEQI 91 as the best testers for the SNP-based heterotic groups 1 and 2. The hybrids, TZEQI 87 × TZEQI 93, TZEQI 77 × TZEQI 91 and TZEQI 80 × TZEQI 91 were identified as the most stable and high yielding across research environments and should be commercialized.

© 2015 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

1. Introduction

Food insecurity and malnutrition are two major challenges confronting countries in sub-Saharan Africa (SSA). Maize (*Zea mays* L.) has a critical nutritional role to play because it is the most important staple food crop with the potential to combat food insecurity presently facing the sub region. Maize is consumed daily in large quantities in various local food preparations, and provides most of the calories, protein, vitamin, and mineral intake in the diets of the poor. In addition, maize is widely fed to babies (2 to 3 months old) until they are weaned at the age of 15 to 24 months and to pre-school children (3 to 5 years old) in several countries without protein supplements. Per capita maize consumption varied from 30 to 90 kg yr^{-1} in coastal countries of WCA and rose at an average of 0.5%/year from 1977 to 1988 in WCA (National Research Council, 1988, USA).

The normal maize has a major nutritional constraint as human food because its protein (about 10%) is deficient in lysine and tryptophan, which are two essential amino acids nutritionally important for both monogastric animals and human beings (Huang et al., 2004). The lysine and tryptophan content of 1.81 and 0.35% in the protein of normal maize endosperm is less than one-half of the concentration recommended for normal human nutrition by the Food and Agriculture Organization (FAO) of

* Corresponding author. Tel.: +234 2241 2626; fax: +234 2241 222.
E-mail address: b.badu-apraku@cgiar.org (B. Badu-Apraku).

http://dx.doi.org/10.1016/j.fcr.2015.07.015
0378-4290/© 2015 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (http://creativecommons.org/licenses/by/4.0/).

the United Nations (FAO/WHO/UNU Expert Committee, 1985; FAO/WHO Expert Consultation, 1990; Prasanna et al., 2001). Consequently, infants fed on normal maize without any balanced protein supplement suffer from malnutrition and develop diseases such as Kwashiorkor. Considerable progress has been made by the International Maize and Wheat Improvement Center (CIMMYT) and the International Institute of Tropical Agriculture (IITA) in developing quality protein maize (QPM) germplasm with the opaque-2 (o2) gene, incorporated along with modifiers that contain twice the amount of lysine (>4.0%) and tryptophan (>0.8%) in the whole grain compared with normal maize (Krivanek et al., 2007). Therefore, maize cultivars combining high grain yield with elevated levels of lysine, tryptophan and the kernel structure of conventional maize have the potential to reduce food insecurity and malnutrition in the sub region.

The savannas of West and Central Africa (WCA) are characterized by low incidence of diseases and pests and high incident incoming solar radiation and therefore could contribute to the achievement of food security in the sub region. However, the agroecology is plagued by *Striga hermonthica* (Del.) Benth parasitism, recurrent drought, and low soil nitrogen (N) and to a lesser extent, lack of productive and adapted maize cultivars. *Striga* can cause total crop failure and many maize farmers in the savannas have been forced to abandon their farmlands due to severe infestation. Parasitism by *Striga* seems to have defied all cultural control options (Bebawi et al., 1984; Odhiambo and Ransom, 1994; Shaxson and Riches, 1998). The use of host plant resistance is considered the most economically feasible and sustainable approach for reducing the effects of *Striga* (DeVries, 2000).

Global warming and its associated effects have changed weather patterns in SSA leading to erratic and unreliable amount and distribution of rainfall, resulting in recurrent drought (Badu-Apraku et al., 2011a). Drought can reduce grain yield of maize by as much as 90% when it occurs at the most sensitive stage of the crop growth i.e. a few days before anthesis to the beginning of grain filling (NeSmith and Ritchie, 1992). Badu-Apraku et al. (2004) reported a grain yield loss of 53% under drought stress and 42% under *Striga* infestation. Consequently, breeding for early maturing cultivars with better tolerance to drought and resistance to *Striga* is crucial to improve productivity and ensure stable maize production in WCA.

Nitrogen is a major requirement for high levels of maize productivity but it is the most limiting nutrient in tropical soils. A fertilizer rate of 90–120 kg N ha^{-1} is recommended for increased maize grain yield in SSA. However, fertilizer application rates are still far below the recommended doses in the sub region due to the unavailability or the exorbitant prices of inorganic fertilizer for resource-poor farmers. The estimated annual loss of maize yield due to low-N stress varies from 10 to 50% per year in SSA (Logrono and Lothrop, 1997). Breeding for tolerance to low-N offers the most economical and sustainable approach for increased maize yields in WCA.

Under field conditions, drought, *Striga*, and soil nutrient deficiencies can occur simultaneously and the combined effect can be devastating (Cechin and Press, 1993; Kim and Adetimirin, 1997). Bänziger et al. (2006) reported that drought and low-N are the most important stress factors that most frequently limit maize production, food security, and economic growth in SSA. Weber et al. (2012) indicated that complex interactions often occur among the stresses, such as drought hindering nutrient up-take, indicating the need to develop genotypes tolerant to these conditions. The development and use of germplasm with tolerance to multiple stresses are therefore crucial for increased productivity and sustainable maize production in SSA.

A large number of QPM inbred lines have been developed in the IITA Maize Program. However, there are no commercial early maturing QPM hybrids. An important requirement for a hybrid program to be commercially successful is the availability of information on the mode of inheritance, combining ability and heterotic patterns among the inbreds in the program. Results of the evaluation of single-cross hybrids derived from 14 early-maturing QPM inbred lines under well-watered, drought stress and low-N conditions in Eastern Africa showed significant mean squares of GCA for grain yield and other agronomic traits whereas SCA mean squares were not significant (Musila et al., 2010). This suggested that additive gene action for grain yield and other agronomic traits was the most important contributor to the heritable variation in agronomic traits in these genotypes. Results of other studies have indicated preponderance of additive over nonadditive gene action (Vasal et al., 1993a,b; Bhatnagar et al., 2004; Musila et al., 2010; Wegary et al., 2013). However, such important information is completely lacking on the gene action conditioning the grain yield of IITA's early QPM inbreds under drought, low-N or *Striga* infestation. There is, therefore, a need to study the genetics of the inheritance of grain yield and other traits of the IITA early-maturing QPM inbreds under the three stress conditions.

Classification of inbreds into heterotic groups is essential not only for maximizing their potential usefulness in the development of productive hybrids and synthetics but also for creating new heterotic groups. However, the heterotic patterns and the extent of diversity in the *Striga* resistant early QPM germplasm in the IITA Maize Program have not been determined. Furthermore, no early QPM inbred testers appropriate for developing stress-tolerant hybrids are available in SSA. Information on heterotic groups and the identification of testers in the early QPM inbreds would be invaluable to the hybrid program at IITA and the national programs in the sub region.

The objectives of the present study were to (i) examine the combining ability for grain yield and inheritance patterns of the set of tropical early QPM yellow inbreds (ii) classify the inbreds into heterotic groups using the SCA effects of grain yield, HSGCA, the HGCAMT and the molecular-based GD methods and identify the best testers; (iii) compare the efficiencies of the heterotic grouping methods in classifying the inbreds and (iv) determine the performance and stability of the inbreds in hybrid combinations under multiple environments.

2. Materials and methods

2.1. Conversion of normal endosperm maize inbreds to QPM

In an effort to mitigate the effects of the major constraints on maize production and productivity in WCA, since 1980 IITA has developed high yielding early and extra-early *Striga* resistant and/or drought and low-N tolerant normal endosperm populations, varieties, hybrids, and inbred lines. The strategy for converting normal inbreds into QPM focused primarily on crossing elite inbred lines to QPM donor sources to obtain materials with the opaque-2(o2) gene followed by repeated selfing with the selection of minor gene modifiers for kernel quality. Details on the procedure adopted in developing the 14 *Striga* resistant and/or drought tolerant early yellow maturing QPM inbreds have been described by Badu-Apraku et al. (2010). Briefly, 15 normal endosperm elite inbred lines, *Striga* resistant and/or drought tolerant were crossed to the broad-based early yellow QPM source population, Pool 18 SR in 2003, in an effort to introgress *Striga* resistance and drought tolerance genes into the early yellow QPM population and subsequently, to extract *Striga* and drought tolerant QPM inbreds. The F_1 crosses were backcrossed to the inbred parents during the major season of 2005 in Ibadan, Nigeria to obtain BC_1. The BC_1 ears were screened under the light box and kernels with the desirable endosperm modification were selected and advanced to the BC_2 stage during the dry season of 2005. The selection for the appropriate

Table 1
Grain yield and other characteristics of the 14 early maturing yellow quality protein maize inbred lines evaluated under drought, low-N and *Striga* infested environments in Nigeria between 2011 and 2012.

S/N	Inbred	Pedigree	Grain yield (kg/ha)				Tryptophan	Protein	Tryptophan content per whole maize protein
			DT	LN	STR	ACR		%	
1	TZEQI 74	TZE COMP5-Y C6S6 Inb 10 × Pool 18 SR QPM BC1S6 2-2-1-1	436	1781	1004	1253	0.086	13.56	0.638
2	TZEQI 76	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 11-39-2-2-2-8	267	1812	2082	1500	+	+	+
3	TZEQI 77	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 11-39-2-2-4-8	456	1439	1422	1198	+	+	+
4	TZEQI 78	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 11-39-2-2-6-8	176	1353	1061	1000	0.083	14.18	0.584
5	TZEQI 79	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 11-39-2-2-8-8	567	1773	1443	1391	0.086	13.33	0.646
6	TZEQI 80	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 2-3-1-1	605	1232	1131	1054	0.095	12.59	0.752
7	TZEQI 81	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 2-3-1-1-4-6	436	1125	3083	1449	0.086	14.14	0.608
8	TZEQI 82	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 2-3-1-1-4-6	642	1595	1262	1276	0.072	13.36	0.542
9	TZEQI 84	TZE COMP5-Y C6S6 Inb 25 × Pool 18 SR QPM BC1S6 4-5-1-1-2-5	356	1192	1087	957	0.074	13.81	0.532
10	TZEQI 87	TZE COMP5-Y C6S6 Inb 31B × Pool 18 SR QPM BC1S6 7-45-2-3-4-7	226	1320	1758	1158	0.095	16.79	0.566
11	TZEQI 89	TZE-Y Pop STR C0 S6 Inb 16 2-3 × Pool 18 SR QPM BC1S6 2-4-1-1-2-8	1232	1419	492	1134	0.076	12.47	0.611
12	TZEQI 91	TZE-Y Pop STR C0 S6 Inb 142 × Pool 18 SR QPM BC1S6 4-35-5-8-4-8	513	1329	747	984	0.070	12.89	0.541
13	TZEQI 92	TZE-Y Pop STR C0 S6 Inb 142 × Pool 18 SR QPM BC1S6 4-35-5-8-8-8	347	1372	723	958	0.068	11.29	0.606
14	TZEQI 93	TZE-Y Pop STR C0 S6 Inb 142 × Pool 18 SR QPM BC1S6 4-35-5-8-7-8	465	980	669	786	0.072	10.97	0.655
	Lsd (0.05)		405	417	839	311			

DT is the Drought environment; LN is the low-N environment; STR is the *Striga* infested environment; ACR is the across research environments; + is the missing values.

endosperm modification during the conversion program was based on a rating scale of 1–5 where 1 = kernels completely translucent with no opaqueness; 2 = 25% opaqueness; 3 = 50% opaqueness; 4 = 75% opaqueness; 5 = 100% opaqueness. The kernels with a score of 2–3 were selected and advanced to the S_2 stage by selfing (Vivek et al., 2008; Badu-Apraku and Lum, 2010). The BC_2 kernels with the desirable endosperm modification were selected under the light box and advanced to the BC_2S_3 stage through three generations of selfing between 2006 and 2008 while screening under the light box for the desirable endosperm modification after each cycle of selfing. Five hundred BC_2S_3 early maturing yellow QPM inbred lines selected from the conversion program were planted at Ikenne during the 2008/2009 dry season for screening for drought tolerance. Based on the results, 270 drought tolerant lines were selected and evaluated under *Striga* infestation at Mokwa during the 2009 growing season. Selected BC_2S_3 lines of the early QPM were advanced to the S_4 and S_5 stages. Based on the results of the *Striga* evaluations, the best 30 lines of the early yellow QPM inbreds were selected and advanced to the S_6 stage during the 2010 growing season. A total of 22 of the 30 yellow grained inbreds were given TZEQ designations and analyzed for lysine and tryptophan contents at the IITA Nutrition Laboratory in August, 2010. The best 14 yellow endosperm QPM lines were selected based on their superior performance under drought and well-watered conditions as well as the tryptophan content for this study (Table 1).

