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Genetic Analysis of Agronomic and Fall Armyworm-Resistance Traits in Maize Hybrids with Varying Levels of Resistance to Stem Borers

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Abstract: Stem borer (SB) and more recently, fall armyworm (FAW) are serious economic pests in maize production in sub-Saharan Africa. It is hypothesized that SB-resistant germplasm may confer resistance against FAW. However, the performance of SB-resistant lines in hybrid combinations and the inheritance of FAW-resistant traits under variable FAW infestations have not been reported. This study was conducted to (i) obtain information on the inheritance of agronomic and FAW-resistant traits under variable FAW infestations; (ii) identify hybrids combining high grain yield (GYLD) and stability under FAW infestations; and (iii) determine the effects of FAW damage on GYLD. Three SB-resistant lines (1393, CKSBL10060 and CML 331) as testers and six open-pollinated varieties (OPVs) as lines were crossed in a line tester scheme to generate eighteen test crosses. The test crosses together with two tester × tester crosses and two checks were evaluated under artificial FAW infestation (AI), natural infestation (NI) and pesticide-protected condition (PC) in Nigeria. Additive and non-additive effects were significant for GYLD, most agronomic and FAW-resistant traits under AI and NI, except ear damage (EDAM) scores under NI, whereas only the non-additive effect was significant for GYLD under PC. Two testers (1393 and CKSBL10060) combined significant and positive GCA effects for GYLD with desirable GCA effects for FAW-resistant traits under AI and NI, whereas CML 331 combined significant and negative GCA effects of GYLD with undesirable GCA effects of FAW resistance under the test conditions. Three OPVs (AWR SYN-W2, AMATZBR-WC4 and TZB-SR) had a significantly positive GCA effect for GYLD and a desirable GCA effect for either leaf damage (LDAM) or EDAM score under AI. The FAW LDAM and EDAM significantly reduced GYLD under AI but not under NI. Three test crosses (AMATZBR-WC4 x CKSBL10060, TZB-SR x CKSBL10060 and TZBR Comp 1-WC2 × 1393) combined high yield with stability and FAW tolerance across the test conditions and thus were recommended for further testing.

Keywords: additive and non-additive effects; fall armyworm; line; tester; test crosses

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1. Introduction

Maize (*Zea mays* L.) is used for food, feed, and as a raw material in industries [1]. In sub-Saharan Africa (SSA), more than 300 million people consume a significant amount of maize, thus implying a continuous increase in maize demand [2]. In contrast to the worldwide average yield (4.9 t ha^{-1}), the average grain yield of maize in SSA is quite low (1.5 t ha^{-1}). Numerous factors, such as the use of low-yielding cultivars, ineffective agronomic practices, and the effects of droughts, diseases and insect pests, contribute to low maize yields in SSA [2,3].

Stem borers [4,5], and more recently, fall armyworms [6] are the two most important insect pests of maize in SSA [7]. Fall armyworm (FAW) larvae feed on maize leaves, stems, ears and kernels [8]. Damaged stems are more prone to lodging and rot infections, while perforated ears can easily be colonized by mycotoxin-producing fungi [9,10]. If FAW infestations are not controlled, they can result in yield reductions of up to 60% [11], with complete crop loss reported in some cases [12,13]. According to [14], it is estimated that annually, FAW would increase the cost of agricultural production in Africa by USD 9.4 billion.

Genetically modified (GM) crops and insecticides have routinely been used to control FAW [15]. Insecticides increase the cost of maize production [16], are hazardous to non-target organisms [17], pollute the environment [18,19] and pose health risks to animals and humans [13,20]. The cultivation of GM crops, on the other hand, is still a developing alternative in SSA [21]. The high cost of GM seeds, regulatory requirements, the need for technical competence to create and distribute transgenic technologies, and the requirement for transgenic product monitoring are major barriers to the adoption of GM crops [22]. Despite the heavy reliance on these two control methods for FAW management, several cases of resistance development have reduced their efficacy [15,23,24].

Breeding for host plant resistance using conventional breeding approaches is an effective and environmentally friendly means of managing stem borers [25] and fall armyworms [26] in maize and provides inherent control at the same cost as the seed. Empirical studies have demonstrated that stem borer-resistant germplasm may confer resistance against FAW and that simultaneous improvement for resistance to both pests is feasible [27–31] reported strong correlations in resistance indices for FAW and southwestern corn borer (SWCB) and mapping studies by various researchers [32,33] identified similar heritable components conferring resistance to both pests.

Since the outbreak of FAW in SSA, researchers in the International Maize and Wheat Improvement Center (CIMMYT) and the International Institute of Tropical Agriculture (IITA) and partners have screened various maize germplasm sources under natural and artificial FAW infestation pressure in free and no-choice experiments [13,34]. Artificial infestation is expensive and requires a high level of expertise to successfully rear larvae. Therefore, with limited funding, researchers have relied on the natural pressure of infestation at FAW hotspots. However, the effectiveness of this cost-saving strategy in comparison to the artificial infestation method has not been examined. Using either or both infestation methods, moderately resistant FAW maize genotypes, mostly from stem borer-resistant backgrounds, were identified and are currently being used for the development of maize germplasm (hybrids and improved open-pollinated varieties) with tolerance to FAW in SSA [34,35].

Studies have shown that resistance to FAW is quantitatively inherited [33,36] and influenced by the environment [36,37], but information on the inheritance of FAW resistance and its stability across environments is limited [38]. A few studies on the performance of fall armyworm-tolerant genotypes in hybrid combinations and the gene action for FAW resistance under variable infestation conditions were reported. Previous studies conducted in temperate environments by various researchers found that additive gene effects were of higher significance than non-additive gene effects in conditioning FAW resistance in maize [9,39,40]. Contrary to these findings, [41] found that non-additive genetic effects were more important than additive genetic effects for the inheritance of grain yield and FAW resistance in a study in Southern Africa. Presently, information on the gene action governing the inheritance of traits in maize under FAW-stressed conditions in WCA is unknown. In order to offer baseline knowledge to guide future breeding decisions, a detailed genetic investigation is required. For yield, agronomic traits, and insect resistance in maize, the line x tester design was extensively used to estimate genetic variance components and deduce combining ability effects [41–44]. Therefore, a line-by-tester analysis of agronomic performance and FAW resistance would be appropriate to provide useful information on the gene action of these traits, as well as the heterotic responses among FAW-tolerant germplasm resources in WCA.

Breeding for durable resistance to FAW will necessitate the use of genetically diverse maize germplasm to produce well-buffered genotypes with horizontal resistance to cope with pest evolution pressure due to climate change [45]. When selecting pest-resistant varieties, it is noteworthy to consider germplasm with improved agronomic and stable grain yield performance. High-yielding and stable hybrids were created by crossing genotypes from various institutions [46,47]. For example, planned crosses involving IITA and CIMMYT inbreds were successfully exploited in the production of high-yielding [48] and stress-tolerant [49–51] maize varieties. On the basis of this assumption, it is sensible to postulate that combining different stem borer-resistant and FAW-tolerant genotypes should produce high-yielding FAW-tolerant hybrids with a variety of adaptable traits suitable for cultivation in WCA.

This study was undertaken to (i) obtain information on the inheritance of agronomic and FAW-resistant traits under variable infestations; (ii) identify hybrids combining high grain yield and stability across FAW-infested environments; and (iii) determine the effects of FAW damage on grain yield under two infestation conditions.

2. Materials and Methods

2.1. Germplasm

Nine parental genotypes, including six open-pollinated varieties (OPVs) and an inbred line from IITA, and two inbreds from CIMMYT, with varying levels of resistance to stem borers and FAW, were used in this study. The pedigree, source population and stress reactions of the genotypes are presented in Table 1. The OPVs, designated as line, and the inbreds, designated as testers, were crossed in a Line × Tester mating design to generate 18 top-cross hybrids and two single-cross hybrids obtained from crossings among the testers. The 20 experimental hybrids were evaluated alongside two checks, namely a population cross hybrid (PCH) between two heterotic IITA borer-resistant populations (TZBR Comp. 1-WC2 × TZBR Comp. 2-WC2) and a three-way cross commercial check hybrid (SAMMAZ 22) popularly grown in Nigeria. All genotypes studied were white-kernelled.

Table 1. Source populations and stress adaptation(s) for the maize genotypes used for the study.

