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Genetic Basis of Yield and *Striga* Resistance in Infested and Non-Infested Maize Hybrids

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ABSTRACT

Maize production in sub-Saharan Africa is severely constrained by *Striga hermonthica* infestation, a parasitic weed that causes substantial yield losses in farmers' fields. Therefore, developing maize genotypes that combine high grain yield with resistance or tolerance to *Striga* infestation is essential for improving smallholder farmers' productivity and livelihoods. In this study, we evaluated the response of selected top-cross maize hybrids to *Striga hermonthica* infestation and identified high-yielding hybrids suitable for cultivation in affected environments. Thirty-two top-cross hybrids and eight commercial checks were evaluated under artificial *Striga*-infested and non-infested conditions across four environments in Nigeria using a 10 × 4 alpha-lattice design with two replications. Significant genotypic differences in grain yield and *Striga*-related traits were observed among the hybrids under both conditions. The variance attributable to general combining ability (GCA) was greater than that due to specific combining ability (SCA) for grain yield and *Striga* damage parameters, indicating that additive gene effects predominantly control the inheritance of these traits. One parental line (TZISTR2014) was identified as a desirable general combiner for improved grain yield, whereas TZISTR1872 was identified as a good combiner for reduced *Striga* emergence count. Four top-cross hybrids (FAWSYN-1/TZISTR2014, FAWSYN-1/TZISTR2024, FAWSYN-2/TZISTR1318, and FAWSYN-1/IITAZI2305), together with two commercial checks (Oba Super 9 and Oba Super 11), exhibited superior grain yield and *Striga* infestation tolerance. Among these, FAWSYN-1/TZISTR2014 showed reduced *Striga* emergence, whereas FAWSYN-1/IITAZI2305, FAWSYN-1/TZISTR2024, and FAWSYN-2/TZISTR1318 displayed favorable responses to *Striga* damage. These hybrids represent valuable genetic resources for developing improved

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populations and extracting inbred lines for producing high-yielding *Striga*-resistant maize hybrids in sub-Saharan Africa.

KEYWORDS: maize; *Striga hermonthica*; combining ability; genetic analysis; yield

ABBREVIATIONS

DF, degrees of freedom; Env, environment; Rep, replication; Gen, genotype; GY, grain yield; DA, days to anthesis; DS, days to silk; ASI, anthesis–silking interval; PLTH, plant height; EH, ear height; HC, husk cover; EASP, ear aspect; STRRAT2, *Striga* rating at 10 weeks after planting; STRCOT2, *Striga* count at 10 weeks after planting

INTRODUCTION

Maize (*Zea mays* L.) is one of the most important cereal crops cultivated worldwide and plays a major role in sub-Saharan Africa (SSA) food security. It serves as a staple food for humans, livestock feed, and a raw material for flour, starch, ethanol, corn oil, and glucose [1–3]. In addition to its diverse uses, maize is nutritionally valuable, containing approximately 72% starch, 10% protein, 4.8% oil, 8.5% fiber, 3% sugar, and 1.7% ash [4]. Maize production in SSA is constrained by several biotic and abiotic stresses despite its importance. The parasitic weed *Striga hermonthica* (purple witchweed) is among the most devastating biotic constraints, causing severe yield losses in maize fields [5]. *Striga* infestation affects nearly two-thirds of the arable land in the savanna regions of SSA and can force farmers to abandon heavily infested fields. Continuous cropping and shortened fallow periods resulting from increasing population pressure on agricultural land have exacerbated the problem [6]. Yield losses caused by *Striga* infestation may range from 50% to complete crop failure depending on infestation severity, maize genotype, soil fertility status, and environmental conditions [7,8].

Several control strategies have been proposed to manage *Striga* infestation, including hand weeding [9], crop rotation and intercropping, herbicide application [10], the use of trap or catch crops [11], and improved soil fertility through nitrogen fertilization [12]. However, none of these methods alone can provide effective and sustainable control of the parasite. Consequently, integrated management strategies are often recommended. Among these approaches, the use of *Striga*-resistant or -tolerant maize varieties is widely considered the most practical and cost-effective option for smallholder farmers in SSA [13,14].

In *Striga* research, resistance is generally classified into pre- and post-attachment mechanisms. Pre-attachment resistance involves reduced stimulation of *Striga* seed germination or inhibition of haustorium initiation, whereas post-attachment resistance occurs when *Striga* fails to establish or develop after attachment to the host root [15–17]. Under field conditions, resistance is often indirectly assessed using indicators such as *Striga* emergence counts and damage ratings. Resistance is evaluated based on the number of emerged *Striga* plants, which reflects the overall host response but does not allow differentiation between pre- and post-attachment resistance mechanisms. In contrast, tolerance describes the host plant's capacity to maintain relatively high grain yield despite the parasite's presence [18,19]. Therefore, breeding maize varieties with improved resistance or tolerance to *Striga* infestation has become an important objective in maize improvement programs across SSA.

The identification of genotypes of maize with high levels of resistance and tolerance has been widely recommended as an effective breeding strategy [20–23]. This approach exploits the natural genetic variation in maize germplasm to develop high-yielding cultivars with improved *Striga* resistance. Successful development of *Striga*-tolerant maize hybrids depends largely on a clear understanding of gene action, inheritance patterns, and parental line combining ability. Such information enables breeders to identify superior parents, design effective hybridization schemes, and adopt appropriate breeding strategies for developing improved cultivars [24,25]. Previous studies have used combining ability analyses to investigate the inheritance of *Striga* resistance in maize [26–28]. However, the relative importance of the effects of additive and non-additive genes remains inconsistent across studies. Some authors have reported that additive gene action predominantly controls grain yield and *Striga* emergence [27,28], whereas others have suggested that non-additive effects have a greater contribution [29]. These results indicate that the genetic control of *Striga* resistance may vary depending on the germplasm used. Therefore, evaluating newly developed maize lines is important to determine the genetic basis of yield performance and resistance to *Striga* infestation.

Assessing the combining ability of inbred lines derived from diverse germplasm sources provides valuable information for hybrid development and selection of superior parental lines. Such knowledge is essential for breeding programs aimed at developing maize hybrids with improved grain yield and enhanced resistance to *Striga* infestation. Therefore, the objectives of this study were to (i) evaluate the general and specific combining ability of maize inbred lines and their hybrids, respectively, under *Striga*-infested and non-infested conditions; (ii) identify parental lines that combine high grain yield with resistance to *Striga* parasitism; and (iii) identify high-yielding maize hybrids that exhibit tolerance to *Striga* infestation.

MATERIALS AND METHODS

Genetic Materials and the Experimental Design

Sixteen inbred maize lines selected for drought tolerance and *Striga* resistance (DTSTR), together with two fall armyworm (FAW)–resistant synthetic testers (FAWSYN-1 and FAWSYN-2), were used as parental materials for the development of top-cross hybrids. The 16 inbred lines were crossed with the two testers using a Line × Tester mating design, generating 32 top-cross hybrids (Table 1). The crosses were produced at the IITA Ibadan Research Field Nursery during the dry season (December 2023–April 2024). The resulting 32 top-cross hybrids, along with eight hybrid checks released by private seed companies and national research programs for *Striga* resistance, were evaluated using a 10 × 4 alpha-lattice experimental design with two replications. The hybrids were evaluated as follows:

Table 1. List of inbred lines and synthetic testers used in the experiment.