2.2. Generation of diallel crosses

The 14 yellow QPM inbreds selected for the present study were planted during the dry season of 2010 in the breeding nursery of IITA at Ibadan, Nigeria. All possible crosses were made among the inbred lines using the diallel mating scheme to produce 91 single-cross hybrids without the reciprocals. The diallel crosses plus nine hybrid checks were used for the present study.

2.3. Field evaluations

Four field experiments were conducted between 2010 and 2012 (Table 2). In the first experiment, there were two set of trials; the inbred and hybrid trials. The inbred trial consisted of 100 early white and yellow QPM inbreds (including the 14 inbreds used in the diallel crosses). The hybrid trial comprised 91 single-cross QPM hybrids generated from diallel crosses involving 14 early yellow QPM inbred lines plus nine early maturing, drought tolerant, and *Striga* resistant open-pollinated varieties and normal endosperm hybrid checks. The inbreds and single cross hybrids plus the checks (hereafter referred to as hybrid trials) were evaluated separately in field trials under induced moisture stress during the dry seasons of 2010/2011 and 2011/2012 at Ikenne (6°53′N, 30°42′E, 60 m altitude, 1200 mm annual rainfall). Early maturing open-pollinated varieties and normal endosperm hybrids were used as checks for the hybrid trials because at the time of this experiment, there were no early maturing QPM hybrids that combined drought tolerance at flowering and grain-filling with *Striga* resistance to serve as checks. Drought was induced for both the inbred and hybrid trials by withdrawing irrigation water from 28 days after planting (DAP) until maturity so that the maize plants relied on water stored in the soil for growth and development. During the first 3 weeks of growth, the plants were irrigated using a sprinkler system, which provided 17 mm of water each week. The soil at the experiment station at Ikenne is eutric nitrosol (FAO classification, 2006) and the experimental fields are flat and fairly uniform, with high water-holding capacity. A total of 60 kg N ha^{-1}, 60 kg P ha^{-1} and 60 kg K ha^{-1} was applied at planting with an additional 60 kg N ha^{-1} top-dressed at 4 weeks after planting (WAP).

In the second experiment, the inbred and hybrid trials were evaluated under artificial *Striga* infestation at Mokwa (9°18′N, 5°4′E, 457 m altitude, 1100 mm rainfall) and Abuja (9°16′N 7°20′E, 300 m altitude, 1500 mm rainfall) in the southern Guinea savanna of

Table 2
Summary information on the four experiments conducted in this study.

Experiment	Year	Location	Genetic materials	Study conditions
1	2010–2012	Ikenne	Set A: 100 white and yellow QPM inbreds Set B: 91 single cross hybrids + 9 OPVs	Induced drought
2	2011–2012	Mokwa and Abuja	Set A: 100 white and yellow QPM inbreds Set B: 91 single cross hybrids + 9 OPVs	Artificial *Striga* Infestation
3	2011–2012	Mokwa and Ile-Ife	Set A: 100 white and yellow QPM inbreds Set B: 91 single cross hybrids + 9 OPVs	Low soil N
4	2011–2012	Mokwa and Ikenne	Set B: 91 single cross hybrids + 9 OPVs	Optimal

Nigeria in 2011 and 2012. Infestation with *Striga* was done according to the method of Kim (1991) and Kim and Winslow (1991). *Striga hermonthica* seeds collected from sorghum fields in the preceding season and stored for at least 6 months were used. Ethylene gas was injected into the soil 2 weeks before artificial infestation to stimulate suicidal germination of existing *Striga* seeds. Fertilizer application was delayed until about 21–25 DAP when 30 kg ha^{-1} each of N, P, and K were applied as NPK 15–15–15. Weeds other than *Striga* were controlled by hand weeding.

In the third experiment, the inbreds and the single-cross hybrids plus the checks were planted separately in low-N (30 kg N ha^{-1}) environments at Mokwa and Ile-Ife (7°28′N 4°33′E, 244 m altitude, 1200 mm rainfall) during the 2011 and 2012 major growing seasons. The soil at Mokwa is a luvisol (FAO classification, 2006) with 0.27, 0.04 and 0.48% organic carbon, organic nitrogen and phosphorus content (by volume). On the other hand, the soil at Ile-Ife is characterized as Alfisol (Soil Survey Staff, 1999) with 0.084% organic nitrogen. The experimental fields had been depleted of N by planting maize for several years and removing the biomass after each harvest. Soil samples were taken before planting in all the test environments and N content was determined at IITA's Analytical Services Laboratory, Ibadan, by the Kjeldahl digestion and colorimetric method (Bremner and Mulvaney, 1982). Fertilizers were applied to bring the total available N to 30 kg N ha^{-1} at 2 WAP. Also, single superphosphate (P_2O_5) and muriate of potash (K_2O) were each applied to the low-N blocks at the rate of 60 kg ha^{-1}.

In the fourth experiment, the single-cross hybrids plus the checks were evaluated under optimal growing environments at Mokwa in 2011 and Ikenne in 2011 and 2012 during the normal growing season in Nigeria. The optimal environments consisted of the environments where water and nitrogen (90 kg N ha^{-1}) were not limiting. These trials received 60 kg N ha^{-1}, 60 kg P ha^{-1} and 60 kg K ha^{-1} at 2 WAP with an additional 60 kg N ha^{-1} top-dressed at 4 WAP.

A 10 × 10 randomized incomplete-block design with two replications was used in each of the four experiments for both the inbred and hybrid trials. The experimental units were single-row plots, each 4 m long with spacing of 0.75 m between two adjacent rows and 0.40 m between plants within the row in all trials. Three seeds were planted per hill, and the seedlings were later thinned to two per hill about 2 weeks after emergence to give a final population density of about 66,000 plants ha^{-1}. All experiments except those under *Striga* infestation were kept weed-free with the application of Atrazine and Gramoxone, respectively as pre- and post-emergence herbicides at 5 L/ha each of Primextra and Paraquat, and subsequently, by hand weeding.

2.4. Data collection

In the drought, low-N and optimal experiments, data were recorded for days to 50% silking, and days to anthesis as the number of days from planting to when 50% of the plants had emerged silks and had shed pollen. The anthesis-silking interval (ASI) was calculated as the difference between days to 50% silking and 50% anthesis. Plant and ear heights were measured as the distance from the base of the plant to the height of the first tassel branch and the node bearing the upper ear. Root lodging (the percentage of plants leaning more than 30° from the vertical), and stalk lodging (the percentage of plants broken at or below the highest ear node) were recorded. Stay-green characteristic was recorded for both the drought-stress and low-N experiments at 70 DAP on a scale of 1 to 9, where 1 = almost all leaves green and 9 = virtually all leaves dead. Plant aspect was recorded on a scale of 1 to 5 based on general plant type, where 1 = excellent plant type and 5 = poor plant type. Husk cover was rated on a scale of 1 to 5, where 1 = husks tightly arranged and extended beyond the ear tip and 5 = ear tips exposed. Ear aspect was based on a scale of 1 to 5, where 1 = clean, uniform, large, and well-filled ears and 5 = ears with undesirable features. Number of ears per plant (EPP) was computed by dividing the total number of ears harvested per plot by the number of plants in a plot. For trials conducted under drought and low-N, harvested ears from each plot were shelled to determine the percentage grain moisture. Grain yield in kg ha^{-1} was computed from the shelled grain weight, adjusted to 15% moisture. For the optimal and *Striga* experiments, a shelling percentage of 80% was assumed for all cultivars and grain yield (obtained from ear weight and converted to kg ha^{-1}) was adjusted to 15% moisture.

The observations made in the *Striga* experiment were the same as those outlined for the drought experiment except that no data were taken on the stay-green characteristic and plant aspect. In addition, host plant damage syndrome rating (Kim, 1991) and emerged *Striga* counts were taken at 8 and 10 WAP (56 and 70 DAP) in the *Striga* infested plots. *Striga* damage syndrome ratings were scored per plot on a scale of 1–9 where 1 = no damage, indicating normal plant growth and high resistance, and 9 = complete collapse or death of the maize plant, i.e., highly susceptible (Kim, 1991). Even though data were collected on several traits, only those on the most important traits in the studies are presented in the results.

2.5. SNP marker assays

2.5.1. DNA extraction

Samples of young leaves were taken from 8 to 10 seedlings in the field at 2 WAP, bulked and freeze-dried for DNA extraction. Genomic DNA was extracted using a modified CTAB protocol of Saghai-Maroof et al. (1984). The quality of the DNA for genotyping by sequencing (GBS) was ascertained by digesting the DNA with restriction enzyme HindIII. The digested DNA was then transferred into a 96 well plate, properly sealed with rubber plate covers, and sent to the Institute for Genomic Diversity of Cornell University, Ithaca, NY for genotyping.

2.5.2. Genotyping with SNP

Genotype-by Sequencing (GBS) libraries were prepared and analyzed as described by Elshire et al. (2011), using the enzyme ApeKI for digestion and creating a library with unique barcodes for each genotype. Raw reads from the sequenced GBS library were called in the GBS analysis pipeline TASSEL version 3.0.147, an extension to the Java program TASSEL (Bradbury et al., 2007). The filtered sequences were aligned to the maize reference genome B73 RefGen

v1 (Schnable et al., 2009) using the Burrows–Wheeler alignment tool. This procedure provided 143,415 SNPs covering all the ten chromosomes of the maize genome. Out of these, 1451 SNP loci, having not less than 0.05 allele frequency and no missing value, were selected using TASSEL version 4.1.12 and used to analyze the genetic diversity of the inbred lines in the current study. The use of less stringent filtering criteria by allowing some percentage of missing data resulted in more SNPs but the grouping (phylogeny) did not change when larger number of SNPs were used (data not shown). The distribution of the SNP loci on the 10 maize chromosomes (ch) was 232 in ch1, 172 in ch2, 177 in ch3, 169 in ch4, 167 in ch5, 95 in ch6, 143 in ch7, 133 in ch8, 81 in ch9 and 82 in ch10.

2.6. Statistical analysis

Separate analyses of variance (ANOVA) were performed on data collected across years and locations under each research condition with PROC GLM in SAS using a RANDOM statement with the TEST option (SAS Institute, 2011). Subsequently, combined ANOVA were carried out across all 13 test environments. In the combined ANOVA, environment, replicate within environment, and block within replicate × environment interaction were regarded as random factors whereas entries (91 hybrids and nine checks) were treated as fixed effects. Means were separated using the LSD.

General combining ability (GCA) effects of the parents and specific combining ability (SCA) effects of the crosses, as well as their mean squares in each environment and across environments, were estimated on the 91 diallel crosses, excluding the checks, following Griffing's method 4 model 1 (fixed model) (Griffing, 1956) and the DIALLEL-SAS program developed by Zhang et al. (2005) adapted to SAS software version 9.3 (SAS Institute, 2011). The GCA and SCA effects were tested for significance using *t*-test. The standard errors of the GCA and SCA effects were estimated as the square root of the GCA and SCA variances (Griffing, 1956). The relative importance of GCA and SCA was investigated using the method of Baker (1978) as modified by Hung and Holland (2012).

