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Combining ability and heterotic patterns of extra-early maturing white maize inbreds with genes from *Zea diploperennis* under multiple environments

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Abstract Low soil nitrogen (Low N), *Striga hermonthica* and recurrent drought are major constraints to maize production and productivity in sub-Saharan Africa (SSA). Only a few extra-early maturing hybrids with combined tolerance to drought, *Striga* and low N have been commercialized in SSA. The objectives of the study were to determine the general combining ability (GCA) and specific combining ability (SCA) effects of grain yield and other traits, classify the inbreds into heterotic groups using the SCA effects of grain yield, and the heterotic group's SCA and GCA of grain yield (HSGCA) methods, and examine the performance of hybrids under contrasting environments. Sixty-three extra-early white maize inbred lines containing genes from *Zea diploperennis* were crossed to four elite testers to obtain 252 single-cross hybrids and evaluated together with four checks at four locations for 2 years under drought, *Striga*-infested, low N and optimal environments in Nigeria. The GCA and SCA effects were significant (P $\leq$ 0.01) with preponderance of GCA over SCA effects for all measured traits indicating that additive genetic effects were predominant in the lines under all the contrasting environments. The HSGCA was more efficient than the SCA method in the classification of the inbreds into heterotic groups. The hybrids TZdEEI 74 × TZEEI 13 and TZdEEI 74 × TZEEI 29 were high yielding and most stable across research environments. These hybrids should be further evaluated in on-farm trials to confirm the consistency of performance for commercialization in SSA.

Keywords Combining ability · Drought · Heterotic groups · Low soil nitrogen · *Striga hermonthica* · *Zea diploperennis*

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Introduction

Maize (*Zea mays* L.) is one of the most important staple food crops in Africa particularly in West and Central Africa (WCA). It is cultivated under diverse climatic and agro-ecological conditions in the sub-region. It is estimated that, by 2025 maize will become the crop with the highest level of production globally

with demand in developing countries doubling by 2050 (CIMMYT and IITA 2010). Maize is also an important feed for animals especially in the poultry industry.

The savannas of WCA have the greatest potential for maize production due to high solar incoming radiation, less disease and insect pest pressure due to the low humidity and lower night temperatures (Badu-Apraku et al. 2013a). Despite the immense potential of maize in the savannas, production is greatly constrained by *Striga hermonthica* parasitism, recurrent drought, and low soil fertility, especially low levels of soil nitrogen (N). Annual maize yield loss of about 15% has been attributed to drought in sub-Saharan Africa (SSA). However, localized losses may be much higher in the marginal areas where the annual rainfall is below 500 mm, or where the soils are sandy or shallow (Edmeades et al. 1995). For example, grain yield losses can even be much higher if drought occurs at the most sensitive stages of crop growth, such as the flowering and grain-filling periods (NeSmith and Ritchie 1992). Changes in climatic conditions resulting from global warming have further increased the probability of drought, even in the forest agro-ecology of WCA (Fakorede and Akinyemiju 2003). Grant et al. (1989) and Badu-Apraku et al. (2012) reported that maize is particularly sensitive to drought during the period covering one week before to two weeks after flowering. Drought during these periods results in an increase in the anthesis-silking interval (ASI) as silk emergence is delayed leading to kernel abortion (Boyle et al. 1991; Edmeades et al. 2000).

Yield losses due to *Striga hermonthica* may range from 10 to 100% depending on the variety and the environmental conditions (Kroschel 1999). *Striga hermonthica* infestation is extremely difficult to control and is a major threat to the rapid spread of maize into the WCA savannas. Available *Striga* control measures include host plant resistance, cultural, chemical, and manual methods (Odhiambo and Ransom 1994; Kim et al. 1998). Of these, the use of host plant resistance or tolerance is considered the most economical and environmentally friendly for resource-poor farmers.

In addition to the losses due to recurrent drought and *Striga*, the soils of WCA are inherently low in N and farmers do not have ready access to inorganic fertilizers because of non-availability, high cost or lack of credit. As a result, most farmers produce maize under low N conditions (McCown et al. 1992; Oikeh and Horst 2001). Estimated yield losses from nitrogen stress alone can be as high as 50% (Wolfe et al. 1988). Nitrogen stress has been reported to reduce final grain number by increasing kernel abortion (Monneveux et al. 2005). This increase in kernel abortion is closely related to lack of post-flowering nitrogen uptake by the crop. Also, nitrogen deficiency reduces leaf area index and hence radiation interception is reduced (Monneveux et al. 2006). The development, deployment and production of low N tolerant maize is therefore a necessary intervention to improve maize production and food security in SSA. Furthermore, under field conditions, drought, *Striga*, and soil nutrient deficiencies can occur simultaneously and the combined effects can be devastating (Cechin and Press 1993; Kim and Adetimirin 1997). Therefore, the development and adoption of early and extra-early maize with tolerance to multiple stresses are vital for increased productivity if maize-based farming systems are to be sustained and expanded. Hence, maize varieties targeted to the drought prone areas of SSA must be tolerant to low N or *Striga* infestation. Thus, breeding for tolerance to drought, *Striga* and low nitrogen has been the focal point of the maize improvement programme of the International Institute of Tropical Agriculture (IITA) during the past two decades. A wide range of high yielding extra-early inbreds and hybrids with tolerance to low N, resistance to *Striga* and also possessing genes for tolerance to drought at the flowering and grain-filling periods, are presently available in SSA to combat these threats (Badu-Apraku and Oyekunle 2012; Badu-Apraku et al. 2013b). Parker and Riches (1993) reported that resistance genes may not exist in cultivated maize to combat the biotic stresses limiting maize production. This has led to the search for novel genes for tolerance to low N, drought and *Striga hermonthica* in the wild relatives of maize, *Zea diploperennis* (Lane et al. 1997).

Due to the high yield potential of maize hybrids, they are used throughout the world for increased maize production. In breeding programs, it is very important to know the combining abilities of inbred lines that are used as parents in hybrid combinations. Increase in maize production can be enhanced by gathering relevant and basic information on the heterotic patterns and combining ability of inbreds. Combining ability studies provide information on the genetics of

the inheritance of traits and enable breeders to select suitable parents for further improvement or use in commercial hybrid breeding programs (Ali et al. 2012).

To revolutionise maize production in the sub-region, a number of countries have adopted hybrid maize production and several high-yielding hybrids in the early, extra-early, intermediate and late maturing groups are presently available for commercial seed production (Badu-Apraku et al. 2013b). Information on the combining abilities and heterotic patterns of inbred lines is important in identifying productive hybrids for commercial production (Badu-Apraku and Oyekunle 2012). Accurate assessment of inbred lines in hybrid combinations is critical to the success of a commercial hybrid program. Also, classification of inbreds into heterotic groups is essential in order to maximize their potential usefulness for the development of productive hybrids and synthetics as well as refining and identifying new heterotic groups.