Genotype	Source Population/Pedigree	Origin	Reaction to Stem Borers	Reaction to Fall Armyworm
Lines				
TZBR Comp 1-WC2	TZBR Comp 1	IITA	Resistant [4,52]	Tolerant [13]
TZBR Comp 2-WC2	TZBR Comp 2	IITA	Resistant [4,52]	Tolerant [13]
TZBR Eld.4-WC2	TZBR Eld. 4	IITA	Resistant [4,52]	Tolerant [13]
AMATZBR-WC4	AMATZBR	IITA	Resistant [4,52]	Tolerant [13]
AWR-SYN-W2	AWR-SYN-W	IITA	Resistant (Ajala et al. unpublished)	Tolerant [35]
TZB-SR	TZB	IITA	Unknown	Unknown
Testers				
CKSBL10060	CML311/MBR C3 Bc F3-1-1-1-B-B-B-B-B	CIMMYT	Resistant [53]	Tolerant [34]
CML 331	(SUWAN8422)/(P47/MP78-518)-#-183-1-2-1-2-2-B Subtropical Recy. W	CIMMYT	Resistant [54]	Tolerant [54]
1393	Guana Caste 7729 x TZSR	IITA	Resistant [55]	Tolerant (Ajala et al. unpublished)
Checks				
TZBR Comp 1-WC2/TZBR Comp 2-WC2		IITA	Resistant	Tolerant (Ajala et al. unpublished)
Sammaz 22	M0826-1	IITA	Unknown	Unknown

2.2. Location of Experimental Sites

The study was conducted at six sites in Nigeria, namely: Ibadan, Benin, Mokwa, Lafia, Dutsin Ma and Zaria. A description of the test locations is shown in Table S1.

2.3. Field Layout and Experimental Design Used for the Study

A randomized complete block design with three replicates was used at all locations. Plots consisted of single rows, each 3 m long with 0.75 m spacing between rows and 0.25 m within rows. Two seeds were sown per hill and seedlings later thinned to one per hill three weeks after planting (WAP) to give a plant population density of 53,333 plants/ha^{-1}.

2.4. Evaluation under Naturally Infested and Protected Conditions

The hybrids were evaluated under natural fall armyworm infestation and protected conditions at Benin, Mokwa, Lafia, Dutsin Ma and Zaria. In order to guarantee FAW infestation from natural populations, the experiment was situated near farmers' fields with older maize plants that were at least four weeks old and had visible symptoms of FAW leaf damage. In each location, 2 sets tagged protected and unprotected were sown in two blocks, 20 m apart. Between the blocks was a strip of densely populated maize cultivars of similar maturity to prevent insecticide drift from the protected trial. For the protected plots, a spray of emamectin benzoate (4′′-Deoxy-4′′-epi-methylamino-avermectin B1) (Ema 19.2 EC) was applied weekly from the 2nd to the 7th week after planting (WAP) to ensure the plots were FAW-stress-free. The strip sown with the densely cultivated cultivar was not protected with insecticides to serve as a refuge for FAW moth and larvae populations. Except for the insecticide applications, all management practices for both the naturally infested and protected plots were the same. Basal fertilizer application was carried out at 2 WAP using NPK 15:15:15 compound fertilizer at the rate of 45 Kg each of N, P and K ha^{-1}, while top-dressing was performed at 6 WAP using urea (46% N) fertilizer at the rate of 45 Kg Nha^{-1}, bringing the total amount of nitrogen applied to 90 Kg Nha^{-1}.

Weeds were controlled by a pre-planting application of glyphosate (*N*-phosphonomethyl glycine) two weeks before planting. A mixture of metolachlor (2-methoxy-1-methylethyl amino oxo-acetic acid) plus atrazine (6-Chloro-N-ethyl-N′-(1-methylethyl)-1, 3,5-triazine-2,4-diamine) and paraquat (1,1′-Dimethyl-4,4′-bipyridinium dichloride) was applied at planting at the rate of 1.6 and 1.0 Kg active ingredient (a.i) ha^{-1}. For the suppression of post-emergence weeds, Nicosulfuron (2-[(4,6-dimethoxypyrimidin-2-yl) carbamoylsulfamoyl]-N, N-dimethylpyridine-3-carboxamide) was sprayed at 4 WAP at a rate of 160 g a.i. ha^{-1}.

2.5. Evaluation under Fall Armyworm Artificially Infested and Protected Conditions

In a separate experiment, the genetic materials were evaluated under FAW artificially infested and protected conditions in the major (early) and minor (late) growing seasons at Ibadan in 2021. In each season, 2 sets were sown and separated following similar protocols with the naturally infested and protected trials. Plants were thinned to one plant per hill at 3 WAP, just before infestation. Each plant in the unprotected trial was infested with ten second instar FAW larvae, 3 WAP. The protected trial served as control. Except for the insecticide applications, all management practices for both the artificially infested and protected plots were the same. Fertilizer application rate and weed control management were similar to the naturally infested and protected trials.

2.6. Data Collection

Data were recorded on agronomic traits in the FAW-infested and FAW-protected trials. The data included days to 50% anthesis (DA), days to 50% silking (DS), plant height (PHT), plant aspect (PASP), ear aspect (EASP). Anthesis-silking interval (ASI) was computed as the difference between days to 50% anthesis and days to 50% silking. Plant aspect was scored on a scale of 1 to 9 based on overall plant appeal, uniformity of plants, disease and pest damage and lodging, with 1 = excellent plant type and 9 = poor plant type. At harvest, ear aspect was rated on a scale of 1–9, with 1 representing clean and well-filled ears, while 9 represented ears with scanty and rotten or damaged kernels. Grain moisture content was determined using a Dickey–John moisture meter, Mini GAC®2500, United States. Grain yield (kg/ha) adjusted to 15% moisture content, was calculated using the formula of [56]:

Grain yield ($Kgha^{-1}$) = Field weight (Kg)/area (m^2) × (100-moisture)/85 × (10,000 × 0.80)

2.7. Fall Armyworm Damage Rating

Visual ratings of FAW damage were carried out on leaves and ears in the FAW-infested trials. Leaf and ear damage ratings were carried out on plot basis of 13 plants per plot. Leaf damage scores were recorded at 2 and 5 WAP on a scale of 1–9, where 1 = no visible damage to the leaves and 9 = 80–100% defoliation of the entire leaf area [27,30]. A genotype with a score of 1 to 2 was considered as resistant, 3 to 5 as tolerant and scores greater than 5 as susceptible [57]. Ear damage was rated at harvest as the extent of damage, i.e., rotten percentage and portions with damaged kernels and frass, by determining the percent area of the ear affected following FAW attack of the ear. The damaged percentage was evaluated by determining the percentage of each cob covered by symptoms using a class rating scale of 1 to 9, in which 1 = 0%, 2 = 1–20%, 3 = 21–30%, 4 = 31–40%, 5 = 41–50%, 6 = 51–60%, 7 = 61–70%, 8 = 71–80%, 9 = 81–100% of the kernels exhibiting visible symptoms of rotten grain [30,57].

2.8. Data Analysis

Each location–treatment combination was considered an environment and analyses of variance (ANOVA) were performed on plot means basis of all genotypes using Proc GLM procedure in SAS 9.3 [58]. Significantly different means were separated using LSD at $p \leq 0.05$. The genotype × environment (G × E) interaction effects for grain yield under natural fall armyworm infestation and protected environments, respectively, was pooled to investigate the yield stability of the genotypes across each test condition using GGE biplot in GEA-R (Version 4.1). The GGE biplots were based on environment-metric preserving, 2-tester-centered, with no scaling [59].

The checks and tester × tester crosses were excluded from the entries and a line × tester analysis was performed for each infestation condition using SAS 9.3 following a linear model:

$$Y_{ijk} = \mu + r(e_k) + e_k + l_i + t_j + (l \times t)_{ij} + (l \times e)_{ik} + [(t \times e)_{jk} + (l \times t \times e)]_{eijk} + \in_{ijk}$$

Y_{ijk} is the measured trait of the genotype of i^{th} line crossed to j^{th} tester evaluated in r replications across k environments; μ is the grand mean; r (*ek*) is the effect of replication nested within the k environments; l and t represent average effects of lines and of testers, respectively, which is equivalent to GCA effects of lines and testers, respectively; l × t = line × tester interaction effects that are equivalent to the SCA effects of the crosses [47]; e is the environmental main effects; $l \times e$, $t \times e$ and $l \times t \times e$ are the interactions of the lines, testers and the lines × testers with the environments; and e_{ijk} is the random experimental error. The hybrid component of variation was divided into variations attributable to Lines (females), Testers (males) and Line × Tester interaction.

