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Fall Armyworm Tolerance of Maize Parental Lines, Experimental Hybrids, and Commercial Cultivars in Southern Africa

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Abstract: Fall armyworm [Spodoptera frugiperda (J./E. Smith); FAW] is negatively impacting sustainable maize production, particularly in smallholder farming systems in sub-Saharan Africa. Two sets of germplasm (commercial cultivars and experimental hybrids, and local and exotic inbred lines) were evaluated under managed and natural FAW infestation to identify FAW tolerant material with superior grain yield performance. Significant genotypic effects on foliar FAW damage, ear FAW damage, and grain yield were observed. Commercial cultivars were significantly more affected by FAW infestation than experimental hybrids, as evidenced by high foliar and ear damage scores, yet they out-yielded experimental genotypes. The introduced FAW donor lines (CML338, CML67, CML121, and CML334) showed better tolerance to FAW, individually and in hybrid combinations. Local inbred lines, SV1P, CML491, and CML 539, also showed FAW tolerance. Hybrids and open pollinated varieties were more vulnerable to FAW damage at early growth stages, but they grew out of it through the mid to late whorl stages. Inbred lines showed increasing damage as they grew to maturity. Husk cover, ear rot, anthesis date, and plant height were highly correlated with FAW tolerance. The identified local and exotic lines with FAW tolerance will contribute to FAW resistance breeding in southern Africa.

Keywords: ear damage; fall armyworm; foliar damage; maize; resistance



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1. Introduction

Maize is one of the most important food security crops in Africa. In sub-Saharan Africa (SSA) alone, approximately 38 million metric tons of maize per year is produced to feed and sustain over 300 million families [1,2]. While maize production in SSA is dominated by smallholder farmers, production is complicated and compromised by an array of challenges which include drought, poor soil fertility, insect pests and diseases, inferior seed, and limited financial resources [3–5]. The world population is projected to increase by 25% in the next 30 years [6] and there is growing demand for maize in SSA, driven by population growth, rapid urbanization, and per capita consumption demand growth [7,8]. Unlike developed countries, more than 63% of maize produced in SSA is for human consumption [9].

The smallholder farmers of SSA have poor mitigation strategies to the various stresses affecting maize production. In 2016, SSA was invaded by a trans-boundary, polyphagous insect pest: fall armyworm [Spodoptera frugiperda (J.E. Smith); FAW] [10–12]. FAW has caused significant crop yield losses across SSA since its arrival on the continent [13–15].

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Maize is FAW's most preferred crop, and several reports have indicated that most cultivars currently in production across most of SSA are susceptible to the pest [14–16].

Host–plant resistance is the ability of a plant to resist pest damage or injury that causes death of the plant or economic yield loss and it is expressed by the degree of the damage by the pest on the host plant, and is the best long-term strategy for overcoming the effects of this pest [17]. Host–plant resistance has been classified into three different categories, which are non-preference, antibiosis, and tolerance [18]. Antibiosis affects the growth, survival, and reproductive capacity of the pest and it is the major mechanism responsible for FAW resistance in resistant genotypes [19]. Non-preference confers resistance mainly by making the plant not a preferred habitat by the pest mainly because of the presence of hairs on the leaves and stems, thick leaf cuticles, and shiny leaf texture [20]. Tolerance is more of a partial resistance mechanism; it refers to the ability of a plant to survive and yield satisfactorily despite hosting a significant pest population [20]. Partial resistance confers horizontal resistance, which is more durable and takes longer to break down [21,22].

In parts of the world, breeding for resistance to FAW was largely replaced by the introduction of Bt maize. In Brazil, FAW was controlled with insecticides until insecticide resistance developed, which lead to the introduction of Bt maize [21,23]. Bt maize has also effectively managed FAW in the Americas [24]. This is significant, as genetically modified maize represents more than 85% of the maize produced in the USA, Brazil, and Argentina [25]. The use of Bt maize in SSA is probably not feasible (with the exception of South Africa) due to high seed costs and the low maize prices small-scale farmers receive, which is characteristic of the SSA market [12].

There has not been a deliberate study to investigate the response of cultivars under production in SSA to FAW infestation [17,26], yet this information is important in guiding smallholder farmers, breeders, seed companies, and policy makers on the right cultivars in the region. This information will also contribute towards targeted FAW resistance breeding, which needs to be implemented in the region. Therefore, the objectives of this study were to (i) identify locally adapted germplasm (commercial cultivars, experimental hybrids, and inbred lines) with good FAW tolerance and superior yield performance under FAW infestation, (ii) determine agronomic traits correlated with FAW tolerance in maize hybrids, open pollinated varieties (OPVs), and inbred lines, and (iii) estimate the impact of natural FAW infestation on grain yield. This information can guide seed supply systems and breeding in the wake of FAW outbreaks.

2. Materials and Methods

2.1. Germplasm Tested

A collection of 60 genotypes, consisting of old and new commercial cultivars registered for cultivation in Zimbabwe, and experimental hybrids were used (Table 1) as well as 63 inbred lines, some of which are parents in the commercial hybrids (Table 2). This germplasm was developed by the Crop Breeding Institute (CBI) of Zimbabwe, the International Maize and Wheat Improvement Center (CIMMYT), and HarvestPlus, while the cultivars and experimental hybrids were sourced from CBI, CIMMYT, and various seed houses in Zimbabwe. The inbred lines used in the inbred line trial constituted the most prominent parental materials for hybrids developed by CBI and CIMMYT. The commercial cultivars included OPVs and hybrids developed or introduced by CBI since 1909, as well as cultivars developed and released by CIMMYT and different seed houses in Zimbabwe. Some of the cultivars are currently grown in a number of countries across the East and Southern African regions (ESA). As there are currently no FAW susceptible and tolerant checks for the region, this material was screened as is in the FAW hotspot areas.

Table 1. Description of commercial cultivars evaluated for tolerance to fall armyworm under natural infestation in Zimbabwe.

