

Assessing the suitability of stress tolerant early-maturing maize (*Zea mays*) inbred lines for hybrid development using combining ability effects and DArTseq markers

Samuel A. Adewale^{1,2} | Baffour Badu-Apraku¹  | Richard O. Akinwale²

¹International Institute of Tropical Agriculture, Ibadan, Nigeria

²Department of Crop Production and Protection, Obafemi Awolowo University, Ile Ife, Nigeria

Correspondence

Baffour Badu-Apraku, International Institute of Tropical Agriculture, PMB 5320, Ibadan, Oyo State, Nigeria.

Email: b.badu-apraku@cgiar.org

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Abstract

Identification of hybrids for commercialization is crucial for sustainable maize production in sub-Saharan Africa (SSA). One hundred and ninety test crosses, 10 tester \times - tester crosses + 10 hybrid checks were evaluated across 11 environments, 2017 to 2019. Inheritance of grain yield under *Striga* infestation, optimal and across environments was influenced by additive genetic action, but there was greater influence of nonadditive gene action under drought stress conditions. Nine, seven and two inbreds had significant and positive general combining ability (GCA) effects for grain yield under *Striga*-infested, optimal and drought stress environments, respectively, and would contribute high grain yield to their progenies. Heterotic grouping methods based on specific and GCA, GCA effects of multiple traits and DArTseq markers classified the inbreds into five, three and two heterotic groups, respectively, across research conditions. The DArTseq markers method that classified the inbred lines into two major heterotic groups and was one of the most efficient methods should be adopted for practical purposes in maize breeding programmes in SSA. Hybrids TZEI 7 \times TZdEI 352, TZEI 1238 \times TZEI 7 and TZEI 1252 \times TZEI 7 had outstanding grain yield under contrasting environments and should be tested on-farm for commercialization in SSA.

KEYWORDS

combining ability, drought, gene action, heterotic groups—DArTseq markers, *Striga hermonthica*

1 | INTRODUCTION

Maize, the most important staple food crop in sub-Saharan Africa (SSA), has the highest yield potential in the savannas of the subregion. Maize is grown primarily for its carbohydrate-rich grains and its high-energy content has made it very vital in human and animal diets (Badu-Apraku et al., 2010). Despite the great potential, maize production and productivity in the savannas of SSA is significantly limited by biotic factors such as *Striga hermonthica* (Del.) Benth parasitism and abiotic factors

including recurrent drought and low soil nitrogen (low-N). Yield reduction attributable to *Striga* parasitism ranges from 20% to 80% depending on the *Striga* seed bank in the soil, level of host plant resistance or tolerance, soil fertility status and environmental factors notably drought (Atera & Itoh, 2011). Although, several methods including the use of herbicides, hand pulling and high nitrogen fertilization are available for improving maize yield under *Striga* infestation, planting of *Striga*-resistant varieties is considered the most economically practicable and sustainable strategy for combating the menace.

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The occurrence of drought stress in the past two decades has intensified, undoubtedly due to global climate changes combined with reduced soil fertility and water-holding capacity, as well as displacement of maize to marginal areas by high-value crops (Bänzinger et al., 2000). Drought at the flowering and grain filling periods of maize are the most sensitive. During the past decade, an important strategy employed by maize scientists in enhancing maize production and productivity in SSA is the concurrent improvement of maize germplasm for resistance to *Striga* and tolerance to drought, instead of selecting maize genotypes that are resistant or tolerant to either of the stresses. This is because these stresses involve a common adaptive mechanism (Badu-Apraku, Fakorede, et al., 2011; Bänzinger et al., 1999). In a study that compared the effects of drought and *S. hermonthica* on maize under field conditions, Badu-Apraku et al. (2004) reported grain yield reduction of 53% and 42% under drought and *Striga* infestation, respectively. Therefore, in the Sudan, Southern and Northern Guinea savannas where intermittent drought occurs frequently, introgression of new sources of favourable alleles for drought tolerance into cultivars that possess resistance to *Striga* is crucial, as both stresses often occur simultaneously. Now, farmers in *Striga* endemic agro-ecologies of West and Central Africa (WCA) are demanding cultivars with both *Striga* resistance and tolerance to drought and are reluctant to adopt maize cultivars that are not adapted to both drought-prone and *Striga* endemic environments (Annor et al., 2019).

For a hybrid development programme to be commercially successful, adequate information on the patterns of inheritance, combining ability and heterotic response among the available inbreds in the programme is crucial. Reports on mode of inheritance of grain yield and other agronomic traits under *S. hermonthica* infestation and drought stress conditions have been contradictory (germplasm specific) especially in tropical maize germplasm. Some earlier researchers reported that resistance to *S. hermonthica* is polygenically controlled and influenced by additive gene action (Akanvou et al., 1997; Badu-Apraku, 2007; Kim, 1994). On the other hand, results of some other studies have revealed nonadditive gene action as being more important (Kim, 1991; Sangaré et al., 2018). Similarly, Guei and Wassom (1992) and Badu-Apraku, Oyekunle, et al. (2011) found the nonadditive gene action to be more important in regulating the inheritance of grain yield under drought stress. Contrarily, results of other studies have revealed the predominance of additive gene action in controlling the inheritance of grain yield under drought stress (Badu-Apraku et al., 2004; Edmeades et al., 1999; Meseka et al., 2013). This calls for more studies to confirm the mode of gene action controlling the inheritance of grain yield of newly developed inbred lines under the contrasting stress conditions.

Information on the combining abilities and heterotic groups of these inbreds would be very useful to breeding programmes in the tropics, as it would facilitate efficient planning of crosses to develop outstanding high-yielding hybrids for stress and nonstress environments. Adequate information on hybrid performance under contrasting environmental stresses can be obtained using mating designs such as diallel (Akinwale et al., 2014; Badu-Apraku et al., 2015; Konate

et al., 2017), North Carolina Design II (Oyekunle & Badu-Apraku, 2013) and line \times tester (Amegbor et al., 2017; Ertiro et al., 2017; Fan et al., 2009). However, when several inbred lines as well as proven inbred testers (from previous studies) are available for hybrid development, production of testcrosses becomes the most efficient alternative approach for determining the combining abilities and heterotic patterns of inbred lines (Agbaje et al., 2008). The genetic materials used in the present study were newly developed inbred lines with improved levels of tolerance to drought stress and resistance to *Striga*.

Heterotic grouping methods used by researchers influence greatly the assignment of maize lines into a particular heterotic group. Several heterotic grouping methods including the specific combining ability (SCA) effects of grain yield, heterotic grouping based on the general combining ability (GCA) and SCA effects of grain yield (HSGCA), heterotic grouping based on the GCA effects of multiple traits (HGCAMT) and molecular markers have been used for grouping inbred lines (Badu-Apraku et al., 2013; Fan et al., 2008). Application of molecular markers such as simple sequence repeats (SSR) and single nucleotide polymorphism (SNP) in the heterotic grouping of inbred lines has been less efficient and reports have been contradictory (Akinwale et al., 2014; Badu-Apraku, Fakorede, Talabi, et al., 2016; Menkir et al., 2004). As a result of the inconsistencies, the Diversity Array Technology sequencing (DARtseq) markers was selected for the heterotic grouping of tropical early maize inbred lines in the present study. The advent of next-generation sequencing has greatly facilitated the development of a rapid SNP discovery method, known as DARtseq™. The DARtseq™ was developed utilizing the DARt marker platform in combination with next generation sequencing platforms (Cruz et al., 2013; Raman et al., 2014). The DARtseq approach, a variant of genotyping-by-sequencing, implements complexity reduction methods that effectively targets the genome fraction containing predominantly active genes (Baloch et al., 2017). Several studies have reported the potential of these markers in diversity and population structure assessment in many crops (Abbasov et al., 2020; Allan et al., 2020; Badu-Apraku et al., 2021).

