

## Article

# Enhancing Drought Tolerance and *Striga hermonthica* Resistance in Maize Using Newly Derived Inbred Lines from the Wild Maize Relative, *Zea diploperennis*

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**Abstract:** Recurrent drought and *Striga hermonthica* (Del.) Benth parasitism constrains maize production in sub-Saharan Africa (SSA). Transfer of resistance genes from wild relatives can improve resistance to drought and *Striga* in tropical maize. The objectives of this study were to (i) determine the combining ability of 12 extra-early yellow maize inbreds derived from *Zea diploperennis* and tropical maize germplasm; (ii) classify the inbreds into heterotic groups using heterotic grouping based on the general combining ability (GCA) of multiple traits (HGCAMT) method; (iii) examine hybrid performance under contrasting environments; and (iv) examine the stability of hybrid combinations involving the inbreds. Sixty-six diallel crosses involving the inbreds plus four checks were evaluated for two years under drought, *Striga*-infested and rainfed environments in Nigeria. Significant differences ( $p < 0.05$ ) were observed for the effects of genotype, environment, genotype  $\times$  environment, GCA and specific combining ability (SCA) on grain yield and other measured traits. Inbred lines such as TZdEEI 7  $\times$  TZEEI 63 derived from *Z. diploperennis* and tropical germplasm exceeded the checks by a range of 28 to 41%. Across environments, the hybrid TZdEEI 1  $\times$  TZdEEI 7, which was derived from *Z. diploperennis*, was the highest-yielding with a grain yield of 4302 kg ha<sup>-1</sup>. The results revealed the predominance of GCA over SCA effects for most measured traits, suggesting that additive gene action governed the inheritance of *Striga* resistance and drought tolerance related traits in the inbreds. The 12 inbreds were classified into three heterotic groups, while TZEEI 79 and TZdEEI 7 were identified as inbred testers and TZdEEI 7  $\times$  TZEEI 12 as a single-cross tester across environments. Hybrid TZdEEI 9  $\times$  TZEEI 79 was the highest-yielding and most stable. Other promising hybrids were TZdEEI 7  $\times$  TZEEI 79, TZdEEI 1  $\times$  TZdEEI 7 and TZdEEI 12  $\times$  TZEEI 95. These hybrids should be extensively tested on-farm for potential commercialization in SSA. Overall, our results highlighted the importance of harnessing beneficial alleles from wild relatives of maize for improvement of resistance to *Striga* and tolerance to drought in adapted maize germplasm.



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## 1. Introduction

Maize (*Zea mays* L.) is a widely adapted major staple food crop, providing calories for over 300 million people in sub-Saharan Africa (SSA). There is a rapid increase in the importance of the crop due to its wide adaptation to varying agroecologies, relative ease of production, processing, storage, and transportation [1]. However, *Striga hermonthica* (Del) Benth parasitism and recurrent drought are fighting against its increased production and productivity, particularly in the savannas. The savannas constitute the maize belts of SSA and are characterized by high incident solar radiation, low night temperature and low disease and pest incidence [2]. Yield losses of 10 to 100% have been recorded under *Striga*

infestation, depending on the type of cultivars grown, climatic conditions, soil fertility status and level of infestation [3]. Resistance to *Striga* describes the ability of the host plant to stimulate the germination of *Striga* seeds but prevent the attachment of the parasites to its roots or kill the attached parasites. Under *Striga* infestation, resistant cultivars support significantly fewer *Striga* plants and produce greater yield than susceptible cultivars [4–6]. Contrarily, tolerance to *Striga* denotes the ability of the host plant to support equal levels of *Striga* infestation as susceptible cultivars [7], without impairment of growth or grain yield losses [8,9]. *Striga* resistance and tolerance are highly complementary defense mechanisms. The combination of these two mechanisms is a good strategy for reducing *Striga* infection and reproduction levels in infested fields. Recurrent drought could result in yield loss of as high as 90% when it occurs from a few days before anthesis to the end of the grain-filling period [10]. Current climate change-related projections present more grim implications for agriculture in Africa, including maize production [11]. Studies have revealed that genetic enhancement of maize for drought tolerance could result in genetic gains [12,13]. Edmeades et al. [14] reported that the deployment of cultivars with drought-tolerance genes is an important strategy to stabilize maize production in areas with recurrent drought. Therefore, cultivars with enhanced tolerance to drought could serve as invaluable germplasm resources in environments with erratic occurrences of varying intensities of drought [15].

Over decades, the characterization of germplasm and breeding programs have revealed that cultivated plants, in general, have relatively lower levels of tolerance to biotic and abiotic stresses when compared to crop wild relatives [16]. Useful variation has been identified in teosinte (*Zea diploperennis* Iltis, Doebley and Guzman) and incorporated into maize gene pools via hybridization and backcrossing and/or selection [17]. This has provided proof that useful phenotypic variation can be tapped from teosinte for the improvement of domesticated maize. Tropical maize populations introgressed with various traits from teosinte have been developed. These include resistance to *Striga* [18–20], gray leaf spot [21], southern corn leaf blight, southern corn rust, and maize streak virus [18], drought tolerance [22] and kernel composition traits [23]. Several outstanding varieties, inbreds and breeding populations with desirable characteristics, including resistance to *Striga* and tolerance to drought, have been developed [24]. They were developed by substituting three of the maize chromosomes with three chromosomes from *Z. diploperennis*, which was achieved by creating a BC<sub>1</sub>F<sub>3</sub> generation of maize × perennial teosinte BC<sub>1</sub>F<sub>3</sub> [24].

By 2008, several *Striga* tolerant extra-early maturing (80–85 days to physiological maturity) inbred lines and varieties with yellow-endosperm had been developed in the International Institute of Tropical Agriculture–Maize Improvement Program (IITA-MIP), Nigeria. The problem with the available *Striga*-tolerant inbred lines and varieties at the time was that they allowed the reproduction of the parasite, thereby increasing the *Striga* seed bank after each planting season. To overcome this problem, *Z. diploperennis* was crossed to an adapted intermediate maturing yellow maize variety SUWAN 1-SR. The resulting F<sub>1</sub> was backcrossed four times to SUWAN 1-SR under artificial infestation with *Striga* to obtain a *Z. diploperennis* BC<sub>4</sub> population from which the intermediate maturing inbred line TZSTRI 106 was extracted. The extra-early maturing inbred lines used in the present study were developed by crossing TZSTRI 106 to the extra-early yellow population TZEE-Y Pop STR C4 to improve the level of *Striga* resistance.

Promotion and commercialization of maize hybrids by farmers as compared to the use of open-pollinated varieties (OPVs) are expected to increase grain yield by 50–100% [25]. However, the success of a commercial hybrid program depends on the availability of information on the combining ability and heterotic groupings of inbred lines. Combining ability analysis for determining the general (GCA) and specific combining ability (SCA) is a powerful tool for identifying cultivars that may be hybridized to exploit heterosis and to select outstanding crosses for direct use or further breeding [26]. Genetic analysis provides information on the type of gene action governing quantitative traits and thus assists breeders in selecting suitable parental lines for hybrid populations [27,28]. Several mating

designs are used for determining the combining ability of maize cultivars. The diallel mating design allows statistical separation of progeny performance into GCA and SCA.

By 2013, a large number of extra-early maturing yellow endosperm maize inbred lines were available. The classification of inbreds into heterotic groups would facilitate the production of high-yielding hybrids, involving lines of opposing heterotic groups. The heterotic grouping based on the GCA of multiple traits (HGCAMT) had been an effective method for classifying inbreds into heterotic groups [29], making them the method of choice for the present study. The objectives of this study, therefore, were to (i) determine the combining ability of a set of 12 newly developed yellow endosperm extra-early maturing maize inbreds derived from *Z. diploperennis* under *Striga* infestation and drought stress; (ii) classify the inbreds into heterotic groups using the HGCAMT method; (iii) identify extra-early maturing inbred and single-cross hybrid testers and (iv) examine the performance and stability of hybrid combinations involving the inbreds.

## 2. Materials and Methods

### 2.1. Genetic Materials Used for the Study

In 2008, a program was initiated at IITA to develop *Striga*-resistant extra-early yellow inbred lines and varieties. *Z. diploperennis* was crossed to an adapted intermediate maturing yellow maize variety SUWAN 1-SR. The resulting F<sub>1</sub> was backcrossed four times to SUWAN 1-SR under artificial infestation with *Striga* to obtain a *Z. diploperennis* BC<sub>4</sub> population from which the intermediate maturing inbred line TZSTRI 106 was extracted. The extra-early maturing inbred lines used in the present study were developed by crossing TZSTRI 106 to the extra-early yellow population TZEE-Y Pop STR C4 to improve the level of resistance to *Striga*. The BC<sub>2</sub>S<sub>1</sub> families were evaluated under artificial *Striga* infestation at Abuja and Mokwa, Nigeria, in 2010, and the resistant lines were backcrossed to TZEE-Y Pop STR C4. Following repeated selfing of the BC<sub>2</sub>S<sub>1</sub> families, the lines were advanced to the BC<sub>2</sub>S<sub>7</sub> stage and were evaluated under *Striga* infestation and screened for drought tolerance. Based on the evaluations, several *Striga*-resistant and drought-tolerant extra-early yellow maize inbreds were identified for the IITA-MIP. Twelve *Striga*-resistant and/or drought-tolerant extra-early maturing yellow maize inbred lines (Table S1) derived from *Z. diploperennis* were selected for the present study. The inbred lines were crossed in all possible combinations using the diallel mating design Method 4, which involves F<sub>1</sub>'s only [30], to obtain 66 single-cross hybrids in the breeding nursery at IITA, Ibadan, Nigeria, in 2013. Seeds from the reciprocal crosses were bulked, assuming no reciprocal effects on drought tolerance and *Striga* resistance in maize [31]. The 66 single-cross yellow endosperm hybrids plus four hybrid checks were used for the present study.