Code	Name	Source	Year of Release	Production Region	Grain Color and Texture	Market Statu
1	Salisbury white	СВІ	Unknown	Zimbabwe and ESA	WD	Inactive
2	Southern cross	CBI	Unknown	Zimbabwe and ESA	W	Inactive
3	Hickory king	CBI	Introduced	Zimbabwe and ESA	W	Inactive
4	R200	CBI	1971	Zimbabwe	Y	Inactive
5	R201	CBI	1971	Zimbabwe	W	Active
6	R215	CBI	1974	Zimbabwe	W	Active
7	ZS107	CBI	1985	Zimbabwe	W	Inactive
8	ZS240	CBI	1992	Zimbabwe	Y	Inactive
9	ZS255	CBI	1998	Zimbabwe	W	Inactive
10	ZS259	CBI	2005	Zimbabwe	W	Inactive
11	ZS261	CBI	2006	Zimbabwe	W	Active
12	ZS263	CBI	2011	Zimbabwe	W	Active
13	ZS265	CBI	2011	Zimbabwe	W	Active
14	ZS269	CBI	2014	Zimbabwe	W	Active
15	ZS271	CBI	2014	Zimbabwe	W	Active
16	ZS273	CBI	2014	Zimbabwe	W	Active
17	ZS275	CBI	2014	Zimbabwe	W	Active
18	ZS225	CBI	2016	Zimbabwe	W	Active
19	SR52	CBI	1962	Zimbabwe and ESA	WD	Inactive
20	ZS242A	CBI	2015	Zimbabwe and ESA	OF	Active
21	ZS246A	CBI	2016	Zimbabwe and ESA	OF	Active
22	093WH03	CBI	Experimental	Zimbabwe	WD	NA
23	093WH123	CBI	Experimental	Zimbabwe	WD	NA
24	113WH330	CBI	Experimental	Zimbabwe	WF	NA
25	ZM309	CIMMYT	2009	Zimbabwe and ESA	WF	Active
26	ZM401	CIMMYT	2009	Zimbabwe and ESA	W	Active
27	ZM421	CIMMYT	2002	Zimbabwe and ESA	W	Active
28	ZM521	CIMMYT	2002	Zimbabwe and ESA	W	Active
29	CZH1258	CIMMYT	Experimental	N/A	W	N/A
30	NTS51	NTS	2014	Zimbabwe	W	Active
31	PAN53	PANNAR	2007	Zimbabwe and ESA	W	Active
32	PAN4M-23	PANNAR		Zimbabwe and ESA	W	Active
33	PAN-7M-81	PANNAR	2013	Zimbabwe and ESA	W	Active
34	PHB30G19	PIONEER	2008	Zimbabwe and ESA	W	Active
35	Shasha301	Champion	Experimental	N/A	W	N/A
36	Shasha302	Champion	Experimental	N/A	W	N/A
37	SeedCo Exp1	SeedCo	Experimental	N/A	W	N/A
38	SeedCo Exp2	SeedCo	Experimental	N/A	W	N/A
39	Manjanja MN421	Mukushi	2015	Zimbabwe, South Africa, Zambia	W	Active
40	Mutsa MN521	Mukushi	2014	Zimbabwe, South Africa, Zambia	W	Active
41	Maka MN625	Mukushi	2018	Zimbabwe, South Africa, Zambia	W	Active
42	Mukwa	Mukushi	2016	Zimbabwe, South Africa, Zambia	W	Active

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Table 1. Cont.

Code	Name	Source	Year of Release	Production Region	Grain Color and Texture	Market Status
43	Pris601	Pristine	2010	Zimbabwe and ESA	W	Active
44	ZAP61	Agriseeds	2008	Zimbabwe and ESA	W	Active
45	ZAP63	Agriseeds	2015	Zimbabwe and ESA	W	Active
46	ZAP43	Agriseeds	2015	Zimbabwe and ESA	W	Active
47	ZAP55	Agriseeds	2015	Zimbabwe and ESA	W	Active
48	CML338/CML67	CIMMYT	Experimental	N/A	YF	N/A
49	CML338/CML334	CIMMYT	Experimental	N/A	YFL	N/A
50	CML331/CML67	CIMMYT	Experimental	N/A	WF	N/A
51	DJ271-28	CIMMYT	Experimental	N/A	W	N/A
52	CIM52/CML139	CIMMYT	Experimental	N/A	WF	N/A
53	CIM53/CML345	CIMMYT	Experimental	N/A	WF	N/A
54	CIM54/CML334	CIMMYT	Experimental	N/A	WDL	N/A
55	CIM55/CML334	CIMMYT	Experimental	N/A	WDL	N/A
56	CIM56/CML334	CIMMYT	Experimental	N/A	WDL	N/A
57	CIM57/CML345	CIMMYT	Experimental	N/A	WF	N/A
58	CIM58/CML121	CIMMYT	Experimental	N/A	YD	N/A
59	CML543/CML334	CIMMYT	Experimental	N/A	WDL	N/A
60	CML571/CML338	CIMMYT	Experimental	N/A	YDL	N/A

WD, White and Dent; W, White; Y, Yellow; WF, White and Flint; WDL, White and Dent like; WFL, White and Flint like; YD, Yellow and Dent; YF, Yellow and Flint; YDL, Yellow and Dent like; YFL, Yellow and Flint like; OD, Orange and Dent; OF, Orange and Flint; ODL, Orange and Dent like; OFL, Orange and Flint like.

Table 2. Description of inbred lines evaluated for fall armyworm tolerance in Zimbabwe.

Name	Source Germplasm	Adaptation/Program	Maturity	Grain Color/Texture	Heterotic Group
2Kba, SV1P,	CBI	Africa MA/ST	Very Early	W	
N3.2.3.3; NAW5885, K64R, RA214P, RA150P, WCoby1P, YCoby7P, QRD69P, RS98P, RS61P, PR15P, RA267P, RA294P, GQL5, WW01408	СВІ	Africa MA/ST	Early/Intermediate/ Late	W	N3/SC
RL17P, EL77P, HX482P, HX439, HS253, BC108P	СВІ	Africa MA/ST	Intermediate/Late	Y	N3/SC
CLHP0003, CLHP0005, CLHP00306, CLHP00478, DPTY9 *9, CLHP00476, CLHP0286, CLHP00448	HarvestPlus	Africa MA/ST	Early/Intermediate/Late	O	A/B
CZL1112, CZL12010, CZL1227, CZL1315, CZL1311, CZL15025	27, CZL1315, CIMMY I Africa MA/ST		Early/Intermediate/ Late	W	A/B
DJL173833, DJL173527, CIMExp60	Atrica MA/SI		Intermediate/Late	W	A/B

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Table 2. Cont.

Name	Source Germplasm	Adaptation/Program	Maturity	Grain Color/Texture	Heterotic Group
CML67	Antigua	Lowland	Late	Y, SD	
CML334	CIMMYT	NA	Late	W, F	
CML139	CIMMYT	Subtropical	Intermediate	Y, SF	
CML181	CIMMYT	Subtropical	Intermediate	W, D	
CML300	SintAmTSR	Lowland	Early	Y, F	
CNL312	P500	Subtropical	Intermediate	W, SF	A Tester
CML331	REC	Subtropical	Early	W, SD	AB
CML338	P590B	Subtropical	Early	Y, SF	В
CML346	P390	Lowland	Intermediate	W, F	В
CML395	IITA	Africa MA/ST	Late	W, SF	B Tester
CML442	REC	Africa MA/ST	Intermediate	W, D	A Tester
CML444	P43	Africa MA/ST	Late	W, SD	B Tester
CML491	REC	Lowland	Late	W, F	A
CML511	Recycled	Africa MA/ST	Early/Intermed	W	В
CML539	CIMMYT	Africa MA/ST	Early/Intermed	W, SF/SD	A
CML541	CIMMYT	NA	Intermed/Late	W	В
CML543	CIMMYT	NA	Intermed/Late	W	В
CML547	CIMMYT	NA	Intermed/Late	W	В
CML566	CIMMYT	NA	Late	W	В
CML571	CIMMYT	NA	Early/Intermed	W	В

W, White; Y, Yellow; O, Orange; D, Dent; F, Flint; SD, Semi-dent; SF, Semi-flint; MA, Mid-altitude; ST, Sub-tropical; Intermed, Intermediate; NA, Not available.