Genotype	Type	Description
TZISTR2014	Inbred line	Drought tolerance and *Striga* resistance
TZISTR2042-1	Inbred line	Drought tolerance and *Striga* resistance
IITATZI2300	Inbred line	Drought tolerance and *Striga* resistance
IITAZI2305	Inbred line	Drought tolerance and *Striga* resistance
TZISTR1121	Inbred line	Drought tolerance and *Striga* resistance
TZISTR1129	Inbred line	Drought tolerance and *Striga* resistance
TZISTR1305	Inbred line	Drought tolerance and *Striga* resistance
TZISTR1318	Inbred line	Drought tolerance and *Striga* resistance
TZISTR1320	Inbred line	Drought tolerance and *Striga* resistance
TZISTR1869	Inbred line	Drought tolerance and *Striga* resistance
TZISTR1872	Inbred line	Drought tolerance and *Striga* resistance
TZISTR1878	Inbred line	Drought tolerance and *Striga* resistance
TZISTR2024	Inbred line	Drought tolerance and *Striga* resistance
TZISTR2042-2	Inbred line	Drought tolerance and *Striga* resistance
TZISTR2129-1	Inbred line	Drought tolerance and *Striga* resistance
TZISTR2129-2	Inbred line	Drought tolerance and *Striga* resistance
FAWSYN-1	Synthetic tester	FAW-resistant synthetic
FAWSYN-2	Synthetic tester	FAW-resistant synthetic
FAWSYN-3	Check-1	
FAWSYN-1	Check-2	
FAWSYN-2	Check-3	
SAMMAZ 51	Check-4	
Oba Super 11	Check-5	
SAMMAZ 24	Check-6	
ZMS 301	Check-7	
Oba Super 9	Check-8	

Description of Study Locations and Evaluation of Field Trials

The 40 maize genotypes, consisting of 32 top-cross hybrids and eight commercial checks, were evaluated under both artificial *Striga*-infested and non-infested conditions across two years and two locations during the 2024 and 2025 rainy seasons. The two locations represent the agro-ecological zones of northern and southern Guinea Savanna in Nigeria. Abuja, representing the Northern Guinea Savanna, is located at approximately 9°04'N, 7°29'E, with an elevation of approximately 476 m above sea level, an average annual rainfall of approximately 1200–1500 mm, mean temperatures ranging from 22 °C to 32 °C, and relative humidity varying between 60% and 80% during the cropping season. Mokwa represents the Savanna of Southern Guinea during the 2023 growing season. It is located approximately 9°18'N, 5°04'E, and receives an average annual rainfall of approximately 1000–1200 mm, with mean temperatures ranging from 24 °C to 34 °C and relative humidity of 55%–75%. The soils at both locations are predominantly sandy loam to loamy soils, which are typical of the Guinea savanna zone and suitable for maize production. The growing season at both locations typically lasts from May to October.

The experimental locations were selected because they represent important maize production environments in the savanna agro-ecological zones of Nigeria, where *Striga hermonthica* infestation is widespread. The IITA maize improvement program routinely uses these sites for *Striga* screening trials because they provide suitable environmental conditions for parasite development and allow reliable evaluation of maize genotypes for resistance and tolerance under field conditions. The experimental fields in the two locations were treated with ethylene gas to induce suicidal germination of residual *Striga* seeds and reduce the residual seed bank from previous experiments. After this treatment, newly prepared *S. hermonthica* seeds collected from farmers' sorghum fields around Abuja and Mokwa in the preceding year were applied at a rate of approximately 3000 germinable seeds per planting hole representing the *Striga*-infested strips. The application of the *Striga* seeds was not direct due to their extremely small size; instead, the seeds were mixed with a small quantity of sand to facilitate uniform distribution during artificial infestation. The sand served only as a carrier for the seeds and was applied in negligible amounts relative to soil volume. Maize seeds were later planted in the same holes as the *Striga* seeds. This procedure is routinely used in *Striga* screening trials to ensure consistent and controlled infestation pressure. Each hybrid was planted in adjacent *Striga*-infested and non-infested strips separated by a 1.5 m alley during planting. Within each strip, genotypes were planted in two-row plots measuring 4 m in length, with 0.75 m spacing between rows and 0.25 m spacing between plants within rows. The infested row of each hybrid was positioned directly opposite the corresponding non-infested row to facilitate the accurate estimation of yield losses attributable to *Striga hermonthica* damage [14]. To eliminate potential *Striga* seed contamination in the non-infested plots, the soil was treated with ethylene 2 weeks before planting. Seeds of S. *hermonthica* were collected from sorghum fields near Abuja and Mokwa during the previous cropping season. For infestation, approximately 8.5 g of sand mixed with *Striga* seeds was applied per planting holes, providing an estimated 3000 germinable *Striga* seeds. Two maize seeds were planted per hill and later thinned to one plant at two weeks after planting (WAP) to achieve a final plant population of approximately 53,333 plants ha^{-1}. Compound fertilizer was applied at a rate of 60 kg N, 60 kg P, and 60 kg K ha^{-1} in two splits: the first at three WAP and the second at five WAP. Weeds other than *Striga* were manually controlled throughout the growing period.

Data Collection

Data were recorded under both *Striga*-infested and non-infested conditions for several agronomic and *Striga*-related traits, including plant stand, days to anthesis (DA), days to silking (DS), anthesis–silking interval (ASI), plant height, ear aspect, and grain yield. The plant stand was recorded after thinning. DA and DS were recorded as the number of days from planting until 50% of the plants in a plot had begun shedding pollen and showing emerged silks, respectively. The anthesis–silking interval (ASI) was calculated as the difference between silking and anthesis dates. Plant height (PLTH) and ear height (EH) were measured on five representative plants per plot at physiological maturity. The plant height was measured from the soil surface to the first tassel branch, and the EH was measured from the soil surface to the upper ear node. The husk cover (HC) was rated on a scale of 1–5, where 1 indicates tightly arranged husks extending beyond the ear tip and 5 indicates exposed husks. Ear aspect (EASP) was visually rated on a scale of 1–5, where 1 indicates clean, uniform, and well-filled ears, and 5 indicates small, poorly filled, and variable ears. Grain yield was determined from ears harvested in each plot and adjusted to 15% grain moisture content.

Striga damage ratings and *Striga* emergence counts were recorded under *Striga*-infested conditions in addition to other traits observed under *Striga*-non-infested conditions. The non-infested strips did not receive *Striga* seed inoculation, and no *Striga* emergence or damage was observed in those plots during the growing season. Therefore, these parameters were not recorded. *Striga* damage was visually rated at 10 WAP using a scale of 1 to 9, where 1 represented no visible damage and 9 represented complete leaf scorching and premature plant death [18]. The number of emerged *S. hermonthica* plants per plot was also counted at 10 WAP.