The proportional contribution of general combining ability (GCA) and specific combining ability (SCA) to the sum of squares was estimated. The GCA testers and GCA line effects for each trait were computed from the adjusted means according to Singh and Chaudhary, (1985). Standard errors (SE) for testing significance of GCA_t and GCA_l estimates for each trait were computed from the mean squares of GCA_t × environment and GCA_l × environment. T-tests were used to test the significance of each GCA effect, with t = GCA/SE_{GCA}.

The variance components and heritability estimates for each trait were calculated based on Restricted Maximum Likelihood Method (REML). The linear regressions of leaf and ear damage scores on grain yield were carried out in R version 4.1.3 [60]. Scatterplots were generated in R using the ggplot functions.

3. Results

3.1. Variation among Maize Genotypes for Grain Yield, Agronomic and FAW-Tolerant Traits

In the analysis of variance, the evaluation conditions differed significantly (Table S2). Under the various treatments, the genotypic effect of maize hybrids was significant for grain yield and most agronomic traits (Table 2). Genotypic effect differed for leaf damage (LDAM) and ear damage (EDAM) scores under artificial infestation (AI) but was only significant for LDAM scores under natural infestation (NI) (Table 2). Under the NI and protected condition (PC), the environment effect was significant for all the traits measured, whereas, under AI, the two growing seasons were not significantly different for all the traits (Table 2). The general combining ability (GCA) effect of the testers was significant for grain yield and most agronomic traits under the artificial and natural infestation conditions but not under the protected condition (PC). Additionally, the tester GCA effect differed for LDAM and EDAM scores under AI. The GCA effect of the lines was significant for grain yield under AI whereas the specific combining ability (SCA) effect of line × tester for grain yield was significant under all three test conditions (Table 2).

3.2. Agronomic Performance and Stability of Maize Genotypes under the Various Test Conditions

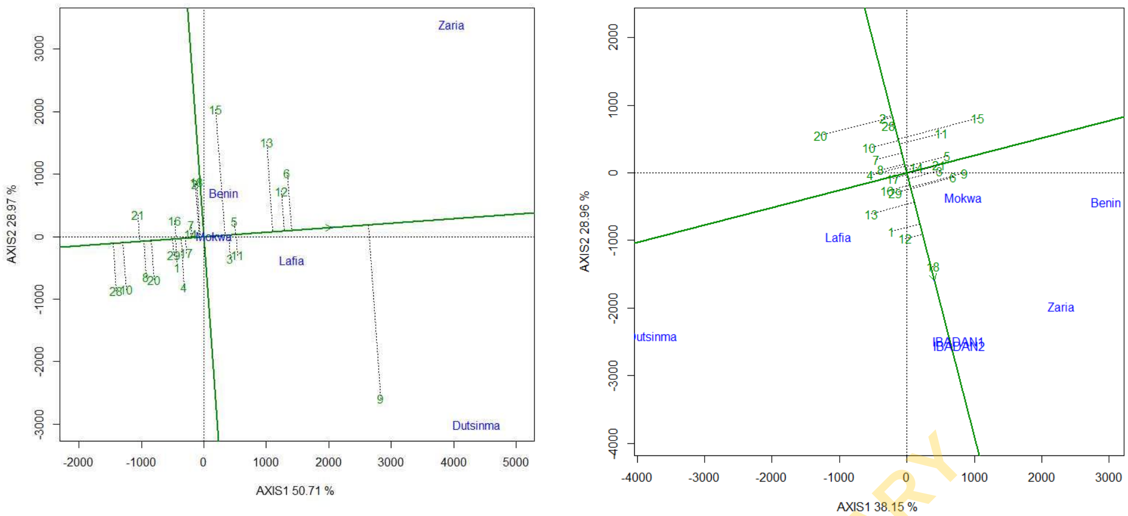
The per se performance of the genotypes differed under the various infestation conditions (Table S3). Under AI, AWR SYN-W2 × 1393 had grain yield markedly more than the grain yields of the check varieties, while TZBR Comp 1-WC2 × 1393, AMATZBR-WC4 × 1393, TZB-SR × 1393 and AMATZBR-WC4 × CKSBL10060 had a grain yield more than the better performing check (Table S3). Three test crosses (AMATZBR-WC4 × CKSBL10060, TZB-SR × CKSBL10060 and TZBR Comp 1-WC2 × 1393) were consistent in agronomic performance under NI as they were under AI and had grain yield significantly more than the FAW-tolerant and commercial hybrid checks (Figure 1a, Table S4). These outstanding test crosses also had desirable lower ear damage scores than both checks under the two FAW infestation conditions. Meanwhile, the grain yields of the tester × tester crosses (1393 × CML331 and 1393 × CKSBL10060) were lower than the yields of most of the test crosses and the better check under AI and NI. However, under the protected condition, almost all the genotypes had competitive grain yields with the better check but TZBR Comp 2-WC2 × CKSBL10060 had a markedly higher yield among the entries. Grain yield was generally higher under PC than under AI and NI (Tables S3–S5).

The projections onto the ordinate and the direction of the abscissa of the average environment coordinate (AEC) of the GGE biplots (Figure 1a,b) measures stability and yield performance, respectively. AMATZBR-WC4 × CML 331, TZB-SR × CML 331, TZB-SR × CKSBL10060, AWR SYN-W2 × CKSBL10060, and TZBR Comp 1-WC2 × 1393 combined high-yield with stability under natural infestation. Under the protected condition, TZBR Comp 2-WC2 × CKSBL10060, TZB-SR × CKSBL10060, AWR SYN-W2 × 1393, AWR SYN-W2 × CKSBL10060, TZBR Comp 1-WC2 × 1393, AMATZBR-WC4 × CKSBL10060 and the check (TZBR Comp 1-WC2 × TZBR Comp 2-WC2) all combined high-yield with stability. Two test crosses (TZB-SR × CKSBL10060 and AWR SYN-W2 × CKSBL10060) consistently combined high yield with stability under NI and PC, whereas, the tester × tester crosses (1393 × CML331 and 1393 × CKSBL10060) consistently ranked low in yield and stability under NI and PC (Figure 1a,b).

Table 2. Mean squares from the ANOVA for agronomic and fall armyworm resistance traits of maize test crosses evaluated under infested and protected environments.