2.2. Trial Sites, Experimental Design and Agronomic Management

The trials were established under managed FAW (FAW control trial) and natural FAW infestation across different sites in Zimbabwe during the 2019 and 2020 summer seasons. Under managed FAW environments, insecticides were used to control FAW, including Thionex (Endosulfan 50%), Carbaryl (Carbaryl 85WP), Dimethoate (Dimethoate 40EC), Karate (Lambda cyhalothrin 5EC), Ecoterex (Deltamethrin and Pirimiphos methyl), Emamectin benzoate/Macten (Emamectin benzoate 5), Super dash (Emamectin benzoate and Acetamiprid), Ampligo (Chlorantraniliprole and Lambda), and Belt (Flubendiamide). A routine FAW control strategy was followed [11] where chemicals were applied when egg masses were spotted on at least 5% of the crop or when 25% of the crop at early whorl stage (or 40% at late whorl stage) showed physical damage caused by the pest and when live pests were visible on the crop. Recommended application rates were used, and the crops were sprayed every two weeks or when the need arose.

The lowveld research sites (Chiredzi and Chisumbanje) have traditionally been used for maize stalk borer screening as they naturally have a high and active infestation population of stem borers, FAW, and other insect pests due to their inherent high temperature and low rainfall characteristic. The other sites in Harare—Gwebi and Kadoma—represent major maize production areas of Zimbabwe, and usually have significant FAW populations during the maize growing season.

The Department of Research and Specialist Services (DR&SS) site—Harare ($17^{\circ}48'$ S, $31^{\circ}03'$ E, 1506 m above sea level (masl), rainfall for 2019 and 2020 respectively 502.7 and 436.3 mm), and Gwebi Variety Testing Centre ($17^{\circ}41'$ S, $30^{\circ}32'$ E, 1448 masl, rainfall for 2019 and 2020 respectively 571.5 and 542.5 mm) were used in both years, while CIMMYT Harare ($17^{\circ}48'$ S, $31^{\circ}85'$ E, 1506 masl, 557.2 mm rainfall for 2019) and Chisumbanje ($20^{\circ}05'$ S, $32^{\circ}15'$ E, 421 masl, 441.9 mm rainfall in 2019) were used only in 2019, and Chiredzi ($21^{\circ}01'$ S, $21^{\circ}25'$ E, 1409 masl, 419.2 mm rainfall in 2020), Rattray-Arnold Research Station (RARS)

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(17°14′ S, 31°14′ E, 1341 masl, 543.8 mm rainfall in 2020), and Kadoma-Cotton Research Institute (18°94′ S, 29°25′ E, 1149, masl, 474.8 mm rainfall in 2020) were used during 2020.

The commercial cultivar experiment was laid out in a $10 \times 6 \alpha$ (0, 1) lattice design, while the inbred line experiment was laid out in a $9 \times 7 \alpha$ (0, 1) lattice design, with both experiments having two replications at each testing site. The experimental unit for all environments was one 4 m row plot, except at DR&SS-Harare and CIMMYT-Harare that had 2 m row plots, with inter-row and intra-row spacing of 0.75 and 0.25 m, respectively. The experimental plants were thinned to one plant per planting station at the two-leaf stage (approximately three weeks after planting) to give a crop population density of about 53,000 plants ha⁻¹. Planting station refers to the position of a plant in row. The plants in the experiments were grown using standard agronomic practices for maize production. Optimal fertilizer rates of 400 kg ha⁻¹ for both compound D (7N:14P:7K) basal applications and ammonium nitrate (AN) (34.5N) for top dressing were applied at all environments. Weeds were controlled using herbicides and hand weeding where necessary.

2.3. Data Collection and Analysis

For trials at each site, the following characteristics were recorded per plot: (i) foliar FAW damage (FFAWD) at 4, 8 and 12 week intervals, (ii) anthesis date (AD), (iii) plant height (PH) at harvesting, (iv) Husk cover (HC), (v) ear FAW damage (EFAWD), (vi) ear rots (ER), and (vii) grain yield (GYD) per plot adjusted to 12.5% moisture content. The presence of FAW was determined through visual assessment of the active larvae and FAW damage scores were the main indicators of the extent of the FAW pressure. FFAWD damage was recorded following the modified Davis scale as described previously [11] where scores 1-2 = resistant, 2-5 = partial resistance, 5-7 = susceptible, 7-9 = highly susceptible [1 = no visible leaf-feeding damage, highly resistant, 2 = few pinholes on 1–2 older leaves, resistant, 3 = several shot-hole injuries on a few leaves (2.5 cm long) on 8–10 leaves, plus a few smallto mid-sized uniform to irregular-shaped holes (basement membrane consumed) eaten from the whorl and/or furl leaves, partially resistant, 6 = several large elongated lesions present on several whorl and furl leaves and/or several large uniform to irregular-shaped holes eaten from furl and whorl leaves, susceptible, 7 = many elongated lesions of all sizes present on several whorl and furl leaves plus several large uniform to irregular-shaped holes eaten from the whorl and furl leaves, susceptible, 8 = many elongated lesions of all sizes present on most whorl and furl leaves plus many mid- to large-sized uniform to irregular-shaped holes eaten from the whorl and furl leaves, highly susceptible, 9 = whorl and furl leaves almost totally destroyed and plant dying as a result of extensive foliar damage, highly susceptible].

EFAWD was scored as follows [11]: 1 = no damage to the ear, highly resistant, 2 = damage to a few kernels (<5) or less than 5% damage to an ear, resistant, 3 = damage to a few kernels (6–15) or less than 10% damage to an ear, resistant, 4 = damage to 16–30 kernels or less than 15% damage to an ear, partially resistant, 5 = damage to 31–50 kernels or less than 25% damage to an ear, partially resistant, 6 = damage to 51–75 kernels or more than 35% but less than 50% damage to an ear, susceptible, 7 = damage to 76–100 kernels or more than 50% but less than 60% damage to an ear, susceptible, 8 = damage to >100 kernels or more than 60% but less than 100% damage to an ear, highly susceptible, 9 = almost 100% damage to an ear, highly susceptible.

All the other agronomic traits were recorded as described previously [27,28]. The collected phenotypic data were subjected to analysis of variance (ANOVA) using Genstat Discovery Software V18.0 [29]. Best linear unbiased predictions (BLUPs) and broad sense heritability estimates (H^2), and genetic correlations between agronomic traits as well as identifying traits correlated with FAW tolerance were estimated using the Multi-environment Trials Analysis in R (META-R) v2.1 R package software [30]. For each trait, sites with H^2 values lower than 20% were dropped from the combined analysis. Means were separated using the Tukey's multiple comparison test in Genstat Discovery Software [29]. In the

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ANOVA model, genotypes were considered fixed, while replications within environments, and environments, were considered random.

3. Results

3.1. Performance of the Commercial Cultivars and Their Corresponding Inbred Line Parents under Natural Fall Armyworm Infestation

Significant (p < 0.05) genotype effects were seen for FAW infestation on both foliar and ear damage across cultivars and inbred lines evaluated (Tables 3 and 4). Grain yield and yield related traits (anthesis date, plant height, and ear rot) differed significantly (p < 0.05) across cultivars and inbred lines evaluated under FAW infestation. The minimum average FFAWD Davis score for cultivars and experimental hybrids was 3.36 while the highest score was 5.73 (Table 3), whereas for inbred lines, the average FFAWD ranged from 2.62 to 6.34 (Table 4). Generally, FFAWD was higher than EFAWD for both cultivars and inbred lines.