### 2.2. Field Evaluations

The present study was conducted in three experiments under stress (one drought and two *Striga*-infested) and non-stress (two rainfed) environments in Nigeria, from 2013 to 2014. In the first experiment, the 66 extra-early, yellow endosperm maize diallel crosses plus four hybrid checks were evaluated under artificial *Striga* infestation at Mokwa (9°18' N, 5°4' E, 457 m ASL, 1100 mm annual rainfall) and Abuja (9°16' N, 7°20,120' E, altitude 300 m, 1500 mm annual rainfall) in the southern Guinea savanna of Nigeria during the 2013 growing season. A 10 × 7 randomized incomplete-block design [32] with two replications was used for each experiment. Each experimental unit comprised single-row plots, 4 m long, with an inter-hill spacing of 0.75 and 0.40 m between plant stands within the hill. The infestation with *Striga* was carried out as described in detail by Kim [33] and Kim and Winslow [34]. Briefly, the *Striga* seeds used for artificial infestation were collected from sorghum (*Sorghum bicolor*) fields at the end of the previous growing season and mixed with finely sieved sand in the ratio of 1:99. About 5000 germinable *Striga* seeds were placed in each planting hole. The sand served as the carrier material and provided adequate volume for rapid and uniform infestation. Three maize seeds were placed in the same hole with the *Striga* seeds at the same time, and the maize seedlings were thinned to two/stand about

2 weeks after emergence to give a final population density of 66,666 plants ha<sup>-1</sup>. Fertilizer application was delayed until about 21 to 25 days after planting (DAP) when 30 kg ha<sup>-1</sup> N, 30 kg ha<sup>-1</sup> P, and 30 kg ha<sup>-1</sup> K was applied as NPK 15–15–15. The reduced rate and delay in the application of fertilizer in *Striga*-infested plots were adopted to induce the production of strigolactones, which stimulate the germination of *Striga* seeds and attachment of the *Striga* plants to the roots of the host plants [33]. Weeds other than *Striga* were controlled by manual weeding.

In the second experiment, the 66 single-cross hybrids and the four hybrid checks were evaluated under induced moisture stress at Ikenne (3°7' E, 6°87' N, 30 m ASL, 1200 mm annual rainfall) during the dry season of 2013/2014. The experimental design was the same as described in the first experiment. The managed drought stress was achieved using the method described by Badu-Apraku et al. [35]. During the first three weeks of growth, the plants were irrigated using a sprinkler irrigation system, which supplied 17 mm of water each week. Irrigation was withdrawn at 21 DAP so that the maize plants had to rely on water in the soil for growth. Apart from the water applied to the nonstress environments, all management practices were the same for both nonstress and drought experiments. Fertilizer was applied at the rate of 60 kg ha<sup>-1</sup> each of N, P, and K at planting. An additional 60 kg ha<sup>-1</sup> N was top-dressed at 2 weeks after planting (WAP).

In the third experiment, the 66 single-cross hybrids plus four hybrid checks were evaluated under rainfed conditions at Ikenne and Bagauda (12°00' N, 8°22' E, 580 m altitude, 800 mm annual rainfall) during the 2014 growing season. The experimental design and population density were the same as described above. Fertilizer was applied at the rate of 60 kg ha<sup>-1</sup> each of N, P, and K at 2 WAP with an additional 60 kg ha<sup>-1</sup> N top-dressed at 5 WAP. The trials were kept weed-free by applying Atrazine and Gramoxone as pre- and post-emergence herbicides at the rate of 5 L ha<sup>-1</sup> each of Primextra and paraquat, respectively, and subsequently complemented by manual weeding.

### 2.3. Data Collection

Data were recorded on both drought and well-watered plots for the number of days to 50% silking (DS) and 50% anthesis (DA). Anthesis silking interval (ASI) was determined as the difference between DS and DA. Plant and ear heights were obtained as the distance from the base of the plant to the height of the first tassel branch and the node bearing the upper ear, respectively. Root lodging (the percentage of plants that were leaning more than 30° from the vertical) and stalk lodging (the percentage of plants that had been broken at or below the highest ear node) were recorded. Stay green characteristic was determined for the drought trial at 70 DAP on a scale of 1 to 9, where 1 = almost all leaves were green and 9 = virtually all leaves were dead. Ear aspect (EASP) was based on free from disease and insect damage, ear size, uniformity of ears, and grain filling, and was determined on a scale of 1 to 9, where 1 = clean, uniform, large, and well-filled ears and 9 = ears with unacceptable features. Plant aspect (PASP) was rated on a scale of 1 to 9 based on plant type, where 1 = excellent and 9 = poor. The number of ears per plant (EPP) was obtained by dividing the total number of ears harvested per plot by the number of plants in a plot. Husk cover (HUSK) was obtained using a scale of 1 to 5, where 1 = ears with husks tightly arranged and extended beyond the ear tip and 5 = ears with tips completely exposed.

The data recorded under *Striga* infestation were the same as those collected in the other experiments with the addition of *Striga* damage syndrome rating [33] and the number of emerged *Striga* plants (ESP) recorded at 8 and 10 WAP. *Striga* damage syndrome rating (SDR) was scored per plot on a scale of 1 to 9 where 1 = no damage, indicating normal plant growth and high level of resistance, and 9 = complete collapse of the maize plant, that is, highly susceptible [33]. For drought trials, ears harvested from each plot were shelled to determine the percentage of grain moisture. Grain yield in kilograms per hectare was computed from the shelled grain weight and adjusted to 15% moisture content. On the other hand, for the rainfed and *Striga*-infested trials, a shelling percentage of 80%

was assumed for all entries, and grain yield, which was obtained from ear weight (after conversion to  $\text{kg ha}^{-1}$ ), was adjusted to 15% moisture content.

#### 2.4. Data Analysis

Data on grain yield and other measured traits were subjected to analysis of variance (ANOVA) for each stress environment and across environments (one drought, two *Striga*-infested and two rain-fed environments) to compute mean squares for each trait. The data were analyzed using SAS [36]. In the combined ANOVA, environments, replicates, and blocks were considered as random factors, while entries (66 hybrids and 4 checks) were considered as fixed effects. The following linear mixed models (Equations (1) and (2)) were used across environments and the drought environment.

$$Y_{ijrs} = \mu + G_i + E_j + GE_{ij} + r_{kj} + B_{sjk} + e_{ijks} \quad (1)$$

$$Y_{ijrs} = \mu + G_i + r_{kj} + B_{sjk} + e_{ijks} \quad (2)$$

where  $Y_{ijrs}$  was the phenotypic performance of the  $i$ th genotype at the  $j$ th environment in the  $r$ th replication of the  $s$ th incomplete block,  $G_i$  was the genetic effects of the  $i$ th genotype,  $E_j$  was the effects of the  $j$ th environment,  $GE_{ij}$  is the interaction effects of  $i$ th genotype and the  $j$ th environment,  $r_{kj}$  was the effects of the  $k$ th replication at the  $j$ th environment,  $B_{sjk}$  was the effects of the  $s$ th incomplete block in the  $k$ th replication in the  $j$ th environment, and  $e_{ijks}$  was residual.

Pearson's correlation was also estimated for each stress environment. Effects of the GCA of the parents and SCA of the crosses, as well as their mean squares in each environment and across environments, were estimated for the  $12 \times 12$  diallel crosses, according to Griffing's method 4, model 1 (fixed model) restricted to  $F_1$ 's only [30] and the DIALLEL-SAS program developed by Zhang et al. [37]. The effects of GCA and SCA for the measured traits were computed from the mean values adjusted for the block effects for each environment and across environments. The statistical model used for the combined diallel analysis across environments is as follows:

$$Y_{ijk} = \mu + E_e + g_i + g_j + S_{ij} + gE_{eg} + sE_{es} + \varepsilon_{ijk} \quad (3)$$

where  $Y_{ijk}$  is the observed measurement for the  $ij$ th cross grown in the  $k$ th environment;  $\mu$  is the grand mean;  $E_e$  is the environment;  $g_i$  and  $g_j$  are the GCA effects of the  $i$ th and  $j$ th inbreds, respectively;  $S_{ij}$  is the SCA effect of the  $ij$ th cross;  $gE_{eg}$  is the interaction effect between GCA and the environment;  $sE_{es}$  is the interaction effect between SCA and the environment, and  $\varepsilon_{ijk}$  is the error term associated with the  $ij$ th cross evaluated in the  $k$ th replication [35]. The following restrictions were imposed on the combining ability effects:  $\sum g_i = 0$ ,  $\sum g_j = 0$  and  $\sum S_{ij} = 0$  for each  $j$  [30]. GCA and SCA effects were tested for significance using a  $t$ -test. The standard errors of the GCA and SCA effects were estimated as the square root of the GCA and SCA variances [30]. The relative importance of GCA and SCA was investigated using the method of Baker [38] as modified by Hung and Holland [39].

Inbred lines were classified into heterotic groups based on the HGCAMT method proposed by Badu-Apraku et al. [29]. The statistical model used for the HGCAMT method to assign the inbreds into the heterotic groups is as follows:

$$Y = \sum_{i=1}^n \left( \frac{Y_i - \bar{Y}_i}{s} \right) + \varepsilon_{ij} \quad (4)$$

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 a 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  $i$ ;  $\varepsilon_{ij}$  is the residual of the model associated with the combination of inbred  $i$  and trait  $j$ .