Source	DF	Grain Yield	Days to Anthesis	Days to Silking	Anthesis-Silking Interval	Plant Height	Plant Aspect	Husk Cover	Ear Aspect	Leaf Damage	Ear Damage
Artificial infestation											
ENVIRONMENT (ENV)	1	74,932.03	0.20	0.00	0.15	65.66	0.01	0.03	0.00	0.59	0.00
REP (ENV)	4	1,299,077 **	22.35 ***	10.59 ***	2.79 *	1375.82 ***	1.45 **	0.27	0.03	27.41 ***	1.20 *
GENOTYPE	17	2,328,014.04 ***	14.81 ***	18.12 ***	3.06 ***	1526.50 ***	0.52 *	0.90 ***	1.45 ***	3.11 ***	4.17 ***
TESTER (GCA)	2	11,730,910 ***	75.28 **	97.98 **	10.80 **	9763.77 ***	0.88	0.27	6.67 **	20.01 **	11.68 **
LINE (GCA)	5	1,778,583 ***	7.82 ***	8.91 ***	3.31 ***	493.52 ***	0.64 ***	1.00 ***	0.71 ***	1.01 **	3.35 ***
LINE × TESTER (SCA)	10	722,150.70 ***	6.20 ***	6.75 ***	1.39 ***	395.54 ***	0.38 ***	0.97 ***	0.78 ***	0.78 ***	3.08 ***
ENV× GENOTYPE	17	15,589.37	0.08	0.11	0.08	6.48	0.03	0.03	0.02	0.08	0.03
ENV × TESTER	2	15,236.34	0.02	0.15	0.06	4.18	0.08	0.04	0.01	0.16	0.01
ENV × LINE	5	9402.01	0.11	0.06	0.07	11.81	0.02	0.01	0.01	0.06	0.01
ENV × LINE × TESTER	10	18,753.65	0.08	0.13	0.10	4.27	0.02	0.03	0.02	0.07	0.04
ERROR	68	276,698.50	0.97	1.39	0.86	69.15	0.28	0.31	0.28	0.74	0.39
Natural infestation											
ENV	4	58,893,022.60 ***	70.95 ***	42.06 ***	12.34 ***	9623.22 ***	15.15 ***	1.00 *	18.10 ***	14.82 ***	10.92 ***
REP (ENV)	10	3,282,784.70 **	4.90	6.86	0.78	423.64	3.10 ***	1.30 ***	2.35 ***	1.64	1.91 *
GENOTYPE	17	2,927,356.80 *	50.55 ***	50.11 ***	0.61	910.52 *	1.06	1.88 **	0.96	2.50 **	1.27
TESTER (GCA)	2	8,120,494.40 **	289.95 **	280.39 **	1.50	2251.46 *	3.09 *	6.73 **	1.34	0.19	0.38
LINE (GCA)	5	872,709.90	17.57 **	23.48 **	0.96	941.40 *	0.68	1.24 **	1.41 *	0.93	1.36
LINE × TESTER (SCA)	10	2,835,253.60 *	14.48 *	13.93 *	0.25	492.57	0.77	1.43 ***	0.50	4.00 ***	1.43
ENV × GENOTYPE	62	2,006,522.40 *	7.91 ***	9.08 ***	1.31 **	501.55	0.75	0.77 ***	0.68	1.04	1.88 ***
ENV × LINE	20	1,838,760.20	4.06	5.47	1.64 **	556.42	0.78	0.87 **	0.40	1.24	1.17
ENV × TESTER	8	3,464,363.60 **	22.01 ***	24.55 ***	1.10	420.52	0.39	0.55	1.84 **	1.24	0.97
ENV × LINE × TESTER	34	1,788,890.30	6.51 **	7.46 **	1.06	486.10	0.82	0.73 **	0.55	0.87	2.50 ***
ERROR	158	1,299,887.10	3.35	3.77	0.79	399.33	0.77	0.36	0.55	0.90	0.98
Protected condition.											
ENV	6	19,891,295.00 ***	158.63 ***	184.84 ***	9.62 ***	4361.45 ***	10.65 ***	34.81 ***	23.68 ***		
REP (ENV)	14	1,622,444.90	5.80	6.28	1.99	921.48 ***	1.25 ***	1.23 ***	0.99 **		
GENOTYPE	17	3,460,751.80 *	52.93 ***	59.86 ***	2.26	1212.89 ***	1.78 **	1.65 ***	1.81 ***		
TESTER (GCA)	2	7,268,464.30	307.88 **	359.98 ***	2.39	6039.88 **	0.99	3.57	1.27		
LINE (GCA)	5	237,9961.20	46.83 **	45.90 *	2.42	586.19 *	1.58	2.83 *	1.18		
LINE ×TESTER (SCA)	10	3,239,604.50 *	5.00	6.82	2.15	560.83	2.03 **	0.68	2.23 **		
ENV × GENOTYPE	102	1,719,106.20 **	9.18 ***	10.31 ***	1.92	336.36 **	0.81 ***	0.72 ***	0.94 *		
ENV × TESTER	12	4,333,152.60 ***	27.22 ***	26.93 ***	2.99 **	712.55 ***	0.96 **	1.07 ***	1.31 ***		
ENV × LINE	30	1,398,100.40	10.09 ***	9.92 ***	1.85 *	231.16	1.08 ***	0.94 ***	0.99 ***		
ENV × LINE × TESTER	60	1,356,799.80 *	5.11	7.17 **	1.74 *	313.73	0.64 ***	0.54	0.84 ***		
ERROR	238	984,151.60	4.29	4.19	1.22	229.44	0.34	0.42	0.41		

*, **, ***: $p \leq 0.05$, 0.01, and 0.001; GCA: General combining ability; SCA: Specific combining ability.



(a) (b)

ENTRY	GENOTYPE
1	AWR SYN-W2 × 1393
2	AWR SYN-W2 × CML 331
3	AWR SYN-W2 × CKSBL10060
4	AMATZBR-WC4 × 1393
5	AMATZBR-WC4 × CML 331
6	AMATZBR-WC4 × CKSBL10060
7	TZBR Eld 4-WC2 × 1393
8	TZBR Eld 4-WC2 × CML 331
9	TZBR Eld 4-WC2 × CKSBL10060
10	TZB-SR × 1393
11	TZB-SR × CML 331
12	TZB-SR × CKSBL10060
13	TZBR Comp 1-WC2 × 1393
14	TZBR Comp 1-WC2 × CML 331
15	TZBR Comp 1-WC2 × CKSBL10060
16	TZBR Comp 2-WC2 × 1393
17	TZBR Comp 2-WC2 × CML 331
18	TZBR Comp 2-WC2 × CKSBL10060
20	1393 × CML 331
21	1393 × CKSBL10060
28	SAMMAZ 22
29	TZBR Comp 1-WC2 × TZBR Comp 2-WC2

(c)

Figure 1. Genotype and genotype × environment (GGE) biplots (mean and stability view) for grain yield of maize hybrids evaluated under (**a**) natural fall armyworm infestation and (**b**) pesticide protected environment. (**c**) Information of genotype.

3.3. Genetic Component Estimates for Grain Yield, Agronomic and FAW-Tolerant Traits

The analysis of the relative contribution to the expression of each trait in the test crosses revealed that the testers contributed a higher proportion (60%) to grain yield under artificial infestation, while the lines and line × tester interactions contributed 22% and 18%, respectively (Figure 2). Meanwhile, under natural infestation and protected conditions, line × tester interactions contributed more to the expression of grain yield. The testers also contributed a higher proportion to the expression of flowering traits in the three test conditions. Leaf damage score was also predominantly determined by the contribution of testers under artificial infestation, whereas line × tester determined the trait expression under natural infestation and the same was seen for the ear damage score (Figure 2).

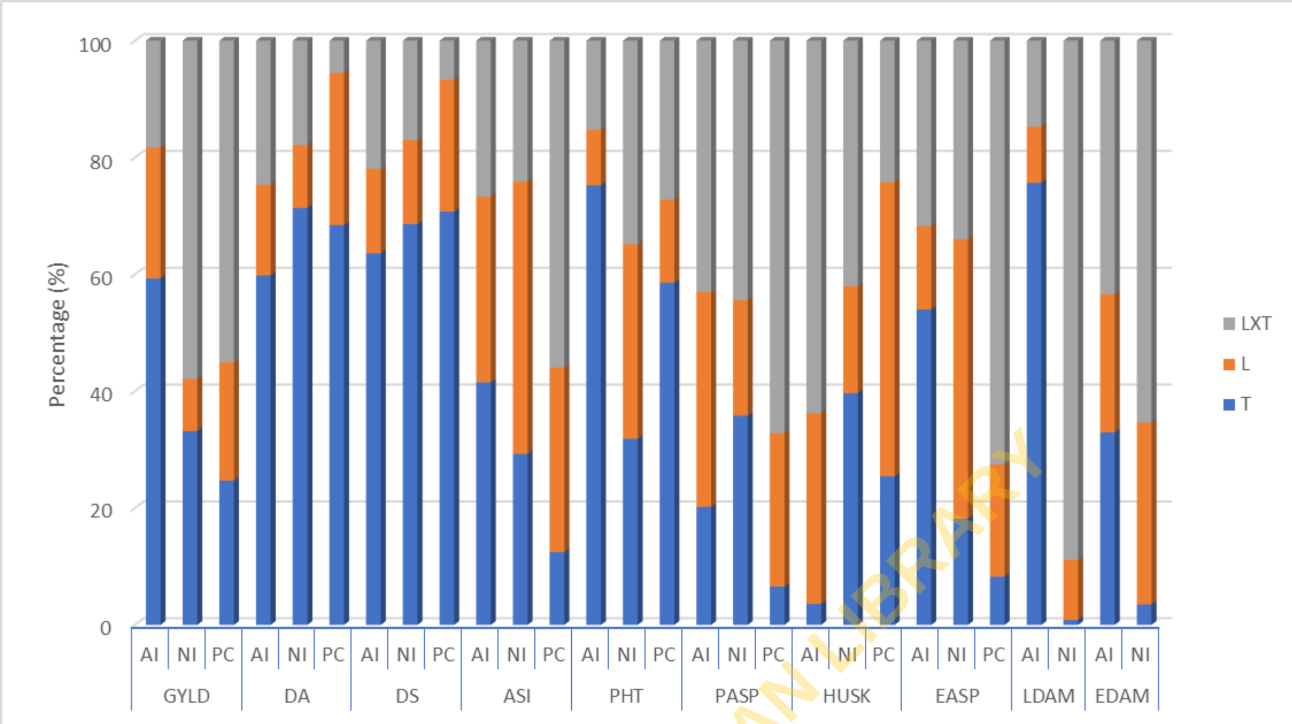


Figure 2. Percentage contributions of testers (T), lines (L) and line x tester (L × T) to the expression of agronomic and fall armyworm-resistance traits of maize hybrids evaluated under infested and protected conditions.