To assign inbred lines into heterotic groups under *Striga* infestation, drought stress, low-N and optimal growing environments, the heterotic group's specific and general combining ability (HSGCA) method proposed by Fan et al. (2008) was used. Also, heterotic grouping based on GCA of multiple traits (HGCAMT) grouping method proposed by Badu-Apraku et al. (2013), the SCA method and Genetic Distance (GD) from SNP markers were adopted for the grouping of the inbreds. Grouping by the HGCAMT method was achieved by standardizing the GCA effects (mean of zero and standard deviation of 1) of the traits that had significant mean squares for G under each study conditions using the following statistical model:

$$Y = \sum_{i=1}^{n} \left(\frac{\left(Y_i - \bar{Y}_i\right)}{s} \right) + \varepsilon_{ij}$$

where *Y* is HGCAMT, which is the genetic value measuring relationship among genotypes based on the GCA of multiple traits *i* to *n*; Y_i is the individual GCA effect of genotypes for trait $_i$, $\bar{Y}_i$ is the mean of GCA effects across genotypes for trait *i*, *s* is the standard deviation of the GCA effects of trait *i* and ε_{ij} is the residual of the model associated with the combination of inbred *i* and trait *j*.

The 14 inbreds were subsequently assigned to heterotic groups based on the Euclidean distance generated from HGCAMT, HSGCA, SCA and SNP-based GD. Ward's minimum variance cluster analysis based on the SNP markers were used to assign the inbred lines to heterotic groups under each contrasting environment and across environments using SAS software version 9.3 (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. To compare the efficiency of the four heterotic grouping methods, the 91 hybrids were arranged from the highest to the lowest based on grain yield under drought, low-N, *Striga*, optimal and across research environments using the method proposed by Fan et al. (2009). The procedure involved the division of the total number of hybrids for each method into two major groups i.e., inter-group and within-group crosses. These two groups were subsequently divided into high yielding hybrids (Yield of group 1 with a mean grain yield ranking among the first 30); intermediate yielding hybrids (Yield group 2 with a mean grain yield between the 31st and the 60th) and low yielding hybrids (Yield group 3 with a mean grain yield between the 61st and the 91st).

In order to obtain information on the performance and yield stability of the single-cross hybrids across the research environments, the yield data were subjected to the additive main effects and multiplicative interaction (AMMI) analysis to assess relationships among cultivars, environments and G × E. The AMMI model was described by Zobel et al. (1988). The model uses principal component analysis to decompose the multiplicative effects (G × E) into a number of interaction principal component axes (IPCAs). The genotype main effect plus G × E interaction (GGE) Windows application software that fully automates biplot analysis (Yan, 2001) was used. The AMMI model equation proposed by Sadeghi et al. (2011) was adopted.

The allele frequency, gene diversity, heterozygosity, polymorphic information content (PIC) and pair-wise Roger's (1972) genetic distance estimates among the inbred lines were computed using PowerMarker version 3.25 (Liu and Muse, 2005).

3. Results

3.1. Analyses of variance and combining ability estimates of grain yield and other traits

Results from the combined analyses of variances (ANOVA) of the genotypes evaluated under drought showed significant genotype (G) and environment (E) effects for all measured traits except E for plant height, ear height and EPP and the G for plant height and husk cover (Table 3). However, no significant differences were observed for the genotype × environment interaction (GEI) mean squares for most measured traits except for grain yield, ear aspect, EPP and husk cover. Under low soil-N environments, the ANOVA combined across two locations and years revealed that mean squares due to G, E, and GEI were significant for all traits except GEI for the stay-green characteristic (Table 3). Similarly, mean squares due to G, E, and GEI under *Striga* infestation were significant for all traits except G for husk cover, *Striga* damage rating at 8 WAP and number of emerged *Striga* plants at 10 WAP and the GEI for ear height, husk cover, *Striga* damage rating at 10 WAP and number of emerged *Striga* plants at 10 WAP. Under optimal growing conditions (well-watered and high soil-N conditions) and across all the four research environments, significant mean squares were detected for G, E, and GEI for all measured traits except E for ear height under optimal conditions (Table 3).

Partitioning of the genotypic mean squares into its components revealed that GCA and SCA mean squares were significant for most traits under drought, low-N, *Striga* infested, optimal, and across test environments (Table 3). However, GCA mean squares for plant height and husk cover as well as SCA mean squares for ASI, plant height and the stay-green characteristic were not significant under drought. Furthermore, there was no significant GCA mean squares for the stay-green characteristic under low-N and the SCA for EPP, husk cover, *Striga* damage at 8 WAP and the number of emerged *Striga* plants at 10 WAP under *Striga* infested

Table 3
Mean squares from the ANOVA of grain yield and other agronomic traits of 91 early maturing yellow-endosperm QPM hybrids evaluated under drought, low-N and optimal environments between 2010 and 2012 in Nigeria.

Source of variation	Df	Grain yield (kg ha^{-1})	Days to anthesis	Days to silk	ASI	Plant height (cm)	Ear height (cm)	Plant aspect	Ear aspect	Ears per plant	Husk cover	LFDTH
Drought environments												
Block/(E × Rep)	36	688,060.6*	8.2*	19.8**	7.1**	2484.9	265.7**	0.4**	0.2	0.06**	0.2**	0.7**
Rep/E	2	3277,172.4**	31.0**	22.9	4.1	4511.6	1116.3**	0.5	0.6**	0.03	0.4*	0.3
Environment (E)	1	13322,380.1**	276.1**	609.5**	65.2**	132.5	34.2	46.1**	11.6**	0.04	6.3**	5.0**
Entry (G)	90	2127,949.2**	13.1**	27.2**	6.4**	2590.3	376.8**	0.4**	0.8**	0.13**	0.3	0.8*
GCA	13	5626,504.1**	27.5**	67.1**	14.3**	2566.7	1254.7**	0.8**	2.1**	0.35**	0.2	2.5**
SCA	77	1535,366.8**	10.5**	20.3**	5.1	2575.7	228.4**	0.3**	0.6**	0.10**	0.3*	0.5
G × E	90	920,096.7**	4.5	9.5	3.9	2669.0	188.2	0.2	0.3*	0.05**	0.2*	0.5
GCA × E	13	1381,297.3**	5.1	8.2	3.3	2897.7	279.9	0.3	0.5**	0.10**	0.2	0.6
SCA × E	77	842,136.2**	4.4	9.6	4	2609.5	151.8	0.1	0.2	0.04	0.2	0.5
Error	180	465,230.8	3.7	8.5	4.7	2403.2	145.3	0.2	0.2	0.03	0.1	0.5
Low soil nitrogen environments												
Block/(E × Rep)	72	2933,062.2**	5.1**	10.3**	2.9**	303.2**	173.7**	0.5**	0.4**	0.02**	0.3**	2.2**
Rep/E	4	2454,747.0	5.2*	9.3	2.1	1243.2**	270.9*	0.5*	0.2	0.05**	0.3	3.3**
Environment (E)	3	85266,017.2**	979.6**	642.3**	37.7**	32,415.7**	6810.8**	25.8**	8.4**	0.22**	78.4**	50.7**
Entry (G)	90	7627,859.7**	8.1**	19.3**	5.9**	1218.7**	834.0*	1.5**	1.5**	0.08**	0.4**	1.5**
GCA	13	17872,507.0**	9.1**	31.1**	17.1**	3407.9**	2997.5**	4.2**	3.3**	0.16**	0.6**	1.3
SCA	77	5836,896.4**	7.9**	16.8**	3.9**	837.8**	440.5**	1.1**	1.1**	0.07**	0.4**	1.5**
G × E	270	2045,726.2**	3.8**	5.8**	2.1*	317.3**	216.2**	0.4**	0.3**	0.02**	0.2**	0.8
GCA × E	39	2353,435.3**	3.7**	4.7	2.5*	459.7**	345.4**	0.5**	0.4**	0.03**	0.4**	0.6
SCA × E	231	1961,018.8**	3.4**	5.7**	2.0	291.9**	188.6**	4.0	0.3**	0.02**	0.2*	0.8
Error	360	1166,818	2.2	4.2	1.7	152.3	96.1	0.2	0.2	0.01	0.2	0.8
Optimal environments												
Block(E × Rep)	54	656,564.3**	4.3**	5.1**	1.0	208.3**	138.1**	0.3*	0.2**	0.02	0.1	
Rep(E)	3	607,453.9	12.4**	3.0	3.4*	160.9	77.0	0.1	0.2	0.01	0.4*	
Environment (E)	2	292648,083.3**	176.2**	48.0**	43.0**	3369.6**	142.6	16.8**	47.0**	1.64**	3.2**	
Entry	90	8431,899.9**	11.7**	24.0**	4.9**	859.8**	645.4**	2.4**	1.1**	0.09**	0.9**	
GCA	13	23996,188.6**	16.2**	49.1**	13.3**	2828.2**	2413.9**	7.2**	3.2**	0.29**	2.3**	
SCA	77	5744,077.1**	10.9**	19.4**	3.2**	520.5**	342.9**	1.6**	0.8**	0.06**	0.6**	
G × E	180	2268,630.5**	4.1**	6.9**	2.3**	262.0**	220.3**	0.6**	0.4**	0.04**	0.3**	
GCA × E	26	3447,977.7**	3.8**	8.5**	2.7**	404.5**	372.0**	0.7**	0.7**	0.08**	0.6**	
SCA × E	154	2058,307.8**	4.0**	6.3**	2.2**	237.0**	193.7**	0.5**	0.4**	0.03**	0.3**	
Error	270	442,699	1.967236	2.6	1.2	124.1	91.4719	0.2	0.1	0.02	0.1	

*, ** Is the significance at 0.05 and 0.01 probability levels, respectively; Rep is the replication; ASI is the Anthesis-silking interval; LFDTH is the stay-green characteristic.

environments (Tables 3 and 4). The GCA × E interaction effect was significant for all traits under low-N, optimal, *Striga* infested conditions and across test environments except for days to silking and the stay-green characteristic under low-N and ear height, ear aspect, and emerged *Striga* plants at 10 WAP under *Striga* infestation. Moreover, under drought conditions, significant mean squares were observed for GCA × E interaction for grain yield, ear aspect, and EPP. Furthermore, significant SCA × E interaction was observed under low-N, optimal, and across research environments for most traits except ASI, plant aspect, and the stay green characteristic under low-N and ear height across research environments. The SCA × E interaction was significant only for grain yield under drought and for grain yield, days to silking, ASI, and *Striga* damage rating at 8 WAP under artificial *Striga* infestation.

The proportions of GCA effects of inbreds for grain yield and other measured traits were larger than those of the SCA effects under all contrasting environments (Fig. 1). The relative importance of GCA to SCA effects for grain yield and most other measured traits increased from stress to non-stress environments. Significant positive GCA effects for grain yield were observed for TZEQI 89, TZEQI 91, TZEQI 92 and TZEQI 93 under drought, low-N, and optimal environments, TZEQI 78, TZEQI 87, TZEQI 91 and TZEQI 92 under *Striga* infestation, and TZEQI 87, TZEQI 89, TZEQI 91, TZEQI 92, and TZEQI 93 across research environments (Table 5). Significant negative GCA effects for the stay-green characteristic were detected for inbreds TZEQI 82 and TZEQI 87 under drought environment and for only TZEQI 87 under low-N. Under *Striga* infested conditions, significant negative GCA effects for *Striga* damage at 10 WAP were observed for inbreds TZEQI 87 and TZEQI 92. Also, TZEQI 84 showed significant negative GCA effects for emerged *Striga* plants at 8 and 10 WAP (Table 5).