Heterotic grouping by the HGCAMT method was performed by standardizing the GCA effects (mean of zero and standard deviation of 1) of observed traits that had significant mean squares across test environments to minimize the effects of different scales of the traits [29]. The standardized GCA effects were subsequently subjected to Ward's minimum variance cluster analysis.

Inbred and single-cross hybrid testers were identified, employing the method proposed by Pswarayi and Vivek [30]. The criteria for identification of an inbred as a tester were (i) display of significant positive GCA effects for grain yield, (ii) classification of the inbred into a heterotic group, and (iii) high per se grain yield of the inbred. The identification of a single-cross tester was based on (a) display of reasonably good GCA effects by the parental inbred lines constituting the single cross; (b) classification of the parental inbred lines of the single-cross hybrid into the same heterotic group; (c) display of high yield potential by the single-cross hybrid to qualify its use as a seed parent for a successful three-way and double-cross hybrid seed production [40].

To identify outstanding single-cross hybrids for commercial production across multiple environments, a modified version of the multiple trait base index (MI) proposed by Badu-Apraku et al. [41] was used. The MI integrated superior grain yield, EPP, anthesis-silking interval, plant and ear aspects, stay-green characteristic, *Striga* damage syndrome rating and a number of emerged *Striga* plants under multiple stress and outstanding grain yield under nonstress environments. This index was used to select the top 15 and worst 10 hybrids. Each trait was standardized to minimize the effects of the different scales. Hybrids with positive MI values were considered as tolerant/resistant to the multiple stresses, while those with negative values were regarded as susceptible. The multiple trait base index was computed according to the following equation:

$$MI = [(2 \times YSTR) + YNSTR + EPP - ASI - EASP - PASP - STGR - (SDR8 + SDR10) - 0.5(ESP8 + ESP10)] \quad (5)$$

where YSTR = grain yield across stress (drought and *Striga*-infested plots), YNSTR = grain yield across rainfed (nonstress) plots, EPP = number of ears per plant across stress, ASI = anthesis-silking interval across stress, EASP = ear aspect across stress, PASP = plant aspect under drought, STGR = stay green characteristic under drought, SDR8 and SDR10 = *Striga* damage rating at 8 and 10 WAP, ESP8 and ESP10 = number of emerged *Striga* plants at 8 and 10 WAP. Therefore, a positive index value indicated tolerance/resistance across stresses, whereas a negative value indicated susceptibility across stresses.

Furthermore, the yield data of the selected 25 hybrids using the MI plus those of the four hybrid checks were subjected to genotype main effect plus genotype  $\times$  environment interaction (GGE) biplot analysis to decompose the G  $\times$  E interactions across environments [42,43]. The GGE biplot was used to identify outstanding single cross hybrids in terms of yield and stability across environments. The GGE biplot model equation is as follows:

$$Y_{ij} - \beta_j = \lambda_1 \zeta_{i1} \eta_{j1} + \lambda_2 \zeta_{i2} \eta_{j2} + \varepsilon_{ij} \quad (6)$$

where  $Y_{ij}$  is the genetic value of the combination between Entry  $i$  and Tester  $j$  for the trait of interest;  $\beta_j$  is the mean of all combinations involving Tester  $j$ , and  $\lambda_2$  are the singular values for PC1 and PC2;  $\zeta_{i1}$  and  $\zeta_{i2}$  are the PC1 and PC2 eigenvectors, respectively, for Entry  $i$ ;  $\eta_{j1}$  and  $\eta_{j2}$  are the PC1 and PC2 eigenvectors, respectively, for Tester  $j$ ; and  $\varepsilon_{ij}$  is the residual of the model associated with the combination of Entry  $i$  and Tester  $j$ .

### 3. Results

#### 3.1. Analysis of Variance across Multiple Environments

Under optimal growing (*Striga*-and drought-free) conditions, significant effects for genotype (G), environment (E), genotype  $\times$  environment (G  $\times$  E) interaction, GCA and SCA were detected for all traits studied except E and G  $\times$  E for plant and ear heights (Table 1). The mean squares due to the environment for *Striga* damage at 8 and 10 WAP

and  $G \times E$  for a number of emerged *Striga* plants at 8 and 10 WAP were not significant under artificial *Striga* infestation. Significant effects of genotype and GCA was observed for all measured traits under drought condition except for anthesis-silking interval, ear height and ear aspect. While for the SCA effect, only days to silking, the number of ears per plant and stay-green characteristics were significant (Table 1).

The analysis of variance across the environments revealed significant effects for genotype, environment,  $G \times E$ , GCA and SCA mean squares for most of the measured traits (Table 1). The few exceptions included the mean squares of environment for *Striga* damage (8 and 10 WAP) and genotype for EPP. The mean squares of  $G \times E$  for plant and ear heights, ears per plant and number of emerged *Striga* plants (8 and 10 WAP) were also not significant. In addition, the mean squares of SCA for ears per plant and the number of emerged *Striga* plants (8 and 10 WAP) across test environments were not significant. The  $GCA \times E$  interaction mean squares were significant for all measured traits except for plant height, plant aspect and the number of emerged *Striga* plants (8 and 10 WAP) across environments. Significant  $SCA \times E$  interactions mean squares were detected for only grain yield, days to anthesis, anthesis-silking interval and husk cover. The heritability of grain yield was 0.73 across environments (Table 1). The heritabilities of *Striga* damage at 8 and 10 WAP were 0.71 and 0.77, respectively. The number of emerged *Striga* plants at 8 and 10 WAP had heritabilities of 0.45 each. The heritability of stay-green characteristics under drought environments was 0.28.

### 3.2. Performance of Hybrids Based on Multiple Trait Index across Environments

The mean grain yield of the entries was  $4013 \text{ kg ha}^{-1}$  under optimal growing conditions and  $2729 \text{ kg ha}^{-1}$  under *Striga* infestation (Table 2). The yield observed under *Striga* infestation represented 32% of the average yield expected under non-infested conditions. In addition, the best *Striga*-resistant hybrid, TZdEEI 7  $\times$  TZEEI 79 ( $4437 \text{ kg ha}^{-1}$ ), exceeded check 2 ( $3202 \text{ kg ha}^{-1}$ ), which was the best resistant check by 39%. Under drought conditions, the highest yielding hybrid was TZdEEI 12  $\times$  TZEEI 63 ( $3883 \text{ kg ha}^{-1}$ ), followed by TZdEEI 7  $\times$  TZEEI 63 ( $3611 \text{ kg ha}^{-1}$ ) and TZdEEI 9  $\times$  TZdEEI 12 ( $3599 \text{ kg ha}^{-1}$ ). Under optimal growing conditions, the high yielding hybrid was TZdEEI 7  $\times$  TZEEI 63 ( $5217 \text{ kg ha}^{-1}$ ), and the lowest was TZdEEI 4  $\times$  TZdEEI 13 ( $2636 \text{ kg ha}^{-1}$ ). TZdEEI 7  $\times$  TZEEI 63 exceeded the checks by a range of 34 to 65%. Across all the environments, TZdEEI 1  $\times$  TZdEEI 7 was the highest yielding hybrid with a grain yield of  $4302 \text{ kg ha}^{-1}$ , followed by TZdEEI 7  $\times$  TZEEI 79 ( $4214 \text{ kg ha}^{-1}$ ) and TZdEEI 7  $\times$  TZEEI 79 ( $4177 \text{ kg ha}^{-1}$ ).

The single cross hybrid, TZdEEI 7  $\times$  TZEEI 79, produced the highest grain yield under both stress environments, while TZdEEI 12  $\times$  TZEEI 95 was the most outstanding in terms of grain yield under nonstress environments (Table 3). The mean grain yield of the hybrids was  $2629 \text{ kg ha}^{-1}$  across stress environments compared with  $4546 \text{ kg ha}^{-1}$  across nonstress environments, indicating a yield reduction of 42% due to the multiple stresses. Grain yield ranged from  $2063 \text{ kg ha}^{-1}$  for TZdEEI 4  $\times$  TZdEEI 11 to  $4438 \text{ kg ha}^{-1}$  for TZdEEI 7  $\times$  TZEEI 79 across multiple environments (Table 3). The top fifteen outstanding hybrids in terms of grain yield were not significantly different, but they significantly exceeded each of the four hybrid checks. Based on the multiple trait index, TZdEEI 7  $\times$  TZEEI 79 was the most outstanding hybrid, while TZdEEI 58  $\times$  TZEEI 63 was the lowest yielding. The outstanding grain yields of the top fifteen hybrids selected based on the multiple trait index were associated with increased ears per plant, reduced anthesis-silking interval, improved ear aspect and stay green characteristic, as well as reduced *Striga* damage under *Striga* infestation.

**Table 1.** Mean squares derived from the combined analysis of variance for grain yield and other agronomic traits of 66 hybrids evaluated across 5 environments (two *Striga*-infested, one drought and two rainfed environments) in Nigeria, 2013–2014.