The magnitude of the genetic components for each trait was influenced by the test conditions (Table 3). Under the three test conditions, additive genetic variance ($\sigma^2{}_A$) was greater than dominance genetic variance ($\sigma^2{}_D$) for grain yield and the majority of agronomic variables. However, the dominant genetic component was of a higher magnitude than the additive component for plant and ear aspect scores under PC, and leaf damage tolerance under NI. Furthermore, broad- and narrow-sense heritability estimates ranged from moderate to high for most traits in all test conditions, except ear damage score under NI where no estimates for genetic components were obtained (Table 3).

Table 3. Genetic components and heritability estimates for agronomic and fall armyworm (FAW)-resistant traits of maize testcross hybrids evaluated under FAW infestations and pesticide-protected conditions in Nigeria.

Genetic Component	**Grain Yield AI NI PC**			**Days to Anthesis AI NI PC**			**Days to Silking AI NI PC**			**Plant Height AI NI PC**			**Plant Aspect AI NI PC**		
$\sigma^2{}_A$	1,402,358.28	289,854.87	331,741.45	9.34	12.30	8.33	11.33	11.84	9.44	979.92	119.05	166.96	0.19	0.07	0.18
$\sigma^2{}_D$	331,782.88	148,443.07	301,695.12	3.60	3.39	0.00	3.75	2.41	0.00	225.95	0.00	52.31	0.10	0.00	0.20
H^2	0.98	0.77	0.88	0.99	0.97	0.95	0.99	0.96	0.95	0.99	0.78	0.93	0.88	0.58	0.91
h^2	0.98	0.51	0.46	0.71	0.76	0.95	0.71	0.80	0.95	0.81	0.78	0.71	0.58	0.58	0.43
	Husk cover AI NI PC_			Ear aspect AI NI PC_			Leaf damage AI NI			Ear damage AI NI_					
$\sigma^2{}_A$	0.43	0.32	0.18	0.82	0.08	0.17	1.67	0.42		2.57	0.00				
$\sigma^2{}_D$	0.40	0.17	0.03	0.35	0.00	0.18	0.12	0.46		1.84	0.00				
H^2	0.95	0.90	0.86	0.97	0.66	0.89	0.95	0.93		0.99	0.00				
h^2	0.49	0.59	0.75	0.68	0.64	0.43	0.88	0.44		0.58	0.00				

$\sigma^2{}_A$: Additive variance; $\sigma^2{}_D$: Dominance variance; H^2: Broad-sense heritability; h^2: Narrow-sense heritability; AI: Artificial infestation; NI: Natural infestation; PC: Protected conditions.

3.4. GCA and SCA Estimates for Agronomic and FAW-Resistant Traits

Two of the resistant stem borer lines used as testers (1393 and CKSBL10060) in this study had a significant positive GCA effect for GYLD under AI but a neutral GCA effect for the trait under NI and PC, respectively. Meanwhile, tester CML331 had a significant negative GCA effect for GYLD under the two FAW infestation conditions and a neutral GCA effect under PC (Table 4). Furthermore, tester 1393 had a significant negative GCA effect for FAW leaf damage, ear damage and ear aspect scores under AI and desirable GCA effects for husk cover under NI and PC.

Table 4. General combining ability effect of testers for grain yield, agronomic and fall armyworm (FAW)-resistant traits under FAW infestation and pesticide-protected conditions in Nigeria.

Tester	Grain Yield AI NI PC			Days to Anthesis AI NI PC			Days to Silking AI NI PC			Plant Aspect AI NI PC		
1393	530 ***	41.58	35.92	0.45 *	0.46	0.65	10.08 ***	3.19	0.75	0.17 ***	0.00	0.08
CML331	−600 ***	−367.85 *	−256.12	1.16 ***	1.73 ***	1.13 **	−19.00 ***	−7.25 ***	1.19 **	−0.02	0.22 ***	0.02
CKSBL10060	70 *	326.27	220.20	−1.62 ***	−2.10 ***	−1.78 ***	8.92 ***	3.31	−1.93 ***	−0.14 **	−0.21 **	−0.10
SE (0.05)	28.7	160.30	151.70	0.18	0.40	0.38	0.36	1.76	0.38	0.03	0.05	0.07
	Husk cover AI NI PC			Ear aspect AI NI PC			Leaf damage AI NI			Ear damage AI NI		
1393	0.08	−0.21 **	−0.16 *	−0.43 ***	0.00	0.06	−0.77 ***	−0.01		−0.56 ***	0.01	
CML331	−0.09	0.29 ***	0.18 *	0.43 ***	0.14	0.06	0.72 ***	0.00		0.58 ***	0.00	
CKSBL10060	0.02	−0.05	−0.02	−0.01	−0.13	−0.12	0.05	0.01		−0.02	−0.01	
SE (0.05)	0.05	0.06	0.07	0.05	0.12	0.08	0.04	0.14		0.05	0.08	

*, **, ***: $p \leq 0.05$, 0.01, and 0.001; AI: Artificial infestation; NI: Natural infestation; PC: Protected condition; SE: Standard error.

CKSBL10060 had desirable GCA effects for days to anthesis and plant aspect score under the two FAW infestation conditions. However, CML331 had significant positive GCA effects for flowering traits under AI and NI, as well as significant positive GCA effects for husk cover, ear aspect, and leaf and ear damage scores under NI, which is undesirable (Table 4).

Three of the six OPVs referred to as lines in the line × tester design had significant positive GCA effects for GYLD under AI (Table 5). Lines AWR SYN-W2 and TZB-SR had significant negative GCA effects for days to anthesis under the infested and protected conditions, whereas TZBR Comp 2-WC2 had a significant positive GCA effect for the same trait (Table 5). TZB-SR had a positive and significant GCA effect on plant height in all conditions (Table 5). For all six lines, ear and leaf damage GCA effects were in opposite directions under AI.

Eight test crosses had significant positive SCA effects for GYLD under AI of which TZB-SR/CKSBL10060 and TZBR Eld 4-WC2/CKSBL10060 also had significant or/and positive SCA effects for the trait under NI and PC (Table 6). In addition, five test crosses (AWR SYN-W2/1393, TZB-SR/CKSBL10060, TZBR Comp 1-WC2/1393, TZBR Comp 2-WC2/CML331 and TZBR Comp 2-WC2/CKSBL10060) combined significant SCA effect for GYLD with desirable SCA effect for leaf and ear damage resistance (Table 6).

Table 5. General combining ability effect of lines for grain yield, agronomic and fall armyworm (FAW)-resistant traits under FAW infestation and pesticide-protected conditions in Nigeria.