Results of studies have shown that heterotic grouping of inbreds based on the HSGCA method is superior to the groupings based on the SCA effects of grain yield (Fan et al. 2009; Badu-Apraku et al. 2013c; Akinwale et al. 2014; Badu-Apraku et al. 2015a). In most of these studies the mating designs used have been the diallel and the North Carolina design II. The line × tester design is probably the most simple and commonly used mating design for genetic studies. Fan et al. (2009) grouped maize inbreds following field evaluations using the line × tester design and reported that the HSGCA grouping method was more efficient than the SCA effects of grain yield. Apart from this study, no other researcher has compared the grouping efficiency of the two methods based on the line × -tester design. Furthermore, there is no published information on the heterotic patterns and combining ability of the numerous extra-early maturing white inbred lines developed by the IITA maize program from crosses between *Zea diploperennis* and normal maize. The objectives of the present study were therefore to (i), determine the general and specific combining ability effects of selected extra-early maturing white inbreds for grain yield and other traits using the line × tester mating design (ii) classify the inbreds into heterotic groups using the SCA effects of grain yield, and the HSGCA of grain yield methods and (iii) examine the performance and stability of selected extra-early maturing white hybrids under drought, low N, *Striga*, optimal and across environments.

Materials and methods

Genetic materials and generation of crosses

An extra-early drought tolerant and *Striga* resistant maize population, TZEE-W Pop STR C_4 was crossed to four IITA intermediate maturing white inbreds, TZSTRI 104, TZSTRI 105, TZSTRI 107, and TZSTRI 108 containing genes for *Striga* resistance from *Zea diploperennis* in an effort to introgress *Striga* resistance genes into the population. The F_1's were backcrossed for two generations to the extra-early population to recover extra-earliness. The backcrosses were selfed for six generations under *Striga* and drought conditions to develop the 63 extra-early inbred lines used in the present study (Supplementary Table 1). A total of 252 single cross hybrids were generated in 2013 from crosses involving the 63 inbred lines and four elite testers identified in previous studies conducted in the IITA maize improvement program viz. TZEEI 13, TZEEI 14, TZEEI 21 and TZEEI 29 at IITA, Ibadan.

Field evaluations

Three experiments were conducted using the 252 single-cross hybrids plus four hybrid checks. The experimental units in all the trials were single-row plots, with spacing of 0.75 m between rows and 0.40 m within rows. The lengths of the single-row plots were 3 m long for all experiments and were laid in 16 × 16 lattice design. Three seeds were sown per hill and seedlings later thinned to two at two weeks after planting (WAP) to give a final plant density of 66,666 plants ha^{-1}.

Experiment 1

In experiment 1, the 256 extra-early maturing maize hybrids were evaluated under managed drought stress during the dry seasons of 2013/2014 and 2014/2015 at Ikenne (lat. 6°87′N, long. 3°7′E, elevation of 60 m above sea level and 1500 mm annual rainfall). In addition, the hybrids were evaluated under optimal environments during the major growing season of

2014 at Ikenne and Bagauda (lat. 12°00′N, long. 8°22′E, elevation 580 m, 800 mm annual rainfall). Bagauda is normally a drought prone environment but drought stress could not be achieved in 2014 due to heavy rainfall throughout the growing season. The induced drought at Ikenne was achieved by withdrawing the irrigation water 21 days after planting (DAP) until maturity so that the maize plants depended on stored water in the soil for growth and development. During the first 21 days after planting, the plants relied on a sprinkler irrigation system which provided 17 mm of water weekly. However, a ''rescue'' irrigation had to be provided at 53 days after planting during the 2014/2015 dry season evaluation due to severe harmattan during January of 2015. The soil at the experiment station at Ikenne is eutric nitrosol (Soil Survey Staff 1999) and the experimental fields are flat and fairly uniform, with high water-holding capacity. Fertilizer was applied to the induced drought trials at the rate of 60 kg ha^{-1} each of N, P and K (15–15–15) at planting. An additional 60 kg ha^{-1} of urea was top-dressed at two WAP. However, under the optimal environments, the fertilizer was applied at 2–3 WAP while the top-dressing was done at 4 to 5 WAP at the same rate as described in the drought trial. The trials were kept weed-free with the application of pre- and post-emergence herbicides, primextra and paraquat each at 5 l/ha and subsequently, by hand weeding.

Experiment 2

The second experiment was conducted under low N (30 kg ha^{-1}) and high N (90 kg ha^{-1}) at Mokwa (lat. 9°18′N, long. 5°4′E, elevation of 457 m above sea level and 1100 mm annual rainfall) and Obafemi Awolowo University Teaching and Research Farm, Ile-Ife (7°28′N, 4°33′E, and 244 m above sea level, 1200 mm annual rainfall) during the 2014 cropping season. The 256 extra-early maturing hybrids used in experiment 1 were also evaluated in fields depleted of nitrogen by continuously planting maize at high population density and removing the plant biomass after harvest. Soil samples were taken before planting for all the test environments and nitrogen, phosphorus and potassium contents were determined at the IITA's analytical services laboratory at Ibadan. The results of the soil analysis showed that the soil at Mokwa contained 0.085% nitrogen, 0.20% potassium and 6.32% phosphorus while the soil at Ile-Ife contained

0.084% nitrogen, 0.358% of potassium and 2.05% phosphorus. Fertilizer was applied to bring the total available N to 90 kg ha^{-1} for the high-N treatment, and 30 kg ha^{-1} for the low N. The N-fertilizer was applied at 2 and 5 WAP. In addition, single super-phosphate (P_2O_5) and muriate of potash (K_2O) were applied to both low N and high-N blocks at the rate of 60 kg ha^{-1}. All other management practices were the same as in Experiment 1.

Experiment 3

In the third experiment, the 256 extra-early maturing hybrids were evaluated under artificial *Striga*-infested and *Striga*-free environments at Mokwa and Abuja (9°16′N, 7°20′E, 300 altitude, 1500 mm rainfall) in the southern Guinea savanna of Nigeria in 2013 and 2014. 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 for the infestations. 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. The delay in fertilizer application was necessary in order to subject maize plants to stress, a condition that favours the production of strigolactones, which stimulate germination of *Striga* seed and the attachment of *Striga* plants to the roots of the maize plants in the *Striga* infested plots (Kim 1991). Weeds other than *Striga* were controlled by hand weeding.

Data collection

Data were collected in the three experiments for days to 50% silking (DS) and anthesis (DA) as the number of days from planting to when 50% of the plants had extruded silks and shed pollen, respectively. Anthesis-silking interval (ASI) was calculated as the difference between DS and DA. Plant height (PLHT in cm) was measured from the base of the plant to the first tassel branch while ear height (EHT in cm), was from the ground to the node bearing the top ear. Number of ears per plant (EPP) was obtained by dividing the total number of ears per plot by the number of plants

harvested. Plant aspect (PASP) was rated on a scale of 1–9, where 1 = excellent and 9 = poor. Ear aspect (EASP) was recorded on a scale of 1–9 where 1 = clean, uniform, large, and well-filled ears while 9 = ears with undesirable features such as diseases, small ears, and ears with poorly filled grains. In addition, stay green characteristic (STGR) was scored for the drought-stress and the 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. Host plant damage syndrome rating (Kim 1991) and number of emerged *Striga* plants were recorded at 8 and 10 WAP in the *Striga*-infested plots at Mokwa, and Abuja. *Striga* damage was scored per plot on a scale of 1–9 where 1 = no damage, indicating normal plant growth, and 9 = complete collapse or death of the maize plant (Kim 1991). In the drought-stress and low N experiments, harvested ears from each plot were shelled and grain moisture was determined using Kett grain moisture tester PM-450. Grain yield (kg ha^{-1}) was computed from the shelled grain weight (kg/plot) at 15% moisture content of each entry. On the other hand, in the *Striga*-infested, *Striga*-free, the well-watered (rain-fed) and high-N experiments, a shelling percentage of 80% was assumed for all hybrids and grain yield (obtained from ear weight and converted to kg ha^{-1}) was adjusted to 15% moisture. Even though data were collected on several traits, only those on the most important traits in the studies are presented in the results.