Optimal															
SOV †	DF	YIELD	DS	ASI	PHT	EHT	PASP	EASP	EPP						
Env	1	1,506,994 **	6.8 **	1.6 **	776.9 **	332.8 **	0.38 **	0.31 **	0.02 **						
Repetition	2	598,147	0.7	0.5	11.9	274.6 **	0.22	3.23 **	0.02						
Hybrid	65	865,461 *	2.2 **	0.9 *	396.0	68.8	0.26 *	0.24 *	0.03 **						
Env*Hybrid	65	841,744 *	2.2 **	0.8	385.6	68.9	0.27 *	0.23 **	0.03 **						
GCA	11	2,998,626 **	28.5 **	3.9 **	2651.7 **	1450.4 **	1.03 **	0.46 **	0.04 **						
SCA	54	1,203,143 **	2.5 **	1.2 **	395.1	105.1 **	0.26 *	0.28 **	0.02 *						
GCA*Env	11	1,241,955 *	4.4 **	2.1 **	634.7 *	114.4 *	0.72 **	0.42 **	0.07 **						
SCA*Env	54	788,767 *	1.7 *	0.7	347.4	59.6	0.17	0.20	0.02 *						
Error	130	545,704	1.0	0.7	324.9	55.3	0.17	0.15	0.01						
Striga															
SOV †	DF	YIELD	DS	ASI	PHT	EHT	SDR1	SDR2	ESP1	ESP2	EPP				
Env	1	39,455,484 **	570.2 **	78.6 **	25,409.5 **	6264.4 **	0.09	1.83	3.63 **	4.23 **	0.62 **				
Repetition	2	784,070	6.4	0.1	1219.7 **	534.6 *	2.43	0.52	0.43 **	0.41 **	0.05				
Hybrid	65	3,176,326 **	12.5 **	3.6 **	452.8 **	203.6 **	4.49 **	3.87 **	0.12 *	0.09 *	0.11 **				
Env*Hybrid	65	1,094,354 *	5.6 **	2.6 *	304.1	136.2	1.56 *	1.06 **	0.08	0.06	0.03 *				
GCA	11	13,626,819 **	52.6 **	9.2 **	1000.5 **	547.3 **	17.58 **	16.55 **	0.28 **	0.21 **	0.45 **				
SCA	54	1,047,522 *	4.4	2.4	341.2 *	133.6	1.82 *	1.29 **	0.09	0.06	0.04 **				
GCA*ENV	11	1,345,046	8.5 **	3.1	433.3 *	182.3	3.01 **	2.58 **	0.09	0.09	0.04				
SCA*ENV	54	1,043,287	5.4 *	2.5	277.8	126.8	1.26	0.75	0.07	0.05	0.03				
Error	130	726,465	3.2	1.8	227.0	113.6	1.10	0.63	0.08	0.06	0.02				
Drought															
SOV †	DF	YIELD	DS	DA	ASI	PHT	EHT	EASP	EPP	PASP	STGR				
Repetition	1	19,449	3.1	2.0	0.1	737.0	185.9	0.03	0.00	1.14	1.32				
Hybrid	65	874,713 **	6.2 **	3.1 **	1.5	382.3 **	176.4	0.71	0.02 **	1.15 *	1.38 *				
GCA	11	2,165,504 **	9.0 **	17.4 **	2.7 *	1004.4 **	535.3 **	1.63 **	0.02 *	1.48 *	1.51 *				
SCA	54	611,774	1.9 *	3.9	1.3	255.6	103.3	0.66	0.02 **	1.09	1.35 *				
Error	65	424,342	1.3	3.0	1.1	303.2	118.6	0.58	0.01	0.72	0.77				
Across															
SOV †	DF	YIELD	DS	DA	ASI	PHT	EHT	HUSK	EASP	EPP					
ENV	5	219,814,222 **	832.5 **	965.3 **	134.0 **	30,657.3 **	6062.6 **	73.50 **	266.12 **	1.57 **					
Repetition	6	618,319	13.1 **	8.6 **	1.0	1243.6 **	316.0 **	0.89 **	1.25 **	0.09					
Hybrid	65	42,095,210 **	26.8 **	22.2 **	4.0 **	1197.8 **	552.1 **	0.89 **	1.67 **	0.15					
Hybrid*ENV	325	1,242,600 **	4.5 **	3.3 **	1.5 **	333.9	106.7	0.48 **	0.59 **	0.12					
GCA	11	14,196,154 **	122.7 **	109.0 **	13.3 **	4741.3 **	2458.1 **	3.14 **	5.37 **	0.22 *					
SCA	54	2,175,206 **	7.3 **	4.5 **	2.1 **	475.9 **	163.8 **	0.44 **	0.91 **	0.14					
GCA*ENV	55	2,590,061 **	9.5 **	7.2 **	2.0 **	434.8 *	140.6 *	1.46 **	1.62 **	0.18 **					
SCA*ENV	270	968,122 **	3.4	2.6 **	1.4	313.3	99.8	0.28 *	0.38	0.11					
Error	390	754,137	2.9	1.9	1.2	300.4	97.6	0.23	0.35	0.11					
Heritability		YIELD	DS	DA	ASI	PHT	EHT	EASP	EPP	PASP	SDR1	SDR2	ESP1	ESP2	STGR
		0.73	0.80	0.86	0.63	0.76	0.84	0.62	0.34	0.37	0.71	0.77	0.45	0.45	0.28

† SOV = sources of variation; ENV = environment; DF = degrees of freedom; YIELD = grain yield; DS = days to silking; DA = days to anthesis; ASI = anthesis-silking interval; PHT = plant height; EHT = ear height; HUSK = husk cover; EASP = ear aspect; EPP = ears per plant; PASP = plant aspect; SDR1 and SDR2 = *Striga* damage rating at 8 and 10 WAP; ESP1 and ESP2 = number of emerged *Striga* plants at 8 and 10 WAP; STGR = stay-green characteristic. \*\*, \* = significant F-test at 0.01 and 0.05 levels of probability, respectively.

**Table 2.** Grain yield (kg ha<sup>-1</sup>) of the hybrids and checks under optimal, Striga, drought and across environments.

PEDIGREE	Optimal	Striga	Drought	Across
TZdEEI 1 × TZdEEI 4	2664	2285	1634	2394
TZdEEI 1 × TZdEEI 5	3864	2924	2661	3179
TZdEEI 1 × TZdEEI 7	4888	4478	2577	4302
TZdEEI 1 × TZdEEI 9	4659	2516	2834	3476
TZdEEI 1 × TZdEEI 11	2698	1359	2614	2196
TZdEEI 1 × TZdEEI 12	4866	3796	2262	3824
TZdEEI 1 × TZdEEI 13	3419	1728	2026	2650
TZdEEI 1 × TZEEI 58	4434	2958	3480	3468
TZdEEI 1 × TZEEI 63	4241	2945	3046	3632
TZdEEI 1 × TZEEI 79	4428	3250	2900	3433
TZdEEI 1 × TZEEI 95	3909	2730	3014	3101
TZdEEI 4 × TZdEEI 5	3698	2405	1504	2544
TZdEEI 4 × TZdEEI 7	3679	1964	1854	2627
TZdEEI 4 × TZdEEI 9	3405	1696	1928	2394
TZdEEI 4 × TZdEEI 11	3128	1453	2498	2435
TZdEEI 4 × TZdEEI 12	3817	1844	2099	2651
TZdEEI 4 × TZdEEI 13	2636	644	1139	1564
TZdEEI 4 × TZEEI 58	4253	1810	1892	2682
TZdEEI 4 × TZEEI 63	4102	1432	1823	2581
TZdEEI 4 × TZEEI 79	3233	1965	1020	2173
TZdEEI 4 × TZEEI 95	4077	2252	2366	2931
TZdEEI 5 × TZdEEI 7	3916	3269	2102	3201
TZdEEI 5 × TZdEEI 9	4846	3599	2051	3940
TZdEEI 5 × TZdEEI 11	4680	2866	3303	3834
TZdEEI 5 × TZdEEI 12	3585	3114	1036	3122
TZdEEI 5 × TZdEEI 13	3473	2336	1346	2637
TZdEEI 5 × TZEEI 58	3979	3190	1933	3258
TZdEEI 5 × TZEEI 63	4169	2842	1781	3133
TZdEEI 5 × TZEEI 79	4386	2925	2602	3427
TZdEEI 5 × TZEEI 95	3579	3385	1559	2983
TZdEEI 7 × TZdEEI 9	4600	3937	2680	3815
TZdEEI 7 × TZdEEI 11	4483	3255	3022	3793
TZdEEI 7 × TZdEEI 12	4081	3619	3254	3694
TZdEEI 7 × TZdEEI 13	4108	2382	2439	3097
TZdEEI 7 × TZEEI 58	3980	4065	2320	3805
TZdEEI 7 × TZEEI 63	5218	3551	3611	4177
TZdEEI 7 × TZEEI 79	4387	4437	3463	4215
TZdEEI 7 × TZEEI 95	4337	4040	2160	3750
TZdEEI 9 × TZdEEI 11	4066	1965	2607	3000
TZdEEI 9 × TZdEEI 12	5008	3516	3599	4033
TZdEEI 9 × TZdEEI 13	4598	888	1517	2357
TZdEEI 9 × TZEEI 58	4712	2878	2183	3405
TZdEEI 9 × TZEEI 63	4051	2569	2407	3178
TZdEEI 9 × TZEEI 79	4530	3747	2838	3717
TZdEEI 9 × TZEEI 95	4831	2974	2325	3549
TZdEEI 11 × TZdEEI 12	4323	3463	2867	3738
TZdEEI 11 × TZdEEI 13	4450	1336	2152	2616
TZdEEI 11 × TZEEI 58	5066	2527	3150	3798
TZdEEI 11 × TZEEI 63	5043	2634	3017	3796
TZdEEI 11 × TZEEI 79	3756	3620	2602	3429
TZdEEI 11 × TZEEI 95	3358	2481	3092	3062

Table 2. Cont.