Line	Grain Yield AI NI PC			Days to Anthesis AI NI PC			Plant Height AI NI PC			Plant Aspect AI NI PC		
AWR SYN-W2	390 ***	23.94	55.06	−0.69 ***	−0.71 *	−1.08 **	−3.56 ***	1.17	−0.45	−0.02	0.09	0.00
AMATZBR-WC4	190 ***	−338.22	−252.05	−0.42 **	0.51	0.46	−1.83 *	3.30	0.69	−0.18 ***	−0.15	−0.22
TZBR Eld. 4-WC2	−520 ***	218.87	-5.55	0.78 ***	0.05	0.28	−6.65 ***	−5.05	−1.96	0.07	−0.06	−0.04
TZB-SR	120 **	−67.57	−160.11	−0.24	−0.65 *	−0.99 **	3.82 ***	8.33 *	4.89 **	0.31 ***	0.16	−0.09
TZBR Comp 1-WC2	−150 ***	240.63	57.02	−0.30 *	−0.24	0.24	0.33	−0.51	−4.14 *	−0.21 ***	−0.02	0.18
TZBR Comp 2-WC2	−30	−77.66	305.63 *	0.88 ***	1.09 ***	1.10 **	7.89 ***	−5.25	0.97	0.03	−0.04	0.18
SE (0.05)	33.3	228.61	136.64	0.14	0.27	0.35	0.84	3.21	1.76	0.04	0.12	0.12
		Husk cover AI NI PC			Ear aspect AI NI PC			Leaf damage AI NI			Ear damage AI NI	
AWR SYN-W2	−0.31 ***	0.18	−0.03	0.01	0.17	0.04	−0.13	0.23	0.24***		0.30	
AMATZBR-WC4	0.15 **	−0.11	−0.17	−0.26 **	−0.27 **	−0.15	0.31 **	−0.01	−0.39 ***		−0.40 **	
TZBR Eld. 4-WC2	−0.27 ***	−0.17	0.00	0.28 ***	0.17	0.02	0.23 *	−0.21	−0.03		0.08	
TZB-SR	0.06	0.02	−0.28 *	−0.14	0.07	−0.17	0.05	−0.13	−0.57 ***		0.03	
TZBR Comp 1-WC2	0.27 ***	0.20	0.26 *	0.16 *	−0.28 **	0.18	−0.29 *	−0.10	0.61 ***		−0.15	
TZBR Comp 2-WC2	0.09	−0.15	0.22 *	−0.05	0.08	0.09	−0.17	0.19	0.15 *		0.04	
SE (0.05)	0.04	0.13	0.11	0.06	0.09	0.12	0.09	0.17	0.05		0.15	

*, **, ***: $p \leq 0.05$, 0.01, and 0.001; AI: Artificial infestation; NI: Natural infestation; PC: Protected condition; SE: Standard error.

Table 6. Specific combining ability effects for grain yield, agronomic and fall armyworm (FAW)-resistant traits under FAW infestation and pesticide-protected conditions in Nigeria.

Line × Tester	Grain Yield AI NI PC			Days to Anthesis AI NI PC			Plant Height_ AI NI PC			Plant Aspect AI NI PC		
AWR SYN-W2/1393	190 ***	−234.55	479.28 *	−0.34 *	0.72	0.44	2.07	3.67	6.19 *	−0.08	−0.18	−0.18
AWR SYN-W2/CML331	290 ***	415.26	−246.38	0.88 ***	−0.02	0.01	8.05 ***	4.67	−3.04	−0.16 *	0.00	0.11
AWR SYN-W2/CKSBL10060	−480 ***	−180.71	−232.89	−0.54 **	−0.79	−0.45	−10.13 ***	−7.59	−3.14	0.23 ***	0.17	0.08
AMATZBR-WC4/1393	30	552.52 *	169.23	0.39 *	−1.70 ***	−0.63	1.13	−7.40	4.90	−0.02	0.13	0.47 ***
AMATZBR-WC4/CML331	−200 ***	−92.46	143.69	−0.69 ***	1.47 **	−0.16	−8.20 ***	5.54	0.66	0.27 ***	0.00	−0.05
AMATZBR-WC4/CKSBL10060	160 **	−460.07	−312.92	0.30	0.97	0.79	7.07 ***	5.42	−5.56	−0.24 ***	−0.23	−0.42 **
TZBR Eld. 4-WC2/1393	−30	−176.11	−313.83	−0.18	−0.90	0.36 *	0.26	−1.38	−1.45	−0.27 ***	−0.03	−0.27 *
TZBR Eld. 4-WC2/CML331	−140 *	−498.04	161.41	0.75 ***	−0.18	−0.22	−3.87 *	2.86	−0.81	0.02	−0.24	0.29 *
TZBR Eld. 4-WC2/CKSBL10060	170 **	674.15 *	152.42	−0.57 **	0.99 *	−0.14	3.61 *	−0.74	2.26	0.24 ***	0.25	−0.02
TZB-SR/1393	−70	−333.79	−306.71	−1.60 ***	0.60	0.00	−10.75 ***	−0.08	−2.13	−0.04	0.09	0.19
TZB-SR/CML331	−130 *	−270.22	−248.30	0.76 ***	1.30 **	0.52	1.70	3.67	−1.62	0.14 *	0.14	0.02
TZB-SR/CKSBL10060	210 ***	604.00 *	555.01 **	0.84 ***	−0.78	−0.52	9.05 ***	−4.27	3.75	−0.10	−0.10	−0.21
TZBR Comp 1-WC2/1393	400 ***	397.19	260.07	0.64 ***	1.12 *	−0.28	8.22 ***	2.06	−1.52	0.01	0.13	−0.17
TZBR Comp 1-WC2/CML331	−200 ***	53.00	171.40	−0.34 *	−0.29	0.00	−1.89	−3.68	5.38	−0.07	−0.15	−0.18
TZBR Comp 1-WC2/CKSBL10060	−200 ***	−450.19	−431.46 *	−0.29	−0.92	0.28	−6.33 ***	2.37	−3.86	0.06	0.01	0.35 **
TZBR Comp 2-WC2/1393	−520 ***	−205.27	−288.04	1.09 ***	0.12	0.11	−0.94	1.14	−5.99 *	0.40 ***	−0.12	−0.04
TZBR Comp 2-WC2/CML331	380 ***	392.44	18.20	−1.35 ***	−1.29 *	−0.15	4.21 *	−6.71	−0.56	−0.21 **	0.33	−0.18
TZBR Comp 2-WC2/CKSBL10060	150 **	−187.18	269.84	0.26	1.08*	0.04	−3.27	6.31	6.55 *	−0.19 **	−0.23	0.23
SE (0.05)	53.2	276.72	189.52	0.17	0.49	0.37	1.65	4.24	2.87	0.06	0.17	0.13

Table 6. *Cont.*

Line × Tester	**Grain Yield AI NI PC**			**Days to Anthesis AI NI PC**			**Plant Height_ AI NI PC**		**Plant Aspect AI NI PC**	
	Husk plant AI NI PC			Ear aspect AI NI PC			Leaf damage AI NI_		Ear damage AI NI_	
AWR SYN-W2/1393	−0.36 ***	0.10	−0.12	−0.12	0.09	−0.46 **	−0.03	−0.01	−0.37 ***	−0.53 **
AWR SYN-W2/CML331	−0.08	−0.13	0.18	0.02	−0.18	0.19	0.18	0.24	0.02	0.44 *
AWR SYN-W2/CKSBL10060	0.44 ***	0.00	−0.06	0.09	0.08	0.27	−0.15	−0.23	0.35 ***	0.09
AMATZBR-WC4/1393	0.39 **	0.05	0.12	0.52 ***	0.06	0.11	−0.41 **	0.23	0.16*	0.34
AMATZBR-WC4/CML331	−0.27 *	0.56 ***	−0.05	0.02	0.04	−0.07	0.00	−0.36 *	0.49 ***	−1.04 ***
AMATZBR-WC4/CKSBL10060	−0.12	−0.55 **	−0.07	−0.54 ***	−0.15	−0.04	0.41 **	−0.03	−0.65 ***	0.47 *
TZBR Eld. 4-WC2/1393	−0.66 ***	0.12	0.14	−0.03	−0.05	−0.10	−0.32 *	−0.03	0.16 *	−0.21
TZBR Eld. 4-WC2/CML331	0.52 ***	−0.51 **	−0.30 *	−0.26 *	−0.05	0.23	0.09	0.09	−0.51 ***	0.07
TZBR Eld. 4-WC2/CKSBL10060	0.14	0.36 *	0.16	0.28 *	0.08	−0.13	0.23	−0.05	0.35 ***	0.15
TZB-SR/1393	0.38 **	−0.01	−0.04	0.13	−0.15	0.34 *	0.22	0.21	0.44 ***	0.30
TZB-SR/CML331	−0.18	0.21	−0.01	−0.10	−0.20	−0.40 **	−0.10	−0.80 ***	0.03	0.07
TZB-SR/CKSBL10060	−0.19	−0.03	0.05	−0.03	0.31 *	0.06	−0.13	0.26	−0.47 ***	−0.34
TZBR Comp 1-WC2/1393	0.17	−0.06	−0.11	−0.54 ***	0.00	−0.16	−0.08	−0.61 ***	−1.11 ***	−0.41 *
TZBR Comp 1-WC2/CML331	−0.13	−0.09	−0.03	0.13	0.20	−0.10	0.24	0.84 ***	0.02	0.53 **
TZBR Comp 1-WC2/CKSBL10060	−0.04	0.11	0.13	0.41 ***	−0.21	0.26	−0.16	−0.23	1.08 ***	−0.12
TZBR Comp 2-WC2/1393	0.08	−0.17	0.01	0.04	0.11	0.27	0.61 ***	0.23	0.72 ***	0.48 **
TZBR Comp 2-WC2/CML331	0.15	0.27	0.20	0.18	0.11	0.15	−0.41 ***	−0.51 ***	−0.06	−0.44 *
TZBR Comp 2-WC2/CKSBL10060	−0.23	−0.13	−0.21	−0.22 *	−0.23	−0.41 **	−0.20	0.28	−0.66 ***	−0.03
SE (0.05)	0.12	0.16	0.12	0.11	0.14	0.15	0.12	0.15	0.07	0.30