Statistical Analysis

Each location–year combination was considered an environment, and the level of *Striga* infestation (infested and non-infested) was treated as an experimental-conditions. Although the infested and non-infested plots were arranged in paired strips within the same field, the two conditions were analyzed as separate experiments because *Striga* infestation substantially alters the growing environment and introduces heterogeneous parasite pressure. Treating the two conditions as separate environments allows a clearer evaluation of genotype performance under both stress and non-stress conditions. Analysis of variance was performed using linear mixed-effects models. In this model, environment, genotype, and their interaction were treated as fixed effects, whereas replications nested within environments and blocks nested within replications were considered random effects. The environment was treated as a fixed effect because the *Striga*-infested and non-infested conditions represented imposed experimental environments designed to evaluate genotype performance under contrasting stress conditions. Line × Tester Analysis of variance (ANOVA) was conducted using the Analysis of Genetic Designs in R software version 5.0 [30], following the procedure described by Singh and Chaudhary [31]. The Henderson method was used to estimate mean squares and partition genetic variance into general and specific combining ability components. The relative importance of additive and non-additive gene effects was assessed using Baker's ratio as follows:

$$\text{Baker's ratio} = [2\ \sigma^2\text{GCA}/(\sigma^2\text{GCA} + \sigma^2\text{SCA})] \quad (1)$$

where σ^2GCA = variance in the general combining ability and σ^2SCA = variance in the specific combining ability.

For each experimental condition, the best linear unbiased estimates (BLUEs) for the 40 hybrids were obtained from a mixed-effect model using the META-R software [32]. These BLUEs were subsequently used to estimate Pearson correlation coefficients among grain yield and other measured traits under both *Striga*-infested and non-infested conditions using the Performance Analytics package in R. To identify maize hybrids combining high grain yield with *Striga* tolerance, the Multi-trait Genotype–Ideotype Distance Index (MGIDI) proposed by Olivoto and Nardino [33] was applied.

RESULTS

Trait Variability among Genotypes

ANOVA conducted under both *Striga*-infested and non-infested conditions revealed that the environment and genotype had significant effects ($p < 0.001$–0.01) on grain yield and most measured traits. However, the genotype × environment interaction was significant only for grain yield under *Striga*-infested conditions and was not significant for any of the traits evaluated under non-infested conditions (Table 2).

Table 2. Mean squares from the analysis of variance for some agronomic and *Striga* damage parameters of maize genotypes evaluated under *Striga*-infested and *non*-infested conditions in Nigeria.

Source of Variation	DF	GY	DA	DS	ASI	PLTH	EASP	STRRAT2	STRCOT2
***Striga*-infested condition**									
Environment (Env)	3	7,795,694**	271.7**	242.1**	0.8	1665.1*	3.4**	67.4***	385.1
Genotype (Gen)	39	1,210,583***	16.8***	16.5***	0.7	335.6***	0.3***	2.3***	260.1***
Env × Gen	117	575,882**	5.6	6.2	0.8	160.0	0.2	1.0	101.4
Residual variance	157	326,314	4.9	5.1	0.8	121.9	0.1	1.1	79.3
***Striga* non-infested**									
Source of variation	**DF**	**GY**	**DA**	**DS**	**ASI**	**PLTH**	**EH**	**EASP**	**HC**
Environment (Env)	3	5,990,889*	284.3**	294.6**	2.9*	1971.9*	1,451.6*	0.8	0.6
Genotype (Gen)	39	1,528,190***	20.8***	21.9***	0.2	443.4**	161.5	0.4***	0.3
Env × Gen	117	546,771	6.0	6.5	0.2	179.2	162.5	0.2	0.3*
Residual variance	157	409,394	7.9	8.6	0.2	213.9	134.0	0.2	0.2

*, **, and *** indicate significance at the 0.05, 0.01, and 0.001 probability levels, respectively.

Mean Performance of the Top 10 and Bottom 5 Hybrids Based on Grain Yield Under *Striga*-Infested Conditions

To facilitate interpretation of genotype performance without overloading the manuscript with extensive genotype-level detail, hybrids were ranked based on BLUEs for grain yield under *Striga*-infested conditions. While the full genotype performance is presented in Tables S1 and S2, the top-performing and lowest-performing groups were presented in this results section to highlight performance contrasts among genotypes. This approach is commonly used in breeding studies to summarize large datasets while retaining biological interpretability. The grain yield (GY) of the top 10 test hybrids ranged from 3104 kg ha^{-1} for FAWSYN-1/TZISTR2014 to 1152 kg ha^{-1} for FAWSYN-2/TZISTR1121. The commercial checks produced GYs ranging from 1519 kg ha^{-1} for ZMS 301 (Check 7) to 3250 kg ha^{-1} for Oba Super 9 (Check 8), with an overall mean of 2121 kg ha^{-1}. The *Striga* damage rating among the top-cross hybrids ranged from 3.7 for FAWSYN-1/TZISTR2014 to 5.8 for FAWSYN-2/TZISTR1121. Among the commercial checks, the ratings ranged from 3.2 for Oba Super 9 (Check 8) to 6.2 for ZMS 301 (Check 7). The number of emerged *Striga* plants among the top-cross hybrids ranged from 6 for FAWSYN-2/TZISTR1121 to 26 for FAWSYN-1/TZISTR2042-2, whereas the counts for the commercial checks ranged from 7 for Oba Super 9 to 44 for ZMS 301. Under non-infested conditions, the top 10 under *Striga*-infestation earlier presented recorded GY ranging from 3853 kg ha^{-1} for FAWSYN-1/TZISTR2014 to 1616 kg ha^{-1} for FAWSYN-2/TZISTR1121. The commercial check hybrids produced GYs ranging from 1669 kg ha^{-1} for FAWSYN-2 (Check 3) to 3152 kg ha^{-1} for Oba Super 11 (Check 5), with an overall mean of 2589 kg ha^{-1} (Table 3).

Four top-cross hybrids—FAWSYN-1/TZISTR2014, FAWSYN-2/TZISTR2014, FAWSYN-2/TZISTR2042-2, and FAWSYN-1/IITAZI2305—ranked among the highest-yielding hybrids under Striga-infested conditions. These hybrids combined relatively high GY with moderate *Striga* damage ratings (3.7, 4.4, 4.6, and 4.7, respectively), *Striga* counts ranging from 13 to 21, and yield reductions ranging from 3.2%–19.4%. Although some lower-yielding hybrids exhibited yield reduction values within a similar range, this pattern was not consistent across all genotypes, indicating that grain yield under infestation and yield reduction are not perfectly associated.

Under non-infested conditions, the hybrids FAWSYN-1/TZISTR2014, FAWSYN-2/TZISTR2014, FAWSYN-1/IITATZI2300, and FAWSYN-2/IITATZI2300 recorded the highest grain yields (3853, 3308, 3292, and 3135 kg ha^{-1}, respectively), which were comparable to or higher than those of the best-performing commercial checks. Conversely, FAWSYN-2/TZISTR1121 and FAWSYN-1/TZISTR1320 were among the lowest-performing hybrids, producing grain yields below the overall mean (1616 and 1813 kg ha^{-1}, respectively).

Table 3. Mean grain yield and *Striga* damage parameters of the top 10 and bottom 5 maize hybrids ranked based on grain yield under *Striga*-infested conditions across four Nigerian environments.