PEDIGREE	Optimal	Striga	Drought	Across
TZdEEI 12 × TZdEEI 13	4742	1902	2864	3180
TZdEEI 12 × TZEEI 58	4245	3446	3170	3681
TZdEEI 12 × TZEEI 63	4349	2884	3883	3682
TZdEEI 12 × TZEEI 79	3767	3355	3271	3612
TZdEEI 12 × TZEEI 95	3673	3648	2874	3638
TZdEEI 13 × TZEEI 58	4202	1300	2596	2567
TZdEEI 13 × TZEEI 63	3974	2323	3121	3190
TZdEEI 13 × TZEEI 79	3544	2469	2623	3029
TZdEEI 13 × TZEEI 95	3769	2270	3149	3066
TZEEI 58 × TZEEI 63	2674	1535	706	1533
TZEEI 58 × TZEEI 79	3050	3574	2324	3063
TZEEI 58 × TZEEI 95	3889	2767	2491	3399
TZEEI 63 × TZEEI 79	4225	3608	1789	3445
TZEEI 63 × TZEEI 95	3860	2306	2705	2888
TZEEI 79 × TZEEI 95	3495	2719	2819	3237
Check 1	3247	2837	1278	2859
Check 2	3882	3202	2224	3233
Check 3	3445	2556	1904	3052
Check 4	3164	2507	2032	2629
Mean	4013	2729	2429	3183

### 3.3. Correlation between Variables under Each Stress Environment

Under optimal conditions, highly significant ( $p < 0.001$ ) correlations were observed between the variables (Table S2). Grain yield showed highly significant and negative correlations with days to anthesis, plant aspect and rear aspect. Days to anthesis were significantly and positively correlated with plant and ear heights, while days to silking showed no significant correlations with plant and ear height (Table S2). Across *Striga* environments, days to anthesis, days to silking, anthesis-silking interval, *Striga* damage (8 and 10 WAP) and ear aspect had significant and negative correlations with grain yield (Table S3). The correlation between *Striga* damage (8 and 10 WAP) and emerged *Striga* counts (8 and 10 WAP) were positive and highly significant ( $p < 0.01$ ). Plant and ear heights had negative correlations with both *Striga* damage and the number of emerged *Striga* plants. Days to anthesis, days to silking, anthesis-silking interval, ear aspect, plant aspect, and stay green characteristic were highly significant ( $p < 0.001$ ) and positively correlated with grain yield (Table S4). The number of ears per plant was positively correlated with grain yield in each stress environment.

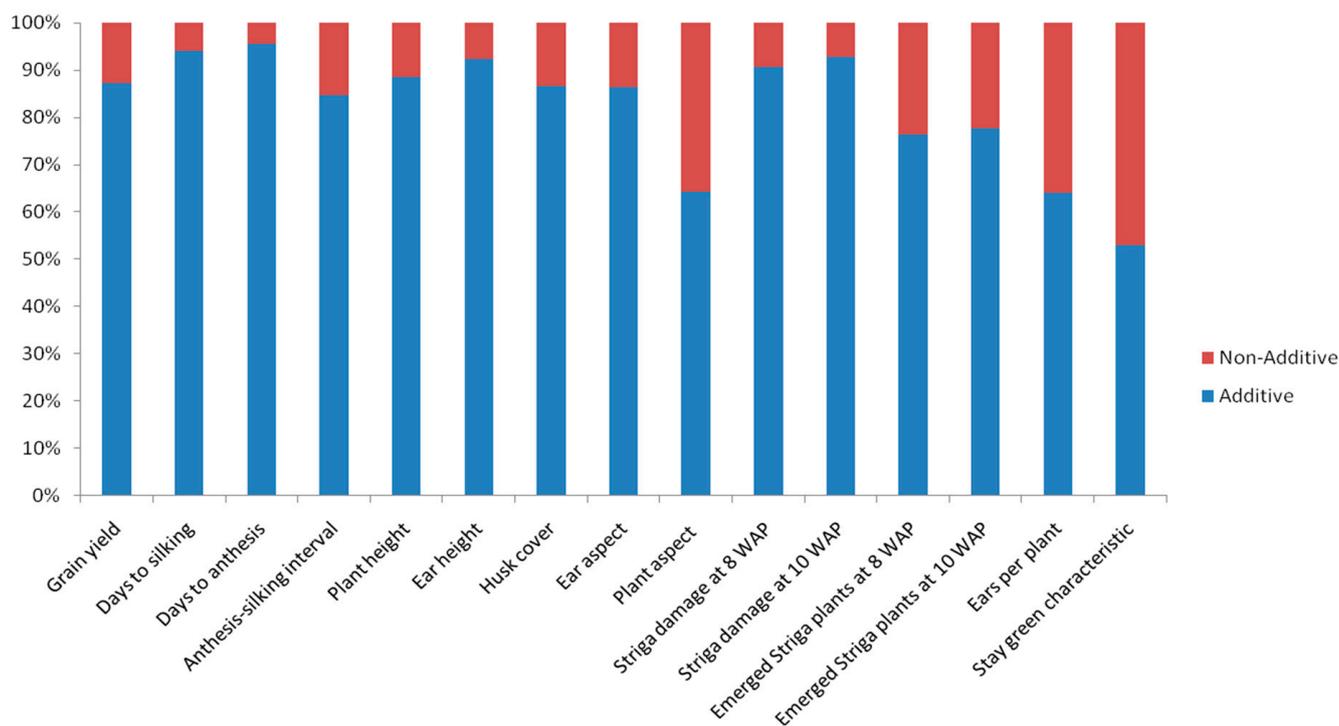
### 3.4. General and Specific Combining Abilities of Inbred Lines across Multiple Environments

There was the preponderance of GCA effects over the SCA effects for grain yield and other measured traits in the set of inbred lines (Figure 1). The inbred TZdEEI 7 had significant positive GCA effects for grain yield under optimal (425\*\*), *Striga* (767\*\*) and across all environments (571) (Table 4). TZdEEI 4 had significant negative GCA effects in each environment and across environments. TZdEEI 12 had significant positive GCA effects under *Striga*, drought and across research environments. However, the inbred TZdEEI 5 had significant positive and negative GCA effects under *Striga* and drought conditions, respectively. TZdEEI 7, TZdEEI 12 and TZEEI 79 had significant and negative GCA effects for *Striga* damage (8 and 10 WAP). Significant and negative GCA effects for the number of emerged *Striga* plants (8 and 10 WAP) were detected for TZdEEI 4, TZEEI 79 and TZEEI 95. The inbred TZdEEI 9 and TZdEEI 13 possessed negative and significant GCA effects for the stay-green characteristic.

**Table 3.** Grain yield and other agronomic traits of hybrids (the best 15 and the worst 10) based on the multiple stress base index with four hybrid checks evaluated under stress (ST), rainfed (NS) and across (ACR) environments in Nigeria, 2013–2014.