*, **, ***: $p \leq 0.05$, 0.01, and 0.001; AI: Artificial infestation; NI: Natural infestation; PC: Protected condition; SE: Standard error.

3.5. Relationship between Grain Yield, Agronomic and Fall Armyworm Tolerance Traits

The relationships between GYLD and the flowering traits under the two FAW infestation conditions were not significant but days to silking was significantly associated with GYLD under PC (Table 7). Under the two infestation conditions, the correlations of GYLD with leaf and ear damage tolerance scores were significant and negative. Additionally, ear aspect score was significantly and negatively correlated with GYLD under the three test conditions, whereas plant height had a positive relationship with the trait under naturally infested and protected conditions (Table 7). The regression analysis of GYLD on leaf and ear damage scores under the two FAW infestations revealed that a unit increase in leaf and ear damage scores under AI will result in a corresponding decline in GYLD by 579.2 Kgha^{-1} and 494.6 Kgha^{-1}, respectively, whereas, under NI, it will result in a yield decline by 409.4 Kgha^{-1} and 314.1 Kgha^{-1}, respectively (Figure 3).

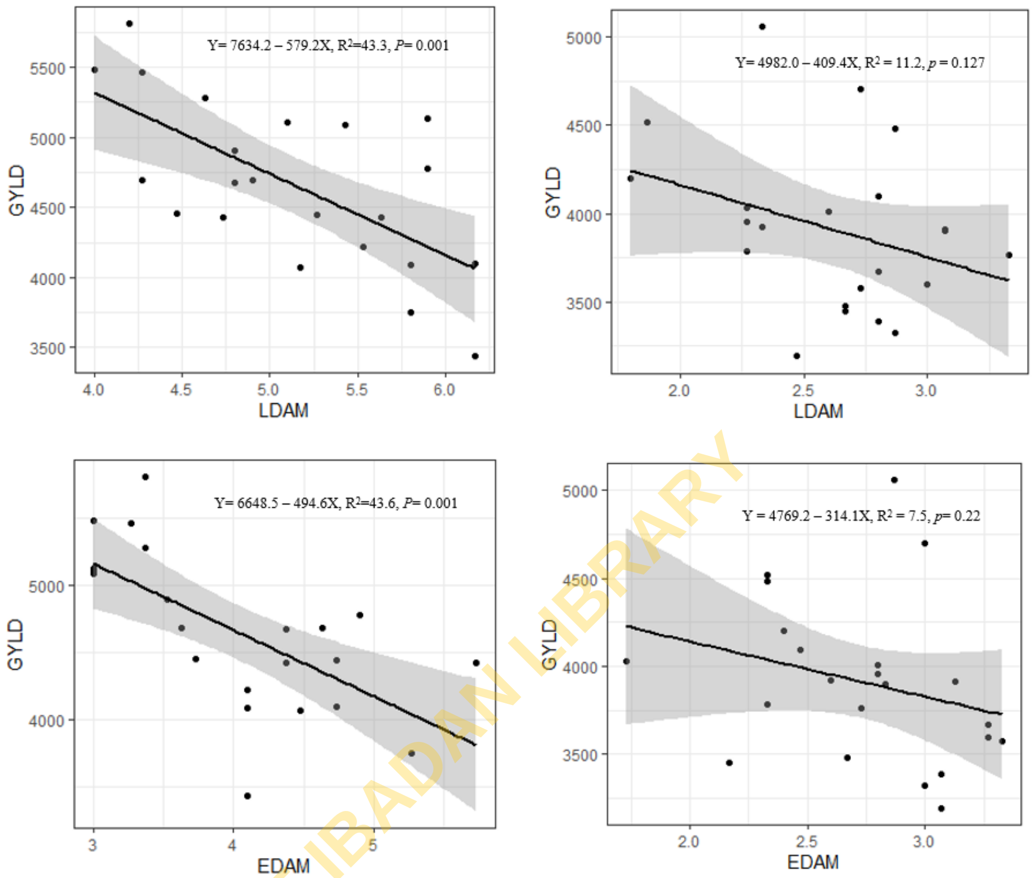


Figure 3. Scatterplots of the regressions of leaf damage (LDAM) and ear damage (EDAM) scores on grain yield (GYLD) of maize hybrids evaluated under artificial and natural fall armyworm infestations in Nigeria.

Table 7. Pearson's correlation coefficients for grain yield, agronomic and fall armyworm (FAW)-resistant traits of maize hybrids evaluated under FAW artificial infestation (Top diagonal), natural infestation (middle diagonal) and pesticide-protected conditions (bottom diagonal) in Nigeria.

	Grain Yield	Days to Anthesis	Days to Silking	Anthesis-Silking Interval	Plant Height	Plant Aspect	Husk Cover	Ear Aspect	Leaf Damage	Ear Damage
Grain yield	-	−0.01	−0.15	−0.30 **	0.64 ***	0.02	0.06	−0.61 ***	−0.45 ***	−0.66 ***
Days to anthesis	−0.01	-	0.89 ***	−0.03	−0.07	0.24 **	0.07	0.04	−0.19 *	−0.18 *
Days to silking	−0.06	0.94 ***	-	0.42 ***	−0.24 **	0.15	0.16	0.11	−0.03	−0.06
Anthesis-silking interval	−0.14 **	−0.18 **	0.16 **	-	−0.39 ***	−0.14	0.23 **	0.16	0.32 **	0.24 **
Plant height	0.28 ***	−0.15 **	−0.16 **	−0.02	-	0.15	0.04	−0.38 ***	−0.63 ***	−0.43 ***
Plant aspect	−0.19 **	0.16 **	0.14 **	−0.06	−0.21 **	-	−0.09	0.02	−0.29 **	−0.11
Husk cover	−0.08	0.00	0.00	−0.02	−0.09	0.30 ***	-	0.01	0.11	−0.04
Ear aspect	−0.32 ***	0.06	0.10	0.11 *	−0.22 ***	0.45 ***	0.11 *	-	0.22 **	0.67 ***
Leaf damage	−0.32 ***	−0.13 *	−0.06	0.21 **	−0.09	−0.09	−0.06	0.13 *	-	0.27 **
Ear damage	−0.13 *	0.03	0.08	0.17 **	0.01	−0.13 *	0.30 ***	0.04	0.30 ***	-
Grain yield										
Days to anthesis	−0.05									
Days to silking	−0.11 *	0.93 ***								
Anthesis-silking interval	−0.16 ***	−0.09	0.28 ***							
Plant height	0.30 ***	−0.18 ***	−0.16 ***	0.04						
Plant aspect	0.02	0.05	0.03	−0.06	−0.09 *					
Husk cover	−0.06	−0.23 ***	−0.24 ***	−0.04	0.02	0.28 ***				
Ear aspect	−0.26 ***	0.07	0.08	0.02	−0.33 ***	0.38 ***	0.26 ***			

*, **, ***: $p \leq 0.05$, 0.01, and 0.001, N = 22.