Statistical analysis

Analyses of variance (ANOVA) was performed separately for data collected under drought, low N, *Striga*-infested and optimal environments as well as across environments on plot means for grain yield, DS, ASI, EPP, PLHT, EHT, STGR, EASP, and PASP with PROC GLM in Statistical Analysis System (SAS) using a RANDOM statement with the TEST option (SAS Institute Inc 2011 version 9.3). Test for homogeneity of variances for grain yield showed no significant differences among year-location combinations (data not shown), thus justifying the analysis across environments. In the ANOVA, locations, replicates, blocks, and hybrids of each experiment were regarded as random factors. Means were separated using the standard errors.

Means generated from the analysis of variance from the study were used for line × tester analysis as described by Singh and Chaudhary (1985). General combining ability (GCA) and specific combining ability (SCA) and their standard errors were computed for grain yield and other measured traits under the research environments using SAS. The variation among hybrids were partitioned into sources due to lines, testers and line × testers. GCA of a tester (male) was obtained based on its performance in F$_1$ hybrid combinations with all possible lines (females). Similarly, GCA of each line was determined based on the performance of F$_1$ hybrid with all possible testers. GCA and SCA effects were determined for each trait under each research environment and across research environments.

The general linear model for line × tester mating design is:

$$Y_{ijkl} = \mu + a_1 + b_{kl} + v_{ij} + (av)_{ijl} + \varepsilon_{ijkl}$$

where Y_{ijkl} = observed value from each experimental unit; μ = population mean; a_1 = location effect; b_{kl} = block or replication effect within each location; v_{ij} = F$_1$ hybrid effect = $g_i + g_j + s_{ij}$. i.e. $v_{ij} = g_i + g_j + s_{ij}$, where g_i = general combining ability (GCA) for the ith parental line; g_j = GCA effects of jth tester; s_{ij} = specific combining ability (SCA) for the ijth F$_1$ hybrid while $(av)_{ijl}$ = interaction effect between ith F$_1$ hybrid and lth location; and ε_{ijkl} = residual effect. The relative importance of GCA sum squares over SCA sum squares for grain yield and other agronomic traits were determined using the ratio proposed by Baker (1978).

Heterotic grouping of the inbred lines under *Striga*-infested, drought, low N, optimal growing environments and across research environments were performed based on SCA of grain yield (Agbaje et al. 2008) and heterotic group's specific and general combining ability (HSGCA) of grain yield proposed by Fan et al. (2009).

To be classified into a heterotic group, a line must have positive SCA effects with one of the testers and negative SCA effects with the other testers, along with mean grain yield equal to or greater than 1 S.E above the grand mean of all testcrosses with the positive SCA tester. Lines that had zero SCA effects were not classified into any of the heterotic groups (Agbaje et al. 2008).

To compare the efficiency of the two heterotic grouping methods, the 252 hybrids were arranged from the highest to the lowest based on grain yield under *Striga*-infested, drought, low N, optimal and across research environments using the method proposed by Badu-Apraku et al. (2015a). 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 further divided into high yielding hybrids (Yield of group 1 with a mean grain yield ranking among the first 84th); intermediate yielding hybrids (Yield group 2 with a mean grain yield between the 85th and the 168th) and low yielding hybrids (Yield group 3 with a mean grain yield between the 169th and the 252nd).

To identify superior hybrids for commercialization under multiple stress environments, a multiple trait base index (MI) that integrated grain yield and other important traits across the three stresses (Badu-Apraku et al. 2015b) was computed as follows:

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

where YLD = grain yield across *Striga*-infested, drought and low N environments, EPP = number of ears per plant under *Striga*-infested, drought and low N environments, EASP = ear aspect across *Striga*-infested, drought and low N environments, PASP = plant aspect across drought and low N environments, ASI = anthesis-silking interval across *Striga*-infested, drought and low N environments, STGR = stay green characteristic across drought and low N environments, SD8 and SD10 = *Striga* damage at 8 and 10 WAP across *Striga*-infested environments, ESP8 and ESP10 = number of emerged *Striga* plants at 8 and 10 WAP across *Striga*-infested environments. The traits used in the base index were standardized with a mean of zero and standard deviation of 1 to minimize the effects of different scales. A positive base index therefore indicated tolerance to the multiple stresses, while a negative value was an indication of susceptibility.

A total of 29 hybrids (top 15 multiple stress tolerant and the ten most susceptible based on the MI plus the four checks) evaluated across ten stress and non stress environments were subjected to the additive main effects and multiplicative interactions (AMMI) biplot analysis. The AMMI analysis was adopted to assess the relationships among the hybrids (G), environments (E), hybrid × environment interactions (GEI) and to obtain information on the performance and yield stability of the hybrids across research conditions as well as to identify hybrids adapted to specific environments. The AMMI model has been described in detail by Zobel et al. (1988), Gauch and Zobel (1988) and Crossa (1990). Three AMMI family models, AMMI0, AMMI1 and AMMI2, are available for studying G × E interactions in multi-environment trials. The most accurate member of the AMMI model family is the AMMI0 because the G × E interactions are small and buried in the noise. However, AMMI1 could be more accurate than AMMI0 when the G × E interaction is only marginally significant. But where the AMMI2 captures more G × E interactions than AMMI1, the AMMI2 model only decreases accuracy (Gauch et al. 2008). In the present study therefore, the AMMI1 was more appropriate and was used to study the GEI.

Results

Analyses of variance and combining ability estimates for grain yield and other traits of extra-early white hybrids

The analysis of variance of the hybrids evaluated under drought, low N, *Striga*-infested, optimal and across research environments showed significant (P ≤ 0.01) hybrid (G), environment (E) and GEI mean squares for grain yield and most of the measured traits (Supplementary Tables 2, 3). Partitioning of the hybrid mean squares into its components revealed that GCA of the lines (GCA$_{line}$), GCA of Tester (GCA$_{tester}$) and the SCA mean squares were significant for grain yield and most other measured traits under drought, low N, *Striga*-infested (Supplementary Table 2), optimal, and across research environments (Supplementary Table 3). It is striking to note that under *Striga*-infested environments the GCA$_{tester}$ and SCA mean squares did not vary for grain yield and most measured traits (Supplementary Table 2). The E × GCA$_{Line}$ and E × GCA$_{Tester}$ interaction mean squares were significant for grain yield and most other measured traits under each and across environments except GCA$_{Tester}$ interaction mean squares under

drought which had only few of the traits showing significant differences. It should be noted that the $E \times GCA_{line}$ and $E \times GCA_{tester}$ interaction mean squares were not significant for grain yield under drought. Similarly, the $E \times SCA$ interaction mean squares did not show significant differences for most of the measured traits under drought, low N, *Striga*-infested, optimal and across research environments (Supplementary Tables 2, 3).