Hybrid	Grain Yield (kg/ha)		*Striga* Response Traits		Yield Impact
Top 10 performers	**Infested**	**Non-infested**	***Striga* rating**	***Striga* count**	**Yield Reduction (%)**
FAWSYN-1/TZISTR2014	3104	3853	3.7	18	19.4
FAWSYN-2/TZISTR2014	3008	3308	4.4	21	9.1
FAWSYN-2/TZISTR2042-2	2515	2597	4.6	15	3.2
FAWSYN-1/IITAZI2305	2417	2917	4.7	13	17.1
FAWSYN-1/TZISTR2042-2	2285	2602	4.6	26	12.2
FAWSYN-1/TZISTR1878	2277	2432	5.0	15	6.4
FAWSYN-2/TZISTR1318	2251	2636	3.8	17	14.6
FAWSYN-2/TZISTR2042-1	2244	2522	3.9	18	11.0
FAWSYN-1/IITATZI2300	2216	3292	4.8	17	32.7
FAWSYN-2/TZISTR1869	2161	2806	4.3	17	23
Bottom Performers					
FAWSYN-2/TZISTR1305	1708	1936	4.1	14	11.8
FAWSYN-1/TZISTR1318	1655	1972	4.7	13	16.0
FAWSYN-2/IITATZI2300	1591	3135	4.9	22	49.2
FAWSYN-1/TZISTR1320	1580	1813	5.3	25	12.9
FAWSYN-2/TZISTR1121	1152	1616	5.8	6	28.7
Checks					
Check 8-Oba Super 9	3250	3096	3.2	7	−5.0
Check 5-Oba Super 11	2626	3152	3.4	16	16.7
Check 4-SAMMAZ 51	2290	2953	4.3	13	22.4
Check 2-FAWSYN-1	1924	2158	4.8	18	10.8
Check 6-Sammaz 24	1738	2755	5.9	29	36.9
Check 1-FAWSYN-3	1721	1842	4.5	15	6.6
Check 3-FAWSYN-2	1542	1669	4.9	10	7.6
Check 7-ZMS 301	1519	2480	6.2	44	38.7
Overall mean	2121	2589	4. 6	17.8	17.5
LSD ($p < 0.05$)	764	905	1.1	10.4	-

Means differ significantly when the difference between two values exceeds the LSD at $p \leq 0.05$.

Combining the Ability Performance of the Parental Lines and the Testers

Under *Striga*-infested conditions, highly significant line effects were observed for grain yield and most of the measured traits ($p < 0.001$). In contrast, the tester (GCA) effects were not significant for any of the evaluated traits (Table 4). The line × tester interaction effect was significant for GY ($p < 0.01$) and *Striga* count ($p < 0.05$). Regarding the interaction with the environment, the environment × line GCA interaction was significant for GY ($p < 0.05$) and DA ($p < 0.05$), whereas the environment × tester GCA interaction was not significant for any of the traits. The environment × SCA interaction was significant only for GY ($p < 0.05$). Baker's ratio values ranged from 0.5 to 0.9, indicating a relatively greater contribution of additive genetic effects for most traits (Figure 1). The contribution of mean squares of GCA to the total variation among hybrids was greater than that of SCA for most of the measured traits.

Table 4. Line-by-tester analysis of variance for some agronomic and *Striga* damage parameters of 16 lines, two testers, and 32 top-cross hybrids evaluated under *Striga*-infested and non-infested conditions across Nigerian environments.

Source of Variation	Df	GY (kg ha^{-1})	DA (days)	DS (days)	ASI (days)	PLTH (cm)	EASP (1–5)	STRRAT2 (1–9)	STRCOT2
***Striga*-infested condition**									
Line (GCA)	15	1,440,446***	18.8***	17.4***	0.8	617.5***	0.4**	1.4	154.9*
Tester (GCA)	1	129,438	11.1	15.8	0.4	0.1	0.7*	0.5	115.8
SCA	15	536,004*	4.2	4.5	0.4	80.0	0.2	1.6	151.9*
Env × Line (GCA)	45	618,453**	7.0*	7.3	0.9	177.0	0.2	0.9	75.0
Env × Tester (GCA)	3	350,017	5.0	9.0	1.6	34.9	0.2	1.9	22.6
Env × SCA	45	459,457*	4.4	5.2	0.5	135.6	0.2	0.8	58.1
Residual	52	285,361	4.3	4.5	0.7	123.2	0.1	1.0	70.1
Baker's ratio		0.7	0.9	0.9	0.8	0.9	0.9	0.5	0.6
***Striga* non-infested**									
Source of Variation	**Df**	**GY (kg ha^{-1})**	**DA (days)**	**DS (days)**	**ASI (days)**	**PLTH (cm)**	**EH (cm)**	**HC (1–5)**	**EASP (1–5)**
Line (GCA)	15	2,287,826***	31.7***	32.9	0.2	660.6**	189.2	0.3	0.5**
Tester (GCA)	1	31,958	0.3	0.7	0.1	0.8	16.4	0.2	0.6
SCA	15	424,405	4.6	5.6	0.1	116.8	126.4	0.3	0.2
Env × Line (GCA)	45	559,195	6.3	7.1	0.2	167.8	170.9	0.3	0.2
Env × Tester (GCA)	3	429,474	5.5	4.8	0.0	107.0	113.1	0.1	0.3
Env × SCA	45	523,749	5.7	6.0	0.1	124.8	215.9	0.3	0.1
Residuals	52	361,045	8.9	9.3	0.2	216.3	163.0	0.2	0.2
Baker's ratio		0.8	0.9	0.9	0.7	0.8	0.6	0.7	0.9

*, **, and *** indicate significance at probability levels of 0.05, 0.01, and 0.001, respectively.

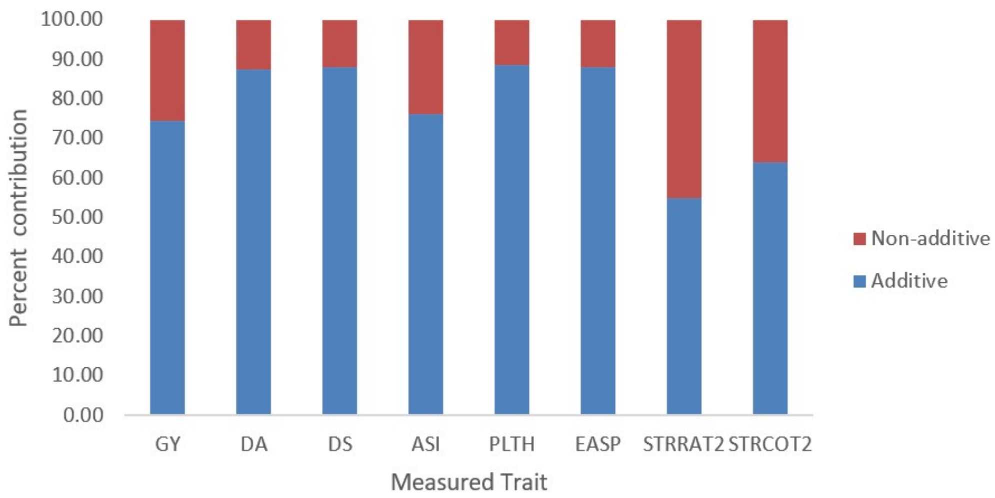


Figure 1. Proportion of additive (lower bar) and non-additive (upper bar) genetic variance for GY and other agronomic traits of 16 inbred lines involved in line × tester crosses evaluated under *Striga*-infested conditions in Nigeria.