The objectives of this study were to (i) assess the combining ability effects of newly developed inbred lines for grain yield and other agronomic traits under drought stress, *Striga* infestation and optimal conditions; (ii) classify the inbreds into heterotic groups using the DARtseq markers and their combining ability effects; (iii) assess the efficiency of the grouping methods in classifying the inbred lines; (iv) determine yield performance and stability of the hybrids across stress and optimal environments.

2 | MATERIALS AND METHODS

2.1 | Genetic materials

Thirty-eight early-maturing white maize (*Zea mays* L.) inbred lines selected based on their responses to *Striga* infestation and drought stress plus five inbred testers were utilized for this study (Tables S1

and S2). The inbred lines were developed from bi-parental crosses involving a broad-based *Striga* resistant population, TZE Comp 5W STR C7 and six drought tolerant inbred lines (TZEI 56, TZEI 31, TZEI 2, TZEI 87, TZEI 65 and TZEI 18) (AdeWale et al., 2020).

2.2 | Generation of testcrosses and field phenotyping

The 38 inbred lines were crossed to five inbred testers (TZEI 7, TZEI 18, TZEI 19, TZEI 31 and TZEI 352) to produce 190 testcrosses using the line \times tester design. The five elite inbred testers were considered as males while the 38 early inbred lines were regarded as females. In addition, the five inbred testers were intermated in a half-diallel mating design to produce 10 tester \times tester hybrids. The 190 testcrosses, 10 tester \times tester hybrids + 10 hybrid checks (including commercial checks ENT 3 \times TZEI 65 commercialized in Nigeria, Ghana and Mali, TZE-W Pop DT STR C4 \times TZEI 7 commercialized in Ghana and TZEI 60 \times TZEI 86 commercialized in Nigeria and Ghana) constituted the hybrid trial. The experimental design was 14 \times 15 alpha lattice design with two replicates. The experimental units were single-row plots, 3 m long, with within row spacing and intra-row spacing of 0.75 and 0.4 m, respectively. Evaluation of the trial was carried out at four experimental sites in Nigeria (Table S3), namely, Mokwa (*Striga*-infested and *Striga*-free conditions) and Kubwa (*Striga*-infested) during the 2017 and 2018 growing seasons, managed drought stress at Ikenne during the 2017/2018 and 2018/2019 dry seasons as well as well-watered (rainfed) conditions at Ikenne during the growing seasons of 2017 and 2018. Additionally, the trials were evaluated under rainfed conditions at Kadawa, a natural terminal drought-prone environment during the 2018 growing season. However, terminal drought was not achieved, and this test environment was considered as an optimal environment. The managed drought stress experiment at Ikenne was carried out as described by Adebayo et al. (2014) and Badu-Apraku, Fakorede, Gedil, et al. (2016). The *Striga* fields at Mokwa and Kubwa were artificially infested with *Striga* by injecting ethylene gas into the soil at about two weeks before planting to induce suicidal germination of existing *Striga* seeds in the soil. The artificial *Striga* infestation procedure proposed by the IITA Maize Improvement Programme was followed (Kim, 1991). Detailed description of the trial management under artificial *Striga* infestation at Kubwa and Mokwa has been described by Badu-Apraku et al. (2020).

In all experiments, three maize seeds were sown in the same hole and seedlings thinned to two plants per stand at two weeks after emergence to obtain a population density of 66 666 plants per hectare. Fertilizer application on the *Striga*-infested maize plots was delayed until about 25 days after planting (DAP) during which 20–30 kg N ha⁻¹, 30 kg P ha⁻¹ and 30 kg K ha⁻¹ were applied as 15–15–15 NPK depending on the fertility status of the soil. The reduced rate of fertilizer application was necessary because *Striga* emergence decreases at high N rate (Badu-Apraku et al., 2020; Kim, 1991). Compound fertilizer (15–15–15 NPK) was applied to the *Striga*-free trials at Ile-Ife, Ikenne, Mokwa and Kadawa at the rate of 60 kg N, P₂O₅

and K₂O per hectare at two weeks after planting with additional 60 kg N ha⁻¹ applied as top dressing at four weeks after planting. In the *Striga*-infested fields, weeds were removed manually leaving the *Striga* plants. The *Striga*-free trials were kept weed-free using primextra and gramoxone at the rate of 5 L/ha each of atrazine and paraquat as pre- and post-emergence herbicides, respectively, and subsequently, by hand weeding.

2.3 | Field data collection

Data were collected on plot basis for measured traits under the three research conditions (drought stress, *Striga* and optimal) on days to anthesis and silking, anthesis–silking interval (ASI), plant and ear heights, number of ears per plant, root, and stalk lodging. Data on plant aspect were collected only under drought stress and optimal conditions. Stay-green characteristic (leaf death score) was scored for the drought-stressed plots at 70 days after planting on a scale of 1–9, where 1 = 0%–10% dead leaf area (almost all leaves green), 9 = 90%–100% dead leaf area (all leaves virtually dead). Under the artificial *Striga* infested environments, data on *Striga* emergence counts and host plant damage severity were collected twice, at eight and 10 WAP (Akinwale et al., 2014; Kim, 1991). Grain yield (kg/ha) under drought was estimated from shelled grain weight per plot adjusted to 15% moisture content. Conversely, in the *Striga*-infested and *Striga*-free environments, grain yield (kg/ha) was estimated by assuming 80% (800 g grain/kg ear weight) shelling percentage of the de-husked ears per plot and adjusting to 15% moisture content.

2.4 | DNA extraction, DArT markers genotyping and quality control

Fresh leaf samples were collected from the 38 inbred lines and five testers (one leaf per plant, 8–10 seedlings per genotype) at two weeks after planting. The leaves were bulked and lyophilized before DNA extraction. Genomic DNA samples were isolated from the freeze-dried leaf tissues using the DArT protocol for genomic DNA extraction available online (www.diversityarrays.com/files/DArT_DNA_isolation.pdf). The quality of genomic DNA was checked by agarose gel electrophoresis and quantity was estimated using Nanodrop ND-2000 spectrophotometer (Thermo Scientific, Wilmington, DE, USA). The extracted DNA were sent to Integrated Genomic Service and Support (IGSS), Nairobi-Kenya for SNP genotyping using the high-throughput DArTseq technology (Raman et al., 2014). Reads and tags found in the resulting sequences were aligned to the *Z. mays* L. reference genome, version AGPV3 (B73 Ref-Gen v4 assembly) (Jiao et al., 2017), giving a raw dataset of 47 440 DArTseq markers. DArTseq markers with missing rate greater than 10%, heterozygosity more than 20%, minor allele frequency (MAF) less than 0.05 as well as those with unknown, and duplicate chromosome positions were eliminated, resulting in 7224 DArTseq markers distributed across the 10 chromosomes, which were employed for the phylogenetic analysis.

2.5 | Data analysis

Analysis of variance (ANOVA) was carried out on plot means for all data collected under each (drought, *Striga*-infested, and optimal growing conditions) and across 11 research environments using PROC GLM and RANDOM statement with test option, all implemented in Statistical Analysis System (SAS Institute, 2011). The location-year combinations, replicates and incomplete blocks within replicate effects were considered as random factors whereas the genotype was considered as a fixed effect in the combined ANOVA. Without the checks, GCA effects of the inbreds, and SCA effects of the crosses as well as their mean squares under each and across research conditions for grain yield and other agronomic traits were estimated for the testcrosses following the line \times tester analysis mating design proposed by Singh and Chaudhary (1985). The source of variation for testers was partitioned into orthogonal contrasts to estimate the significance of contrasts among testers. The testers TZEI 31, TZEI 19, TZEI 18, TZEI 7 and TZdEI 352 were designated as 1, 2, 3, 4 and 5, respectively. The relative contributions of GCA ($GCA_{\text{line}} + GCA_{\text{tester}}$) and SCA effects were computed for grain yield and other measured traits as the proportion of the GCA component to the total genetic sum of squares for each trait (Annor et al., 2019). The larger the percentage of the sum of squares of a trait due to GCA/SCA, the greater the predictability of the trait based on GCA or SCA.