The relative importance of GCA mean squares over SCA sum squares under drought, low N, *Striga*-infested, optimal and across research environments are presented in Supplementary Tables 2 and 3. The contributions of GCA sum of squares to the total variation among hybrids were larger (>0.5) than those of SCA for grain yield and the other measured traits under each and across research environments.

General combining ability effects of lines and testers for grain yield and other traits under drought, low N, *Striga*-infested and optimal environments

The GCA effects of 36 of the 63 inbreds used in the present study did not reach significant positive or negative levels for grain yield and most other measured traits under *Striga*-infestation, drought, low N and across test environments and are therefore not presented in the results of this study. The GCA effects of grain yield and other measured traits of the 31 inbreds with significant positive and/or negative GCA effects for grain yield and other important traits under the contrasting environments are presented in Table 1. Significant positive GCA effects for grain yield were detected for TZdEEI 34, TZdEEI 50, TZdEEI 59, TZdEEI 71, TZEEI 14, and TZEEI 29 under *Striga* infestation, TZdEEI 34, TZdEEI 90 and TZEEI 13 under low N, TZdEEI 23, TZdEEI 45, TZdEEI 47 and TZdEEI 50, TZdEEI 51, TZdEEI 55, and TZdEEI 91 under drought, TZdEEI 34, TZdEEI 54, TZdEEI 55, TZdEEI 68, TZdEEI 71, and TZdEEI 91 under optimal environments. Only TZEEI 29 had significant negative ASI under low N, TZdEEI 70 under drought, TZdEEI 105 and TZEEI 29 under optimal environments. Similarly, only TZEEI 14 had significant negative GCA effects for ASI under *Striga* infestation. The inbreds TZdEEI 23, TZdEEI 51, TZdEEI 54, TZdEEI 55 and TZdEEI 71 had significant negative GCA effects for plant aspect under

drought and TZdEEI 23, TZdEEI 91 under optimal environments. The inbreds TZdEEI 34 and TZdEEI 68 had significant negative GCA effects for ear aspect under low N; TZdEEI 50, TZdEEI 51, TZdEEI 55, TZdEEI 70, TZdEEI 71, TZdEEI 91 and TZEEI 14 under drought; TZdEEI 55 and TZdEEI 70, TZdEEI 71, TZdEEI 91 and TZEEI 29 under optimal environments. Also, inbreds TZdEEI 23, TZdEEI 43 and TZEEI 21 showed significant negative GCA effects for the stay-green characteristic under drought while only TZdEEI 59 and TZEEI 13 displayed significant negative GCA effects for the stay-green characteristic under low N. Under *Striga*-infested conditions, significant negative GCA effects for *Striga* damage at 8 and 10 WAP were observed for inbreds TZdEEI 34, TZdEEI 50, TZdEEI 71 and TZEEI 29 at 8 WAP. In contrast, only TZEEI 29 showed significant negative GCA effects for the number of emerged *Striga* plants at 8 and 10 WAP.

Heterotic grouping of extra-early inbred lines under drought, low N, *Striga*-infested, optimal and across research environments

Under low N, only four of the lines (representing 6.35%) could be grouped by the testers based on the SCA heterotic grouping method. Inbreds TZdEEI 21 and TZdEEI 24 were placed in the TZEEI 13 heterotic group, TZdEEI 89 in the TZEEI 14 group and TZdEEI 26 in the TZEEI 29 heterotic group. No inbred was grouped by tester TZEEI 21. However, using the HSGCA of grain yield grouping method, 56 of the 63 inbreds (82.54%) were grouped by the testers. Of the inbreds classified, seventeen were in the TZEEI 13 group, 13 in the TZEEI 14 group, 12 in the TZEEI 21 group and 14 in the TZEEI 29 group (Table not shown). Under drought, five of the inbred lines were classified into the TZEEI 13 heterotic group, four into TZEEI 14 group, seven into the TZEEI 21 group and two into the TZEEI 29 group while 45 inbreds (representing 71.42%) could not be classified into any of the heterotic groups based on the SCA of grain yield method. In contrast, only 14 lines (23.33%) could not be classified into any of the heterotic groups using the HSGCA method. Under optimal growing environments, the SCA method classified only eight of the inbred lines (12.70%). However, using the HSGCA grouping method, six of the lines were classified into the TZEEI 13 group, 13 into each of the

Table 1 General combining ability (GCA) effects of inbreds and testers for grain yield and other traits under low N (LN), drought (DT), Striga-infested (STR), and optimal (OP) environments

Line	Grain yield (kg ha⁻¹)				Anthesis silking interval				Plant aspect		
	STR	LN	DT	OP	STR	LN	DT	OP	LN	DT	OP
TZdEEI 23	142.93	131.51	535.56*	406.98	0.14	0.02	−0.22	0.00	−0.84**	0.07	−0.21**
TZdEEI 31	−135.07	−610.00	−871.50**	162.8	−0.17	0.27	0.09	0.22	0.53*	0.10	0.09
TZdEEI 34	1125.39*	932.71*	295.24	650.24*	−0.05	−0.41	−0.04	0.19	0.03	−0.09	−0.12
TZdEEI 42	64.40	−262.48	−220.6	−567.24*	−0.05	0.09	0.21	−0.09	0.22	0.20	0.13
TZdEEI 43	−22.96	−188.25	−81.67	−900.34**	−0.05	0.27	0.34	−0.19	0.10	0.16	0.15*
TZdEEI 45	221.71	−404.86	481.93*	99.45	−0.05	−0.10	−0.10	−0.16	−0.34	0.15	0.15*
TZdEEI 47	53.56	39.19	600.19*	303.77	0.01	0.34	−0.41	0.03	−0.22	0.01	0.02
TZdEEI 50	1058.66*	−256.19	597.94*	−221.51	−0.42	−0.10	−0.16	0.03	−0.28	−0.12	0.02
TZdEEI 51	338.98	273.49	818.83**	−69.14	−0.36	0.02	−0.47	0.03	−0.59*	−0.09	−0.04
TZdEEI 54	−358.89	−148.10	190.36	548.82*	1.39*	0.21	0.09	0.06	−0.59*	−0.05	−0.18
TZdEEI 55	−67.73	−154.28	586.27*	1007.12**	0.83	−0.04	0.71*	−0.19	−0.78**	0.04	−0.07
TZdEEI 59	935.76*	130.69	−13.94	22.84	−0.17	−0.10	0.15	−0.06	−0.34	−0.02	−0.07
TZdEEI 68	−15.57	448.58	−76.36	537.29*	−0.11	−0.16	0.28	−0.03	0.16	−0.09	−0.13
TZdEEI 69	37.74	284.83	271.34	183.9	−0.05	−0.35	0.03	0.03	−0.34	−0.09	−0.07
TZdEEI 70	127.87	−14.58	131.15	402.65	−0.05	0.46	−0.79**	−0.16	−0.15	0.04	−0.10
TZdEEI 71	1018.60*	−69.00	406.78	558.97*	−0.17	−0.23	−0.16	0.03	−0.78**	0.01	−0.02
TZdEEI 73	−675.78	−154.57	−185.72	−769.55*	0.14	0.15	0.34	0.03	−0.03	−0.02	0.16*
TZdEEI 78	−354.04	590.73	−190.60	−543.91*	0.20	−0.04	−0.16	−0.03	0.60*	−0.18	0.05
TZdEEI 82	123.79	−519.19	−211.00	−824.29**	−0.36	−0.10	0.09	−0.06	0.10	0.01	0.07
TZdEEI 83	347.44	253.99	−863.12**	60.26	−0.24	−0.04	1.21**	0.00	0.78**	−0.27	−0.09
TZdEEI 84	119.86	41.84	−231.35	−430.28	0.83	−0.16	0.34	−0.19	−0.03	−0.18	0.15*
TZdEEI 85	−155.63	262.32	−539.93*	549.98*	−0.05	−0.16	0.53	−0.13	0.35	0.04	−0.04
TZdEEI 90	344.81	913.30*	−202.54	132.14	0.45	−0.10	0.84**	0.19	0.35	−0.12	0.02
TZdEEI 91	−184.17	489.64	783.28**	837.78**	0.39	−0.16	−0.47	0.09	−0.47	−0.15	−0.16*
TZdEEI 99	−935.31*	−391.46	−290.77	−860.03**	0.20	0.27	0.53	0.16	0.47	0.01	0.19*
TZdEEI 105	359.19	195.15	−560.8*	47.11	−0.05	−0.04	0.15	−0.25*	0.60*	0.04	−0.04
TZdEEI 107	−394.83	−432.29	−717.76**	−893.79**	0.01	−0.54	1.21**	−0.13	0.91**	0.10	0.15*
TZEEI 13	−48.98	345.43*	−51.99	186.65	0.01	0.01	0.05	−0.01	0.13	−0.07	−0.02
TZEEI 14	264.48***	5.74	177.78	56.25	−0.07*	0.00	−0.13	0.06*	−0.19*	−0.04	−0.06
TZEEI 21	−362.98***	−257.61	24.88	−239.16	0.00	0.02	−0.09	−0.07**	−0.16	0.03	0.00