Table 3. Analysis of variance for leaf and ear fall armyworm damage scores and selected agronomic traits of commercial cultivars and experimental hybrids under natural fall armyworm infestation sites in Zimbabwe, during the 2019 and 2020 summer seasons.

Source of Variation	DF	GYD	DF	Avg-FFAWD	DF	EFAWD	DF	AD	DF	ER
Environment	8	104.96 ***	10	138.99 ***	5	78.364 ***	6	2244.24 ***	8	26,140.2 ***
Replication (Environment)	9	4.06 ***	11	1.04	6	3.15 *	7	466.06 ***	9	1517.2 ***
Block (Replication × Site)	162	2.59 ***	198	2.09 ***	108	2.08 ***	126	62.37 ***	161	660.2 ***
Genotype	59	10.32 ***	59	4.77 ***	58	2.71 ***	58	76.37 ***	58	2088.3 ***
Genotype × Environment	448	2.09 ***	570	0.77 **	280	1.39	332	22.96 **	439	514.3 ***
Residuals	296	1.02	397	0.62	197	1.13	239	17.11	277	284.7
Phenotypic variance		3.11		2.20		2.12		41.52		792.69
Genotypic variance		0.57		0.24		0.12		5.35		111.85
$G \times E$ variance		0.57		0.12		0.19		3.30		107.71
Environmental variance		0.95		1.21		0.68		15.77		288.44
PCV (%)		68.57		30.35		53.02		9.50		88.94
GCV (%)		29.48		10.13		12.67		3.36		33.41
Broad-sense heritability (%)		0.82		0.87		0.49		0.76		0.78
LSD		2.09		1.52		2.08		8.15		36.56
Grand mean		2.57		4.88		2.74		67.83		31.66
Minimum		0.94		3.36		2.20		64.04		20.14
Maximum		3.85		5.73		3.27		72.15		60.48

^{*} p < 0.05; ** p < 0.01; *** p < 0.001; DF = degrees of freedom; GYD = grain yield; Avg-FFAWD = average foliar fall armyworm damage; EFAWD = ear fall armyworm damage; AD = anthesis date; ER = ear rot; PCV = phenotypic coefficient of variance; GCV = genotypic coefficient of variance; LSD = least significant difference.

Table 4. Analysis of variance for fall armyworm damage scores and agronomic traits of inbred lines evaluated across natural fall armyworm infestation sites during the 2019 and 2020 seasons.

Source	DF	GYD	DF	FFAWD Average	DF	EFAWD	DF	РН	DF	AD	DF	ER	DF	НС
Environment (E)	6	3.43 ***	9	130.95 **	4	21.92 ***	5	16,905.8 ***	6	2293.32 ***	4	56,525.00 ***	2	394.73 ***
Rep (Env)	7	0.13	10	5.55 ***	5	1.93	6	1145.8 *	7	235.63 ***	5	807	3	5.87
Blk (Rep \times Site)	110	0.25	160	2.97 ***	80	3.23 **	96	822.7 ***	112	108.97 ***	78	2062	48	60.33 *
Genotype (G)	60	0.77 ***	61	10.18 ***	58	4.26 ***	62	970.2 ***	62	260.86 ***	59	2916.00 *	60	90.15 ***
GE	275	0.19	524	0.95 ***	195	1.9	297	477.7	316	150.59 ***	173	1304	111	60.82 *
Residuals	103	0.19	371	0.69	95	1.94	240	412.3	153	27.77	70	1774	96	38.41
P-Variance		0.31		2.54		2.85		648.95		180.33		2840.34		56.96
G-Variance		0.06		0.58		0.62		61.98		15.51		328.78		7.31
GxE-Variance		0.02		0.17		0.05		42.27		114.55		122.75		8.36
Env-Variance		0.04		1.10		0.23		132.39		22.50		614.80		2.88

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Source	DF	GYD	DF	FFAWD Average	DF	EFAWD	DF	PH	DF	AD	DF	ER	DF	НС
PCV (%)		126.03		32.67		55.50		27,036.00		17.81		108.14		241.42
GCV (%)		54.94		15.54		25.97		8.46		5.23		36.79		86.48
Heritability (%)		0.79		0.92		0.77		0.60		0.46		0.68		0.42
LSD		0.82		1.62		2.63		39.44		10.42		71.12		12.83
Grand mean		0.44		4.88		3.04		93.10		75.38		49.29		3.13
Minimum		0.20		2.62		1.89		79.08		69.57		23.62		1.84
Maximum		1.18		6.34		5.18		106.28		90.79		86.29		12.12

^{*} p < 0.05; *** p < 0.01; *** p < 0.001; DF = degrees of freedom; GYD = grain yield; FFAWD-Avg = average foliar fall armyworm damage; EFAWD = ear fall armyworm damage; PH = plant height; AD = anthesis date; ER = ear rot; HC = husk cover; Rep = replication; Env = environment; p-Variance = phenotypic variance; G-Variance = genotypic variance; PCV = phenotypic coefficient of variance; GCV = genotypic coefficient of variance; LSD = least significant difference.

3.2. Private and Public Sector Hybrids and Open Pollinated Varieties with Substantial Levels of Fall Armyworm Tolerance and Superior Yield Performance

In Table 5, the commercial genotypes were grouped according to source of development for easier interpretation. Among the private sector commercial cultivars that were identified as showing tolerance to FAW according to the Davies scoring scale, the hybrids PAN53 (average FFAWD = 4.73, EFAWD = 2.65; GYD = 3.85 t ha $^{-1}$), Mutsa MN521 (average FFAWD = 4.58, EFAWD = 2.88; GYD = 3.63 t ha $^{-1}$), ZAP61 (average FFAWD = 4.77, EFAWD = 3.18; GYD = 3.13 t ha $^{-1}$) and Manjanja MN421 (average FFAWD = 4.74, EFAWD = 2.95; GYD = 3.09 t ha $^{-1}$) had good grain yield potential and showed partial tolerance to FAW. Within the public sector cluster (national breeding program), the DR&SS registered varieties, ZS246A (average FFAWD = 4.51, EFAWD = 2.73; GYD = 3.24 t ha $^{-1}$) and ZS242A (average FFAWD = 4.38, EFAWD = 2.92; GYD = 3.04 t ha $^{-1}$), as well as an experimental hybrid identified as 113WH330 (average FFAWD = 4.81, EFAWD = 2.72; GYD = 3.23 t ha $^{-1}$) were the best in terms of FAW tolerance and grain yield performance. Additionally, in the public sector (CIMMYT breeding program), a total of eight experimental hybrids showing FAW tolerance and good grain yield performance under FAW infestation were identified. All these genotypes had a statistically similar yield.

Table 5. Identified fall armyworm resistant genotypes with acceptable yield among the 60 entries evaluated across natural Fall armyworm infested sites in Zimbabwe during the 2019–2020 seasons.