The 38 inbred lines were assigned to heterotic groups in individual and across research environments by employing the HGCAMT method (Badu-Apraku et al., 2013), HSGCA method (Fan et al., 2008) and genetic distance (GD) based on DArT-SNP markers. Ward's minimum variance cluster analysis based on the Euclidean distance generated from the three methods was used to assign the 38 inbreds into heterotic groups under each environment and across the 11 test environments using SAS version 9.3 (SAS Institute, 2011). For the heterotic grouping based on the DArTseq-SNP markers, the pair-wise GD estimates among the inbred lines were computed using PowerMarker version 3.25 (Liu & Muse, 2005). To compare the effectiveness of the three heterotic grouping approaches, the 190 testcross hybrids were ranked from the best performing to the least performing, taking into consideration their grain yield under drought, *Striga*, optimal and across research environments (Fan et al., 2009). This involved the division of the total number of hybrids for each heterotic grouping procedure into two main groups that is, intergroup and intragroup crosses based on the classification of the inbred lines into the same or different heterotic groups by each grouping method. These two groups were thereafter classified into high-yielding hybrids (Yield Group 1 with average grain yield among the first 63); moderately high-yielding hybrids (Yield Group 2 with average grain yield between the 64th and the 126th) and low-yielding hybrids (Yield Group 3 with average grain yield between the 127th and the 190th). The best grouping method was detected based on the breeding efficiency described by Fan et al. (2009) and adapted by Badu-Apraku, Fakorede, Talabi, et al. (2016). The breeding efficiency was estimated as follows:

$$\frac{[\text{HPWGC} \times 100]}{\text{TNBGC}} + \frac{[\text{LYBGC} \times 100]}{\text{TNWGC}}$$

2

where HPWGC = number of highly productive between-group crosses, TNBGC = total number of between-group crosses, LYBGC = number of low-yielding within-group crosses, and TNWGC = total number of within-group crosses. In order to identify the best performing hybrids across stress environments (*Striga* and drought), the multiple-trait selection index (MI) was estimated as described by Badu-Apraku, Yallou, et al. (2017). The top 15 *Striga* and drought tolerant/resistant and the five most susceptible as well as five checks were selected for genotype main effect plus genotype \times environment interaction (GGE) biplot analysis to break-down the G \times E interactions into its component parts (Yan, 2001), using the genotype \times environment analysis with R for Windows (GEAR) software (Pacheco et al., 2016). The 'mean versus stability view' was used to identify the most promising hybrids with high and stable yield across stress and optimal environments.

3 | RESULTS

3.1 | Analyses of variance of grain yield and other traits of early-maturing white hybrids across research environments

The combined ANOVA of the hybrids across 11 research environments showed highly significant mean squares for grain yield and other measured traits for Env, G and G \times Env (Table 1). The combined ANOVA of the testcrosses under *Striga* infestation, drought and optimal research conditions are presented in Tables S4 and S5. Partitioning of the overall variation of genotypes into lines (GCA_{line}), testers (GCA_{tester}) and line \times tester ($SCA_{\text{line} \times \text{tester}}$) components revealed significant variation for nearly all the measured traits (Table 1). The Env \times GCA_{line} , Env \times GCA_{tester} and E \times $SCA_{\text{line} \times \text{tester}}$ interaction mean squares revealed significant effects for majority of the studied traits across research environments. Orthogonal comparisons between Testers 1, 2, 3, and 4, 5 were significantly different for all measured traits except ear height (Table 1). Comparisons of the differences between Tester s1 and 2, 3 and Testers 2 and 3 were significantly different for grain yield and a few other traits. However, comparison between Testers 4 and 5 was not significantly different for most measured traits including grain yield.

3.2 | Relative contributions of general and specific combining ability effects of the inbred lines

The proportion of GCA ($GCA_{\text{line}} + GCA_{\text{tester}}$) sum of squares to the total genetic effects was consistently higher for all assayed traits under *Striga* infestation and across research conditions except for grain yield and majority of the traits under optimal conditions (Figure 1). Contributions of SCA sum of squares were larger for grain

TABLE 1 Mean squares from the analysis of variance of grain yield and other agronomic traits of early-maturing testcrosses across 11 research environments in Nigeria, 2017–2019

SoV	Df	Yield	DSK	DTA	ASI	PHT	EHT	EPP	SLG	EASP	HC	PASP
Block (Rep*Env)	432	2 301 576**	14.16**	9.26**	2.89**	515.95**	2.90**	.04**	205.97**	1.66**	.79**	1.96**
Rep (ENV)	11	20 863 535**	19.23**	16.94**	4.37**	2046.05**	911.56**	0.11**	446.62**	3.63**	1.70**	5.83**
ENV	10	967 406 125**	4087.07**	2235.22**	52.48**	142 318.60**	56 115.59**	6.65**	46 541.71**	96.98**	136.79**	214.77**
Entry (G)	189	76 69 466**	46.96**	39.36**	5.383**	1195.08**	538.43**	.08**	463.12**	4.37**	3.25**	3.39**
Line	37	15 066 552**	163.14**	13.31**	12.23**	2615.10**	969.57**	.14**	1207.56**	7.73**	9.61**	4.86**
Tester	4	119 285 223**	222.03**	183.61**	42.01**	20 026.23**	9225.66**	1.26**	2076.78**	81.75**	52.45**	5.72**
Contrast 1, 2, 3 vs. 4, 5	1	309 491 471**	129.20**	33.97**	21.15**	8356.32**	16.29	3.55**	5689.86**	16.61**	136.18**	92.46**
Contrast 1 vs. 2, 3	1	11 4832 099**	82.26**	.45	89.06**	15 779.27**	16 127.77**	.00	19.24	3.97	47.00**	75.10**
Contrast 2 vs. 3	1	15 896 851**	7.05	7.33	25.19**	25 303.43**	10 111.08**	0.33**	2775.66**	52.99	3.18	1.72
Contrast 4 vs. 5	1	4 230 965	583.60	615.58**	2.39	24 461.23**	5923.17**	1.01**	.02	41.09**	1.66	15.32**
Line*Tester	148	3 018 130**	21.94**	18.18**	3.98**	306.94**	158.65**	0.05**	263.62**	1.83**	1.40**	1.41**
ENV*Entry	1900	1 594 106**	6.95**	1029.09**	2.79**	189.83**	101.25**	.03**	19.95**	.96**	1.12**	.89**
ENV*Line	400	3 010 611**	11.77**	9.83**	3.43**	382.52**	188.84**	0.05**	313.58**	1.76**	2.06**	1.27**
ENV*Tester	40	13 119 289**	17.93**	12.01**	12.72**	1577.26**	897.69**	0.19**	738.27**	6.98**	12.93**	4.39**
ENV*Line*Tester	1480	1 486 181**	8.43**	5.59**	2.84**	228.58	109.84*	.03**	173.21*	.92**	.91**	1.02
Error	1843	804 088	3.92	2.37	1.74	123.20	65.60	.02	14.55	.54	.52	.62

Note: The testers TZEI 31, TZEI 19, TZEI 18, TZEI 7 and TZdEI 352 were designated as 1, 2, 3, 4 and 5, respectively.