Table 1 continued

Line	Grain yield (kg ha^{-1})				Anthesis silking interval				Plant aspect		
	STR	LN	DT	OP	STR	LN	DT	OP	LN	DT	OP
TZEEI 29	147.48**	−93.56	−150.67	−3.74	0.07*	−0.03*	0.17	0.02	0.22**	0.09	0.07*
SE_Lines	439	356.90	215.20	265.02	0.638	0.24	0.29	0.12	0.22	0.11	0.07
SE_Testers	47.01	118.20	115.70	135.06	0.03	0.03	0.10	0.02	0.07	0.06	0.03

Line	Ear aspect				STGR		Striga damage		Emerged Striga plants	
	STR	LN	DT	OP	STR	LN	8 WAP	10 WAP	8 WAP	10 WAP
TZdEEI 23	−0.25	0.18	−0.43	−0.15	0.41	−0.47*	−0.39	0.04	−3.69	−3.71
TZdEEI 31	−0.13	0.06	0.88**	0.06	0.34	0.22	0.11	−0.09	−4.01	−4.27
TZdEEI 34	−0.81	−0.25*	−0.06	−0.02	−0.34	−0.16	−1.02*	−1.09*	−1.26	−0.15
TZdEEI 42	0.19	0.12	0.38	0.20*	−0.47	0.34	−0.02	−0.02	−1.63	−0.96
TZdEEI 43	0.25	0.21	−0.37	0.26*	−0.16	−0.41*	−0.14	−0.15	−7.94	−7.27
TZdEEI 45	0.00	0.18	−0.24	0.18*	0.47	0.16	−0.02	−0.09	5.18	3.16
TZdEEI 47	−0.19	−0.07	−0.24	−0.13	−0.03	−0.03	0.17	−0.02	5.81	4.04
TZdEEI 50	−0.56	0.00	−0.56*	0.07	0.41	0.03	−1.27*	−1.02*	−4.01	−2.52
TZdEEI 51	0.12	−0.10	−0.68*	0.03	−0.28	−0.22	−0.14	−0.34	−1.13	−1.59
TZdEEI 54	0.12	0.00	−0.43	−0.18	0.47	−0.09	0.29	0.60	6.87	5.41
TZdEEI 55	0.31	0.03	−0.49*	−0.21*	0.22	−0.28	0.29	0.60	17.49*	22.91*
TZdEEI 59	−0.50	−0.07	0.01	0.07	−0.91*	0.16	−0.58	−0.46	−4.13	−5.52
TZdEEI 68	−0.31	−0.32*	−0.12	−0.17	−0.41	−0.22	−0.39	−0.15	−3.88	−3.27
TZdEEI 69	0.06	−0.07	−0.37	−0.13	−0.66	−0.09	−0.14	0.16	−5.26	−5.34
TZdEEI 70	−0.25	0.00	−0.56*	−0.19*	−0.47	0.22	0.17	0.04	−3.69	−3.02
TZdEEI 71	−0.69	0.03	−0.87**	−0.18*	−0.09	−0.16	−1.33**	−1.02*	−5.94	−6.02
TZdEEI 73	0.19	−0.04	0.32	0.17	0.28	0.09	0.29	0.54	−7.63	−9.09
TZdEEI 78	0.12	−0.19	0.13	0.03	−0.41	0.03	−0.02	0.35	1.81	1.23
TZdEEI 82	−0.06	0.09	0.26	0.13	−0.16	0.28	−0.52	−0.46	−6.57	−6.96
TZdEEI 83	−0.25	−0.13	0.88**	−0.13	0.22	0.28	−0.27	−0.21	−5.94	−7.65
TZdEEI 84	0.31	−0.22	0.26	0.04	0.16	0.34	0.48	−0.02	−3.82	−4.46
TZdEEI 85	0.19	−0.16	0.51*	−0.07	−0.28	0.53*	0.86	0.48	−1.69	−2.02
TZdEEI 90	0.00	−0.19	0.19	−0.07	−0.72	0.03	−0.14	−0.09	−6.88	−6.84
TZdEEI 91	0.00	−0.13	−0.68*	−0.24*	−0.16	−0.22	0.17	0.10	2.62	4.29
TZdEEI 99	0.62	0.18	0.26	0.18*	0.91*	−0.03	1.04*	0.73	3.56	3.60

Table 1 continued

Line	Ear aspect				STGR		Striga damage		Emerged Striga plants	
	STR	LN	DT	OP	LN	DT	8 WAP	10 WAP	8 WAP	10 WAP
TZdEEI 105	−0.19	0.03	0.44	−0.02	−0.72	0.09	0.11	−0.09	−3.19	−3.09
TZdEEI 107	0.19	0.15	0.57*	0.12	0.78*	0.28	0.23	0.35	−7.51	−6.34
TZEEI 13	0.05*	−0.04	0.13	0.00	−0.31*	−0.10	0.22**	0.11	2.32*	2.90**
TZEEI 14	−0.23	−0.03	−0.28*	−0.02	0.13	0.31**	−0.07	−0.14	−0.99	−1.11
TZEEI 21	0.31	0.09	0.03	0.10*	0.33*	−0.21**	0.05	0.16	0.55	0.26
TZEEI 29	−0.12	−0.02	0.12	−0.08*	−0.14	0.00	−0.20**	−0.13	−1.88*	−2.04*
SE_Lines	0.38	0.13	0.24	0.09	0.37	0.193	0.45	0.45	7.137	7.762
SE_Testers	0.02	0.05	0.13	0.04	0.12	0.063	0.05	0.13	0.93	0.96

SGTR Stay green characteristic

*, ** Significant F-test at probability levels of 0.05 and 0.01, respectively

TZEEI 14, TZEEI 21 and TZEEI 29 heterotic groups with only 18 of the 63 lines (28.57%) not classified into any heterotic group under optimal environments. Similarly, under *Striga*-infested environments, the SCA effects of grain yield method classified only eight of the 63 inbreds (12.70%) while the HSGCA method classified 74.60% of the inbreds under *Striga*-infested environments (Table not shown). Across the research environments, the SCA effects of grain yield method classified only 13 of the 63 inbreds (20.63%) while the HSGCA method classified 46 (73.02%) of the inbreds (Supplementary Table 4).