Under non-infested conditions, line (GCA) effects were highly significant for GY and DA ($p < 0.001$) and significant for plant height and ear aspect ($p < 0.01$). However, tester (GCA) and line × tester (SCA) effects were not significant for the evaluated traits (Table 4). Baker's ratio values ranged from 0.6 to 0.9, again indicating a predominance of additive gene effects for the traits studied (Figure 2).

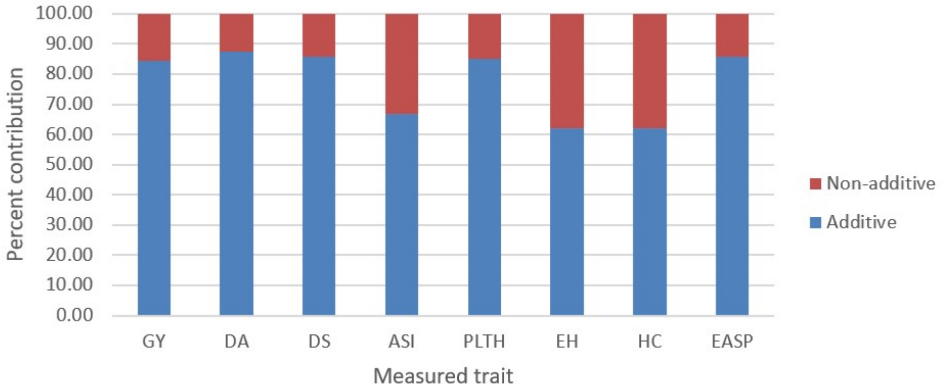


Figure 2. Proportion of additive (lower bar) and non-additive (upper bar) genetic variance for GY and other agronomic traits of 16 inbred lines involved in line × tester crosses evaluated under non-infested conditions across four environments in Nigeria.

General combining ability

The GCA estimates of the parental lines for GY and selected *Striga*-related traits are presented in Table 5. Several lines showed positive GCA estimates for GY under *Striga*-infested conditions; however, only TZISTR2014 exhibited statistically significant effects, indicating its potential to contribute to GY under *Striga* infestation. A similar pattern was observed under non-infested conditions, where several lines displayed positive GCA estimates, but only TZISTR2014 showed a significant effect. For the *Striga* count, TZISTR1872 exhibited a significant and desirable negative GCA estimate, indicating its potential contribution to reducing *Striga* emergence. Although several lines showed negative GCA estimates for the *Striga* damage rating, none of these estimates were statistically significant.

Table 5. Effects of general combining ability on grain yield and *Striga* damage parameters of 16 inbred lines and two testers evaluated under artificial *Striga* infestation across four environments in Nigeria.

PARENTS	GY		STRRAT2	STRCOT2
	Infested	Non-infested		
TZISTR2014	1,053.5***	1,042.0**	−0.5	2.4
TZISTR2042-1	69.0	−147.7	−0.2	0.2
IITATZI2300	−129.8	549.5	0.4	2.5
IITAZI2305	39.4	273.3	0.4	0.6
TZISTR1121	−460.0	−565.6	0.3	1.0
TZISTR1129	23.0	212.3	−0.4	−0.8
TZISTR1305	−249.6	−517.2	−0.0	−4.9
TZISTR1318	−45.3	−274.8	−0.3	−0.7
TZISTR1320	−280.9	−480.6	0.4	5.4
TZISTR1869	17.3	266.7	0.0	4.3
TZISTR1872	−74.9	−169.7	0.14	−7.5*
TZISTR1878	44.1	66.7	0.1	−0.8
TZISTR2024	−160.3	159.1	−0.4	−3.9
TZISTR2042-2	398.3	21.7	0.1	5.5
TZISTR2129-1	−121.2	−401.3	−0.2	−4.1
TZISTR2129-2	−111.8	−96.0	0.0	−2.4
T1 (TESTER 1)	15.0	−30.9	−0.1	0.8
T2 (Tester 2)	−13.6	23.3	0.1	−1.2

*, **, and *** indicate significance at the 0.05, 0.01, and 0.001 probability levels, respectively.

Specific combining ability

The SCA estimates for GY and *Striga*-related traits are presented in Table 6. Under *Striga*-infested conditions, most hybrids showed SCA estimates that were not statistically significant for GY, indicating limited evidence of non-additive genetic effects for this trait. However, significant SCA estimates were observed for some *Striga*-related traits. For example, the hybrid FAWSYN-1/TZISTR1121 exhibited a significant positive SCA estimate for GY under non-infested conditions and significant SCA estimates for *Striga* damage rating and *Striga* count under *Striga*-infested conditions. Similarly, the hybrid FAWSYN-1/TZISTR1121 showed a significant negative SCA estimate for *Striga* damage rating, showed a potential contribution to reduced *Striga* damage. Additionally, the hybrid FAWSYN-2/TZISTR1121 exhibited significant SCA estimates for the *Striga* count. Although several other hybrids showed positive or negative SCA estimates for the evaluated traits, these estimates were not statistically significant.

Table 6. Estimates of the effects of specific combining ability on grain yield and *Striga* damage parameters of 16 inbred lines and two testers evaluated under artificial *Striga* infestation across four environments in Nigeria.