Abbreviations: ASI, anthesis-silking interval; DSK, days to silking; DTA, days to anthesis; EASP, ear aspect; EHT, ear height; ENV, environments; EPP, ears per plant; HC, husk cover; ns, not significant; PASP, plant aspect; PHT, plant height; RLG, root lodging; SLG, stalk lodging; SoV, source of variation.

*Significant at .05 probability levels, respectively.

**Significant at .01 probability levels, respectively.

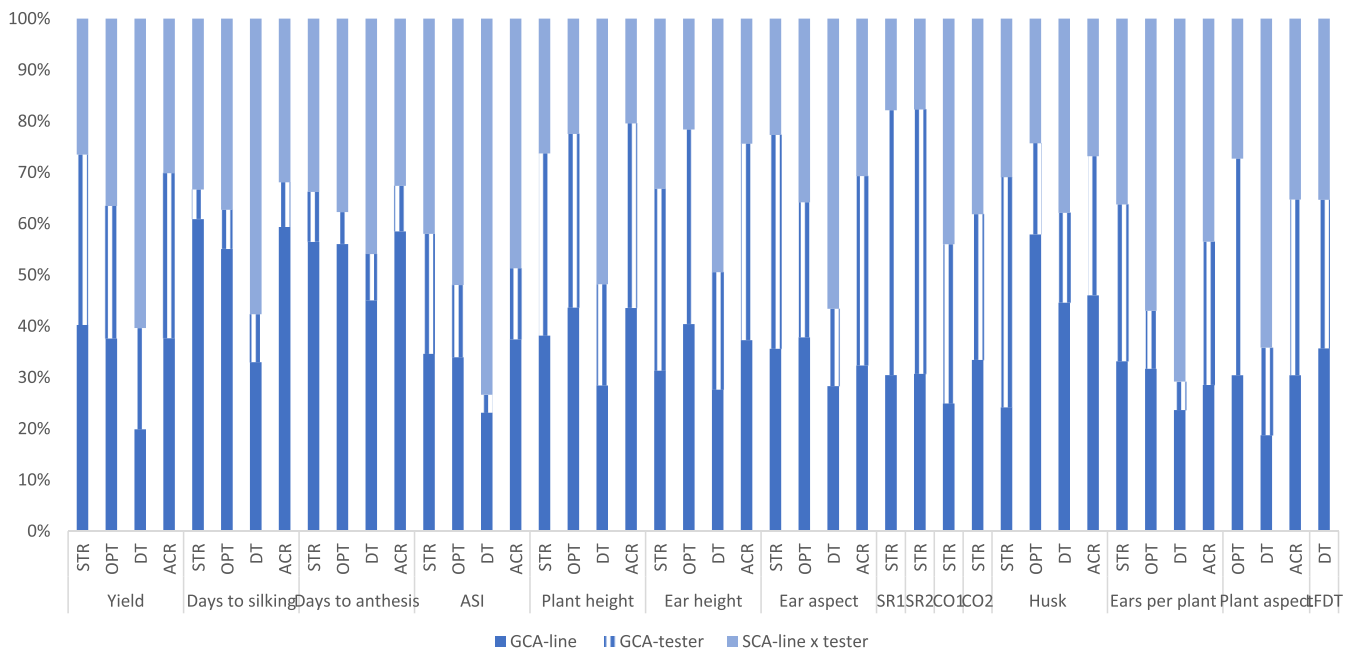


FIGURE 1 Percentage contribution of total genotypic sum of squares of grain yield and other measured traits of early-maturing maize inbreds due to GCA-line, GCA-tester and SCA-line \times tester under each and across research conditions between 2017 and 2019. STR, *Striga*; OPT, optimal; DT, drought; ACR, across; ASI, anthesis–silking interval; LFDT, leaf death score; SR1, *Striga* damage rating at 8WAP; SR2, *Striga* damage rating at 10WAP; CO1, *Striga* emergence counts at 8WAP; CO2, *Striga* emergence counts at 10WAP. [Color figure can be viewed at wileyonlinelibrary.com]

yield, ASI, plant aspect, ear aspect and ears per plant under drought stress conditions.

Of the nine inbreds with significant and positive GCA effects for grain yield under *Striga* infestation, TZEI 1203, TZEI 1252 and TZEI 1348 also displayed positive and significant GCA effects as well as negative and significant GCA effects for both *Striga* damage ratings and *Striga* emergence counts under artificial *Striga* infested conditions (Table 2). The inbred lines TZEI 1321 and TZEI 1323 displayed desirable GCA effects (significant and positive) for grain yield under drought stress conditions. The inbreds TZEI 804, TZEI 811, TZEI 836, TZEI 932, TZEI 1137 and TZEI 1238 had significant and negative GCA effects for leaf death score. The inbred lines TZEI 771, TZEI 916, TZEI 1203, TZEI 1238, TZEI 1241, TZEI 1271 and TZEI 1305 showed significant and positive GCA effects for grain yield under optimal environments.

3.3 | Heterotic grouping of the inbred lines and efficiency of heterotic grouping methods

The HSGCA, HGCAMT and DArTseq marker-based GD methods classified the inbred lines into five, three and two heterotic groups, respectively, across research conditions (Table 3). Similarly, the HSGCA and HGCAMT placed the inbreds into five and three clusters each under *Striga*, drought and optimal conditions (Table S6). Across research environments, 33 out of 38 inbred lines (87%) were classified by the testers based on the HSGCA heterotic grouping method, 26 out of the 38 inbred lines (68%) were grouped by the HGCAMT

method whereas the DArTseq marker-based GD was able to classify 29 out of the 38 inbred lines (76%). In the placement of the inbreds into heterotic groups, there was slight conformity between HSGCA and DArTseq marker-based GD grouping approaches across research environments. For instance, the placement of the inbred lines into heterotic groups followed the same trend such that TZEI 1092, TZEI 811 and TZEI 836 were placed in Group 1.

The HGCAMT, HSGCA and DArT-SNP heterotic grouping approaches detected 52, 61 and 62 high-yielding crosses out of a total of 145, 157 and 147 interheterotic crosses, respectively, across 11 research environments (Table 4). The number of between- and within-group hybrids classified by HSGCA, HGCAMT and DArTseq methods and breeding efficiencies of the grouping methods under *Striga* infestation, drought stress and nonstress research conditions are presented in Table S7. Both the HSGCA and DArT-SNP methods had the highest breeding efficiencies across research conditions, 52.8% and 52.5%, respectively, whereas that of the HGCAMT method was the least efficient (44.6%).