Comparison of the efficiencies of the SCA effect of grain yield and HSGCA heterotic grouping methods

The breeding efficiency is the proportion of superior high yielding hybrids obtained across the total number of inter-heterotic crosses, thus the best heterotic grouping method is the one that permits inter-heterotic group crosses to produce more of the superior hybrids than the intra-group crosses (Fan et al. 2009). Based on this, the SCA method identified 81, 84, 84, 83 and 82 inter-group crosses as high yielding hybrids out of the total inter-group crosses of 234, 248, 244, 244 and 244 recorded under drought, low N, *Striga*, optimal and across research environments, respectively. On the other hand, the HSGCA method identified 76, 82, 81, 81 and 82 high yielding hybrids out of the total inter-group crosses of 204, 198, 205, 208 and 206 under drought, low N, *Striga*-infested, optimal and across research environments, respectively (Table 2). The breeding efficiencies of the HSGCA method were higher (37.3, 41.4, 39.5, 38.9 and 39.8%) under drought, low N, *Striga*-infested, optimal and across research environments, respectively than those of the SCA method (34.6, 33.9, 34.4, 34.0 and 33.6%) (Table 2).

Performance of testcross hybrids and hybrid checks under low soil N, induced drought stress, *Striga* infestation and optimal growing conditions

The top 15 and worst 10 hybrids selected using the multiple stress base index and the four checks are shown in Supplementary Table 5. Under drought, the grain yield of the hybrids ranged from 1464 kg ha^{-1} for TZdEEI 100 × TZEEI 21 to 3857 kg ha^{-1} for

TZdEEI 23 × TZEEI 14 with a mean grain yield of 2567 kg ha^{-1}. Under low N, the mean yield was 4234 kg ha^{-1} and ranged from 2822 kg ha^{-1} for TZdEEI 107 × TZEEI 21 to 5750 kg ha^{-1} for TZdEEI 51 × TZEEI 13. Also, under *Striga*-infestation, a mean grain yield of 3615 kg ha^{-1} was recorded with a range of 1722 kg ha^{-1} for TZdEEI 32 × TZEEI 13 to 5238 kg ha^{-1} for TZdEEI 71 × TZEEI 13. Grain yield under optimal growing conditions ranged from 3176 kg ha^{-1} for TZdEEI 66 × TZEEI 21 to 7259 kg ha^{-1} for TZdEEI 23 × TZEEI 14 with a mean of 5468 kg ha^{-1}. The percent reduction in grain yield of the hybrids ranged from 11 to 64 under *Striga*-infestation, 16 to 74 under drought and from 2 to 37 under low N environments, respectively. The best hybrids out-yielded the best checks by 38.0, 33.8, and 31.7%, under *Striga*-infestation, drought and low N, respectively (Supplementary Table 5). Generally, the reduction in grain yield under the stress conditions was associated with an increase in days to silking, anthesis-silking interval, poor ear and plant aspects, as well as fewer ears per plant.

The significant G, E, and GEI mean squares obtained for grain yield under the contrasting environments prompted the use of the AMMI biplot to decompose the GEI and to examine the yield performance and stability of the extra-early hybrids across test environments. The AMMI biplot for grain yield of selected 29 (best 15 and worst 10 selected hybrids plus the four checks using the multiple stress base index) extra-early maturing maize hybrids across the research environments are presented in Fig. 1. The vertical line represents the grand mean for grain yield. On the other hand, the horizontal line (*y*-ordinate) is the interaction principal component axes 1 (IPCA1) value of zero. Hybrids close to the horizontal line have small interaction with the environment and are considered to be more stable than those farther from it. Therefore, hybrids 5 (TZdEEI 74 × TZEEI 13), 8 (TZdEEI 21 × TZEEI 14), 11 (TZdEEI 74 × TZEEI 29), 14 (TZdEEI 111 × TZEEI 13), 10 (TZdEEI 74 × TZEEI 14) and 26 (Check 1-TZEEI 21 × TZEEI 29) were identified as the most stable and high yielding across the research environments due to their closeness to the zero IPCA1 score and display of grain yield greater than the mean grain yield. Hybrids 13 (TZdEEI 23 × TZEEI 14) and 3 (TZdEEI 64 × TZEEI 14) displayed grain yields

Table 2 Number of inter- and intra-group hybrids classified by specific combining ability of grain yield (SCA) and heterotic group's specific and general combining abilities (HSGCA) methods into Yield Groups 1 (top 84 hybrids), 2 (middle 84 hybrids), and 3 (lowest 84 hybrids) arranged in descending order, along with the breeding efficiency (BE) of the grouping methods under drought, low-N, *Striga*-infested, and across environments

Yield group	Cross type	SCA	HSGCA
Drought environments			
1	Inter-group	81	76
1	Intra-group	3	8
2	Inter-group	77	71
2	Intra-group	7	13
3	Inter-group	76	57
3	Intra-group	8	27
BE		34.6	37.3
Low soil nitrogen environments			
1	Inter-group	84	82
1	Intra-group	0	2
2	Inter-group	84	75
2	Intra-group	0	9
3	Inter-group	80	41
3	Intra-group	4	43
BE		33.9	41.4
Striga-infested environments			
1	Inter-group	84	81
1	Intra-group	0	3
2	Inter-group	81	72
2	Intra-group	3	12
3	Inter-group	79	52
3	Intra-group	5	32
BE		34.4	39.5
Optimal environments			
1	Inter-group	83	81
1	Intra-group	1	3
2	Inter-group	83	69
2	Intra-group	1	15
3	Inter-group	78	58
3	Intra-group	6	26
BE		34.0	38.9
Across environment			
1	Inter-group	82	82
1	Intra-group	2	2
2	Inter-group	80	65
2	Intra-group	4	19
3	Inter-group	82	59
3	Intra-group	2	25
BE		33.6	39.8