Hybrid	Yield (kg ha <sup>-1</sup> )			EPP		ASI (Days)		EASP		STGR	SDR1	SDR2	ESP1	ESP2	MI
	ST	NS	ACR	ST	NS	ST	NS	ST	NS			ST			
TZdEEI 7 × TZEEI 79	4112	4928	4438	1.00	0.94	1.75	1.14	4.5	2.7	3.3	2.7	3.8	26.7	28.6	13.76
TZdEEI 9 × TZEEI 79	3445	5163	4132	0.90	0.89	1.48	0.39	4.4	2.7	3.5	2.8	3.9	31.0	34.8	10.64
TZdEEI 7 × TZdEEI 12	3497	4757	4001	1.02	0.88	0.99	0.46	4.7	3.1	4.0	2.6	3.9	38.3	40.3	10.21
TZdEEI 1 × TZdEEI 7	3844	4991	4303	1.09	1.05	1.79	0.86	4.5	3.0	6.0	2.9	3.8	45.3	48.8	9.76
TZdEEI 7 × TZdEEI 9	3518	5047	4130	0.96	0.89	0.73	0.71	4.7	3.1	3.5	3.3	4.5	46.2	53.2	9.68
TZdEEI 9 × TZdEEI 12	3544	4328	3857	1.00	1.12	0.71	1.07	4.7	3.0	4.0	4.0	4.9	26.2	33.3	9.26
TZdEEI 11 × TZEEI 79	3281	5274	4078	0.89	0.97	1.85	1.37	4.2	2.6	3.8	3.3	3.9	24.8	30.4	9.18
TZdEEI 1 × TZEEI 79	3134	5078	3912	0.90	0.74	1.82	1.38	4.5	2.7	2.7	4.3	4.5	28.5	38.0	8.66
TZdEEI 12 × TZEEI 95	3390	5602	4275	0.95	0.75	1.37	0.91	4.5	2.9	3.6	3.8	4.8	30.0	38.6	8.57
TZdEEI 12 × TZEEI 79	3327	5038	4011	0.91	0.94	1.62	0.96	4.8	3.1	3.7	3.6	4.1	42.8	42.3	8.24
TZdEEI 58 × TZEEI 79	3158	4360	3638	0.85	0.88	1.80	1.65	4.9	3.1	3.4	2.5	4.2	36.1	42.9	8.19
TZdEEI 1 × TZdEEI 12	3285	4633	3824	1.01	0.95	1.58	0.51	4.8	3.0	3.2	4.2	4.3	26.5	32.5	7.98
TZdEEI 5 × TZEEI 79	2818	5402	3852	0.84	0.89	0.62	1.21	4.8	2.3	3.4	4.8	5.3	29.7	37.1	6.49
TZdEEI 7 × TZEEI 63	3571	5142	4199	0.88	0.92	1.84	0.92	4.7	2.6	3.5	3.9	4.6	52.2	58.0	6.44
TZdEEI 7 × TZEEI 95	3413	4330	3780	0.97	0.99	1.90	1.21	5.5	3.2	4.1	3.4	4.8	31.4	36.0	5.93
Check 2 †	2876	4391	3482	0.89	0.92	1.91	1.79	4.6	2.7	4.5	4.0	4.8	21.1	22.6	5.30
Check 1	2316	4819	3318	0.85	0.84	2.64	1.99	5.5	2.9	4.5	3.6	4.8	27.6	34.1	0.65
Check 3	2339	3513	2808	0.84	0.94	2.74	1.42	5.5	3.3	5.6	4.6	5.7	3.8	6.3	-2.40
Check 4	2349	4114	3055	0.80	1.07	2.20	1.21	5.6	3.2	4.8	5.0	5.9	38.2	36.6	-3.00
TZdEEI 5 × TZdEEI 13	2006	4161	2868	0.77	0.93	3.42	1.88	5.7	3.2	3.0	5.6	6.2	44.6	51.8	-7.26
TZdEEI 1 × TZdEEI 13	1827	4668	2964	0.79	0.90	2.73	1.17	5.7	3.0	4.7	6.2	6.2	44.8	49.1	-7.39
TZdEEI 4 × TZdEEI 11	1801	2456	2063	0.75	0.90	2.07	0.60	5.7	3.6	3.2	5.8	6.5	48.1	52.3	-8.98
TZdEEI 13 × TZEEI 58	1732	4589	2875	0.55	0.95	1.47	1.64	6.1	2.9	3.2	6.4	7.2	47.5	53.8	-9.58
TZdEEI 4 × TZEEI 58	1837	4604	2944	0.61	1.00	3.81	1.36	6.0	3.2	5.3	5.7	6.5	28.5	31.5	-10.53
TZdEEI 4 × TZEEI 63	1562	4055	2559	0.68	0.93	3.10	2.12	6.2	3.0	4.8	5.9	6.7	33.3	37.4	-11.37
TZdEEI 11 × TZdEEI 13	1608	3857	2508	0.68	0.89	3.27	1.81	6.1	2.9	3.3	6.9	7.4	45.2	49.8	-11.84
TZdEEI 9 × TZdEEI 13	1097	4694	2536	0.60	1.02	3.86	0.62	6.6	3.1	3.6	6.7	7.1	76.6	84.9	-16.38
TZdEEI 4 × TZdEEI 13	808	4186	2159	0.61	1.04	3.58	0.84	6.8	3.1	4.1	6.9	7.8	27.7	35.4	-17.80
TZdEEI 58 × TZEEI 63	1247	3557	2171	0.52	0.88	4.46	2.58	6.3	3.3	5.3	5.7	6.7	53.3	59.4	-17.98
Mean	2629	4546	3396	0.85	0.98	2.21	1.20	5.3	3.0	4.0	4.6	5.4	40.6	45.5	
LSD	758	1216	663	0.15	0.75	1.39	1.13	0.74	0.49	1.64	1.21	0.97	26.91	28.79	

† Check 1 = TZEEI 79 × TZEEI 82; Check 2 = TZEEI 79 × TZEEI 76; Check 3 = (TZEEI 82 × TZEEI 79) × TZEEI 58; Check 4 = (TZEEI 95 × TZEEI 58) × (TZEEI 82 × TZEEI 79); YIELD = grain yield; EPP = ears per plant; ASI = anthesis-silking interval; EASP = ear aspect; STGR = stay-green characteristic; SDR1 and SDR2 = *Striga* damage rating at 8 and 10 WAP; ESP1 and ESP2 = emerged *Striga* plants at 8 and 10 WAP; MI = multiple trait base index.



**Figure 1.** Proportion of additive (lower bar) and non-additive (upper bar) genetic variance for grain yield and other agronomic traits of 12 extra-early yellow inbred lines involved in diallel crosses evaluated across drought, *Striga*-infested and rainfed environments in Nigeria, 2013–2014.

**Table 4.** General combining ability (GCA) effects of extra-early yellow maize inbred parents for grain yield and other agronomic traits across 5 environments (two *Striga*-infested, one drought and two rainfed environments) in Nigeria, 2013–2014.

S/N	Parent	YIELD † (kg ha <sup>-1</sup> )				SDR1	SDR2	ESP1	ESP2	STGR
		Optimal	<i>Striga</i>	Drought	Across					
1	TZdEEI 1	21	102	−1	−46	0.09	−0.13	0.57	0.42	0.08
2	TZdEEI 4	−585 **	−1119 **	−689 **	−860 **	0.69 **	1.02 **	−10.15 **	−10.83 *	0.32
3	TZdEEI 5	4	279 **	−521 **	−11	0.01	−0.13	7.30	7.72	−0.03
4	TZdEEI 7	425 **	767 **	271	571 **	−0.79 **	−0.73 **	13.45 **	12.69 **	0.07
5	TZdEEI 9	363 *	103	−83	63	−0.31	−0.16	4.77	4.42	−0.43 *
6	TZdEEI 11	101	−164	390 **	−166	0.44 **	0.12	−3.33	−3.21	−0.12
7	TZdEEI 12	150	602 **	338 *	334 *	−0.59 **	−0.61 **	−5.23	−6.01	0.57 **
8	TZdEEI 13	−256	−1026 **	−43	−424 **	1.39 **	1.24 **	2.05	2.69	−0.38 *
9	TZEEI 58	−29	−40	−114	38	0.09	0.04	8.32 *	8.09	0.07
10	TZEEI 63	123	−173	133	−37	0.16	0.34 **	5.70	6.87	0.07
11	TZEEI 79	−210	572 **	82	313 *	−1.06 **	−0.93 **	−11.93 **	−11.58 **	−0.08
12	TZEEI 95	−106	97 **	237	226	−0.11	−0.06	−11.50 **	−11.26 **	−0.18

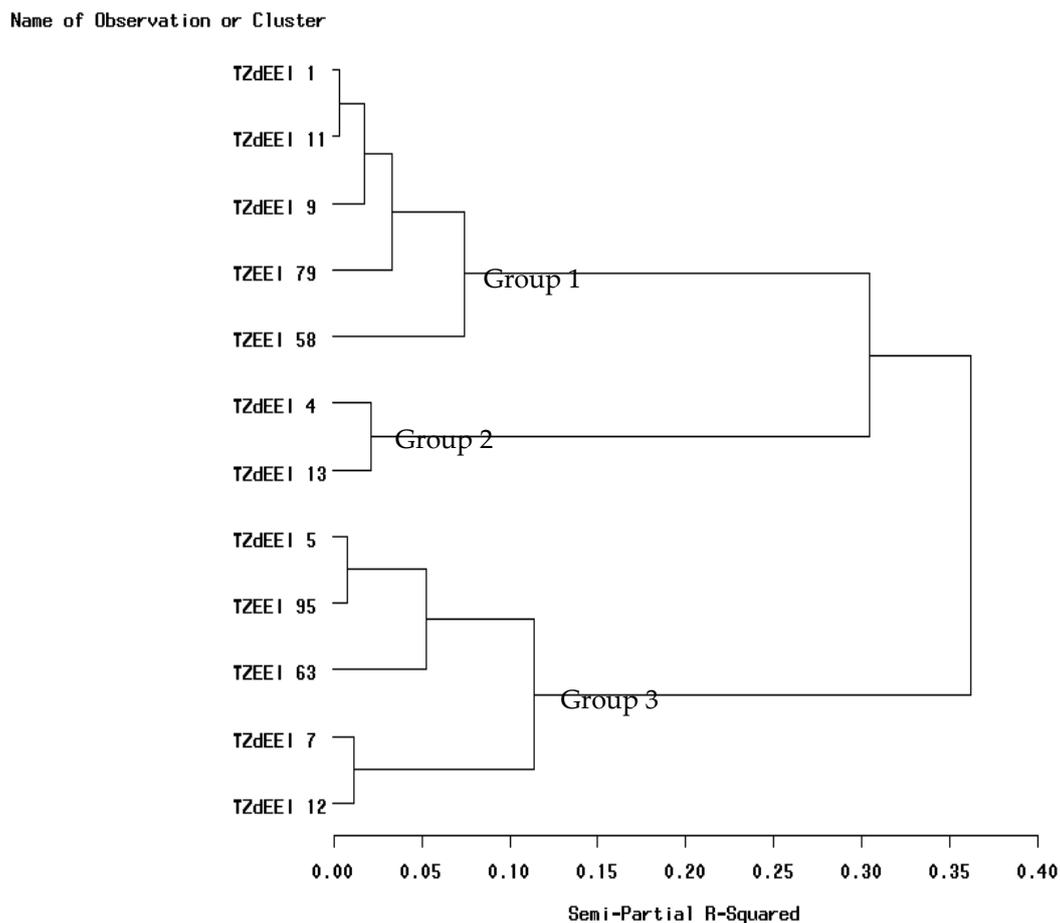
† YIELD = grain yield; SDR1 and SDR2 = *Striga* damage rating at 8 and 10 WAP; ESP1 and ESP2 = emerged *Striga* plants at 8 and 10 WAP; STGR = stay-green characteristic. \*\*, \* = significant F-test at 0.01 and 0.05 levels of probability, respectively.