3.4 | Yield performance and stability of hybrids under stress and optimal conditions

Nine out of the 15 top performing hybrids across stress conditions had inbred tester TZEI 352 involved in their crosses while two each of the worst five hybrids had testers TZEI 31 and TZEI 19 involved in their crosses (Table 5). The hybrid TZEI 7 \times TZEI 352 obtained from intermating among the testers recorded the highest grain yield across

TABLE 2 General combining ability effects of grain yield and other agronomic traits of 38 early maturing maize inbred lines across four *Striga*-infested, two drought and five optimal environments in Nigeria, 2017–2019

Inbred	Yield (kg/ha)			Days to anthesis		
	Striga	Drought	Optimal			
TZEI 762	65.83**	-417.40*	101.00	.04*	-0.32	-0.47
TZEI 769	102.73	-28.49	22.36	0.01	-2.65**	-2.44**
TZEI 771	250.00	328.20	961.44**	-0.02	0.68	0.28
TZEI 804	70.56	140.31	-135.22	0.02	-2.36**	-1.94**
TZEI 806	215.43	56.76	-328.29	0.05**	-0.85	-0.64*
TZEI 807	177.53	-288.79	197.17	-0.04	-0.24	-0.44
TZEI 811	-1131.18**	28.72	216.65	-0.04*	1.98**	1.61**
TZEI 835	-701.39**	-345.04	-386.40	-0.08**	0.90**	0.57*
TZEI 836	-529.03*	38.35	-424.14*	-0.05**	0.73**	0.74**
TZEI 868	-674.64**	-474.60*	-672.86**	0.00	1.13**	0.94**
TZEI 907	-456.21*	229.66	-404.17	-0.04*	0.21	0.06
TZEI 916	-495.12*	120.43	447.52*	0.00	1.93**	1.86**
TZEI 932	-512.26*	287.30	-391.83	0.01	1.32**	1.36**
TZEI 933	-193.48	-170.31	-288.51	0.03	1.29**	1.58**
TZEI 934	-699.46**	212.53	-159.45	0.01	0.28	0.16
TZEI 968	-493.96*	216.38	-79.63	-0.04	-0.46	-0.70**
TZEI 972	-734.1**	-221.94	-33.53	-0.03	0.81**	0.54*
TZEI 1021	-171.81	-136.66	340.43	0.03	-1.14**	-0.62*
TZEI 1028	-27.38	220.54	317.85	-0.02	1.54**	1.41**
TZEI 1092	68.68	-707.56**	-559.17**	0.01	2.19**	1.62**
TZEI 1107	-1283.8**	-71.83	-708.55**	0.00	-0.75**	-0.15
TZEI 1134	588.71**	-39.49	120.55	0.00	-0.24	-0.45
TZEI 1137	-305.36	-281.37	-1110.67**	0.03	0.29	0.50
TZEI 1145	-70.83**	-666.20**	-746.32**	-0.04	-0.03	0.27
TZEI 1203	947.65**	127.62	898.46**	0.07**	-0.64*	-0.28
TZEI 1207	538.94*	218.71	-129.65	0.04	-0.91**	-0.53
TZEI 1225	-199.14	185.44	96.69	-0.01	-0.08	-0.25
TZEI 1237	401.65	170.66	-134.42	0.00	-0.18	-0.02
TZEI 1238	289.82	129.24	720.96**	0.01	0.33	0.33
TZEI 1241	176.41	221.44	682.86**	0.00	1.63**	1.49**
TZEI 1252	1178.65**	-216.71	249.14	0.05*	-0.89**	-0.89**
TZEI 1271	445.71*	-252.63	572.71**	-0.03	-0.40	-0.72**

TABLE 2 (Continued)

Inbred	Yield (kg/ha)			Drought	Optimal	Ears per plant	Days to silking		Days to anthesis
	Striga						Across		
TZEI 1305	394.95		478.09*	98.71		-0.02	-0.45		-0.24
TZEI 1321	-0.72		-103.42	530.75**		-0.04*	-0.98**		-1.09**
TZEI 1323	601.51**		372.68	411.97*		0.02	-0.85**		-0.61*
TZEI 1341	6.18		-23.74	142.64		0.00	-1.25**		-1.49**
TZEI 1344	911.45**		-353.07	-103.45		0.06**	-1.97**		-1.70**
TZEI 1348	1292.49**		379.75	306.12		0.04*	0.40		0.35
S. E	221.07		217.66	20.09		0.02	0.31		0.28

TABLE 2 (Continued)

Inbred	Anthesis-silking interval		Plant aspect	Husk cover	Plant height	Striga damage rating at 10 WAP		Striga emergence count at 10 WAP	Leaf death score
	Across	Ear aspect				Striga	Striga		
TZEI 762	0.18	-0.06	0.49**	0.56**	-13.57**	-0.57**	-0.10*		0.56*
TZEI 769	-0.37*	0.02	0.06	0.67**	-1.14	0.28	-0.08		0.01
TZEI 771	0.49**	-0.21	-0.49**	-0.04	5.00**	-0.12	0.00		0.11
TZEI 804	-0.47**	-0.05	0.06	0.05	-0.35	-0.17	0.00		-0.94**
TZEI 806	-0.22	-0.08	0.07	-0.30**	-4.81**	-0.27	0.05		0.11
TZEI 807	0.25	0.12	-0.03	0.20	0.84	-0.09	0.02		0.16
TZEI 811	0.46**	0.09	-0.17	-0.16	0.98	0.96**	0.04		-0.59*
TZEI 835	0.31	0.40**	0.31**	0.35**	-3.75*	0.36*	0.13**		-0.04
TZEI 836	-0.11	0.25*	0.26*	0.30*	-5.01**	0.68**	0.09*		-0.49*
TZEI 868	0.14	0.35**	0.38**	0.13	-5.38**	0.33	0.02		-0.14
TZEI 907	0.22	0.12	0.01	0.03	3.09	0.58**	0.04		0.16
TZEI 916	0.08	-0.11	-0.37**	-0.15	3.18	0.03	0.11*		-0.39
TZEI 932	0.00	-0.03	-0.14	-0.19	4.31**	0.23	0.10*		-0.64**
TZEI 933	-0.31	0.02	0.14	-0.05	2.41	-0.27	0.12**		0.16
TZEI 934	0.23	0.11	-0.02	0.06	-0.62	0.53**	0.19**		-0.09
TZEI 968	0.21	0.24*	0.08	0.55**	-5.17**	0.81**	0.03		0.71**
TZEI 972	0.32*	0.23*	0.11	0.37**	-3.79*	0.53**	0.14**		0.76**
TZEI 1021	-0.47**	0.02	-0.06	0.43**	0.51	0.13	0.01		0.71**
TZEI 1028	0.13	-0.10	-0.17	0.07	9.19**	0.01	0.08		0.31
TZEI 1092	0.40*	0.43**	0.33**	-0.31*	1.25	-0.19	-0.16**		1.01**
TZEI 1107	-0.63**	0.47**	0.24*	0.07	-3.74*	1.11**	0.02		-0.09

TABLE 2 (Continued)

Inbred	Anthesis-silking interval Across	Ear aspect	Plant aspect	Husk cover	Plant height	Striga damage rating at 10 WAP Striga	Striga emergence count at 10 WAP	Leaf death score
TZEI 1134	0.26	-0.06	0.02	-0.22	3.79*	-0.14	-0.11*	0.06
TZEI 1137	-0.67**	0.35**	0.38**	-0.02	-1.24	-0.34	-0.01	-0.84**
TZEI 1145	-0.67**	0.54**	0.42**	-0.28*	-2.57	0.38*	0.02	0.11
TZEI 1203	-0.23	-0.57**	-0.27*	-0.49**	1.39	-0.59**	-0.11*	-0.34
TZEI 1207	-0.33*	-0.27*	-0.23	-0.25*	2.11	-0.39*	-0.07	-0.19
TZEI 1225	0.15	-0.03	-0.09	-0.10	-1.17	0.16	0.02	0.01
TZEI 1237	-0.05	-0.13	0.06	0.20	0.54	-0.17	-0.04	0.01
TZEI 1238	0.12	-0.33**	-0.44**	-0.38**	2.66	0.13	0.01	-0.49*
TZEI 1241	0.19	-0.29**	-0.34**	-0.16	6.96**	0.06	-0.05	0.01
TZEI 1252	-0.05	-0.28**	0.09	-0.17	-2.63	-1.27**	-0.13**	0.11
TZEI 1271	0.28	-0.10	-0.27*	0.00	10.65**	-0.14	-0.01	0.11
TZEI 1305	-0.21	-0.09	-0.07	-0.26	1.16	0.01	-0.07	0.11
TZEI 1321	0.20	-0.03	-0.21	-0.16	-2.46	-0.19	-0.05	0.16
TZEI 1323	-0.26	-0.19	-0.11	0.28**	4.51**	-0.14	-0.07	-0.14
TZEI 1341	0.38*	-0.10	-0.11	-0.08	-4.49**	-0.07	0.02	-0.34
TZEI 1344	-0.15	-0.32**	0.26*	-0.21	-6.30**	-0.94**	-0.10*	-0.09
TZEI 1348	0.17	-0.34**	-0.17	-0.37**	3.68*	-1.27**	-0.11	0.46
S. E	0.17	0.12	0.12	0.13	1.76	0.19	0.04	0.25