greater than the grand mean across environments but had a strong positive interaction with the IPCA1 suggesting that they were adapted to high-yield environment (MK14HN). On the other hand, hybrids 1 (TZdEEI 51 × TZEEI 13), 2 (TZdEEI 71 × TZEEI 13), 6 (TZdEEI 71 × TZEEI 29), 7 (TZdEEI 70 × TZEEI 14), 9 (TZdEEI 91 × TZEEI 13), 12 (TZdEEI 54 × TZEEI 13) and 15 (TZdEEI 59 × TZEEI 13) displayed grain yield greater than the grand mean but had a strong negative interaction with IPCA1 scores suggesting that the hybrids were adapted to low-yield environments (IF14LN, IF14HN, IK14OPT and BG14OPT).
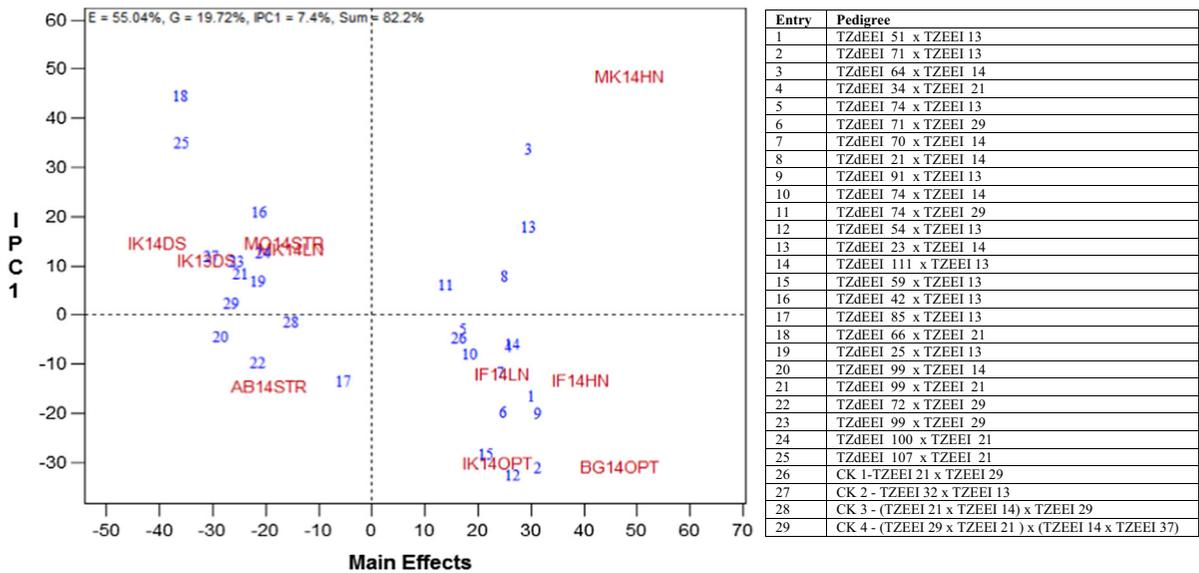
Discussion

General combining ability effects of lines and testers for grain yield and other traits under drought, low N, *Striga*-infested, optimal and across research environments

The highly significant mean squares observed for grain yield and other measured traits of the hybrids under drought, low N, *Striga*-infested, optimal and across research environments implied that there was adequate genetic variation among the genotypes to facilitate improvement of the traits under the contrasting environments. The significant environment mean squares for most measured traits under low N, *Striga*-infestation, drought and optimal growing conditions showed that the test environments were unique in discriminating among the genotypes and that there is a need to test the hybrids in a wide range of environments (Badu-Apraku et al. 2011a). The significant GEI for grain yield and most other measured traits under low N, *Striga*-infestation and optimal growing conditions indicated differential response of the hybrids to the test environments and underscored the need for the extensive testing of the hybrids to identify the high yielding and most stable across multiple environments over years (Moghaddam and Pourdad 2009) before recommendations are made for release and commercialization. The yield reduction of 23% obtained under low N in this study falls within the range of 20–30% proposed by Bolanos and Edmeades (1996) as the expected average yield in the same location under optimal conditions to allow for the identification of genotypes that perform well under

optimal conditions. However, the lack of significant GEI mean squares for most measured traits under drought implied that most of the traits behaved similarly in the two drought environments and that the performance of the genotypes under drought stress will not be significantly influenced by the environment. The presence of significant GCA and SCA mean squares for most traits under *Striga*, low N, drought, optimal and across research environments indicated that there was scope for the improvement of most of the traits through selection and that additive and non-additive genetic effects were both important in the set of inbreds under each and across environments. The results of the present study confirmed the presence of multiple stress tolerant genes in the extra-early maturing inbred lines derived from *Zea diploperennis* (Badu-Apraku et al. 2013b). The results also implied that the testers used in the present study were effective in discriminating among the inbreds under the contrasting environments. Furthermore, the results revealed that the elite inbred testers were effective in classifying the inbred lines derived from *Zea diploperennis* into the established heterotic groups under each and across research environments. The significant interaction of GCA with environment for most measured traits under *Striga*-infested, drought, low N, optimal and across research environments showed that there was large variation in the combining ability of the 63 lines and the four testers under the contrasting environments. Similar results were reported in earlier studies (Gutierrez-Gaitan et al. 1986; Badu-Apraku et al. 2011a).

The preponderance of GCA effects over SCA effects for grain yield and other measured traits under drought, low N, *Striga*-infested, optimal and across research environments suggested that additive gene action was more important than the non-additive in controlling the inheritance of the traits. The predominance of GCA over SCA effects under each and across environments indicated that early generation testing would be effective and promising hybrids may be identified based solely on the prediction from GCA effects. The results of the present study are in disagreement with the findings of Betrán et al. (2003) who found non-additive gene action to be more important for grain yield under low N, drought and optimal environments. The differences in the results of the present study and that of Betrán et al. (2003) may be attributed to the differences in the

Entry	Pedigree
1	TZdEEI 51 x TZEEI 13
2	TZdEEI 71 x TZEEI 13
3	TZdEEI 64 x TZEEI 14
4	TZdEEI 34 x TZEEI 21
5	TZdEEI 74 x TZEEI 13
6	TZdEEI 71 x TZEEI 29
7	TZdEEI 70 x TZEEI 14
8	TZdEEI 21 x TZEEI 14
9	TZdEEI 91 x TZEEI 13
10	TZdEEI 74 x TZEEI 14
11	TZdEEI 74 x TZEEI 29
12	TZdEEI 54 x TZEEI 13
13	TZdEEI 23 x TZEEI 14
14	TZdEEI 111 x TZEEI 13
15	TZdEEI 59 x TZEEI 13
16	TZdEEI 42 x TZEEI 13
17	TZdEEI 85 x TZEEI 13
18	TZdEEI 66 x TZEEI 21
19	TZdEEI 25 x TZEEI 13
20	TZdEEI 99 x TZEEI 14
21	TZdEEI 99 x TZEEI 21
22	TZdEEI 72 x TZEEI 29
23	TZdEEI 99 x TZEEI 29
24	TZdEEI 100 x TZEEI 21
25	TZdEEI 107 x TZEEI 21
26	CK 1-TZEEI 21 x TZEEI 29
27	CK 2 - TZEEI 32 x TZEEI 13
28	CK 3 - (TZEEI 21 x TZEEI 14) x TZEEI 29
29	CK 4 - (TZEEI 29 x TZEEI 21) x (TZEEI 14 x TZEEI 37)

Fig. 1 Grain yield performance and stability of 25 extra-early maturing maize hybrids (*top 15* tolerant and *10* most susceptible based on the multiple trait base index) and four checks evaluated across 10 environments in Nigeria, under drought during the 2013/2014 and 2014/2015 dry seasons and *Striga*-infested, low N and optimal growing conditions in 2014. *BG14OPT* Bagauda optimum, 2014; *IF14HN* Ile-Ife high N, 2014; *IF14LN* Ile-Ife low N, 2014; *IK13DS* Ikenne drought stress, 2013/2014; *IK14DS* Ikenne drought stress, 2014/2015; *IK14OPT* Ikenne optimum, 2014; *MK14LN* Mokwa low soil nitrogen, 2014; *MK14HN* Mokwa high soil nitrogen, 2014; *AB14ST* Abuja *Striga* infested, 2014; *MO14STR* Mokwa *Striga* infested, 2014

genetic materials used and the research conditions as well as the levels of stresses achieved in the different studies.