Table S5 shows the SCA effects of grain yield and agronomic traits of extra-early yellow maize hybrids under optimal, *Striga*, drought and across environments. The hybrids TZdEEI 1 × TZdEEI 11 had negative SCA effects for grain yield under optimal (−1322 \*\*), *Striga* (−1231), drought (−408) and across environments (−1276 \*\*). TZEEI 58 × TZEEI 63 had significant negative SCA effects for grain yield in each environment and across environments. TZdEEI 13 × TZEEI 95 had positive SCA effects for grain yield in each environment

and across environments. Under *Striga* infestation, TZdEEI 13 × TZEEI 63 (1063) had significant positive SCA for grain yield while TZEEI 58 × TZEEI 63 had significant positive SCA effects for *Striga* damage rating at 8 and 10 WAP. Under drought conditions, the hybrid TZdEEI 5 × TZdEEI 11 had the highest positive SCA for grain yield (1263 \*\*) followed by TZdEEI 1 × TZEEI 58 (882 \*). The SCA effects for the stay-green characteristic were not significant; however, TZdEEI 1 × TZdEEI 7 had the highest SCA (1.87), followed by TZdEEI 5 × TZdEEI 12 (1.47) and TZdEEI 5 × TZdEEI 7 (1.47).

### 3.5. Classification of Inbred Lines into Heterotic Groups and Identification of Testers

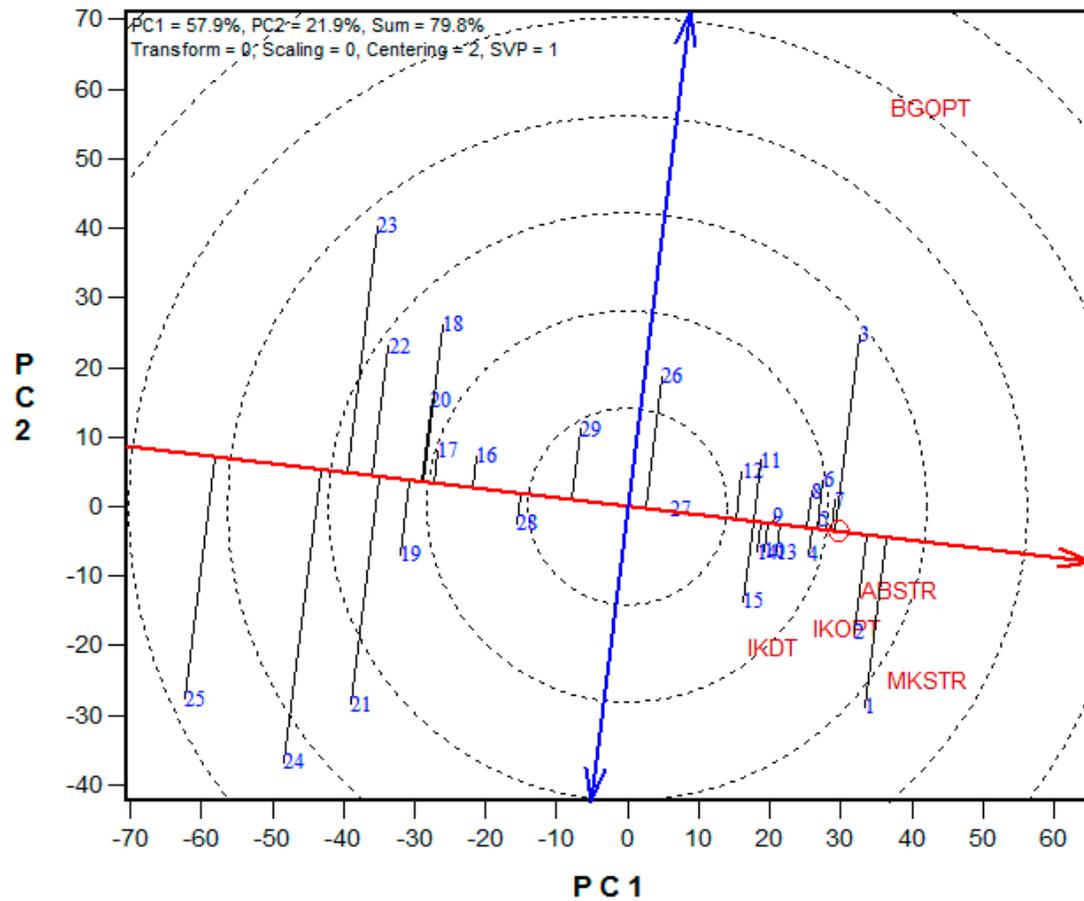
The 12 inbreds used in the present study were classified into three heterotic groups using the HGCAMT method (Figure 2). It is striking to note that the HGCAMT method classified the inbreds TZdEEI 4 and TZdEEI 13, with significant and negative GCA effects for grain yield into heterotic group 2 while inbreds TZdEEI 7 and TZdEEI 12 (two out of the three inbreds with significant and positive GCA effects for grain yield) were placed in heterotic group 3. Based on the criteria described earlier for the identification of an inbred tester, TZEEI 79 was selected as a tester for heterotic group 1 and TZdEEI 7 for heterotic group 3. However, no inbred in group 2 satisfied the criteria for selection as a tester. Furthermore, the hybrid TZdEEI 7 × TZdEEI 12 was identified as a single-cross tester because the parental lines (TZdEEI 7 and TZdEEI 12) were characterized by significant and positive GCA effects for grain yield. The parents were classified into the same heterotic group by the HGCMAT method, with the hybrid displaying a grain yield value that was higher than the mean grain yield of the hybrids in the trial.



**Figure 2.** Dendrogram of 12 extra-early maize inbred lines derived from the heterotic grouping based on the general combining ability (GCA) of multiple traits (HGCAMT) method using Ward's minimum variance cluster analysis across research environments.

### 3.6. Performance of Hybrids Based on GGE Biplot Analyses across Environments

The highly significant genotype and GEI for grain yield across test environments justified the need for the use of the GGE biplot to decompose the GEI and to examine the yield performance and stability of the hybrids across test environments. The “mean performance and stability” view of the GGE biplot analysis of selected 29 extra-early maturing maize hybrids (15 best and 10 worst hybrids plus four hybrid checks) evaluated across five environments in Nigeria in 2013 and 2014 are presented in Figure 3. The thick single-arrow black line that passes through the biplot origin (intercept of the vertical and horizontal axis) and the average tester (center of the inner-most concentric circle with an arrow) is referred to as the average-tester coordinate axis (ATC). The double-headed arrow line (ATC ordinate) separates entries with below-average means (to the left side of the line) from those with above-average means. A set of lines, parallel to the double-headed arrow line, spans the entire range of the entries, grouping them based on their mean performance. The average performance of a genotype is approximated by the projection of its marker on the ATC. The stability of the genotypes is determined by their projections onto the average-tester coordinate  $y$ -axis single-arrow line (ATC abscissa). The greater the absolute length of the projection of a genotype, the less stable it is. Based on these criteria, TZdEEI 9  $\times$  TZEEI 79 was the most stable hybrid with competitive yield across environments. Other outstanding hybrids identified as high yielding but unstable included TZdEEI 7  $\times$  TZEEI 79, TZdEEI 1  $\times$  TZdEEI 7 and TZdEEI 12  $\times$  TZEEI 95.



Entry	Pedigree
1	TZdEEI 7 × TZEEI 79
2	TZdEEI 1 × TZdEEI 7
3	TZdEEI 12 × TZEEI 95
4	TZdEEI 7 × TZEEI 63
5	TZdEEI 9 × TZEEI 79
6	TZdEEI 7 × TZdEEI 9
7	TZdEEI 7 × TZEEI 58
8	TZdEEI 11 × TZdEEI 79
9	TZdEEI 12 × TZEEI 79
10	TZdEEI 7 × TZdEEI 12
11	TZdEEI 1 × TZEEI 58
12	TZdEEI 11 × TZdEEI 58
13	TZdEEI 5 × TZdEEI 9
14	TZdEEI 7 × TZdEEI 11
15	TZdEEI 1 × TZEEI 79
16	TZdEEI 4 × TZEEI 79
17	TZdEEI 4 × TZEEI 63
18	TZdEEI 9 × TZdEEI 13
19	TZdEEI 11 × TZdEEI 13
20	TZdEEI 4 × TZdEEI 9
21	TZdEEI 1 × TZdEEI 4
22	TZdEEI 58 × TZEEI 63
23	TZdEEI 4 × TZdEEI 13
24	TZdEEI 4 × TZdEEI 11
25	TZdEEI 1 × TZdEEI 11
26	Check 1: TZEEI 79 × TZEEI 82
27	Check 2: TZEEI 79 × TZEEI 76
28	Check 3: (TZEEI 82 × TZEEI 79) × TZEEI 58
29	Check 4: (TZEEI 95 × TZEEI 58) × (TZEEI 82 × TZEEI 79)

**Figure 3.** Genotype × environment interaction (GGE) biplot analysis of grain yield of selected 15 best and 10 worst extra-early maize hybrids plus four extra-early hybrid checks evaluated under *Striga* infestation at Mokwa (MKST13) and Abuja (ABST13) and rainfed conditions at Ikenne (IKOP13) and Bagauda (BGOP13) during the 2013 growing season and under drought at Ikenne (IKDS13/14) during the 2013/2014 dry season.