TABLE 3 Summary of the heterotic groups of 38 early-maturing white inbred lines identified by different heterotic grouping methods across 11 research environments between 2017 and 2019

Heterotic grouping approach	Group 1	Group 2	Group 3	Group 4	Group 5
HSGCA	TZEI 18, TZEI 1092, TZEI 1225, TZEI 762, TZEI 811, TZEI 836, TZEI 932	TZEI 19, TZEI 1021, TZEI 1137, TZEI 1238, TZEI 1241, TZEI 1271, TZEI 1305, TZEI 1321, TZEI 769, TZEI 907, TZEI 968	TZEI 31, TZEI 1028, TZEI 807, TZEI 868, TZEI 916, TZEI 933, TZEI 934, TZEI 972	TZEI 7, TZEI 1107, TZEI 1145, TZEI 1207, TZEI 1237, TZEI 1341, TZEI 771, TZEI 804, TZEI 835	TZdEI 352, TZEI 1134, TZEI 806
HGCAMT	TZEI 806, TZEI 934, TZEI 7, TZEI 1341, TZEI 1321, TZEI 18, TZEI 807, TZEI 1225, TZEI 1237, TZEI 1305, TZEI 1134	TZEI 1203, TZdEI 352, TZEI 1348, TZEI 1252, TZEI 1344, TZEI 762	TZEI 1092, TZEI 1107, TZEI 1137, TZEI 1145, TZEI 811, TZEI 907, TZEI 19, TZEI 835, TZEI 836, TZEI 868, TZEI 31, TZEI 968, TZEI 972		
DArT-SNP based GD	TZEI 1092, TZEI 1107, TZEI 18, TZEI 7, TZEI 19, TZdEI 352, TZEI 811, TZEI 835, TZEI 836	TZEI 1134, TZEI 1305, TZEI 1137, TZEI 1203, TZEI 1237, TZEI 1271, TZEI 1238, TZEI 1241, TZEI 1225, TZEI 1321, TZEI 1323, TZEI 1341, TZEI 1344, TZEI 1145, TZEI 1207, TZEI 1252, TZEI 807, TZEI 1348, TZEI 31, TZEI 771, TZEI 804, TZEI 762, TZEI 806, TZEI 769			

TABLE 4 Number of between and within-group hybrids classified by HSGCA, HGCAMT and DArTseq grouping approaches into yield groups 1 (top 63 hybrids), 2 (middle 63 hybrids) and 3 (lowest 64 hybrids), arranged in descending order, as well as breeding efficiency (B.E) of the grouping methods across 11 research environments, 2017 to 2019

Yield group	Cross type	HGCAMT	HSGCA	DArT-SNP
1	Inter	52	61	62
1	Intra	11	2	1
2	Inter	53	54	48
2	Intra	10	9	15
3	Inter	40	42	37
3	Intra	24	22	27
B.E		44.6	52.8	52.5

stress and under nonstress environments. Grain yield of the testcross hybrids varied from 1281 kg/ha for TZEI 968 × TZEI 19 to 4447 kg/ha for TZEI 1305 × TZdEI 352 across stress conditions and 3688 kg/ha for TZEI 972 × TZEI 31 to 6982 kg/ha for TZEI 771 × TZdEI 352 across nonstress conditions. The highest yielding testcross hybrids out-yielded the best hybrid check TZE-W Pop DT C5 STR C5 × ENT 11 by 13% across stress conditions. Grain yield of the TZEI 7 × TZdEI 352 obtained from intermating among the testers outperformed the best check by 20% across stress conditions. The superior

performance of the testcrosses with positive index values was generally associated with higher grain yield, shorter ASI, taller plants, minimal *Striga* damage symptoms, reduced *Striga* emergence, delayed leaf senescence, improved plant aspect and increased ears per plant. The principal component axis (PCA) 1 and 2 of the 'mean versus stability' view of the GGE biplot accounted for 63.4% of the overall variation in grain yield of the hybrids across environments (Figure 2). The hybrids TZEI 7 × TZdEI 352, TZEI 1238 × TZEI 7 and TZEI 1252 × TZEI 7 were identified as high yielding and most stable whereas hybrids TZEI 807 × TZEI 31 and TZEI 972 × TZEI 31 were the lowest yielding and most stable across environments.

4 | DISCUSSION

The presence of significant mean squares for grain yield and most studied traits for the hybrids in the present study indicated sufficient genetic variability among the testcrosses to allow good advances from selection for improvement in grain yield as well as drought tolerance and *Striga* resistance adaptive traits. The significant G × E mean squares for grain yield and most other measured traits under each and across research conditions implied contrasting responses of the genotypes in contrasting environments and the necessity for identifying high-yielding as well as stable hybrids across environments (Amegbor et al., 2017). The significant GCA_{line} , GCA_{tester} and $SCA_{line \times tester}$

TABLE 5 Grain yield and other agronomic traits of selected hybrids (best 15 and worst 5 based on the multiple base index) plus checks evaluated under multiple stress and nonstress environments in Nigeria, 2017 and 2019