	Cultivar Name	Entry	GYD t ha ⁻¹	Rank	FFAWD 4 wks	FFAWD 8 wks	FFAWD 12 wks	FFAWD Avg	EFAWD
	PAN53	31	3.85	1	5.31	5.06	3.81	4.73	2.65
Private Sector	Mutsa MN521	40	3.63	4	5.15	4.79	3.93	4.58	2.88
Cultivars	Manjanja MN421	39	3.09	15	5.25	5.02	4.17	4.74	2.95
Cultivars	ZAP61	44	3.13	13	5.23	4.98	4.25	4.77	3.18
Public Sector	ZS246A	21	3.24	9	5.26	4.90	3.72	4.51	2.73
(DR&SS)	ZS242A	20	3.04	20	5.17	4.60	3.59	4.38	2.92
Cultivars	113WH330	24	3.23	10	5.37	5.04	4.09	4.81	2.72
	CZH128	29	3.60	5	4.97	5.10	4.13	4.78	2.59
	CIMExp/334	55	3.35	7	5.35	4.66	3.65	4.40	2.54
Public Sector	CML571/CML338	60	3.13	12	4.88	4.17	3.39	4.09	2.39
	CIMExp54/CML334	54	3.08	16	5.33	4.68	3.87	4.48	2.70
(CIMMYT)	CIMExp52/CML139	52	3.06	17	5.32	5.02	3.61	4.55	2.47
Experimentals	CML338/CML334	49	3.03	21	5.16	4.15	3.46	4.02	2.24
	CIMExp58/CML121	58	3.00	22	4.76	3.74	3.54	3.78	2.20
	CML543/CML334	59	3.00	23	5.26	4.64	4.19	4.49	2.50
	Heritability		0.82		0.52	0.82	0.77	0.87	0.49
	Grand Mean		2.57		5.38	5.10	4.26	4.88	2.74

GYD = grain yield; FFAWD-Avg = average foliar fall armyworm damage; FFAWD 4 wks = foliar fall armyworm damage at 4 weeks after crop emergence; FFAWD 8 wks = foliar fall armyworm damage at 8 weeks after crop emergence; FFAWD 12 wks = foliar fall armyworm damage at 12 weeks after crop emergence; EFAWD = ear fall armyworm damage.

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With the exception of CZH128 (average FFAWD = 4.78, EFAWD = 2.59; GYD = 3.60 t ha⁻¹), the other seven hybrids were crosses between a FAW resistant donor inbred line parent with a CIMMYT elite line, designated as CIMMYT maize line (CML) or an experimental inbred line parent. For example, genotype 55 (CIMExp/CML334) (GYD = 3.35 t ha⁻¹), a cross between a CIMMYT experimental inbred line and a late flowering FAW resistant donor inbred line parent, CML334, ranked seventh for grain yield performance among the 60 evaluated genotypes under natural FAW infestation.

There was a general trend of decreasing FFAWD scores for FAW resistant hybrids from 4 to 12 weeks after planting (Table 5). All commercial cultivars and experimental hybrids had the lowest scores at 12 weeks after crop emergence. FFAWD tolerance of some of the genotypes is likely due to non-preference resulting from increased pubescence on stems and leaves. This was particularly true for the experimental hybrids from crosses between FAW resistant donor inbred line parents (such as genotype CML338/CML67) that had minimal damage on leaves, silks, and ears.

3.3. Grain Yield and Agronomic Performance of Cultivars, Experimental Hybrids, and Inbred Lines under Control (Managed Fall Armyworm) Conditions

The mean grain yield performance under control conditions in the commercial cultivar/hybrid trial was 5.99 t ha^{-1} , while the mean average FFAWD and EFAWD scores were 0.36 and 0.44 respectively (Table 6). The top 10 commercial genotypes and top 10 inbred lines in terms of yield, with their associated characteristics, were also listed in Table 6. The best performers were PAN-7M-81 (GYD = 8.96 t ha^{-1} , average FFAWD = 2.46, EFAWD = 2.51), PHB30G19 (GYD = 8.87 t ha^{-1} , average FFAWD = 2.44, EFAWD = 1.94), PAN-4M-23 (GYD = 8.62 t ha^{-1} , average FFAWD = 2.63, EFAWD = 2.14), PAN53 (GYD = 8.40 t ha^{-1} , average FFAWD = 2.70, EFAWD = 1.92), Mukwa (GYD = 8.39 t ha^{-1} , average FFAWD = 2.52, EFAWD = 2.28), ZS265 (GYD = 7.78 t ha^{-1} , FFAWD = 2.62, EFAWD = 1.90), ZS269 (GYD = 7.65 t ha^{-1} , Avg-FFAWD = 2.63, EFAWD = 2.16), and NTS51 (GYD = 7.64 t ha^{-1} , average FFAWD = 2.47, EFAWD = 2.38). The hybrids CIMExp/CML345 and CML338/CML334 were the only two experimental hybrids that were among the best 10 yielding entries under control conditions.

Table 6. Grain yield and agronomic performance of the best ten cultivars and experimental hybrids and best ten inbred lines evaluated under managed fall armyworm conditions in Zimbabwe during the 2019–2020 seasons.

Cultivar Name	Genotype	GYD	Rank	PH	ЕН	AD	FFAWD 4 wks	FFAWD 8 wks	FFAWD 12 wks	FFAWD Avg	EFAWD	ER
PAN-7M-81	33	8.96	1	192.01	83.50	71.02	2.43	2.36	2.64	2.46	2.51	17.36
PHB30G19	34	8.87	2	184.03	78.61	68.18	2.63	2.26	2.52	2.44	1.94	8.99
PAN4M-23	32	8.62	3	174.09	74.55	70.07	2.65	2.37	2.76	2.63	2.14	20.44
PAN53	31	8.40	4	184.53	74.38	69.13	2.70	2.47	2.64	2.70	1.92	15.66
Mukwa	42	8.39	5	174.64	74.80	69.60	2.46	2.48	2.64	2.52	2.28	19.42
CIMExp/345	53	7.95	6	175.50	62.58	68.83	2.49	2.33	2.61	2.46	2.04	14.78
CML338/CML334	49	7.82	7	195.12	74.56	69.29	2.52	2.27	2.64	2.46	2.01	25.83
ZS265	13	7.78	8	178.15	81.18	69.13	2.49	2.58	2.87	2.62	1.90	14.57
ZS269	14	7.65	9	189.93	79.82	70.55	2.64	2.49	2.64	2.63	2.16	13.95
NTS51	30	7.64	10	185.38	69.66	68.66	2.50	2.47	2.52	2.47	2.38	21.69
Heritabili	ity	0.80		0.65	0.59	0.63	0.18	0.42	0.24	0.36	0.44	0.68
Grand Me	ean	5.99		176.45	71.48	69.36	2.60	2.45	2.69	2.62	2.22	23.81
LSD		2.73		29.09	21.92	4.92	1.48	1.10	1.56	0.97	1.32	25.74
Inbred lines												
CML121	55	1.16		1		8	6.47	2.62	2.97	2.69	1.78	
CML304	27	1.09		2		8	3.22	3.08	3.32	3.13	3.15	
SV1P	9	1.05		3		7	0.87	3.23	3.06	3.06	3.22	

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Cultivar Name	Genotype	GYD	Rank	РН	ЕН	AD	FFAWD 4 wks	FFAWD 8 wks	FFAWD 12 wks	FFAWD Avg	EFAWD	ER
CML334	48	1.05		4		8	6.16	2.83	3.55	3.09	2.77	
CML491	30	1.01		5		8	0.45	3.62	3.49	3.40	3.70	
CML338	47	0.95		6		7	6.28	2.75	2.89	2.78	1.63	
CZL1112	61	0.95		7		8	0.44	4.00	4.21	3.98	2.47	
DPTY9 * 9	38	0.94		8		7	8.80	3.52	3.07	3.25	3.45	
CML539	46	0.92		9		7	6.70	3.49	3.54	3.49	3.48	
CZL1315	40	0.91		10		7	9.08	3.48	3.36	3.24	2.84	
Heritabil	ity	0.20						0.63	0.66		0.69	
Grand Me	ean	0.77						3.96	4.12		81.94	
LSD		1.35				9	9.34	2.03	2.48	1.81	1.96	

GYD = grain yield; FFAWD-Avg = average foliar fall armyworm damage; FFAWD 4 wks = foliar fall armyworm damage at 4 weeks after crop emergence; FFAWD 8 wks = foliar fall armyworm damage at 8 weeks after crop emergence; FFAWD 12 wks = foliar fall armyworm damage at 12 weeks after crop emergence; EFAWD = ear fall armyworm damage; AD = anthesis date.