	GY			
Top-Cross Hybrids	**Infested**	**Non-infested**	**STRRAT2**	**STRCOT2**
FAWSYN-1/TZISTR2014	−2.9	204.7	−0.4	−2.3
FAWSYN-1/TZISTR2042-1	−279.8	−207.2	0.1	−1.9
FAWSYN-1/IITATZI2300	319.7	146.6	−0.1	−1.6
FAWSYN-1/IITAZI2305	230.2	52.5	−0.4	−3.2
FAWSYN-1/TZISTR1121	278.8	354.9*	−0.7*	10.3***
FAWSYN-1/TZISTR1129	15.6	−74.2	0.1	1.0
FAWSYN-1/TZISTR1305	−23.4	79.6	0.1	−2.6
FAWSYN-1/TZISTR1318	−269.4	−214.6	0.5	−0.7
FAWSYN-1/TZISTR1320	−189.5	−151.6	0.4	4.8
FAWSYN-1/TZISTR1869	−195.4	50.7	0.4	0.6
FAWSYN-1/TZISTR1872	−101.3	145.6	0.4	−0.7
FAWSYN-1/TZISTR1878	191.3	−114.9	−0.1	−0.3
FAWSYN-1/TZISTR2024	38.5	61.0	−0.5	−2.8
FAWSYN-1/TZISTR2042-2	−139.0	−1.3	0.1	3.9
FAWSYN-1/TZISTR2129-1	60.0	92.8	−0.1	0.9
FAWSYN-1/TZISTR2129-2	55.8	−363.1*	0.2	−2.1
FAWSYN-2/TZISTR2014	1.6	−197.0	0.4	2.7
FAWSYN-2/TZISTR2042-1	278.5	214.9	−0.1	2.3
FAWSYN-2/IITATZI2300	−321.0	−139.0	0.1	2.0
FAWSYN-2/IITAZI2305	−231.6	−44.9	0.4	3.6
FAWSYN-2/TZISTR1121	−280.1	−347.2*	0.7*	−9.9*
FAWSYN-2/TZISTR1129	−17.0	81.9	−0.1	−0.6
FAWSYN-2/TZISTR1305	22.1	−71.9	−0.1	3.0
FAWSYN-2/TZISTR1318	268.1	222.2	−0.5	1.1
FAWSYN-2/TZISTR1320	188.1	159.3	−0.4	−4.4
FAWSYN-2/TZISTR1869	194.1	−43.0	−0.4	−0.2
FAWSYN-2/TZISTR1872	99.9	−137.9	−0.4	1.1
FAWSYN-2/TZISTR1878	−192.7	122.6	0.1	0.7
FAWSYN-2/TZISTR2024	−39.8	−53.3	0.5	3.2
FAWSYN-2/TZISTR2042-2	137.6	9.0	−0.1	−3.5
FAWSYN-2/TZISTR2129-1	−61.4	−85.1	0.1	−0.5
FAWSYN-2/TZISTR2129-2	−57.2	370.8*	−0.2	2.5

* and *** indicate significance at the 0.05, 0.01, and 0.001 probability levels, respectively.

Selection of Outstanding Top-Cross Hybrids with *Striga* Tolerance Using MGIDI

The measured traits were grouped into two factors based on the MGIDI analysis. The first factor (FA1) was associated with plant height (PLTH), *Striga* damage rating (STRRAT2), EASP, and grain yield (GY), whereas the second factor (FA2) was mainly associated with *Striga* count (STRCOT2). MGIDI analysis predicted desirable genetic gains for all evaluated traits relative to the ideotype. The predicted selection gain was 35.28% for traits targeted for increase and −36.08% for traits targeted for reduction (Table 7). Six genotypes were identified as superior based on the MGIDI index using a selection intensity of 15%. These included four newly developed top-cross hybrids and two commercial check hybrids, namely, Oba Super 9 (Check 8) and Oba Super 11 (Check 5) (Figure 3). Among the selected hybrids, three were derived from crosses involving FAWSYN-1.

Table 7. Factorial loadings and predicted genetic gains of 32 top-cross hybrids and 8 commercial checks based on the MGIDI.

Traits	Factor	Xo	Xs	Predicted Gain	Sense	Goal
Plant height	FA1	118.43	125.47	5.95	increase	100
Striga rating	FA1	4.56	3.88	−14.82	decrease	100
Ear aspect	FA1	2.63	2.37	−9.93	decrease	100
Grain yield	FA1	2,032.40	2,628.49	29.33	increase	100
Striga count	FA2	16.53	14.55	−11.93	decrease	100

FA1 = factor analysis 1; FA2 = factor analysis 2; Xo = population mean before selection; Xs = population mean of the selected individuals.

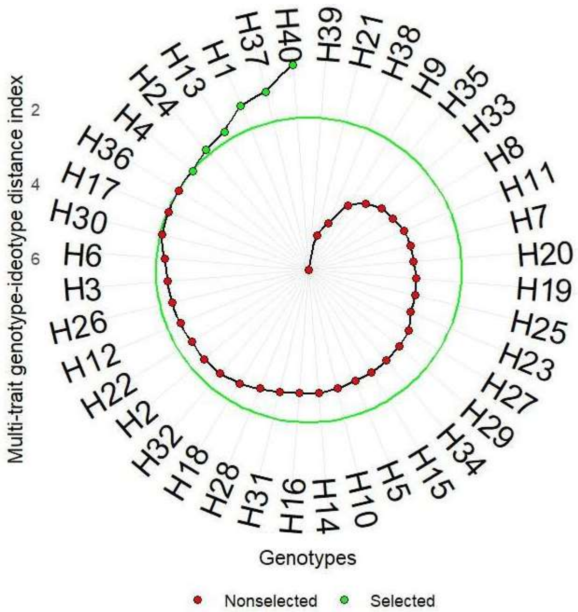
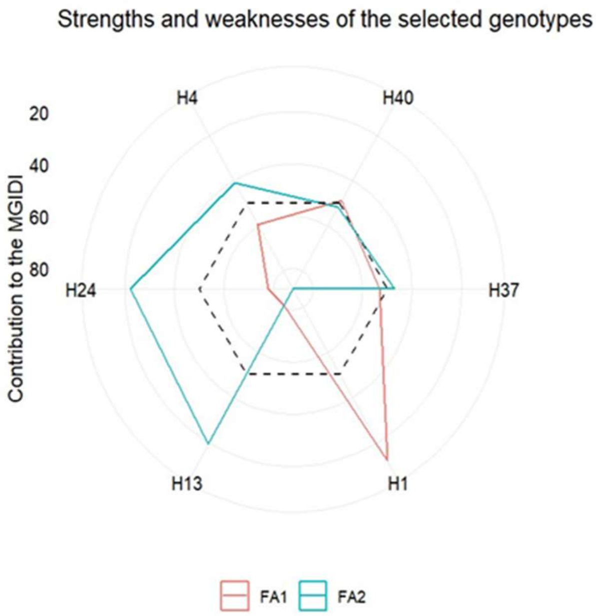


Figure 3. View of the selected (green dots) and non-selected (red dots) hybrids based on the multi-trait genotype–ideotype distance index. The lower the MGIDI of a genotype on the left side of the graph, the closer the genotype is to an ideotype. The green circle is the cut-off MGIDI value that determines the genotype to be selected based on the individual MGIDI estimate.

The four best-performing top-cross hybrids identified using the MGIDI index were FAWSYN-1/TZISTR2014, FAWSYN-1/TZISTR2024, FAWSYN-2/TZISTR1318, and FAWSYN-1/IITAZI2305. These hybrids combine desirable levels of grain yield with improved *Striga* infestation tolerance. The MGIDI results also revealed the selected hybrids' strengths and weaknesses (Figure 4). The proportion of each factor contributing to the MGIDI value indicated the traits that influenced the performance of individual hybrids.

The hybrids FAWSYN-1/TZISTR2014 (H1) and Oba Super 9 (H40) showed strengths associated with FA1, including plant height, *Striga* damage rating, ear aspect, and GY. In contrast, hybrids FAWSYN-1/IITAZI2305 (H4), FAWSYN-2/TZISTR1318 (H24), FAWSYN-1/TZISTR2024 (H13), and Oba Super 11 (H37) were strongly associated with FA2, which was primarily related to *the Striga* count (Table 7 and Figure 4).