Hybrid	Yield		DYSK		ASI		PLHT		RAT1		RAT2		CO1		CO2		EPP		LDS		PASP		BI	
	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS
TZEI 7 × TZdEI 352	4843	7125	55	55	1.2	1.8	153	168	4.0	4.0	26.5	38.3	0.91	1.03	2.3	3.5	3.0	3.0	18.4					
TZEI 1207 × TZdEI 352	4414	5370	56	53	1.8	1.0	158	171	2.5	3.0	16.5	22.3	0.91	0.94	3.2	3.8	3.6	18.1						
TZEI 1305 × TZdEI 352	4447	6261	57	53	2.0	0.9	163	184	2.3	2.9	16.9	24.0	0.82	0.99	3.9	4.5	3.5	15.9						
TZEI 1321 × TZdEI 352	4042	5784	56	53	2.0	1.1	153	170	2.8	3.3	15.0	19.9	0.88	0.94	3.4	3.8	3.5	15.7						
TZEI 1344 × TZdEI 352	4131	5000	56	52	2.3	1.5	146	157	2.0	2.4	12.8	14.9	0.90	1.00	3.6	5.0	4.1	15.5						
TZEI 1021 × TZdEI 352	4088	6075	55	51	1.1	0.3	162	181	2.9	3.6	17.1	20.9	0.87	1.02	4.2	4.3	3.8	14.2						
TZEI 1252 × TZEI 7	4154	5394	55	52	2.5	0.9	145	165	2.8	3.5	20.4	21.4	0.87	1.01	2.9	4.3	4.6	13.9						
TZEI 1237 × TZdEI 352	3854	6306	57	53	2.3	0.5	155	170	2.6	3.4	13.0	18.4	0.93	0.92	4.4	5.0	3.9	13.4						
TZEI 1028 × TZdEI 352	4146	6051	58	56	1.8	1.3	165	183	3.0	3.6	20.0	27.1	0.85	0.99	3.7	5.0	3.8	13.0						
TZEI 1348 × TZEI 7	3962	5642	56	53	2.3	0.8	150	160	3.1	3.6	26.3	27.8	0.84	0.94	3.0	4.5	4.4	12.3						
TZEI 771 × TZdEI 352	3904	6982	59	54	3.0	0.9	156	187	3.0	3.4	18.4	21.9	0.81	0.99	3.9	5.0	2.8	11.5						
TZEI 762 × TZEI 7	3602	5501	56	52	1.6	1.0	139	152	3.1	4.0	16.4	21.1	0.85	0.94	2.8	5.0	4.8	11.32						
TZEI 1238 × TZEI 7	3684	7107	57	53	2.4	0.9	154	172	3.9	4.6	16.6	21.0	0.76	1.00	2.9	4.5	3.6	10.67						
TZEI 1348 × TZEI 18	4302	6203	58	54	2.6	1.6	147	169	2.9	3.5	23.5	31.5	0.81	0.97	4.1	5.0	4.4	9.89						
TZEI 1203 × TZEI 7	3599	6093	56	53	2.5	0.8	146	170	3.6	4.5	13.1	21.88	0.81	0.97	2.9	5.3	4.3	9.18						
TZEI 835 × TZEI 7	1804	4811	61	54	5.2	1.1	139	167	5.0	5.9	34.1	46.8	0.48	0.81	3.9	6.5	4.8	-14.9						
TZEI 1021 × TZEI 19	1513	5787	59	53	2.8	1.0	142	175	5.8	6.4	41.3	44.3	0.51	0.94	5.1	6.3	4.4	-15.1						
TZEI 807 × TZEI 31	1310	4490	59	54	3.1	0.8	137	168	5.3	6.0	25.4	33.9	0.48	0.85	4.2	7.5	4.6	-16.0						
TZEI 972 × TZEI 31	1431	3688	59	54	3.0	0.3	134	162	5.8	6.4	37.8	46.0	0.48	0.92	4.4	6.5	5.0	-16.9						
TZEI 968 × TZEI 19	1281	5431	59	53	4.8	1.5	138	164	6.4	7.5	38.6	46.9	0.44	0.89	5.2	5.8	4.4	-21.1						
TZE-W pop DT C5 STR C5 × ENT 11 (check)	3889	7520	56	53	1.3	1.0	162	193	4.3	5.0	26.0	35.0	0.88	0.98	3.3	4.0	4.0	12.1						
ENT 11 × TZEI 65 (check)	3285	6315	56	53	2.5	0.3	135	165	4.0	4.3	38.5	39.0	0.75	1.01	3.3	6.0	4.3	2.95						
TZE-W pop DT STR C4 × TZEI 7 (check)	2725	5945	55	53	2.2	1.5	139	164	5.3	5.63	33.4	34.9	0.75	0.92	3.1	4.8	4.5	0.79						
TZEI 86 × TZEI 60 (check)	2525	6362	57	52	2.7	0.5	152	180	5.4	5.9	40.0	39.3	0.67	0.84	4.3	4.8	3.9	-3.81						
ENT 3 × TZEI 65	2280	5057	59	52	4.6	1.6	136	160	5.6	6.1	32.6	39.6	0.65	0.91	3.3	5.3	4.3	-8.21						
S.e.d	317	362	1	1	0.5	0.3	5	4	0.3	0.3	5.0	5.0	0.05	0.04	0.4	0.6	0.3							
Grand mean	2748	5405	58	53	2.6	1.1	146	169	4.4	5.1	26.6	31.6	0.72	0.93	3.6	5.5	4.3							

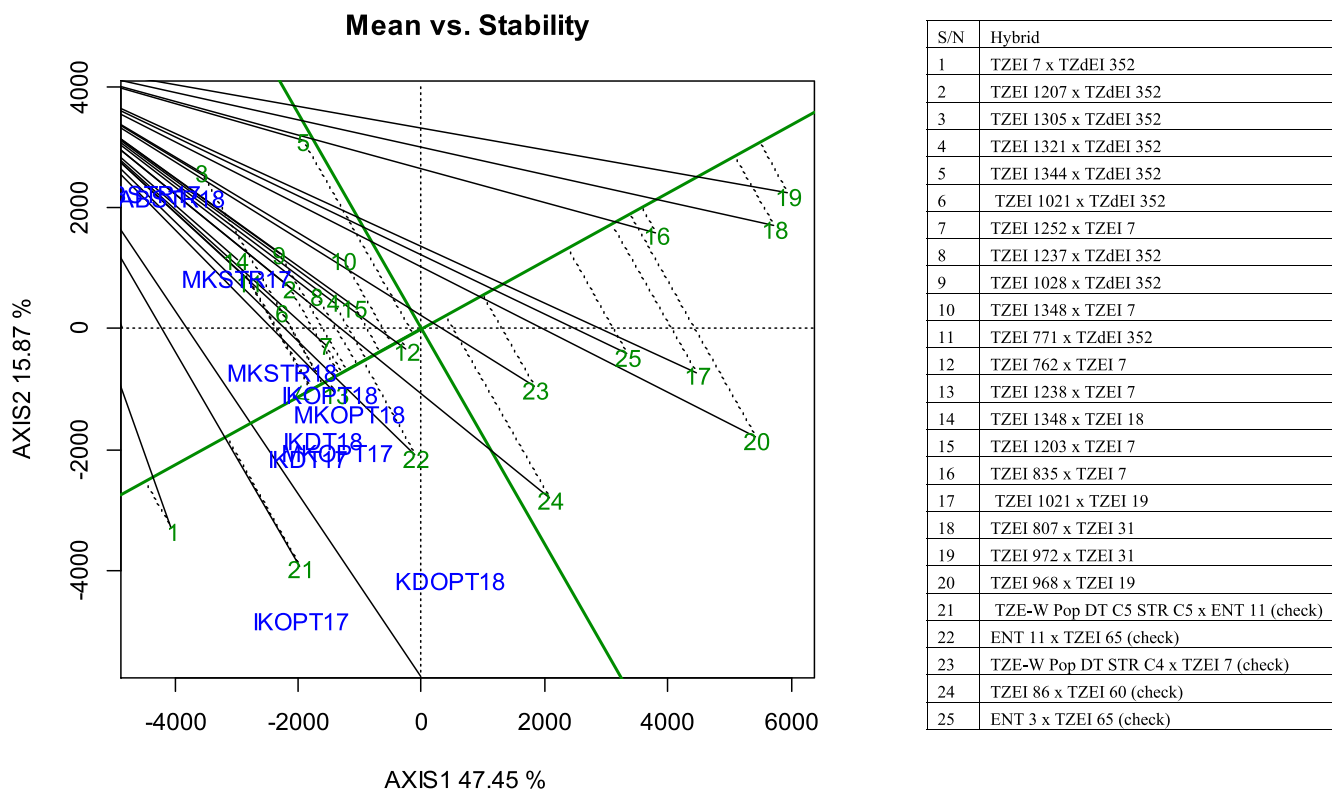


FIGURE 2 Mean yield performance and stability of 15 best and worst five early maturing maize hybrids plus five hybrid checks evaluated across 11 environments (*Striga*-infested, drought and optimal) in Nigeria, 2017–2019. MKSTR17—Mokwa *Striga*-infested 2017; MKSTR18—Mokwa *Striga*-infested 2018; MKOPT17—Mokwa optimal 2017; MKOPT18—Mokwa optimal 2018; ABSTR17—Abuja *Striga*-infested 2017; ABSTR18—Abuja *Striga*-infested 2018; IKOPT17—Ikenne optimal 2017; IKOPT18—Ikenne optimal 2018; IKDT17—Ikenne drought 2017; IKDT18—Ikenne drought 2018; KDOPT18—Kadawa optimal, 2018. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13077)]

mean squares obtained for grain yield and most measured traits under each and across research conditions revealed significant genetic differences in the performance of the inbred lines and testers, and both additive and nonadditive genetic effects were important in the set of inbreds. The significance of linear contrasts for most orthogonal comparisons across research environments for grain yield and other assayed traits emphasized the differences in the relative rankings of the inbreds by the testers. The lack of significant orthogonal comparisons observed between Tester 4 (TZEI 7) and Tester 5 (TZdEI 352) for grain yield across research environments indicated close correspondence in the relative rankings of the inbred lines for grain yield performance.