In contrast to this, grain yields were not significantly different for inbred lines under control conditions at Harare during the 2019 and 2020 summer seasons (Table 6). However, genotypes showed differential performance (p < 0.05) for average FFAWD, FFAWD at 12 weeks, EFAWD and AD while there were no differences across genotypes for FFAWD at 8 weeks. The mean GYD for inbred lines under managed FAW was 0.77 t ha⁻¹, and the means for average FFAWD and EFAWD were 3.88 and 3.37 respectively.

3.4. Sources of Fall Armyworm Tolerance in Public Sector Breeding Programs

For the selected public sector (National and CIMMYT breeding programs) FAW resistant genotypes (listed in Table 5), parental inbred lines making up the hybrids were tracked in inbred line trials in order to explore sources of tolerance among the publicly available maize germplasm pools in Zimbabwe (Table 7). From the national breeding program registered cultivars, the parental inbred line CLHP0005 (average FFAWD Rank = 9; average FFAWD = 4.39; EFAWD = 4.61; GYD = 0.5 t ha $^{-1}$), which is a parental line in the hybrids ZS246A and ZS242A, proved to be the best source for FAW resistance. From the CIMMYT breeding program, an inbred line parent identified as CML334 (average FFAWD Rank = 8; average FFAWD = 4.35; EFAWD = 2.01; GYD = 0.48 t ha $^{-1}$), a parental line in the experimental hybrid, CIMExp/CML334, was identified as the best source of FAW resistance.

Comparing mean grain yields attained under natural FAW infestation (2.57 t ha $^{-1}$) against 5.99 t ha $^{-1}$ realized under managed conditions, FAW infestation caused a yield loss of 57.1% in hybrids and OPVs evaluated under the commercial cultivar and experimental hybrid trials (Tables 5 and 6). Slightly lower, but similar yield damage was also observed on inbred lines where the average grain yield performance under FAW stress was 0.39 t ha $^{-1}$ while it was 0.77 t ha $^{-1}$ under managed conditions (Tables 6 and 7). This translates to a yield penalty of 49.4%.

The other potential sources of FAW resistance, but that are not involved as parents in the selected hybrid genotypes, were CML67 (average FFAWD Rank = 1; average FFAWD = 2.75; EFAWD = 3.48; GYD = 0.50 t ha $^{-1}$), CML121 (average FFAWD Rank = 2; Avg-FFAWD = 3.05; EFAWD = 2.33; GYD = 0.57 t ha $^{-1}$), CML338 (average FFAWD Rank = 3; average FFAWD = 3.63; EFAWD = 2.82; GYD = 0.62 t ha $^{-1}$); CML346 (average FFAWD Rank = 4; average FFAWD = 3.79; EFAWD = 2.47; GYD = 0.44 t ha $^{-1}$), SV1P (average FFAWD Rank = 5; average FFAWD = 3.89; EFAWD = 2.46; GYD = 1.05 t ha $^{-1}$), and CML331 and CML491, with the majority of them being CIMMYT FAW tolerance donor lines (Table 7). The most susceptible lines were WW01408 (average FFAWD Rank = 61; average FFAWD = 6.04; EFAWD = 3.02; GYD = 0.28 t ha $^{-1}$) and HX482P (average FFAWD

Rank = 62; average FFAWD = 6.39; EFAWD = 3.17; GYD = 0.28 t ha⁻¹) (Table 6). The inbred lines SV1P and CML491 are parents of commercial cultivars.

Table 7. Fall armyworm tolerance and grain yield performance of inbred parental lines of FAW resistant public commercial and experimental hybrids and other FAW resistant inbred lines evaluated under natural FAW infested sites in Zimbabwe during the 2019–2020 seasons.

	Genotype Name	Genotype Code	FFAWD Average	Rank	FFAWD 4 wks	FFAWD 8 wks	FFAWD 12 wks	EFAWD	GYD t ha ⁻¹	ER%	AD	НС	PH
Parental inbred lines	CLHP0005	25	4.39	9	4.61	4.61	4.93	3.47	0.50	41.77	73.49	4.88	102.58
	CML304	27	4.60	10	4.43	5.13	4.67	2.41	0.51	35.14	74.01	4.18	104.94
	CZL1227	42	4.86	16	4.53	5.06	5.33	2.48	0.61	35.50	77.32	4.47	97.08
	CML444	28	5.67	52	4.67	6.22	6.04	2.80	0.35	61.78	76.19	3.50	92.80
	CML543	57	6.02	60	4.95	6.58	6.49	2.36	0.23	36.56	76.97	2.08	88.51
	CML395	34	5.81	54	5.03	6.51	6.19	2.39	0.39	35.45	75.83	2.04	91.21
	CML334	48	4.35	8	4.46	4.66	4.96	2.01	0.48	42.08	77.70	2.32	99.74
	CML312	33	5.19	29	4.05	5.53	5.84	2.72	0.39	46.26	75.81	4.61	98.92
	CLHP00478	36	5.19	30	4.73	5.50	5.43	2.73	0.35	34.74	73.07	4.24	94.61
	CML139	51	5.34	35	4.66	6.00	5.71	1.96	0.30	46.97	76.75	1.86	98.22
	CML571	52	4.65	11	4.17	5.23	4.46	3.82	0.30	48.33	74.49	1.96	97.53
	CLHP0003	24	4.91	18	4.50	5.26	5.11	3.23	0.45	42.81	73.13	5.03	97.10
	CIMExp54	60	5.08	24	4.47	5.57	5.11	2.60	0.61	33.04	74.15	2.88	92.70
Other good inbred lines	CML67	50	2.75	1	3.44	2.97	2.83	3.48	0.50	23.62	73.09	2.66	76.63
	CML121	55	3.05	2	3.69	3.01	3.78	2.33	0.57	29.06	73.77	1.96	92.84
	CML338	47	3.63	3	4.29	3.66	4.10	2.82	0.62	35.30	72.18	1.87	93.50
	CML346	53	3.79	4	4.09	4.10	4.04	2.47	0.44	26.25	73.89	2.42	96.68
	SV1P	9	3.89	5	4.12	4.07	4.38	2.46	1.05	29.75	69.61	2.53	100.57
	CML331	49	4.26	6	4.26	4.64	4.80	2.81	0.59	43.84	74.96	4.55	89.04
	CML491	30	4.30	7	4.29	4.67	4.88	2.89	0.99	28.53	73.43	1.86	92.15
Most	WW01408	23	6.04	61	4.72	6.56	7.00	3.02	0.28	45.31	75.32	3.03	82.84
susceptible	HX482P	18	6.39	62	4.42	7.08	7.23	3.17	0.28	61.81	76.34	2.33	80.63
	Heritability		0.90		0.59	0.88	0.86	0.72	0.74	0.68	0.40	0.42	0.66
	Mean		5.14		4.50	5.52	5.59	2.95	0.39	49.29	75.46	3.13	89.93
	LSD		1.60		1.51	2.21	2.26	2.73	0.69	71.12	10.41	12.83	36.58