The GCA effect of an inbred is important for the improvement of a target trait in a population and for the development of synthetic varieties and hybrids (Akinwale et al. 2014). The significant and positive GCA effects observed for grain yield of the inbreds TZdEEI 51, TZdEEI 23, TZdEEI 45, TZdEEI 47, TZdEEI 50, TZdEEI 55 and TZdEEI 91 under drought, TZdEEI 34 and TZdEEI 90 under low N implied that these inbreds possess favorable alleles for grain yield and would contribute high yield to their progenies under drought and/or low N as suggested by Badu-Apraku et al. (2015a). Similarly, under *Striga*-infestation, TZdEEI 34, TZdEEI 50, TZdEEI 59, and TZdEEI 71 and fourteen other inbred lines recorded significant and positive GCA effects for grain yield under optimal conditions indicating that the inbreds would contribute high yield to their progenies under optimal conditions. On the other hand, the significant and negative GCA effects observed for the stay-green characteristic of inbreds TZdEEI 21, TZdEEI 59, TZdEEI 74 under low N and TZdEEI 22,

TZdEEI 23, TZdEEI 33, TZdEEI 43 and TZdEEI 72 under drought environments indicated that these inbreds will slow down the rate of leaf senescence of their progenies. The significant negative GCA effects detected under *Striga* infestation for *Striga* damage of inbreds TZdEEI 16, TZdEEI 34, TZdEEI 50 and TZdEEI 71 and TZdEEI 34, TZdEEI 50 and TZdEEI 71 at 8 and 10 WAP, respectively implied that the inbreds possess genes for *Striga* tolerance which could easily be introgressed into tropical white maize populations for improvement of the tolerance to *Striga* and for development of *Striga* tolerant hybrids and synthetic varieties. Furthermore, TZdEEI 55 showed significant negative GCA effects for the number of emerged *Striga* plants at 8 and 10 WAP, indicating that it possesses genes for resistance to *Striga*. Furthermore, the significant negative GCA effect displayed by inbred (tester) TZEEI 29 for *Striga* damage at 8 WAP and number of emerged *Striga* plants at 8 and 10 WAP indicated that this inbred possessed both tolerance and resistance genes and it could be an invaluable source of favourable alleles for improving tropical maize populations for *Striga* resistance.

Heterotic grouping of the inbred lines based
on specific combining ability and heterotic group's
specific and general combining ability
and comparison of their efficiencies

The SCA effects of grain yield method and the
HSGCA method were used to classify the inbreds into
four heterotic groups. The HSGCA method was the
most efficient in the classification of the inbreds into
heterotic groups under drought, low N, *Striga*-
infested, optimal and across environments. The SCA
method could classify only 28.6, 4.8, 12.7, and 12.7%
of the inbreds into a heterotic group under drought,
low N, *Striga*-infested and optimal environments,
respectively while the HSGCA method classified 77.8,
87.3, 73.0, 73.0 and 69.8% of the inbreds under
drought, low N, *Striga*-infested, optimal and across
research environments, respectively. These results
also indicated that the testers TZEEI 13, TZEEI 14,
TZEEI 21 and TZEEI 29 possess favourable alleles for
grain yield and are efficient for use in hybrid maize
development programs for yield improvement under
multiple stress and optimal 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
HSGCA method identified distinct heterotic groups in
which intra-group mean yields were significantly
lower than the inter-group mean yields under low N,
drought, optimal and *Striga*-infested environments.
Based on the breeding efficiency, the HSGCA method
was identified as the more efficient grouping method
under the contrasting environments.

Performance of extra-early maturing maize single
cross hybrids across research environments

An important objective of the present study was to
examine the combining abilities of the 63 inbred lines
crossed to the four testers and also the yield perfor-
mance of the hybrids under contrasting environments.
The yield reduction of the hybrids under *Striga*-
infestation was 34% of the average yield expected
under optimal growing conditions. This reduction in
grain yield is greater than the 20–30% reported by
Bolanos and Edmeades (1996) and Badu-Apraku et al.
(2011a) under stress conditions. However, the yield

reduction obtained under *Striga*-infestation was far
less compared to the results of earlier study conducted
by Badu-Apraku et al. (2011b) who reported yield
reduction of 77%. Nevertheless, the present results
indicated that the artificial *Striga* infestation was
severe enough to facilitate the discrimination of *Striga*
resistant and susceptible hybrids. The hybrids TZdEEI
74 × TZEEI 13, TZEEI 21 × TZEEI 29, TZdEEI
74 × TZEEI 29 and TZdEEI 21 × TZEEI 14 were
identified by the AMMI biplot as the highest yielding
and most stable across multiple stress environments
and should be extensively tested on-farm to confirm
the consistency of the performance and commercial-
ized. On the other hand, hybrids TZdEEI 23 × TZEEI
14, TZdEEI 64 × TZEEI 14, TZdEEI 51 × TZEEI
13, TZdEEI 71 × TZEEI 13, TZdEEI 71 × TZEEI
29, TZdEEI 70 × TZEEI 14, TZdEEI 91 × TZEEI
13, TZdEEI 54 × TZEEI 13 and TZdEEI
59 × TZEEI 13 were superior in specific environ-
ments and should be tested extensively in those
environments and commercialized.

Conclusions

The GCA and SCA effects were significant with GCA
effects more important than SCA effects for all
measured traits indicating that additive genetic effects
were predominant in the lines. The HSGCA method
was more efficient than the SCA effects of grain yield
method in grouping the extra-early inbreds under the
contrasting environments. The elite inbred tester,
TZEEI 29 displayed significant positive GCA effects
for grain yield, significant negative GCA effects for
Striga damage and number of emerged *Striga* plants
indicating that the inbred possessed both *Striga*
tolerance and resistance genes and could be an
invaluable source of favourable alleles for improving
tropical maize populations for *Striga* resistance. The
hybrids TZdEEI 74 × TZEEI 13, TZdEEI
21 × TZEEI 14, TZdEEI 74 × TZEEI 29, TZdEEI
111 × TZEEI 13 and TZdEEI 74 × TZEEI 14 were
identified as the highest yielding and most
stable across environments and should be tested
extensively in on-farm trials and considered for
commercialization in SSA. The results of this study
have clearly established that maize productivity in
WCA can be improved significantly by selecting
genotypes with improved resistance to *Striga*,

tolerance to drought and increased adaptability to low-N production environments. Furthermore, the results of this study have indicated conclusively that breeding for multiple stress tolerant hybrids using genes from *Zea diploperennis* is an achievable breeding goal.

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