Entries	Code	Genotype
1	H1	FAWSYN-1/TZISTR2014
4	H4	FAWSYN-1/IITAZI2305
13	H13	FAWSYN-1/TZISTR2024
24	H24	FAWSYN-2/TZISTR1318
37	H37	Check 5-Oba Super 11
40	H40	Check 8-Oba Super 9

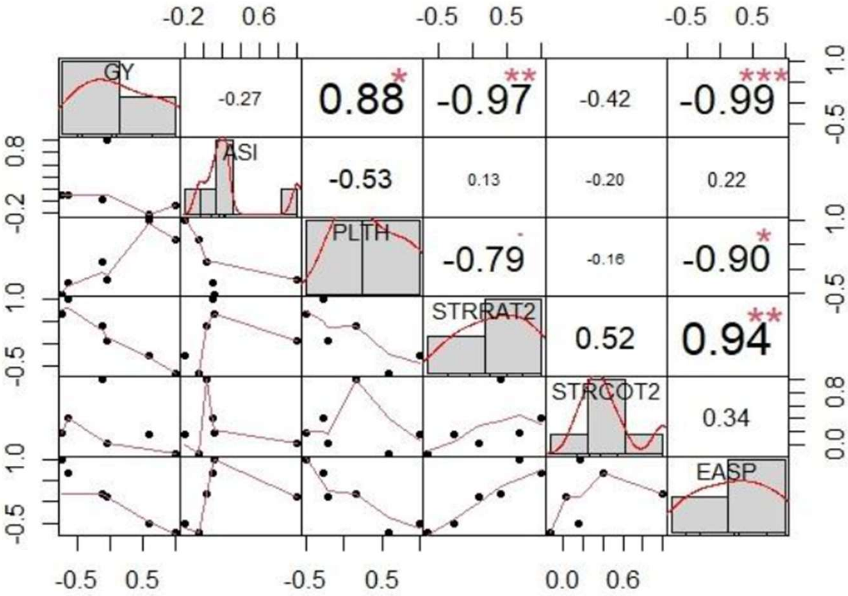
Figure 4. Radar plot showing the strengths and weaknesses of the hybrids selected by MGIDI. Red and green represent the two factors, respectively, and the factor protruding the most from the genotype is indicated as the genotype strength.

Correlations among Traits under *Striga*-Infested and non-Infested Conditions

Figure 5A shows the relationships among traits under *Striga*-infested conditions. GY was strongly positively correlated with plant height (r = 0.88*) but significantly negatively correlated with *Striga* damage rating (r = −0.97**) and ear aspect (r = −0.99**). Plant height was also negatively correlated with ear aspect (r = −0.90*), indicating that taller plants tended to produce ears with better visual quality. Furthermore, the *Striga* damage rating was positively correlated with ear aspect (r = 0.94**), suggesting that higher levels of *Striga* damage were associated with poorer ear quality.

Under *non*-infested conditions (Figure 5B), GY was positively and significantly correlated with plant height (r = 0.93**) but negatively correlated with ear aspect (r = −0.97**) and husk cover (r = −0.90*). These relationships indicate that plant architecture and ear characteristics play important roles in determining GY performance under both stress and non-stress conditions.

(A)



(B)

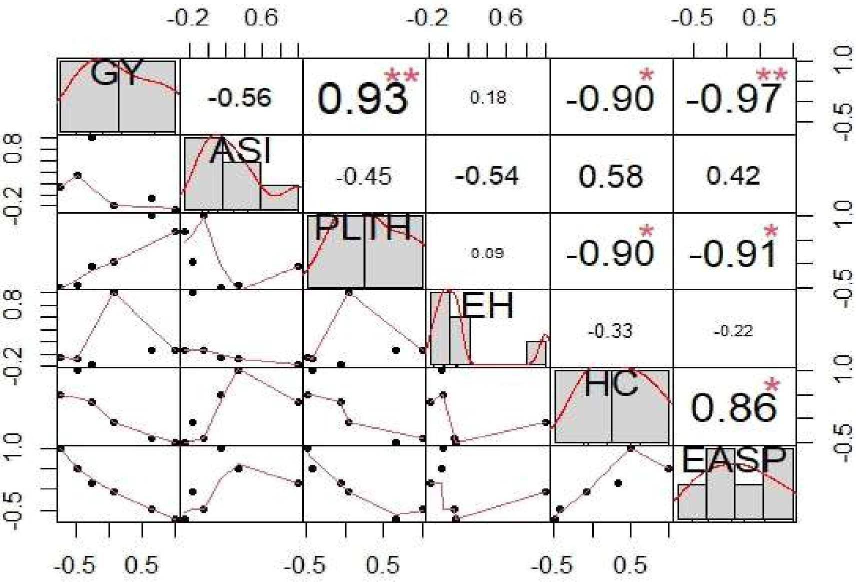


Figure 5. Correlation matrix showing the relationships between grain yield and selected agronomic and *Striga*-related traits. (**A**) *Striga*-infested conditions, (**B**) Non-infested conditions. In both graphs, the upper-right triangle displays Pearson correlation coefficients, with asterisks indicating statistical significance (*p ≤ 0.05, **p ≤ 0.01, ***p ≤ 0.001). The diagonal panels display the traits and their distributions. The lower-left triangle shows scatter plots with fitted trend lines illustrating the traits' pairwise relationships.

DISCUSSION

This study evaluated the genetic basis of GY and *Striga hermonthica* resistance in maize top-cross hybrids in both *Striga*-infested and non-infested environments in Nigeria. The results provide insights into the magnitude of genetic variability, the relative importance of additive and non-additive gene effects, and the performance of parental lines and hybrids under contrasting conditions. Understanding these genetic mechanisms is essential for identifying superior parental lines and developing high-yielding maize hybrids in SSA with improved tolerance to *Striga* infestation.

The significant effects of environment and genotype on GY and most measured traits under both *Striga*-infested and non-infested conditions indicate substantial genetic variability among the evaluated maize hybrids. Such variability is essential for effective selection and genetic improvement in breeding programs. Previous studies evaluating maize genotypes in *Striga*-infested and non-infested environments have reported similar findings [34,35]. The significant genotype × environment interaction observed for GY under *Striga*-infested conditions suggests that environmental factors influenced hybrid performance. This indicates that the relative performance of hybrids may vary across test locations, emphasizing the importance of multi-environment evaluation when identifying stable and high-yielding hybrids. Previous studies have reported comparable observations on maize performance under *Striga* infestation [34,36]. In contrast, the absence of significant genotype × environment interaction for *Striga* damage rating and *Striga* emergence count suggests that these traits were relatively stable across environments and were largely controlled by genetic factors. Akinwale et al. [37] reported similar results, although some other studies [28,38,39] have documented significant environmental effects for these traits.