GYD = grain yield; FFAWD-Avg = average foliar fall armyworm damage; FFAWD 4 wks = foliar fall armyworm damage at 4 weeks after crop emergence; FFAWD 8 wks = foliar fall armyworm damage at 8 weeks after crop emergence; FFAWD 12 wks = foliar fall armyworm damage at 12 weeks after crop emergence; EFAWD = ear fall armyworm damage; GYD = grain yield; ER = ear rot; AD = anthesis date; HC = husk cover; PH = plant height.

Genotypes that had higher EFAWD had corresponding higher levels of ER. Generally, ER increased with increasing levels of FFAWD, EFAWD, and open HC. CML67 had the lowest FFAWD scores, lowest incidence of ER, and lower levels of open HC compared to HX482P, which had higher FFAWD and EFAWD scores and ER counts (Table 7). Four of the FAW resistant donor inbred lines (CML67, CML121, CML346, and CML338) had good HC ranging between 1.86–2.66, which was comparable to that of SV1P and CML491. Line CML331 had HC counts that were comparable to those of CML304, CLHP0003, CLHP0005, and CML543. Contrary to the observation on commercial cultivars and experimental hybrids, inbred lines showed a general trend of increasing FFAWD from 4–12 weeks under FAW infestation across genotypes (Table 7). Ear rots were generally high, and they were significantly higher (p < 0.05) in older inbred lines, particularly those with higher FFAWD scores, such as HX482P and WW01408. Similarly, higher levels of poor HC were associated with high levels FFAWD and EFAWD.

3.5. Genetic Correlations between Fall Armyworm Damage Parameters and Grain Yield and Yield Related Variables across Genotypes and Environments

In both hybrids/OPVs and inbred line trials, FAW damage had significantly negative effects (p < 0.05) on grain yield performance across genotypes except for EFAWD on inbred lines where the correlation was very small, positive, and insignificant (Table 8). For hybrids/OPVs the negative correlation between GYD and FAW damage was highest between GYD and EFAWD (r = -0.57; p < 0.0001) and FFAWD at 12 weeks (r = -0.56;

p < 0.0001) (Table 8). ER had the highest negative effect on grain yield (r = -0.90, p < 0.0001). The associations between the different FAWD parameters were all positive and highly significant (p < 0.0001), ranging from a lowest of r = 0.52 between EFAWD and FFAWD at 8 weeks, and a highest of r = 0.99 between FFAWD at 4 and 8 weeks as well as between average FFAWD and FFAWD at 8 weeks (Table 8).

Table 8. Genetic correlations between grain yield and yield related traits with fall armyworm damage scores at different crop growth stages determined under natural fall armyworm infestation in Zimbabwe during 2019–2020 seasons.

Traits	GYD	FFAWD 4 wks	FFAWD 8 wks	FFAWD 12 wks	Avg FFAWD	EFAWD	AD	РН	НС
FFAWD_4_wks	-0.47 ***								
FFAWD_8_wks	-0.31 *	0.66 ***							
FFAWD_12_wks	-0.56 ***	0.99 ***	0.98 ***						
Avg_FFAWD	-0.43 ***	0.70 ***	0.99 ***	0.89 ***					
EFAWD	-0.57 ***	0.55 ***	0.52 ***	0.53 ***	0.43 ***				
AD	-0.29 *	0.73 ***	0.16	0.13	0.20	-0.38 **			
PH	0.56 ***	-0.46 ***	-0.27 *	-0.14	-0.18	-0.25	0.38 **		
HC	NA	NA	NA	NA	NA	NA	NA	NA	NA
ER	-0.90 ***	0.44 ***	0.53 ***	0.89 ***	0.58 ***	0.46 ***	0.56 ***	-0.05	NA
Traits	GYD	FFAWD 4 wks	FFAWD 8 wks	FFAWD 12 wks	Avg FFAWD	EFAWD	AD	РН	НС
FFAWD 4 wks	-0.99 ***								
FFAWD 8 wks	-0.48***	0.09							
FFAWD 12 wks	-0.44 **	0.54 ***	0.99 ***						
Avg FFAWD	-0.52 ***	0.03	1.00 ***	0.99 ***					
EFAWD	0.03	0.83 ***	0.14	0.62 ***	0.31 *				
AD	-0.54 ***	0.99 ***	0.72 ***	0.67 ***	0.63 ***	-0.21			
PH	-0.03	-0.07	-0.23	-0.13	-0.22	-0.74 ***	0.21		
HC	-0.83 ***	-0.01	0.04	-0.07	-0.09	0.46 ***	0.09	0.02	
ER	-0.67 ***	1.00 ***	0.68 ***	1.00 ***	0.75 ***	0.49 ***	0.12	-0.32 *	0.99 ***

* p < 0.05; ** p < 0.01; *** p < 0.001; GYD = grain yield; Avg-FFAWD = average foliar fall armyworm damage; FFAWD 4 wks = foliar fall armyworm damage at 4 weeks after crop emergence; FFAWD 8 wks = foliar fall armyworm damage at 8 weeks after crop emergence; FFAWD 12 wks = foliar fall armyworm damage at 12 weeks after crop emergence; EFAWD = ear fall armyworm damage; AD = anthesis date; PH = plant height; HC = husk cover; ER = ear rot.

Again, ER showed high positive and highly significant (p < 0.0001) correlations with FAWD parameters. Similarly, PH positively and significantly (p < 0.001) correlated with GYD and AD (Table 8). For inbred lines, the associations between FAWD parameters were all positive and highly significant (p < 0.0001) except for average FFAWD with FFAWD at 4 weeks (r = 0.03) and EFAWD with FFAWD at 8 weeks (r = 0.14).

EFAWD correlated highly negatively (r = -0.74, p < 0.0001) with PH. In contrast, EFAWD showed positive and highly significant associations with HC (r = 0.46; p < 0.0001) and ER (r = 0.49; p < 0.0001). Plant height was negatively associated with GYD and all FAW damage parameters, but only significantly for EFAWD (r = -0.74; p < 0.0001) (Table 8).