3.2. Groupings of inbreds and relationships among heterotic grouping methods

Results of the grouping of the 14 early maturing yellow QPM inbreds using dendrograms constructed based on the SCA, HSGCA, HGCAMT and SNP markers are presented in Table 6. The SCA effects of the grain yield method classified the inbreds into three heterotic groups each under drought, optimal growing conditions, and across research environments but four under low-N and *Striga* infested environments. In contrast, the HSGCA method identified three groups each under drought, low-N, *Striga* infested, optimal growing conditions, and across research environments. The HGCAMT identified two groups each under drought, low N, and across research environments and three groups each under *Striga* and optimal growing conditions. Furthermore, the SNP-based GD method classified the inbreds into two heterotic groups across research environments. In general, there was close correspondence in the classification of the inbreds into heterotic groups based on the different grouping methods (Table 6).

3.3. Comparison of the efficiencies of the SCA, HSGCA, HGCAMT and SNP-based GD methods and the identification of testers across test environments

The breeding efficiency was defined as the percentage of superior high yielding hybrids obtained across the total number of

Table 4
Mean squares from the combined analysis of variance of grain yield and other agronomic traits of 91 early maturing yellow endosperm QPM hybrids evaluated under *Striga* infestation and across test environments between 2010 and 2012 in Nigeria.

Source of variation	Df	Grain yield (kg ha^{-1})	Days to anthesis	Days to silk	ASI	Plant height(cm)	Ear height(cm)	Ear aspect	Ears per plant	Husk cover	*Striga* damage rating		*Striga* emergence count	
											8 wk	10 wk	8 wk	10 wk
Striga infestation														
Block(E × Rep)	72	1484,194.3**	3.9**	5.8**	1.8*	292.3**	196.2*	0.9**	0.02**	0.4**	1.1**	2.2**	0.8**	0.8**
Rep/E	4	9685,207.5**	3.3	13.0**	7.0**	2644.2**	2698.6**	2.9**	0.16**	0.7*	6.1**	10.7**	3.1**	2.8**
Environment (E)	3	82481,958.3**	692.2**	942.8**	48.2**	55,290.6**	8036.7**	32.8**	0.51**	62.2**	481.1**	225.6**	147.2**	98.2**
Entry (G)	90	4314,640.9**	9.4**	17.5**	3.5**	730.6**	432.4**	1.8**	0.04**	0.4	0.8	1.8**	0.9**	0.5
GCA	13	5236,316.6**	13.8**	41.1**	11.6**	2263.0**	1054.3**	2.5**	0.12**	0.9**	1.6**	3.4**	1.3**	0.6
SCA	77	3762,091.8**	8.3**	12.2**	1.9*	458.3**	318.4**	1.6**	0.02	0.3	0.6378	1.4**	0.8**	0.4
G × E	270	1576,760.8**	2.8**	4.6**	2.0**	221.5*	161.4	0.7**	0.02*	0.4	0.7**	1.1	0.7*	0.5
GCA × E	39	2057,373.2**	4.5**	6.1**	3.4**	301.6**	114.51	0.6	0.04**	0.5**	0.7*	2.0**	0.9*	0.5
SCA × E	231	1467,832.7**	2.4	4.2**	1.7*	207.33	105.03	0.4	0.02	0.2	0.7*	1.0	0.6	0.5
Error	360	745,750.0	2.1	3.2	1.4	174.5	138.1	0.5	0.01	0.2	0.5	0.9	0.5	0.4
Across environments														
Block(E × Rep)	234	1616,526.0**	5.0**	9.2**	2.8**	629.7**	186.5**	0.5**	0.03**	0.3				
Rep/E	13	4379,733.0**	10.3**	11.1**	4.2*	1927.3**	970.3**	0.9**	0.07**	0.4**				
Environment (E)	12	167161,301.0**	642.4**	1023.1**	2.3**	66,165.8**	15,315.3**	197.5**	2.26**	300.5**				
Entry (G)	90	16924,012.0**	28.6**	63.8**	12.8**	2931.9**	1698.5**	3.9**	0.16**	0.9**				
GCA	13	36972,713.0**	44.2**	146.9**	44.0**	8017.1**	6537.7**	8.8**	0.41**	1.8**				
SCA	77	13194,069.7**	25.6**	47.6**	6.8**	2061.2**	852.3**	3.0**	0.12**	0.8**				
G × E	1080	1825,263.0**	3.9**	6.5**	2.4**	606.4**	199.1**	0.4**	0.04**	0.3**				
GCA × E	156	3105,706.8**	5.0**	8.3**	3.2**	753.3**	298.9**	0.6**	0.08**	0.5**				
SCA × E	924	1577,472.4**	3.5**	6.1**	2.3*	576.0*	158.19	0.4**	0.03**	0.2**				
Error	1170	762,218.0	2.3	4.2	2.0	498.9	113.7	0.2	0.02	0.2				

*, ** Is the significance at 0.05 and 0.01 probability levels, respectively; Rep is the replication; ASI is the anthesis-silking interval.

Table 5
General combining ability (GCA) effects for grain yield and other agronomic traits of the 14 early maturing yellow-endosperm QPM inbred lines evaluated in diallel crosses under drought, low-N, *Striga* infestation, optimum conditions and across test environments between 2011 and 2012 in Nigeria.

Inbred	Grain yield (kg ha^{-1})					Days to silk					Anthesis silking interval					Plant aspect		
	DT	LN	OPT	STR	ACR	DT	LN	OPT	STR	ACR	DT	LN	OPT	STR	ACR	DT	LN	OPT
TZEQI 74	−8.79	−196.14	136.04	211.88	34.88	−0.01	−1.03**	−1.00**	−1.14**	−0.90**	0.36	−0.32*	−0.46**	−0.33*	−0.25**	0.01	0.15*	0.09
TZEQI 76	−329.66**	−169.32	−129.22	51.61	−116.75	1.84**	0.4	0.89**	0.83**	0.87**	0.32	0.31*	0.53**	0.43**	0.40**	0.26**	−0.03	0.09
TZEQI 77	−315.42**	−416.19**	−378.03*	−22.1	−270.62**	1.65**	0.97**	1.20**	0.66*	1.03**	0.53	0.41**	0.43**	0.29*	0.40**	0.15	0.18**	0.17*
TZEQI 78	−445.09**	−94.33	−366.12*	244.81*	−106.66	1.05*	0.41	0.63**	0.98**	0.74**	0.63*	0.53**	0.32*	0.54**	0.50**	0.09	0.07	0.27**
TZEQI 79	−527.73**	−608.80**	−582.93**	−243.35*	−477.91**	0.63	0.48	0.73**	0.46	0.56**	0.49	0.74**	0.82**	0.49**	0.64**	0.06	0.23**	0.28**
TZEQI 80	−54.23	−309.77*	−598.93**	−284.07*	−329.28**	−0.8	−0.03	0.06	−0.37	−0.23	−0.74*	−0.06	0.02	−0.31*	−0.23*	0	0.15*	0.27**
TZEQI 81	−77.23	−126.12	−311.13	−256.46*	−201.40**	−0.1	−0.14	0.12	−0.3	−0.12	−0.31	−0.25	0.06	−0.15	−0.16	−0.03	0.06	0.20**
TZEQI 82	−35.99	−449.30**	−695.34**	−378.07**	−420.57**	−1.47**	0.54*	0.27	−0.07	−0.02	−0.85*	0.13	0.03	−0.27*	−0.17	−0.07	0.26**	0.39**
TZEQI 84	−95.46	−214.3	−480.57**	116.3	−155.74*	1.61**	0.13	0.14	0.38	0.44**	0.78*	0.17	−0.08	0.13	0.19	0.14	0.10	0.14
TZEQI 87	210.83	260.27	307.67	389.60**	303.40**	−0.78	−0.28	−0.23	−0.34	−0.36*	−0.06	−0.10	0.02	−0.2	−0.1	−0.20*	−0.06	−0.12
TZEQI 89	451.09**	350.33**	550.84**	−430.75**	171.77*	−0.26	0.4	0.24	0.86**	0.40*	−0.18	0.23	0.17	0.44**	0.22*	−0.19*	−0.09	−0.26**
TZEQI 91	372.66**	664.04**	909.33**	367.22**	584.49**	−1.07*	−0.5	−0.66**	−0.58*	−0.65**	−0.35	−0.41**	−0.64**	−0.2	−0.39**	−0.11	−0.32**	−0.53**
TZEQI 92	239.87*	633.69**	756.41**	286.87*	494.71**	−0.45	−0.29	−0.29	−0.17	−0.28	0.15	−0.52**	−0.40**	−0.40**	−0.35**	−0.07	−0.37**	−0.52**
TZEQI 93	615.16**	675.94**	881.97**	−53.5	489.69**	−1.85**	−1.08**	−2.09**	−1.18**	−1.46**	−0.76*	−0.84**	−0.82**	−0.46**	−0.71**	−0.04	−0.34**	−0.46**
SE	114.94	137.11	177.78	**122.01**	**80.28**	0.46	0.28	0.241	**0.28**	**0.18**	0.3	0.14	0.15	**0.14**	**0.1**	0.08	0.06	0.07

Inbred	Ear aspect					Ears per plant					LFDTH		*Striga* damage rating		Emerged *Striga* plants	
	DT	LN	OPT	STR	ACR	DT	LN	OPT	STR	ACR	DT	LN	8 wk	10 wk	8 wk	10 wk
TZEQI 74	−0.08	0.08	−0.01	−0.06	−0.01	0.06*	0.04**	0.07**	0.03*	0.05**	0.44**	−0.04	0.10	0.07	0.08	−1.88
TZEQI 76	0.20*	0.14**	−0.01	−0.09	0.06	−0.03	−0.04**	−0.02	0.02	−0.01	0.13	0.07	0.04	−0.11	−2.02	−1.13
TZEQI 77	0.19*	0.13*	0.17*	0.09	0.14*	−0.11**	−0.04**	−0.05**	−0.01	−0.04**	−0.17	0.10	−0.03	−0.03	−1.2	−1.72
TZEQI 78	0.18*	0.07	0.1	−0.13	0.05	−0.09**	−0.06**	−0.04*	0.03*	−0.03**	−0.08	0.11	0.00	−0.11	−0.75	0.44
TZEQI 79	0.32**	0.27**	0.19**	0.24*	0.25**	−0.15**	−0.04**	−0.10**	0.01	−0.06**	−0.04	0.07	−0.04	0.04	−0.77	−0.34
TZEQI 80	−0.05	0.14**	0.28**	0.26**	0.17**	0.02	0.003	−0.05*	−0.03	−0.02	−0.19	0.11	0.23	0.24	−1.59	−1.47
TZEQI 81	0.16*	0.05	0.11	0.27**	0.14*	0.01	−0.01	−0.05**	−0.05**	−0.03	−0.1	0.11	0.08	0.14	0.18	0.30
TZEQI 82	0.07	0.20**	0.23**	0.22*	0.19**	0.02	−0.05**	−0.08**	0.02	−0.02*	−0.38**	0.09	0.11	0.34*	0.07	0.81
TZEQI 84	0.15*	0.04	0.16*	−0.12	0.05	−0.11**	−0.02	−0.01	0.03*	−0.02	−0.13	0.06	−0.08	−0.15	−3.95*	−4.68*
TZEQI 87	−1.19*	−0.13**	−0.08	−0.34**	−0.18**	0.07*	0.03**	0.08**	0.06**	0.06**	−0.21*	−0.20*	−0.17	−0.35*	3.51*	2.81
TZEQI 89	−0.24**	−0.10**	−0.12	0.19*	−0.06	0.08**	0.02	0.06**	−0.08**	0.01	0.00	−0.18	0.11	0.22	1.38	1.41
TZEQI 91	−0.31**	−0.30**	−0.35**	−0.33**	−0.32**	0.11**	0.06**	0.05**	0.00	0.05**	0.15	−0.08	−0.13	−0.11	0.38	0.91
TZEQI 92	−0.14*	−0.33**	−0.39**	−0.16	−0.27**	0.04	0.04**	0.06**	0.00	0.03**	0.25*	−0.11	−0.29	−0.29*	2.93	3.14
TZEQI 93	−0.28**	−0.24**	−0.28**	−0.05	−0.21**	0.09**	0.06**	0.09**	−0.05**	0.04**	0.33**	−0.12	0.07	0.09	1.76	1.42
SE	0.07	0.05	0.08	**0.10**	**0.07**	0.03	0.01	0.02	**0.01**	**0.01**	0.10	0.10	**0.17**	**0.14**	**1.61**	**1.81**

*, ** is the significance at 0.05 and 0.01 probability levels, respectively; DT is the Drought environment; LN is the low-N environment; STR is the *Striga* infested environment; ACR is the across research environments; OPT is the optimal environments; LFDTH is the stay-green characteristic.