The predominance of GCA over SCA sum of squares for grain yield and most other assayed traits under *Striga*-infested, optimal and across research conditions was an indication that additive gene action was more important in the inheritance of these traits and that GCA was the major component accounting for the variations among the 190 testcrosses assessed. The predominance of GCA action over SCA under *Striga* infestation indicated that selection for resistance to *S. hermonthica* based solely on the prediction from GCA would be effective in early generations (Akinwale et al., 2014; Badu-Apraku, Oyekunle, et al., 2011; Yallou et al., 2009; Zebire et al., 2020). Contrarily, Kim (1991) and Sangaré et al. (2018) reported that nonadditive

genetic action was more important for grain yield and other traits under *Striga* infestation. The predominance of SCA over GCA action (nonadditive gene action) for grain yield and majority of the traits under drought stress conditions is consistent with the findings of Guei and Wassom (1992) and Badu-Apraku, Oyekunle, et al. (2011). Contrarily, Adebayo et al. (2014), Ertiro et al. (2017) and Adewale et al. (2018) reported the preponderance of additive gene action for grain yield and other traits under drought stress conditions. The disparity between the findings from this study and those of earlier researchers may be attributed to the sources of the inbred lines used for this study, the intensity of drought stress conditions in the drought stress experiments and the influence of environmental conditions such as the types of soil and climate that might have directly affected the emergence, severity and biotypes of *Striga* species in the different locations and years of the *Striga* experiments.

Inbred lines with outstanding GCA effects for maize grain yield and other agronomic traits could be used to develop heterotic populations for further improvement and for developing high-yielding and multiple stress-tolerant varieties in WCA (Akinwale et al., 2014). Desirable GCA effects of TZEI 1203, TZEI 1252 and TZEI 1348 observed for grain yield under *Striga* and across research environments, *Striga* damage ratings and number of emerged *Striga* plants implied that these inbred lines possessed beneficial alleles and might

have contributed alleles for higher grain yield to their progenies. Similarly, inbred lines TZEI 1321 and TZEI 1323 manifested significant and positive GCA effects for grain yield under drought conditions indicating that the lines might have contributed beneficial alleles for higher grain yield to their hybrids under drought stress. Under optimal conditions, TZEI 771, TZEI 916, TZEI 1203, TZEI 1238, TZEI 1241, TZEI 1271 and TZEI 1305 were identified as inbred parents with significant positive/negative GCA effects for grain yield and other agronomic traits. Parental lines identified in the present study with favourable and stable GCA effects for grain yield and other desirable agronomic traits could be used in hybrid development and recurrent selection programmes for the development of synthetic populations that could be improved for *Striga* resistance and drought tolerance, or used for inbred recycling as well as testers for evaluating newly developed inbred lines (Akinwale et al., 2014; Ertiro et al., 2017; Makumbi et al., 2011).

Unlike the temperate maize germplasm, distinct heterotic patterns have not been identified among tropical maize germplasm and this has been attributed to the existence of several cultivars which are yet to be field tested (Badu-Apraku, Fakorede, & Akinwale, 2017). The 38 inbred lines used in our study were classified into two, three and five heterotic groups by the DArTseq-SNP based GD, HGCAMT and HSGCA methods, respectively. Regarding the placement of inbred lines into the same heterotic group, there was little conformity between the HSGCA and the DArTseq-SNP methods. An efficient heterotic grouping method is expected to identify groups that allow interheterotic group crosses to display higher heterosis than within-group crosses. The HSGCA and DArTseq grouping methods were the most efficient in classifying the inbreds into heterotic groups with the highest breeding efficiencies of 52.8% and 52.5%, respectively across 11 research environments. In a similar study, Annor et al. (2020) identified the HSGCA grouping method as the most effective in classifying early yellow tropical maize inbred lines across similar environmental conditions (*Striga* infestation, drought and optimal). Molecular markers have also proved to be powerful tools for defining heterotic groups and examining relationships among inbred lines. For instance, Badu-Apraku et al. (2015) identified the SNP-marker method as the most efficient in classifying early maturing quality protein inbred lines into heterotic groups under multiple stress environments. Therefore, for a practical maize breeding programme, the DArTseq marker-based GD method, which was identified as one of the most efficient grouping methods for the early maturing white inbred lines of the IITA-MIP in the present study and classified the inbred lines into two groups, should be adopted for grouping and realigning the IITA-MIP early maturing white maize inbred lines into two heterotic groups. The adoption of the DArTseq marker-based GD method for grouping of the early white inbred lines would facilitate the achievement of the present goal of the IITA-MIP to reduce the number of the heterotic groups of the early maturing white endosperm maize inbred lines into heterotic groups A and B categories (Badu-Apraku et al., 2021). This will greatly improve the efficiency of parent selection of the hybrid programme while reducing the number of heterotic groups to a manageable number.

Using the multiple trait base index, 9 of the 15 top-performing testcrosses had inbred TZdEI 352 involved in their crosses. This

implied that the tester TZdEI 352 possessed multiple stress tolerant genes, especially for *Striga* resistance. The results of the present study buttressed the findings of Akaogu et al. (2019) who recommended that TZdEI 352 should be used as a parent in hybrid development, to maximize maize production and productivity in *Striga* endemic agro-ecologies of SSA. The hybrid TZEI 7 × TZdEI 352 obtained from intermating among the testers in the present study, testcross hybrids TZEI 1238 × TZEI 7 and TZEI 1252 × TZEI 7 were identified as the high-yielding and most stable hybrids across *Striga*-infested, drought and nonstress research conditions. These hybrids should be tested extensively in on-farm trials for commercialization in SSA.

5 | CONCLUSIONS

The inheritance of grain yield under *Striga* infestation, optimal and across research environments was influenced by additive genetic effects but there was greater influence of nonadditive effects under drought stress conditions. Nine, seven and two inbred lines had significant and positive GCA effects for grain yield under *Striga* infestation, optimal and drought stress environments, respectively. These inbred lines could be important sources of beneficial alleles for development of outstanding tropical maize hybrids and improvement of breeding populations. The DArTseq marker-based GD method, which was one of the most efficient methods and classified the inbred lines into two groups, should be adopted for grouping and realigning the early maturing white maize inbred lines into two heterotic groups. Outstanding hybrids TZEI 7 × TZdEI 352, TZEI 1238 × TZEI 7 and TZEI 1252 × TZEI 7 should be tested extensively in on-farm trials for commercialization in SSA.

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CONFLICT OF INTEREST

The authors declare that there is no competing interest.

AUTHOR CONTRIBUTIONS

Samuel Adewale, Baffour Badu-Apraku and Richard Akinwale conceptualized, designed and executed the experiments. Samuel Adewale analysed the data and drafted the manuscript. All authors critically reviewed the manuscript.

DATA AVAILABILITY STATEMENT

The datasets used in this study have been deposited at the IITA CKAN repository.

ORCID

Baffour Badu-Apraku  <https://orcid.org/0000-0003-0113-5487>

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