4. Discussion

The devastating effect of FAW is limiting maize yield in Africa and Asia. Under severe infestation, FAW is capable of reducing the grain yield of maize by up to 53%, depending on the genotype susceptibility and severity of the infestation [30]. The development and deployment of host-resistant varieties is a safe and cost-effective approach to mitigating yield losses, especially among poorly resourced smallholder farmers. To develop resistant varieties, the presence of genetic variability among genotypes and effective screening methodologies are a pre-requisite [25,35,61].

In the present study, the differences among the FAW infestation treatment indicated that the conditions of evaluation differed and thus evoked variable responses among the experimental maize hybrids. Under the three evaluation conditions, the significant genotypic effect of the maize hybrids for grain yield (GYLD) and most agronomic traits indicated that selection can be made among the genotypes for enhanced yield and agronomic performance. Additionally, the genotypic differences for leaf damage (LDAM) and ear damage (EDAM) scores under the artificial FAW infestation (AI) condition and LDAM score under the natural infestation (NI) condition signified that the genotypes varied for FAW resistance in the test conditions.

The significant environment effect for all the traits measured under natural FAW infestation and protected conditions indicated that the test environment differed, probably due to variation in the climatic, edaphic, disease and FAW infestation conditions in the respective environment. Significant G $\times$ E effects of genotype, tester and line for GYLD and some agronomic traits under natural FAW infestation and protected conditions indicated that the test environments were unique [61].

An understanding of the relative value of different testers in eliciting genetic diversity among new lines is necessary for resistant hybrid breeding programs [62]. In the present study, the significant GCA effect of both tester and line, as well as the significant SCA effect for GYLD, most agronomic traits and FAW-resistant traits under artificial infestation suggested that these traits were both governed by additive and non-additive gene effects under this test condition. Additionally, the significant GCA effect of the tester and significant SCA effect for GYLD and most agronomic traits under the natural infestation condition is indicative of the presence of additive and non-additive gene effects in the control of these traits. However, for FAW leaf damage resistance under NI, the non-additive gene effect was more important. The testers' contributions to the inheritance for GYLD and leaf damage resistance under AI, and flowering traits under the three test conditions were comparatively larger than those of the lines and underscores that the testers contributed more than the lines in the inheritance of these traits in hybrid combinations. Conversely, the relative contributions of the lines for ASI, PHT, EASP and EDAM under natural infestation and ASI and husk cover under protected conditions indicated that the lines were more important than the testers in the inheritance of these traits under those conditions. The presence of additive and non-additive gene effects implied that most of the measured traits can be improved through hybridization, backcrossing, and recurrent selection to develop maize hybrids or synthetics [50]. In addition, the result also implies that potential testers can be identified to discriminate for high yield, excellent agronomic performance and FAW resistance under these varying infestation conditions. The high broad-sense heritability estimates and moderate to high narrow-sense heritability estimates reaffirmed the presence of dominance and additive gene effects in the inheritance of the measured traits. This result is contrary to the result of [41] who reported low-to-moderate narrow-sense heritability for GYLD, agronomic traits and FAW tolerance among 60 experimental maize hybrids evaluated in Zambia. The high estimates of additive gene effects in the present study suggest that these traits can respond to selection and thus can be improved by recurrent selection techniques.

The stem borer-resistant lines of IITA (1393) and CIMMYT (CKSBL10060), which were also previously validated for FAW tolerance, had significant and positive GCA effects for GYLD and desirable GCA effects for at least two FAW-resistant or agronomic traits under AI. These lines also produced significantly higher grain yields in hybrid combinations (AMATZBR-WC4 × CKSBL10060, TZB-SR × CKSBL10060 and TZBR Comp 1-WC2 × 1393) than the two checks included in this study. They can be exploited in FAW-resistant hybrid breeding programs as it is evident that these testers possess alleles conferring FAW resistance. Inbred line 1393 (TZI4) from IITA, Ibadan has shown cross-resistance to various stem borers such as the African pink stem borer (IITA, 1986), the European corn borer [55] and the African sugarcane borer [4]. CKSBL10060 from CIMMYT Kenya is resistant to the spotted stalk borer and the maize stalk borer and is a valuable resource in CIMMYTs multiple-borer resistance breeding efforts in East and Southern Africa. On the other hand, the tester CML331, which was previously characterized for resistance to the sugarcane borer and tolerance to the FAW by CIMMYT (Mexico) [54], had significant and negative GCA effects for GYLD under the three test conditions and undesirable GCA effect for leaf and ear damage scores under AI. This tester did not produce outstanding test crosses, especially under AI, suggestive of its unsuitability for broad-based FAW-resistant hybrid breeding programs in WCA. The GCA effects of the respective testers for GYLD and FAW resistance were indicative of their heterotic affinities under the various test conditions. This result shows similarity to a previous study in which GCA and SCA effects of testers showed a pattern for heterotic affinity and were used to assign lines into heterotic groups [50]. Furthermore, the OPV (AWR SYN-W2), which combined significant and positive GCA effects for GYLD with desirable GCA effects for agronomic traits under the three test conditions, can serve as a source population for the extraction of inbred lines for FAW-resistant variety development. Similarly, AMATZBR-WC4 and TZB-SR also combined significant GCA effects for GYLD under AI with desirable leaf damage or/and ear damage scores, thus showing merit for FAW resistance/tolerant inbred line extraction. Five of the eighteen test crosses (AWR SYN-W2/1393, TZB-SR/CKSBL10060, TZBR Comp 1-WC2/1393, TZBR Comp 2-WC2/CML331 and TZBR Comp 2-WC2/CKSBL10060) were identified and considered tolerant [57] due to their lower leaf, ear damage, and higher GYLD yield under FAW infestation.

The significant negative correlation coefficients between GYLD and EASP, LDAM and EDAM scores under the two infestation conditions denoted adverse correlation effects of the traits on yield. From the regression models, the significant decline in GYLD due to an increase in leaf and ear damage scores occasioned by artificial FAW infestation, and the concomitant non-significant decline in yield under natural infestation implied that the artificial FAW infestation was more severe than the natural infestation. This could be attributed to the increased pest pressure and more uniform infestation achieved under the artificially infested as compared to the naturally infested environment. The direct effect of leaf damage score on grain yield is a function of leaf feeding and whorl damage by FAW larvae thereby reducing the photosynthetic efficiency of the plant which, in turn, impairs assimilate translocations for vegetative growth, cob formation and grain filling. The older caterpillars burrow into the maize cob, damaging the maize ear and kernels, and predisposing the cob to secondary infections [63]. This is evidenced by the significant relationship between ear damage score and grain yield under the artificial FAW infestation. Nevertheless, specific combinations of the FAW-tolerant lines (OPVs) and testers (inbreds) identified in this study show promise for FAW resistance and are recommended for further testing.

5. Conclusions

The presence of significant additive and non-additive effects for grain yield, most agronomic traits and fall armyworm (FAW)-resistant traits of maize test cross hybrids evaluated under artificial and natural FAW infestations indicated that these traits can be improved under the test conditions. The two testers (1393 and CKSBL10060) identified for their significant GCA effects for GYLD and desirable GCA effects for FAW-resistant traits could be improved and serve as source populations for inbred extraction for the development of FAW-tolerant maize hybrids. In addition, the test crosses that combined high yield with stability and FAW tolerance could be used as a source for the development of high-yielding, adaptive and FAW-tolerant open-pollinated maize varieties for poorly resourced farmers.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/agronomy12123042/s1, Table S1: Description of the test locations used for evaluation of genotypes under fall armyworm-infested and non-infested growing conditions in Nigeria in 2021; Table S2: Mean squares from the ANOVA for grain yield and agronomic traits of maize hybrids evaluated under artificial, natural FAW infestations and protected environments, and fall armyworm-resistant traits in infested environments in Nigeria; Table S3: Mean performance of grain yield, agronomic and fall armyworm (FAW)-resistant traits of maize hybrids evaluated under artificial FAW infestation in two growing seasons in Ibadan, Nigeria; Table S4: Mean performance of grain yield, agronomic and fall armyworm (FAW)-resistant traits of maize hybrids evaluated under natural FAW infestation across five locations in Nigeria; Table S5: Mean performance of grain yield and agronomic traits of maize hybrids evaluated under insecticide protection across seven environments in Nigeria.

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