Table 6
Summary of the heterotic groups of 14 early-maturing yellow QPM inbred lines identified by different heterotic grouping methods under drought, low-N, *Striga* infestation, optimal conditions, and across the three research environments.

Method	Group			
	1	2	3	4
Drought environment				
SCA	TZEQI 74,TZEQI 78,TZEQI 77, TZEQI 79, TZEQI 84,TZEQI 80, TZEQI 87, TZEQI 82	TZEQI 76, TZEQI 81, TZEQI 89	TZEQI 91, TZEQI 93, TZEQ1 92	
HSGCA	TZEQI 74, TZEQI 77, TZEQI 79, TZEQI 78, TZEQI 80, TZEQI 82, TZEQI 87	TZEQI 76, TZEQI 81, TZEQI 84, TZEQI 89	TZEQI 91, TZEQI 93, TZEQI 92	
HGCAMT	TZEQI 74, TZEQI 92, TZEQI 87, TZEQI 89, TZEQI 91, TZEQI 93, TZEQI 80, TZEQI 81, TZEQI 82	TZEQI 76, TZEQI 77, TZEQI 84, TZEQI 78, TZEQI 79		
SNP based GD	TZEQI 74, TZEQI 89, TZEQI 87, TZEQI 76, TZEQI 78, TZEQI 79, TZEQI 77, TZEQI 80, TZEQI 82, TZEQI 81	TZEQI 84, TZEQI 91, TZEQI 93, TZEQI 92		
Low-N environment				
SCA	TZEQI 74, TZEQI 87, TZEQI 89, TZEQI 84, TZEQI 77	TZEQI 76, TZEQI 79, TZEQI 78	TZEQI 91, TZEQI 93, TZEQI 92	TZEQI 80, TZEQI 81, TZEQI 82
HSGCA	TZEQI 74, TZEQI 77, TZEQI 76, TZEQI 79, TZEQI 84, TZEQI 87, TZEQI 89, TZEQI 78	TZEQI 80, TZEQI 81, TZEQI 82	TZEQI 91, TZEQI 93, TZEQI 92	
HGCAMT	TZEQI 74, TZEQI 76, TZEQI 80, TZEQI 84, TZEQI 81, TZEQI 87, TZEQI 89, TZEQI 77, TZEQI 82, TZEQI 78, TZEQI 79,		TZEQI 91, TZEQI 92, TZEQI 93	
SNP based GD	TZEQI 74, TZEQI 89, TZEQI 87, TZEQI 76, TZEQI 78, TZEQI 79, TZEQI 77, TZEQI 80, TZEQI 82, TZEQI 81	TZEQI 84, TZEQI 91, TZEQI 93, TZEQI 92		
Striga infested environment				
SCA	TZEQ1 74, TZEQI 84, TZEQI 87, TZEQI 89, TZEQI 91, TZEQI 93, TZEQI 92	TZEQI 80, TZEQI 81, TZEQI 82	TZEQI 76, TZEQI 77	TZEQI 78, TZEQI 79
HSGCA	TZEQI 74, TZEQI 89, TZEQI 76, TZEQI 77	TZEQI 78, TZEQI 79, TZEQI 91, TZEQI 93, TZEQI 92	TZEQI 80, TZEQI 81, TZEQI 84, TZEQI 87, TZEQI 82	
HGCAMT	TZEQI 74, TZEQI 76, TZEQI 77, TZEQI 78, TZEQI 79, TZEQI 84	TZEQI 80, TZEQI 81, TZEQI 82, TZEQI 89	TZEQI 87, TZEQI 92, TZEQI 91, TZEQI 93	
SNP based GD	TZEQI 74, TZEQI 89, TZEQI 87, TZEQI 76, TZEQI 78, TZEQI 79, TZEQI 77, TZEQI 80, TZEQI 82, TZEQI 81	TZEQI 84, TZEQI 91, TZEQI 93, TZEQI 92		
Optimal environment				
SCA	TZEQI 74, TZEQI 84, TZEQI 82, TZEQI 80, TZEQI 87, TZEQI 89, TZEQI 81	TZEQI 76, TZEQI 79, TZEQI 77, TZEQI 78	TZEQI 91, TZEQI 93, TZEQI 92	
HSGCA	TZEQI 74, TZEQI 80, TZEQI 82, TZEQI 84, TZEQI 81, TZEQI 87, TZEQI 89	TZEQI 76, TZEQI 77, TZEQI 79, TZEQI 78	TZEQI 91, TZEQI 93, TZEQI 92	
HGCAMT	TZEQI 74, TZEQI 80, TZEQI 82, TZEQI 84, TZEQI 81, TZEQI 87, TZEQI 89	TZEQI 76, TZEQI 77, TZEQI 79, TZEQI 78	TZEQI 91, TZEQI 93, TZEQI 92	
SNP based GD	TZEQI 74, TZEQI 89, TZEQI 87, TZEQI 76, TZEQI 78, TZEQI 79, TZEQI 77, TZEQI 80, TZEQI 82, TZEQI 81	TZEQI 84, TZEQI 91, TZEQI 93, TZEQI 92		
Across research environments				
SCA	TZEQI 74, TZEQI 87, TZEQI 89, TZEQI 84, TZEQI 76, TZEQI 77, TZEQI 78, TZEQI 79	TZEQI 80, TZEQI 81, TZEQI 82	TZEQI 91, TZEQI 93, TZEQI 92	
HSGCA	TZEQI 74, TZEQI 87, TZEQI 89, TZEQI 76, TZEQI 77, TZEQI 78, TZEQI 79, TZEQI 84	TZEQI 80, TZEQI 81, TZEQI 82	TZEQI 91, TZEQI 93, TZEQI 92	
HGCAMT	TZEQI 76, TZEQI 78, TZEQI 84, TZEQI 77, TZEQI 79, TZEQI 80, TZEQI 82, TZEQI 81	TZEQI 74, TZEQI 87, TZEQI 89, TZEQI 91,TZEQI 92, TZEQI 93		
SNP based GD	TZEQI 74, TZEQI 89, TZEQI 87, TZEQI 76, TZEQI 78, TZEQI 79, TZEQI 77, TZEQI 80, TZEQI 82, TZEQI 81	TZEQI 84, TZEQI 91, TZEQI 93, TZEQI 92		

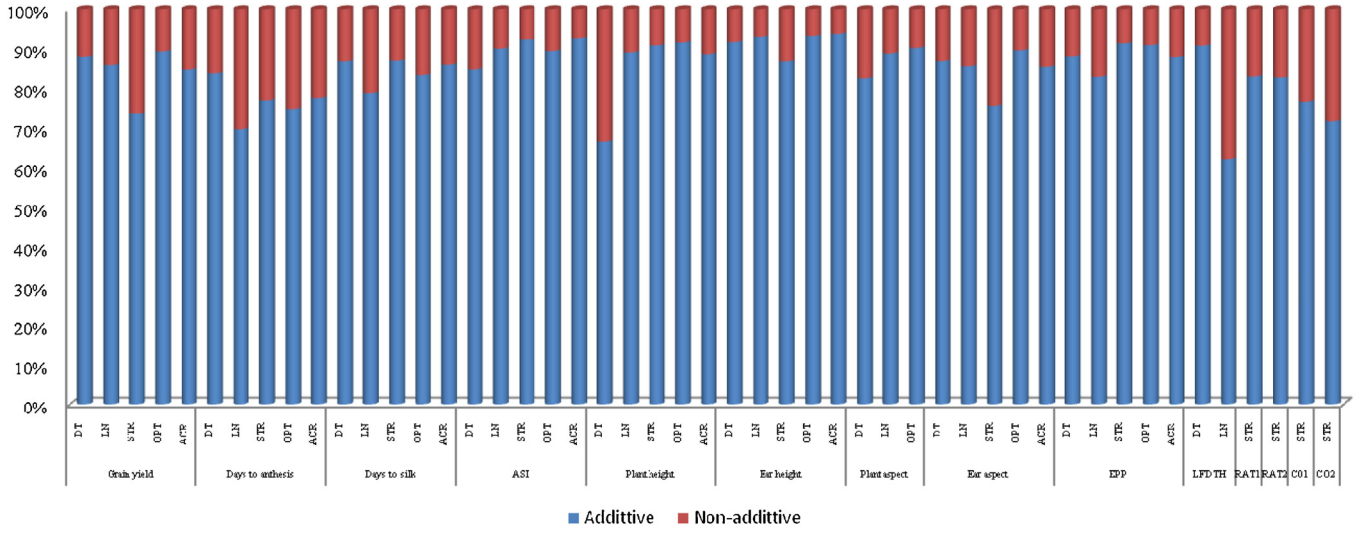


Fig. 1. Proportion of additive (lower bar) and non-additive (upper bar) genetic variance for grain yield and other agronomic traits under drought, low-N, *Striga* infestation, optimal conditions and across test environments in a diallel among 14 early yellow QPM inbred lines. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

inter-heterotic crosses, i.e., the best heterotic grouping method is the one that allowed inter-heterotic group crosses to produce more of the superior hybrids than the within-group crosses (Fan et al., 2009). Based on this, the SCA method identified 26 high yielding hybrids, HSGCA 25, HGCAMT 10, and SNP-based 21 out of the total intergroup crosses under drought (Table 76). Under low-N, the SCA method identified 30 high yielding hybrids, HSGCA 28, HGCAMT 27, and the SNP-based method 24 out of the total number of inter-group crosses identified by the grouping methods (Table 7). Also, 23 high yielding inter-group crosses were identified by the SCA, 24 by the HSGCA methods, 25 by HGCAMT and 16 by the SNP-based method under *Striga* infested environments. Under optimal environments, the SCA, HSGCA and HGCAMT methods each identified 28 high-yielding hybrids out of the total intergroup crosses; the SNP-based method identified 25. Across research environments 29 high yielding hybrids were identified by the SCA method, 29 by the HSGCA, 22 by the HGCAMT and 25 by the SNP.

The breeding efficiency of the SNP-based method was the highest under drought (53%) and exceeded that of the SCA method by 15%, HSGCA method by 28%, and the HGCAMT by 136% (Table 8). Similarly, the SNP-based method had the highest breeding efficiency of 40% under *Striga* infested, 63% under optimal conditions, and 63%, across research environments. However, under low-N the HGCAMT method was the best and had the highest breeding efficiency of 82% followed by the SNP-based method (60%).

Since the SNP-based method was the most efficient in the classification of the inbreds into heterotic groups in the present study, it was used to identify inbred testers based on the display of significant positive GCA effects, classification into heterotic groups and per se grain yield of inbreds (Pswarayi and Vivek, 2008) (Table 1). Based on these criteria, inbred TZEQI 87 was identified as the best testers for the SNP-based group 1 and TZEQI 91 for group 2 for the classification of other inbreds into heterotic groups across test environments.

Table 7
The number of hybrids within the first 30 arranged in descending order of their yield (group 1), from 31st to 60th (Group 2) and from 61st to 91st (Group 3).