#### 4. Discussion

The highly significant environment and genotype mean squares detected for grain yield and most other agronomic traits across environments indicated that there was significant genetic variability among the extra-early yellow maize hybrids. The significant variability will allow good progress from selection for improvements of the measured traits. These results agreed with the findings of Badu-Apraku et al. [29,41,44,45] and Badu-Apraku and Oyekunle [46]. This shows that crop wild relatives can be used to introgress genetic variation into elite maize cultivars. It has been reported that the genetic base of maize cultivars has narrowed down. The narrow genetic base has made it more vulnerable to new epidemics and decreased yield due to more difficult and less predictable maize growing environments [17]. Thus, crop wild relatives can be used to improve the genetic base of maize because useful genetic variation exists in the crop wild relatives of maize. The lack of significant E means squares for *Striga* damage (8 and 10 WAP) indicated that the *Striga*-infested environments were similar in the expression of the *Striga* damages. Additionally, the lack of significant  $G \times E$  mean squares for plant and ear heights, ears per plant and number of emerged *Striga* plants (8 and 10 WAP) implied that the expressions of these traits were consistent from one environment to the other. The significant GCA and SCA mean squares for most measured traits indicated that both additive and non-additive gene actions were important in the inheritance of grain yield and other traits. The existence of additive gene action in the present study implied that progress had been made in developing *Striga* and drought-tolerant maize hybrids with genes from *Z. diploperennis*. Amegbor et al. [20] also reported progress in developing drought-tolerant maize hybrids with genes from *Z. diploperennis* based on the additive gene action observed. The hybrid TZdEEI 7  $\times$  TZEEI 79 has the potential of producing a higher yield under *Striga* infestation. This hybrid was derived from *Z. diploperennis* and tropical germplasm. Gethi and Smith [47] reported that  $F_1$  crosses involving three *Z. mays*  $\times$  *Z. diploperennis* backcross-derived lines, although un-adapted to the environmental conditions in Kenya, East Africa, had significantly fewer *Striga* plants compared with susceptible checks. Under drought conditions, the hybrid TZdEEI 12  $\times$  TZEEI 63 displayed the potential for producing a high yield. This hybrid was also derived from a cross between *Z. diploperennis* and tropical germplasm, which agreed with the results of the study of Gethi and Smith [47] and further indicated that favorable alleles were introgressed from *Z. diploperennis*.

The yield observed under stress environments represented 58% of the average yield obtained under nonstress environments, indicating a yield reduction of 42% due to the stresses, which was more than that observed by Bolanos and Edmeades [48]. Empirical estimates of maize yield reduction under artificial *Striga* infestation in WCA have been variable: 80% [49], 53.7% [50], 68% [51], 42% [52], and 39% [53]. Additionally, a yield reduction of 49% under drought has been reported [20]. Possible factors responsible for these differences include the levels of *Striga* infestation, soil fertility, and level of resistance/tolerance to *Striga* of the maize genotypes studied as well as the differences in the environmental conditions. Across research environments, hybrids such as TZdEEI 7  $\times$  TZEEI 79, TZdEEI 12  $\times$  TZEEI 63, and TZdEEI 1  $\times$  TZdEEI 7 had good performances. These hybrids should be extensively evaluated in on-farm trials to confirm the consistency of their performance under *Striga*-infested and drought environments for commercialization in SSA. Furthermore, the hybrid TZdEEI 7  $\times$  TZEEI 79 was the most outstanding based on the multiple trait base index. The outstanding grain yields of the top fifteen hybrids selected based on the multiple trait index were associated with increased ears per plant, reduced ASI, improved ear aspect and stay-green characteristic. It was also associated with reduced *Striga* damage under stress environments. These results confirmed that the multiple trait index was effective in the selection of promising hybrids with superior grain yield and other desirable agronomic traits.

The higher proportion of GCA effects of inbreds for grain yield and other measured traits than those of the SCA effects across test environments indicated that additive gene action played a dominant role in the expression of the measured traits. In addition, there

is a chance to identify potentially discriminating testers across environments. These findings are consistent with the results of Badu-Apraku et al. [29] and Badu-Apraku and Oyekunle [46], who reported the preponderance of additive gene action compared to the non-additive portion in extra-early maturing maize inbreds evaluated under contrasting environments. However, the results of this study disagree with the findings of Gethi and Smith [47], Yallou et al. [19] and Badu-Apraku et al. [44,54], who demonstrated that non-additive gene action was more important than additive gene action in the control of the inheritance of host-plant damage. Similarly, under drought conditions, additive gene action largely controlled the inheritance of the traits, which was contrary to the reports of Njeri et al. [55] and Umar et al. [56]. The differences in the results of this study and those of earlier workers may be attributed to the fact that the inbred lines used in the present study were derived from composites of a wide range of germplasm, including *Z. diploperennis*. Furthermore, the differences in the intensity of stress factors in the environments under which the studies were conducted could also lead to the differences observed. A high GCA estimate indicated higher heritability and fewer environmental effects, as also evident from the heritability values of the traits studied. It may also result in fewer gene interactions and higher achievement in selection. Thus, one parent of the worst combination could make the best combination if the other parent is selected properly. This also indicated that GCA was the main component accounting for the differences among the single-cross hybrids and that early generation testing will be effective. In addition, the selection of promising hybrids will be successful based solely on the prediction from GCA effects. This makes hybrid variety improvement more effective and less costly because testing based on a single representative tester should be enough for initial hybrid selections. The additive mode of inheritance will enhance the development of maize hybrids that are resistant to *Striga* without the need for special breeding techniques.

As reported by Makumbi et al. [57], inbred lines with favorable GCA effects could be used as parents to form a synthetic population for tolerance to stressful environments. The inbreds, TZdEEI 7, TZdEEI 12 and TZEEI 79 with significant positive GCA across the test environments could contribute favorable alleles for the improvement of grain yield in the development of productive hybrids. The inbred lines, TZdEEI 7, TZdEEI 12 and TZEEI 79, which displayed significant negative GCA effects for *Striga* damage (8 and 10 WAP), could serve as sources of favorable alleles for *Striga* tolerance. Furthermore, TZdEEI 4, TZEEI 79 and TZEEI 95 with significant and negative GCA effects for emerged *Striga* plants (8 and 10 WAP) are likely to serve as invaluable sources for *Striga* resistance. The inbred lines such as TZdEEI 9 and TZdEEI 13 with negative GCA effects for stay green characteristic could contribute to drought tolerance in maize improvement programs.

It is desirable to group inbreds based on several traits, particularly in a situation where lines and hybrids are being developed for resistance or tolerance to multiple stresses. The HGCAMT method recommended for efficient grouping of inbred lines under *Striga* infestation [58] and drought stress was also effective in the present study. The method classified the extra-early inbreds into three contrasting heterotic groups. The inbreds of each heterotic group may be recombined to form heterotic populations, which could be improved through the recurrent selection to increase the frequency of *Striga* and drought tolerance alleles. In GCA determination, SCA usually acts as a masking effect. By using genetically broad testers from different heterotic groups or increasing the number of testers, the SCA impact can be decreased because parental choice only based on the SCA effect has limited value in breeding programs. The inbreds, TZEEI 79 and TZdEEI 7 identified as testers, could be used to classify other extra-early yellow inbreds into heterotic groups and thus enhance the development of high-yielding hybrids for commercialization.

The GGE biplot analysis identified TZdEEI 9 × TZEEI 79 as the most stable single-cross hybrid with competitive grain yield across test environments. However, the hybrids TZdEEI 7 × TZEEI 79, TZdEEI 1 × TZdEEI 7 and TZdEEI 12 × TZEEI 95 were high yielding but less stable across environments. These outstanding hybrids should be tested extensively in those environments where they showed outstanding performances to confirm the

consistency of their performance and promoted for commercialization to improve food security in SSA. Results of the present study have confirmed that the introgression of *Striga* resistance from the wild relative of maize, *Zea diploperennis*, into the background of cultivated maize is a resourceful approach for the improvement of maize.

## 5. Conclusions

Additive gene action was more important than the non-additive in the inheritance of yield, *Striga* and drought resistance. GCA was the main component accounting for the differences among the maize hybrids, and the selection of promising hybrids for *Striga* and drought resistance is possible based solely on the prediction from GCA effects. The single cross hybrids that have high SCA effects for grain yield and other traits under the stress conditions can be recommended for extensive evaluation to confirm the consistency of performance of the hybrids in contrasting environments. They can also be used as parents for the development of three-way hybrids in breeding programs. In addition, the inbred lines that exhibited high GCA effects for grain yield under the stresses can be used as resource materials in hybridization programs. Inbreds TZEEI 79 and TZdEEI 7 were identified as testers, while TZdEEI 7 × TZEEI 12 was identified as a single-cross hybrid tester across environments. The single-cross hybrid TZdEEI 7 × TZEEI 79 was identified by the multiple trait index and TZdEEI 9 × TZEEI 79 by the GGE biplot as the most promising across environments. These hybrids should be further tested for consistency of performance in on-farm trials and commercialized to improve food security and contribute to the alleviation of poverty in SSA. The outstanding performance of hybrids derived from *Zea diploperennis* inbred lines has confirmed the importance of harnessing beneficial alleles from crop wild relatives for improvement of resistance to *Striga* and tolerance to drought.

**Supplementary Materials:** The following are available online at <https://www.mdpi.com/2073-4395/11/1/177/s1>, Table S1: Reactions of the maize inbred lines to *Striga* infestation and drought conditions. Table S2: Correlations between variables under optimal environment. Table S3: Correlations between variables under *Striga* environment. Table S4: Correlations between variables under drought environment. Table S5: SCA effects of extra-early yellow maize inbred parents for grain yield and other agronomic traits across 5 environments (two *Striga*-infested, one drought and two rainfed environments) in Nigeria, 2013–2014.

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