The significant GCA effects observed for most traits under both experimental conditions indicate that additive gene effects played a major role in controlling GY and related traits. Although both additive and non-additive gene effects contributed to trait inheritance, GCA had a larger contribution than SCA, suggesting that additive gene action was predominant in determining hybrid performance. These findings agree with previous reports indicating that additive gene effects are particularly important for GY and *Striga*-related traits in tropical maize germplasm [40–42]. The significant interaction between environment and GCA for several traits under *Striga*-infested conditions indicates that the parental lines' ability to combine varied across environments. This highlights the importance of evaluating breeding materials across multiple environments to identify stable and broadly adapted parental lines and hybrids. However, the SCA × environment interaction was not significant for most traits except GY under *Striga*-infested conditions. This suggests that non-additive gene effects were relatively stable across environments for most traits. The higher contribution of GCA relative to SCA for GY, *Striga* damage rating, *Striga* count, and other measured traits across environments further supports the predominance of additive gene effects. However, the estimated GCA effects should be interpreted primarily in relation to the specific testers employed rather than as definitive indicators of general combining ability across a broader range of genetic backgrounds because only two testers were used in this study. This observation is consistent with earlier studies that reported additive gene action as the major genetic component controlling yield and stress tolerance traits in tropical maize germplasm [24,43]. However, these results differ from those of other studies that reported a stronger influence of non-additive gene effects in the inheritance of host plant damage caused by *Striga* infestation [34,44–46]. Such differences may arise from variations in genetic backgrounds, environmental conditions, and experimental materials used in different studies.

Understanding combining ability and gene action controlling important agronomic traits is essential for designing effective breeding strategies. Combining ability analysis enables breeders to identify superior parental lines and select appropriate hybrid combinations for crop improvement [47,48]. In this study, several inbred lines exhibited favorable effects of GCA on GY under both *Striga*-infested and non-infested conditions, although not all showed statistically significant effect. Among these inbreds, TZISTR2014 in particular showed positive and significant GCA effects on GY across both conditions, indicating that this line possesses favorable alleles for improving yield performance. Similarly, the TZISTR1872 parental line exhibited desirable negative GCA effects on the *Striga* emergence count. Therefore, this line represents a valuable genetic resource for improving *Striga* resistance and tolerance in maize breeding programs. Previous studies evaluating the combining ability of maize inbred lines under *Striga*-infested conditions reported similar observations [49,50]. Specific combining ability reflects the performance of particular cross combinations and is primarily associated with non-additive genetic effects, such as dominance and epistasis [51]. In this study, several top-cross hybrids exhibited positive SCA effects on GY under *Striga*-infested conditions. Among these hybrids, FAWSYN-1/IITATZI2300 and FAWSYN-1/IITAZI2305 also showed desirable negative SCA effects for *Striga* damage rating and *Striga* count, suggesting their potential suitability for cultivation in *Striga*-prone environments.

Improving maize performance under *Striga* infestation requires the simultaneous consideration of several agronomic and stress-related traits. In *Striga*-prone environments, superior genotypes are expected to combine high GY with reduced *Striga* emergence count, lower damage ratings, and desirable plant architecture that supports productivity under stress. Such a combination of traits represents an ideal plant type or ideotype for maize production in *Striga*-infested environments. Ideotype-based breeding provides a useful framework for selecting genotypes that integrate multiple desirable characteristics associated with yield potential and *S. hermonthica* tolerance. Because these traits are often genetically and physiologically interconnected, multi-trait selection approaches are particularly valuable for identifying hybrids that best approximate the target ideotype. The application of the MGIDI index allowed the simultaneous selection of hybrids with high GY and improved tolerance to *Striga* infestation. The MGIDI approach is increasingly used in plant breeding because it integrates multiple traits into a single selection index, enabling breeders to identify genotypes that approach the desired ideotype [52]. The identification of six superior hybrids using MGIDI analysis demonstrates the usefulness of this method for selecting genotypes with balanced performance across multiple traits. Among the selected hybrids, FAWSYN-1/TZISTR2014 exhibited reduced *Striga* emergence, suggesting the presence of favorable alleles associated with resistance mechanisms that limit parasite establishment. In contrast, FAWSYN-1/IITAZI2305, FAWSYN-1/TZISTR2024, and FAWSYN-2/TZISTR1318 were associated with improved GY, plant height, and reduced *Striga* damage, indicating their potential as promising hybrids for cultivation in *Striga*-infested environments.

Trait correlation analysis further provided useful insights into the relationships between agronomic and *Striga*-related traits. The strong negative correlations observed between GY and *Striga* damage rating indicate that higher levels of *Striga* infestation increased yield losses. In particular, GY showed a strong positive correlation with plant height and a strong negative correlation with *Striga* damage rating and ear aspect, indicating that plant vigor and reduced *Striga* damage were important contributors to improved yield performance under *Striga*-infested conditions. Previous studies evaluating maize performance under *Striga* stress have reported similar relationships [8,45,49,53]. These findings confirm that *Striga* damage rating is an important indicator trait that can be used in the selection of maize genotypes with improved tolerance to *Striga* infestation. GY was also positively correlated with plant height under both *Striga*-infested and non-infested conditions, suggesting that plant vigor may contribute to improved productivity under stress environments. Similar positive relationships between plant height and GY have been reported in maize breeding studies [49,54].

CONCLUSIONS

This study revealed substantial genetic variability among the evaluated maize top-cross hybrids in both *Striga*-infested and non-infested environments. The predominance of effects of general combining ability (GCA) effects for most traits suggested that additive gene action contributed significantly to the inheritance of GY and *Striga*-related traits. Although only TZISTR2014 was statistically significant for GY among the lines, it represents a potentially useful genetic resource for hybrid development. However, these combining ability estimates should be interpreted primarily in relation to the specific testers used because the evaluation involved only two testers and may require validation across a broader set of testers before general conclusions about combining ability can be made. Similarly, TZISTR1872 displayed negative and significant GCA estimates for the *Striga* count, suggesting its potential usefulness as a source of resistance or tolerance, although further validation is required. Trait correlation analysis further indicated that GY was positively associated with plant height and negatively associated with *Striga* damage rating, highlighting the importance of plant vigor and reduced parasite damage for improving maize productivity under *Striga*-infested conditions. The MGIDI-based multi-trait selection identified four promising top-cross hybrids—FAWSYN-1/TZISTR2014, FAWSYN-1/TZISTR2024, FAWSYN-2/TZISTR1318, and FAWSYN-1/IITAZI2305—that combined high GY with improved *Striga* infestation tolerance. These hybrids represent promising candidates for further evaluation and deployment in *Striga*-prone environments. Furthermore, they can serve as valuable source populations for extracting new inbred lines and developing improved maize hybrids in SSA with enhanced productivity and *Striga* resistance.

SUPPLEMENTARY MATERIALS

The following supplementary materials are available online, Table S1: Mean grain yield and other agronomic parameters of 40 hybrids comprising 32 topcrosses and 8 commercial checks evaluated under *Striga*-infested conditions across four environments in Nigeria; Table S2: Mean grain yield and other agronomic parameters of 40 hybrids comprising 32 topcrosses and 8 commercial checks evaluated under non-infested conditions across four environments in Nigeria.

DATA AVAILABILITY

The raw data from this study are available upon request from the corresponding author.

AUTHOR CONTRIBUTIONS

Conceptualization, YK, WM, SM, AA, and AM; methodology, YK, WM, SM, and AM; validation, YK, WM, SM, AA, and AM; formal analysis, YK, ISA; investigation, YK; data curation, YK; writing—original draft preparation, YK; writing—review and editing, YK, WM, SM, AA, ISA, AM and JD; supervision, AA and WM.

CONFLICTS OF INTEREST

The authors declare that they have no conflicts of interest.

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