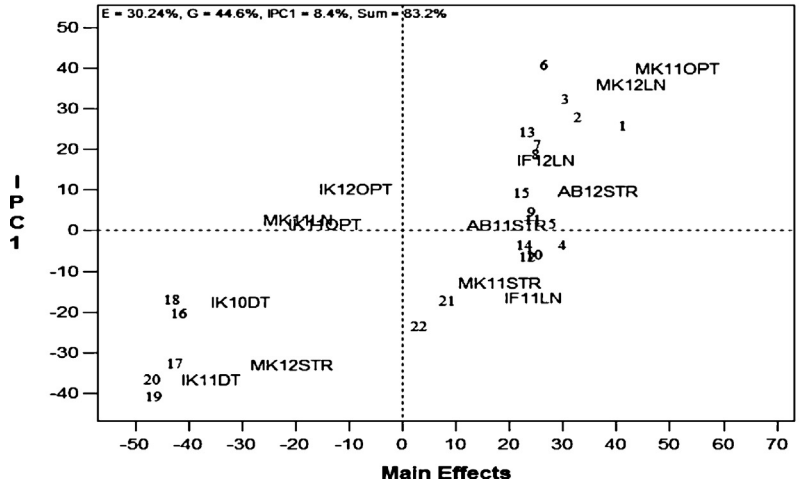
Yield group	Cross type	SCA	HSGCA	HGCAMT	SNP-based
Drought environment					
1	Inter	26	25	10	21
1	Intra	4	5	20	9
2	Inter	18	19	20	15
2	Intra	12	11	10	15
3	Inter	13	17	15	4
3	Intra	18	14	16	27
Low-N environment					
1	Inter	30	28	27	24
1	Intra	0	2	3	6
2	Inter	23	18	5	9
2	Intra	7	12	25	21
3	Inter	19	11	1	7
3	Intra	12	20	30	24
Striga infested environment					
1	Inter	23	24	25	16
1	Intra	7	6	5	14
2	Inter	23	22	24	17
2	Intra	7	8	6	13
3	Inter	19	19	15	7
3	Intra	12	12	16	24
Optimal environment					
1	Inter	28	28	28	25
1	Intra	2	2	2	5
2	Inter	19	19	20	7
2	Intra	11	11	10	23
3	Inter	14	14	14	8
3	Intra	17	17	17	23
Across environments					
1	Inter	29	29	22	25
1	Intra	1	1	8	5
2	Inter	28	16	19	8
2	Intra	2	14	11	22
3	Inter	31	12	7	7
3	Intra	0	19	24	24

3.4. Performance of early maturing yellow QPM hybrids

Grain yields ranged from 18 kg ha^{-1} for TZEQI 91 × TZEQI 93 to 3164 kg ha^{-1} for TZEQI 82 × TZEQI 93 across drought environments (data not shown). The QPM hybrid TZEQI 82 × TZEQI 93 out-yielded the best normal endosperm drought tolerant hybrid

Table 8
Breeding efficiency (%) of SCA, HSGCA, HGCAMT, and SNP-based heterotic grouping methods under drought, low-N, optimal conditions and across research environments.

Environment	SCA	HSGCA	HGCAMT	SNP-Based
Drought	45.61	40.98	22.22	52.50
Low-N	41.67	49.12	81.82	60.00
Striga	35.38	36.92	39.06	40.00
Optimal	45.90	45.90	45.16	62.5
Across	50.88	50.88	45.83	62.50



Entry	Pedigree
1	TZEQI 78 X TZEQI 92
2	TZEQI 78 X TZEQI 93
3	TZEQI 76 X TZEQI 92
4	TZEQI 79 X TZEQI 92
5	TZEQI 87 X TZEQI 93
6	TZEQI 79 X TZEQI 91
7	TZEQI 78 X TZEQI 91
8	TZEQI 81 X TZEQI 91
9	TZEQI 80 X TZEQI 91
10	TZEQI 84 X TZEQI 91
11	TZEQI 77 X TZEQI 91
12	TZEQI 87 X TZEQI 91
13	TZEQI 81 X TZEQI 93
14	TZEQI 80 X TZEQI 92
15	TZEQI 89 X TZEQI 93
16	TZEQI 77 X TZEQI 79
17	TZEQI 80 X TZEQI 81
18	TZEQI 91 X TZEQI 93
19	TZEQI 81 X TZEQI 82
20	TZEQI 80 X TZEQI 82
21	CHECK 1 - TZEI 24 X TZEI 17
22	CHECK 2 - TZEI 16 X TZEI 8

Fig. 2. AMMI biplot of grain yield and the first interaction principal component axis (IPCA 1) of best 15 and worst 5 (based on mean grain yield across environments) early maturing yellow QPM hybrids plus two checks evaluated across 13 environments between 2011 and 2012 in Nigeria. IK11OPT and IK12OPT = Ikenne under optimal growing conditions, 2011 and 2012; IK11DT and IK12DT = Ikenne under drought stress, 2011 and 2012; MK11LN and MK12LN = Mokwa under low N, 2011 and 2012; IF11LN and IF12LN = Ile-Ife under low-N, 2011 and 2012; MK11HN and MK12HN = Mokwa under high-N, 2011 and 2012; IF11HN and IF12HN = Ile-Ife under high-N, 2011 and 2012; MK11STR and MK12STR = Mokwa under *Striga* infestation, 2011 and 2012; AB11STR and AB12STR = Abuja under *Striga* infestation, 2011 and 2012.

check, TZEI 16 × TZEI 8 by 20% and the drought susceptible normal endosperm hybrid check, TZEI 9 × TZEI 11 by 100% across drought environments. Under low-N environments, yields ranged from 1106 kg ha^{-1} for TZEQI 78 × TZEQI 79 to 5532 kg ha^{-1} for TZEQI 78 × TZEQI 92 (data not shown). The outstanding low-N tolerant QPM hybrid, TZEQI 78 × TZEQI 92 out-yielded the low-N tolerant normal hybrid check, TZEI 16 × TZEI 8 by 50% and the low-N susceptible normal endosperm hybrid check, TZEI 23 × TZEI 16 by 72%. Across *Striga* infested environments, yields ranged from 1008 kg ha^{-1} for TZEQI 80 × TZEQI 82 to 5074 kg ha^{-1} for TZEQI 78 × TZEQI 92 (data not shown). The best *Striga* resistant QPM hybrid, TZEQI 78 × TZEQI 92 out-yielded the best *Striga* resistant normal endosperm hybrid check, TZEI 16 × TZEI 8 by 45% and the most *Striga* susceptible normal endosperm hybrid check TZEI 9 × TZEI 16 by 78% (data not shown). Under optimal environments, yields ranged from 605 kg ha^{-1} for TZEQI 80 × TZEQI 81 to 6002 kg ha^{-1} for TZEQI 78 × TZEQI 92. The yield of the top performing QPM hybrid TZEQI 78 × TZEQI 92 was about 188% of that of the least performing normal hybrid check and 154% of that of the best normal hybrid check (data not shown). Across test environments grain yields ranged from 881 kg ha^{-1} for TZEQI 81 × TZEQI 82 to 4925 kg ha^{-1} for TZEQI 78 × TZEQI 92. The QPM hybrid TZEQI 78 × TZEQI 92 out-yielded the best normal endosperm hybrid check TZEI 16 × TZEI 8 by 44% and the lowest-yielding normal endosperm hybrid check, TZEI 9 × TZEI 16 by 71%. It is striking that the QPM hybrid TZEQI 78 × TZEQI 92 was the outstanding hybrid under both low-N, and *Striga* infested conditions and across test environments (data not shown).

The AMMI biplot was adopted to examine the stability of the performance of the early QPM hybrids across the contrasting environments. The biplot showed a large variability among the thirteen environments and wide yield range among the 22 genotypes (Fig. 2). The hybrids, 5 (TZEQI 87 × TZEQI 93), 11 (TZEQI 77 × TZEQI 91) and 9 (TZEQI 80 × TZEQI 91) were the most stable and relatively high yielding across environments due to their small interaction with the environments as revealed by their closeness to the zero IPCA1 score and display of grain yield greater than the mean grain yield. However, hybrid 1 (TZEQI 78 × TZEQI 92) was the highest yielding across environments but had a strong positive interaction with IPCA1 indicating that it was probably adapted to favorable environments. Similarly, hybrids 2 (TZEQI 78 × TZEQI 93), 3 (TZEQI 76 × TZEQI 92), 7 (TZEQI 78 × TZEQI 91), 8 (TZEQI 81 × TZEQI 91), 13 (TZEQI 81 × TZEQI 93) and 6 (TZEQI 79 × TZEQI 91) had mean grain yield greater than the grand mean but were adapted to favorable environments. In contrast, hybrid 4 (TZEQI 79 × TZEQI 92), 14 (TZEQI 80 × TZEQI 92), 10 (TZEQI 84 × TZEQI 91) and 12 (TZEQI 87 × TZEQI 91) had grain yield above the grand mean but negative interaction with IPCA1 scores suggesting that the hybrids were probably adapted to low-yield environments.

4. Discussion

4.1. Inheritance of grain yield and other traits of early maturing yellow QPM inbreds

The presence of genetic variability is of prime importance for progress from selection for improved grain yield under drought, low-N and *Striga* infestation. The differential response of genotypes to varying environmental conditions constitutes a major constraint in the identification of superior maize cultivars for narrow or wide adaptation. The observed significant G and E effects for most measured traits indicated that the test environments were unique and that there was adequate genetic variability among the early yellow QPM inbreds to allow good progress from selection for improvements of such traits. This result is consistent with the findings of Badu-Apraku et al. (2011a, 2013) for normal endosperm maize inbreds. The lack of significant GEI mean squares for most measured traits except for grain yield, ear aspect, EPP and husk cover under drought stress implied that most of the traits used to select for tolerance to drought were stable and not affected by GEI. It is therefore anticipated that the phenotypic and genotypic correlations between these traits and grain yield would not be reduced under drought. These results are in agreement with the findings of Badu-Apraku et al. (2011a, 2013). The presence of a significant

G, E, and GEI for grain yield and most other traits under low-N, *Striga*-infested and optimal environments suggested differential responses of the genotypes to the contrasting environments and the need to identify high yielding and stable genotypes across the test environments (Badu-Apraku et al., 1995, 2003; Sabaghnia et al., 2008; Moghaddam and Pourdad, 2009). The presence of a significant GEI for grain yield of the early cultivars confirmed the need for the extensive testing of hybrids in multiple environments over years before hybrid recommendations are made.

The presence of significant GCA and SCA mean squares for most traits under the four research conditions and across test environments indicated that additive and non-additive genetic effects were important in this set of genotypes under all test environments. The results of the present study suggested that there was scope for the improvement of most measured traits using hybridization, backcrossing, and recurrent selection methods to develop hybrids and synthetics as well as population development. The results also implied that there was a chance to identify a potentially discriminating tester under the contrasting environments as well as superior inbreds with good combining abilities. Furthermore, the results implied that the inbreds could be classified into distinct heterotic groups under each research environment, and that those that could serve as ideal testers could be identified under the contrasting environments. The results of the present study indicated that both additive and non-additive gene actions were important in the inheritance of all measured traits except the number of emerged *Striga* plants at 8 WAP and *Striga* damage at 10 WAP. However, there was the preponderance of GCA over SCA mean squares for grain yield and other measured traits under all the contrasting environments with the relative importance of GCA to SCA effects for grain yield and most other measured traits increasing from stress to nonstress environments. The implication of this result is that additive gene action was more important than non-additive gene action for these traits and that GCA was the major component accounting for the differences among the inbreds evaluated in the present study. The results of this study is partially in agreement with the findings of several other authors (Kim, 1994; Akanvou et al., 1997) who reported that additive genetic effects were more important in controlling host plant damage syndrome rating and grain yield while nonadditive gene action controlled the number of emerged *Striga* plants under *Striga* infestation. Furthermore, the results of this study are in disagreement with the findings of Gethi and Smith (2004), Yallou et al. (2009), and Badu-Apraku et al. (2007, 2011b) who showed that nonadditive gene action was more important than additive gene action in the control of the inheritance of host plant damage. Similar results indicating the preponderance of additive gene action over non-additive gene action have been reported by several workers in studies involving the inheritance of quantitative traits in QPM germplasm. For example, Vasal et al. (1993a,b) showed the preponderance of additive gene action for grain yield. Bhatnagar et al. (2004) reported the preponderance of additive gene action for root and stalk lodging in a study involving selected white QPM inbred lines. In addition, Musila et al. (2010) reported the preponderance of additive gene action for grain yield, anthesis date, ASI and EPP in adapted early maturing QPM inbred lines evaluated under low-N, drought, and optimal environments. In contrast, Wegary et al. (2013) reported GCA effects to be more important under drought, while SCA effects were more important under low-N and optimal conditions for grain yield. The differences in the results reported in the studies may be due to the fact that the inbred lines used in the different studies were derived from diverse germplasm sources and these might have had some genes with different modes of action (Badu-Apraku et al., 2013). The results of the present study suggest that the gene actions controlling grain yield and most measured traits under drought, low-N and *Striga* infestation were similar in this set of early yellow QPM inbreds. The implication is that drought, low-N tolerance and *Striga* resistance in either of the parental inbred lines would be sufficient to obtain hybrids with an acceptable performance under these stresses. Moreover, the predominance of GCA over SCA effects indicated that early generation testing may be effective and promising hybrids could be identified and selected based solely on the prediction from GCA effects.

The significant interaction of GCA with environment for most measured traits under low-N, optimal, *Striga* infestation and across test environments indicated that there was significant variation in the combining ability of the lines under different environments. Similar results have been reported in earlier studies (Gutierrez-Gaitan et al., 1986; Vasal et al., 1993a; Badu-Apraku et al., 2011a,b) and this emphasizes the need for testing inbred lines in contrasting environments to identify those with stable performance for the development of multiple stress tolerant hybrids. This is particularly important for *Striga* resistance in view of possible variability in strains between locations and year-to-year variation in the parasite population since *S. hermonthica* is an outcrossing species. Furthermore, the significant GCA × environment interaction suggested the need to select different parental lines for hybrid development under each environment.

Evaluation of inbred lines under contrasting environments is very desirable to facilitate the selection of stable testers and hybrids (Scott, 1967; Badu-Apraku et al., 2013). The significant SCA × environment interaction for grain yield and most measured traits under the research conditions, and across research environments, suggested that the yield performance and the expression of the traits of the hybrids were not consistent in the varying environments and that there is a need to select different parental lines for hybrid development under each environment (Akinwale et al., 2014). This result provides a justification for our strategy of evaluating the crosses across multiple test environments in an effort to identify the tester with a consistent performance in contrasting environments (Badu-Apraku et al., 2013). This result corroborates the earlier findings of Kang (1996) and of Akinwale et al. (2014), who reported that the environment plays a predominant role in the phenotypic expression of agronomic traits, and that ignoring environmental components in the field would impede progress and advances from selection.

The GCA effect of an inbred is dependent on its relative importance as a tester for the improvement of a target trait in a population and as a parent for the development of synthetic varieties and hybrids. Genotypes that are outstanding in terms of GCA and SCA for grain yield and other agronomic traits could be employed for the development of heterotic populations for further improvement and for developing high yielding synthetic varieties and hybrids (Akinwale et al., 2014). The significant and positive GCA effects observed for grain yield of the inbreds TZEQI 89, TZEQI 91, TZEQI 92 and TZEQI 93 under drought, low-N, and optimal environments, TZEQI 78, TZEQI 87, TZEQI 91 and TZEQI 92 under *Striga* infestation, and TZEQI 87, TZEQI 89, TZEQI 91, TZEQI 92 and TZEQI 93 across research environments indicated that these inbreds possess favorable alleles for grain yield and would contribute high yields to their progenies. Significant and negative GCA effects were observed for the stay-green characteristic of inbred TZEQI 82 and of TZEQI 87 under drought stress and under low-N indicating that the two inbreds will transmit the trait to their progenies or will slow down the rate of leaf senescence. These inbreds could be used to improve this trait in QPM germplasm. Under *Striga*-infestation, significant negative GCA effects were detected for *Striga* damage at 10 WAP for inbreds TZEQI 87 and TZEQI 92 indicating that the inbreds are tolerant to *Striga* and could be used to improve other QPM germplasm. Also, TZEQI 84 showed significant negative GCA effects for the number of emerged *Striga* plants at 8 and 10 WAP, indicating that the inbred possesses genes for resistance to *Striga* that

could be introgressed into QPM germplasm. The inbred TZEQI 93 showed significant negative GCA effects for days to silking and ASI under drought, low-N, *Striga* infested, optimal, and across research environments suggesting that it will contribute favorable alleles for earliness to the progenies under the contrasting environments. Inbreds TZEQI 74 and TZEQI 87 showed significant positive GCA effects for EPP under each and across research environments, indicating that they would contribute favorable alleles to the trait in their progenies.

4.2. Groupings of inbreds, relationships among heterotic grouping methods, and identification of testers

The SCA effects of grain yield method and the HSGCA method classified the inbreds into three groups each; the HGCAMT and the SNP-based GD methods had two groups across research environments. There was close correspondence in the classification of the inbreds using the grouping methods across environments in terms of placement of inbred lines into the same heterotic group. However, SNP-based method was the most efficient in the classification of the inbreds into heterotic groups and was used to identify the best testers across research environments.

According to Fan et al. (2009), an efficient heterotic grouping method is expected to identify groups which allow inter-heterotic group crosses to display higher heterosis than within-group crosses. On the basis of the mean values of intra- and inter-heterotic groups, the SNP-marker based method was identified as the most efficient because it identified distinct heterotic groups in which intra-group mean yields were significantly lower than in all inter-group mean yields. However, under low-N, the HGCAMT method was the best method with the highest breeding efficiency of 82% followed by the SNP-based method (60%). The breeding efficiency of the SNP-based method was the highest under drought (53%), *Striga* infestation (40%), optimal conditions (63%), and across research environments (63%). This result is striking because heterotic grouping based on GD derived from molecular markers has sometimes produced contrasting results depending on the species, markers (Hamblin et al., 2007) for comparison and used for genotyping a given marker type (Semagn et al., 2012, 2014). The correspondence of GD-based heterotic grouping is further compounded by the quality of the existing heterotic groups, which were not sufficiently diverged (Semagn et al., 2012; Menkir et al., 2010; Benchimol et al., 2008; Shieh and Thseng, 2006). Nevertheless, numerous examples of such successful heterotic grouping of maize have been reported (Lanza et al., 1997; Balestre et al., 2008). For example, Akinwale et al. (2014) reported that the classification of 28 early maturing inbreds based on SSR marker-based GD was closely related to that based on the SCA method under a *Striga* free environment. He indicated that the GD method was not as effective as the HSGCA method in classifying the early maturing inbreds under both *Striga* infested and *Striga* free environments. In the present study, the grouping of the inbred lines by SNP markers was closely related to their pedigree data and their combining ability and proved more effective than HSGCA. The implications of these results are that SNP markers could be invaluable in planning and reducing the number of planned crosses in a breeding program before using the more expensive field performance based methods, and that both methods would be necessary for final heterotic grouping. The discrepancy in the result of this study and the earlier report by Akinwale et al. (2014) suggested that SNP markers could be more effective in assessing diversity among tropical early maize and subsequently assigning them into distinct heterotic group than SSR markers. However, further studies are needed to confirm this.

A good tester is characterized by the ability to discriminate between lines within its heterotic group and those from other groups. Also, a good tester should be representative of the inbreds within its group and should be effective in classifying other inbreds into distinct heterotic groups in line × tester analyses. In this study, using the criteria that the best tester should display significant positive GCA effects, should be classified into a heterotic group and the per se grain yield of the inbred should be highest in the group (Pswarayi and Vivek, 2008) inbred TZEQI 87 was identified as the best tester for the SNP-based heterotic group 1 and TZEQI 91 for group 2. The identified testers could be used to group the large number of early yellow QPM inbreds in the IITA Maize Program yet to be field-tested.

4.3. Performance of early maturing yellow QPM hybrids across research environments

An important objective of the present study was to identify outstanding QPM early yellow hybrids for commercialization in SSA. Even though there are several reports indicating that certain QPM cultivars can produce yields equal to those of conventional cultivars currently under cultivation in developing countries and that generally experimental varieties performed better than the checks in several regions of the world (National Research Council, 1988), such reports are limited in the sub region. Results of this study has clearly established that QPM early hybrids with grain yield, *Striga* resistance, drought and Low-N tolerance, comparable with or superior to their normal endosperm hybrid versions have been developed in our program. For example, in the present study, the QPM hybrid TZEQI 78 × TZEQI 92, out-yielded the best normal endosperm hybrid check TZEI 16 × TZEI 8, by 44%. Similarly, the best *Striga* resistant QPM hybrid, TZEQI 78 × TZEQI 92, out-yielded the best *Striga* resistant normal endosperm hybrid check, TZEI 16 × TZEI 8 by 45% and the most *Striga* susceptible normal endosperm hybrid check, TZEI 9 × TZEI 16, by 78% suggesting severe parasitic pressure to facilitate the identification of superior hybrids with genes for *Striga* resistance. Also, the QPM hybrid TZEQI 82 × TZEQI 93, out-yielded the best normal endosperm drought tolerant hybrid check, TZEI 16 × TZEI 8, by 20% and the drought susceptible normal endosperm hybrid check, TZEI 9 × TZEI 11, by 100% across drought environments, indicating that the drought was severe enough to allow the discrimination of drought tolerant and susceptible genotypes. Under low-N environments, the most outstanding low-N tolerant QPM hybrid, TZEQI 78 × TZEQI 92, out-yielded the low-N tolerant normal hybrid check, TZEI 16 × TZEI 8, by 50% and the low-N susceptible normal endosperm hybrid check, TZEI 23 × TZEI 16, by 72%, an indication of the severe low-N stress in the experiment. The hybrids, TZEQI 87 × TZEQI 93, TZEQI 77 × TZEQI 91 and TZEQI 80 × TZEQI 91 were identified as the most stable and relatively high yielding across environments and should be extensively evaluated in on-farm trials to confirm the consistency of performance and commercialized. On the other hand, hybrids TZEQI 78 × TZEQI 93, TZEQI 76 × TZEQI 92, TZEQI 78 × TZEQI 91, TZEQI 81 × TZEQI 91, TZEQI 81 × TZEQI 93 and TZEQI 79 × TZEQI 91 had mean grain yield greater than the grand mean but were adapted to favorable environments. These hybrids could be released for production in the specific environments where they had outstanding performance.

5. Conclusions

The inbreds TZEQI 87 and TZEQI 92 had significant and positive GCA effects for grain yield, significant and negative GCA effects for *Striga* damage at 10 WAP, TZEQI 84 had negative and significant GCA effects for the number of emerged *Striga* plants across research environments. The favorable alleles from these inbreds should be introgressed into the early maturing QPM breeding populations of the sub region for improvement of the target traits. Additive gene action was more important than non-additive gene action for

the measured traits, indicating that GCA was the major component accounting for the differences among the inbreds evaluated in the present study. A program may be initiated to develop heterotic populations by inter crossing the inbred lines in each of the identified heterotic groups which could be improved using reciprocal recurrent selection to synthesize more genetically diverse and superior inbred lines. The hybrids, 5 (TZEQI 87 × TZEQI 93), 11 (TZEQI 77 × TZEQI 91) and 9 (TZEQI 80 × TZEQI 91) were identified as the most stable and high yielding across environments and should be extensively evaluated in on-farm trials to confirm the consistency of performance and commercialized.

Acknowledgments

The financial support of the Drought Tolerant Maize for Africa (DTMA) Project and the International Institute of Tropical Agriculture (IITA) for this study is gratefully acknowledged. Special thanks are also due to the staff of the IITA Maize Improvement Program and Bioscience in Ibadan, Nigeria, for technical assistance.

References

Akanvou, L., Doku, E.V., Kling, J., 1997. Estimates of genetic variances and interrelationships of traits associated with *Striga* resistance in maize. Afr. Crop Sci. J. 5, 1–8.

Akinwale, R.O., Badu-Apraku, B., Fakorede, M.A.B., Vroh-Bi, I., 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.

Badu-Apraku, B., Lum, A.F., 2010. Grain yield response of normal and quality protein maize cultivars in stress and nonstress environments. Agron. J. 102, 381–394.

Badu-Apraku, B., Fajemisin, J.M., Diallo, A.O., 1995. The performance of early and extra-early varieties across environments in West and Central Africa. In: Badu-Apraku, B., Akoroda, M.O., Ouedraogo, M., Quin, F.M. (Eds.), Contributing to Food Self-Sufficiency: Maize Research and Development in West and Central Africa. Proceedings of a Regional Maize Workshop, 29 May-2 June, 1995. IITA, Cotonou, Benin Republic, pp. 149–159.

Badu-Apraku, B., Menkir, A., Lum, A.F., 2007. Genetic variability for grain yield and components in an early tropical yellow maize population under *Striga hermonthica* infestation. Crop Improv. 20, 107–122.

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

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

Badu-Apraku, B., Fakorede, M.A.B., Menkir, A., Kamara, A.Y., Adam, A., 2004. Effects of drought-screening methodology on genetic variances and covariances in Pool 16 DT maize population. J. Agric. Sci. 142, 445–452.

Badu-Apraku, B., Abamu, F.J., Menkir, A., Fakorede, M.A.B., Obeng-Antwi, K., The, C., 2003. Genotype by environment interactions in the regional early variety trials in West and Central Africa. Maydica 48, 93–104.

Badu-Apraku, B., Menkir, A., Ajala, S.O., Akinwale, R.O., Oyekunle, M., Obeng-Antwi, K., 2010. Performance of tropical early-maturing maize cultivars in multiple stress environments. Can. J. Plant Sci. 90, 1–22.

Badu-Apraku, B., Oyekunle, M., Fakorede, M.A.B., Vroh, I., Akinwale, R.O., Aderounmu, M., 2013. Combining ability, heterotic patterns and genetic diversity of extra-early yellow inbreds under contrasting environments. Euphytica 192, 413–433.

Baker, R.J., 1978. Issues in diallel analysis. Crop Sci. 18, 533–536.

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

Bänziger, M., Sentimela, P., Hodson, D., Biniganavile, V., 2006. Breeding for improved abiotic stress tolerance in maize adapted to southern Africa. Agric. Water Manage. 80, 212–224.

Bebawi, F.F., Eplec, R.E., Harris, C.E., Norris, R.S., 1984. Longevity of witchweed (*Striga asiatica*) seed. Weed Sci. 32, 494–497.

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

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

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

Bremner, J.M., Mulvaney, C.S., 1982. Nitrogen-total. In: Page, A.L., et al. (Eds.), Methods of Soil Analysis. Part 2. Agron. Monogr. , 2nd ed. ASA and SSSA, Madison, pp. 595–624.

Cechin, I., Press, M.C., 1993. The influence of nitrogen on growth and photosynthesis of sorghum infected with *Striga hermonthica* from different provenances. Weed Res. 3, 289–298.

DeVries, J., 2000. The inheritance of *Striga* reactions in maize. In: Haussmann, et al. (Eds.), Breeding for Striga Resistance in Cereals. Proc. Workshop. IITA, Ibadan. Margraf Verlag, Weikersheim, pp. 73–84.

Elshire, R.J., Glaubitz, J.C., Sun, Q., Poland, J.A., Kawamoto, K., 2011. A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS ONE 6 (5), e19379.

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

Fan, X.M., Chen, H.M., Tan, J., Xu, C.X., Zhang, Y.M., Huang, Y.X., Kang, M.S., 2008. A new maize heterotic pattern between temperate and tropical germplasms. Agron. J. 100, 917–923.

FAO/WHO Expert Consultation, 1990. Protein Quality Evaluation, FAO/WHO Nutrition Meetings. Food and Agriculture Organization/World Health Organization, Rome.

FAO/WHO/UNU Expert Committee, 1985. Energy and Protein Requirements, FAO/WHO Nutrition Meetings. Food and Agriculture Organization/World Health Organization, Geneva.

FAO, 2006. World Reference Base for Soil Resources: A Framework for International Classification, Correlation and Communication. FAO, Rome, pp. 103.

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

Griffing, B., 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Aust. J. Biol. Sci. 9, 463–493.

Gutierrez-Gaitan, M.A., Cortez-Mendoza, H., Wathika, E.N., Gardner, C.O., Oyervides-Garcia, M., Hallauer, A.R., Darrah, L.L., 1986. Test cross evaluation of Mexican maize populations. Crop Sci. 26, 99–104.

Hamblin, M.T., Warburton, M.L., Buckler, E.S., 2007. Empirical comparison of Simple Sequence Repeats and single nucleotide polymorphisms in assessment of maize diversity and relatedness. PLoS ONE 2, e1367.

Huang, S., Adams, W.R., Zhou, Q., Malloy, K.P., Voyles, D.A., Anthony, J., Kriz, A.L., Luethy, M.H., 2004. Improving nutritional quality of maize proteins by expressing sense and antisense zein genes. J. Agric. Food Chem. 52, 1958–1964.

Hung, H.Y., Holland, J.B., 2012. Diallel analysis of resistance to fusarium ear rot and fumonium contamination in maize. Crop Sci., http://dx.doi.org/10.2135/cropsci2012.03.0154

Kang, M.S., 1996. Using genotype-by-environment interaction for crop cultivar development. Adv. Agron. 62, 199–252.

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

Kim, S.K., 1994. Genetics of maize tolerance of *Striga hermonthica*. Crop Sci. 34, 900–907.

Kim, S.K., Adetimirin, V.O., 1997. Responses of tolerant and susceptible maize varieties to timing and rate of nitrogen under *Striga hermonthica* infestation. Agron. J. 89, 38–44.

Kim, S.K., Winslow, M.D., 1991. Progress in breeding maize for *Striga*-tolerance/resistance at IITA. In: Ransom, J.K. (Ed.), Proc. 5th Intl. Symp. Parasitic Weeds, Nairobi. 24–30 June, 1991. IITA, Ibadan, Nigeria, pp. 494–499.

Krivanek, A.F., De Groote, H., Gunaratna, N.S., Diallo, A.O., Friesen, D., 2007. Breeding and disseminating quality protein maize (QPM) for Africa. Afr. J. Biotechnol. 6, 312–324.

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

Liu, K., Muse, S.V., 2005. Power marker: integrated analysis environment for genetic marker data. Bioinformatics 21, 2128–2129.

Logrono, M.L., Lothrop, J.E., 1997. Impact of drought and low nitrogen on maize production in Asia. In: Edmeades, G.O., et al. (Eds.), Developing Drought- and Low N-Tolerant Maize. Proceedings of a Symposium. March 25–29, 1996. CIMMYT, El Batan, Mexico, pp. 39–43.

National Research Council, 1988. Quality Protein Maize. National Academic Press, Washington, DC.

NeSmith, D.S., Ritchie, J.T., 1992. Effects of water-deficits during tassel emergence on development and yield components of maize (*Zea mays* L.). Field Crops Res. 28, 251–256.

Menkir, A., Adetimirin, V.O., Yallou, C.G., Gedil, M., 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.

Moghaddam, M.J., Pourdad, S.S., 2009. Comparison of parametric and non-parametric methods for analyzing genotype × environment interactions in safflower (*Carthamus tinctorius* L.). J. Agric. Sci. 147, 601–612.

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

Odhiambo, G.D., Ransom, J.K., 1994. Long-term strategies for *Striga* control. In: Jewell, D.C., Waddington, S.R., Ransom, J.K., Pixley, K.V. (Eds.), Maize Research for Stress Environments. Proc. 4th Eastern and Southern Africa Regional Maize Conf., Harare, Zimbabwe. 28 Mar—Apr, 1994. CIMMYT, Harare, Zimbabwe, pp. 263–266.

Prasanna, B.M., Vasal, S.K., Kassahun, B., Singh, N.N., 2001. Quality protein maize. Curr. Sci. 81, 1308–1319.

Pswarayi, A., Vivek, B.S., 2008. Combining ability amongst CIMMYT's early maturing maize (*Zea mays* L.) germplasm under stress and non-stress conditions and identification of testers. Euphytica 162, 353–362.

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

Sabaghnia, N., Sabaghpour, S.H., Dehghani, H., 2008. The use of an AMMI model and its parameters to analyse yield stability in multi-environment trials. J. Agric. Sci. 146, 571–581.

Sadeghi, S.M., Samizadeh, H., Amiri, E., Ashouri, M., 2011. Additive main effects and multiplicative interactions (AMMI) analysis of dry leaf yield in tobacco hybrids across environments. Afr. J. Biotech. 10, 4358–4364.

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

SAS Institute Inc., 2011. Base SAS® 9. 3 Procedures Guide. SAS Institute Inc, Cary, NC.

Shaxson, L., Riches, C., 1998. Where once there was grain to burn: a farming system in crisis in eastern Malawi. Outlook Agric. 27, 101–105.

Schnable, P.S., Ware, D., Fulton, R.S., Stein, J.C., Wei, F., 2009. The B73 maize genome: complexity, diversity, and dynamics. Science 326 (5956), 1112–1115.

Scott, G.E., 1967. Selecting for stability of yield in maize. Crop Sci. 7, 549–551.

Semagn, K., Babu, R., Hearne, S., Olsen, M., 2014. Single nucleotide polymorphism genotyping using Kompetitive Allele Specific PCR (KASP): overview of the technology and its application in crop improvement. Mol. Breed. 33, 1–14.

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

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

Soil Survey Staff, et al. (Eds.), 1999. Soil taxonomy: a basic system of soil classification for making and interpreting soil survey. Agricultural Handbook 43, 2nd ed. Natural Resource Conservation Service USDA, Washington, US Government Printing Office, pp. 869–873.

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

Vasal, S.K., Srinivasan, G., González, F., Beck, D.L., Crossa, J., 1993b. Heterosis and combining ability of CIMMYT's quality protein maize germplasm: II. Subtropical. Crop Sci. 33, 51–57.

Vivek, B.S., Krivanek, A.F., Palacios-Rojas, N., Twumasi-Afriyie, S., Diallo, A.O., 2008. Breeding Quality Protein Maize (QPM): Protocols for Developing QPM Cultivars. CIMMYT, Mexico, DF.

Weber, V.S., Melchinger, A.E., Magorokosho, C., Makumbi, D., Bänziger, M., Atlin, G.N., 2012. Efficiency of managed-stress selection for maize grain yield under optimal rainfed, low-N, and random abiotic stress conditions in Southern Africa. Crop Sci. 52, 1011–1020.

Wegary, D., Vivek, S.B., Labuschagne, M.T., 2013. Combining Ability of Certain agronomic traits in Quality Protein Maize under stress and non-stress environments in Eastern and Southern Africa. Crop Sci., http://dx.doi.org/10.2135/cropsci2013.09.0585

Yallou, C.G., Menkir, A., Adetimirin, V.O., Kling, J.G., 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. GGEbiplot-a Windows application for graphical analysis of multienvironment trial data. Agron. J. 94, 1396–1401.

Zhang, Y., Kang, M.S., Lamkey, K.R., 2005. DIALLEL-SAS: a comprehensive program for Griffing's and Gardner–Eberthart analyses. Agron. J. 97, 1097–1106.

Zobel, R.W., Wright, M.J., Gauch, H.G., 1988. Statistical analysis of a yield trial. Agron. J. 80, 388–393, http://dx.doi.org/10.2134/agronj198.8.00021962008000030002x.