4. Discussion

This study evaluated two sets of germplasm for their tolerance to FAW and superior grain yield performance on sites with naturally moderate to high FAW infestation, designated as natural infestation environments, as well as under controlled FAW conditions (managed FAW). FAW populations were not quantified, but infestation pressure in all environments was sufficient to cause a differential response across genotypes. No other pests were observed on the trials during the growing season, although Chiredzi and Chisumbanje do often have stalk borer infestation. This implies that varietal screening for FAW tolerance can be effectively implemented under natural FAW infestation. The

current study is the second reported study that has evaluated germplasm resources in SSA under natural FAW infestation after the first [31]. The findings are encouraging for national research programs and other breeding programs across SSA that have no access to artificial screening environments for FAW tolerance breeding, as they can effectively evaluate their breeding materials under natural FAW infestation. The highly significant differences between genotypes demonstrated that there is sufficient genetic variability for effective FAW tolerance breeding. Average FFAWD scores as low as 4.49 and as high as 5.98 were observed in the hybrid/OPV germplasm set while 2.75 and 6.39 were the lowest and highest average FFAWD scores recorded on inbred lines. These differ from the average FFAWD and EFAWD values of 2.62 and 2.22, respectively, for cultivars, and 3.88 and 3.37, respectively, for inbred lines, observed under managed FAW conditions. Generally, FFAWD scores were lowest and highest on inbred lines compared to commercial cultivars and experimental hybrids. This is primarily because hybrids and OPVs, which constituted the commercial cultivars and experimental hybrids, are generally vigorous and tend to tolerate FAW attacks better than inbred lines. This concurs with a previous study [32] which reported that vigorous genotypes, particularly those showing heterosis, can out-perform their inbred line counterparts that are affected by slow growth and inbreeding depression.

Vigorous genotypes showed a general tendency to grow out of FFAWD as they developed from young to mature plants. Highest FFAWD scores were observed at 4 weeks after crop emergence and the scores improved from 8–12 weeks after crop emergence. Genotype CML543/CML334 had a Davis score of 6.43 at 4 weeks after crop emergence, and then recorded 5.70 and 4.66 at 8 and 12 weeks after crop emergence, respectively. In contrast, inbred line FFAWD scores generally increased over time of 4, 8 and 12 weeks after crop emergence. This further supports the fact that inbred lines are less vigorous, weaker and have slower growth compared to hybrids and landraces [33,34], hence they tend to suffer more foliar FAW damage compared to hybrids and OPVs. Maize generally has the capacity to recover from moderate to average FAW foliar damage [25]. However, this is only possible under good moisture and nutrient conditions.

Lower FFAWD scores were noted on hybrids constituted from CIMMYT lines and FAW donor lines as well as crosses between donor lines. This indicates that FAW donor lines included in this study have the potential to resist FAW and can be used to quickly develop hybrids that can be used in the interim to protect smallholder farmers' maize crop from FAW damage. The experiences from the Americas were reviewed as possibly helping in reducing the impact of FAW in Africa and Asia, which highlighted varietal acceptance concerns due to preferences [12] which is an issue in this study as well. The most resistant donor lines were CML67, CML121, and CML338, which have red and yellow grains and may not be readily accepted by farmers and consumers in Zimbabwe and most of ESA due to color preference for white maize [20]. In contrast, the lines CML346, CML139, and CML334 showed acceptable FAW tolerance both as hybrid parents and inbred lines. The three have white flint-like to flint grains, hence hybrids constituted from these may be quickly accepted by farmers in the region. It is therefore imperative that maize breeders consider these in developing white maize hybrids that can be rapidly released to counter the effects of FAW attack on maize. In addition, as was suggested by the water efficient maize for Africa (WEMA) project findings [11,35], gene stacking through introgression crosses among FAW resistant donor lines, together with elite and adapted FAW resistant lines such as SV1P and CML491, can result in good tolerance against FAW.

Two orange maize cultivars ZS242A and ZS246A, and four white grain cultivars, which include the very early—early maturing hybrids, Manjanja MN421 and Mutsa MN521 and the medium maturity hybrids PAN53 and ZAP61, were the only commercial hybrids that were among the top performers under FAW infestation. The list of the least resistant cultivars to FFAWD was dominated by most of the hybrids that are currently active and dominant on the market, as well as some old OPVs released by DR&SS. This suggests that most smallholder farmers who have limited capacity to control FAW using chemicals may suffer significant FFAWD damage from the pest. However, GYD rankings of cultivars and

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experimental varieties evaluated under FAW infestation showed that the pool of current commercial cultivars, despite being susceptible to FAW damage, still out-yielded most experimental varieties constituted from FAW donor lines. This was also reported in a previous study in the Americas [36] which found that agronomically good genotypes were susceptible to FAW, but they still yielded better than the resistant, but agronomically poor genotypes. In southern Africa it was reported [14,15] that cultivars in commercial production are susceptible to FAW, with yield losses in the range of 11.5–16.4%. There is need to introgress FAW tolerance in parental lines of commercial cultivars so that they can perform better under FAW infestation. The three hybrids PAN53, ZS246A, and Mutsa MN521 that were identified among the most FFAWD resistant cultivars, were also among the top 10 grain yielders under FAW infestation. Inbred lines CLHP0005 and CML304 are parental lines for ZS242A, and CLHP0005 is also a parent of the hybrid ZS246A. These two hybrids exhibited superior grain yield performance and low FFAWD scores under natural FAW infestation. This implies that the superior performance of ZS242A and ZS246A under FAW infestation was due to the superiority of their parental inbred lines under FAW infestation conditions, particularly CLHP0005. Further improvement through FAW tolerance introgression on these lines will likely enhance FAW tolerance in these improved cultivars.

The inbred lines SV1P and CML491 are commercial inbred lines developed and registered by DR&SS and CIMMYT respectively. In this study, these two inbred lines demonstrated outstanding tolerance to FAW damage and the ability to yield significantly better under FAW infestation compared to most of the commercial inbred lines evaluated. SV1P is a parent of commercial cultivar ZS259 that is currently off the market in Zimbabwe, and was not included in this study. The quality protein maize (QPM) inbred line CML491 is a parent of a released QPM maize hybrid in Zimbabwe, ZS225Q. The hybrid was included in the study, but it was omitted from the analysis due to poor germination. The superior tolerance to FAW of CML491 was also noted and reported previously [31] in Zambia. Further breeding using these two inbred lines has good potential for the development of elite, adapted, and productive lines with enhanced FAW resistance.

SV1P is an extra early maturing genotype. This suggests that most of its FAW tolerance could have been due to early growth and development. This inbred line has the ability to grow fast, therefore flowering and maturing early. This could allow its rapid growth through the most vulnerable and preferred growth stages by FAW [11,33]. A study in Zambia [32] identified an extra early OPV, Pool 16, among the genotypes selected for good tolerance to FAW. The current study noted that AD was highly significant and positively correlated with FFAWD, this indicates that genotypes that mature early have the capacity to escape FAW damage as observed in this study as well as previously [31]. Again, CML539 was selected among the genotypes that exhibited low levels of FAW damage during early stages of growth. CML539 is an early maturing inbred line developed by CIMMYT. In the current study, the inbred line CML539 was again identified among the top 10 grain yielders under FAW infestation, with a yield of 0.92 t ha⁻¹. Another local commercial line, DPTY9...*9 was among the best grain yielders under FAW infestation.

A number of studies have reported that depending on level of infestation, FAW damage can cause yield losses of up to 100% [37–40]. Comparing the grain yields realized under natural FAW infestation with those attained under managed FAW conditions, the current study showed a yield penalty of between 49–57% due to FAW infestation. This concurs with 2017 figures reported in Kenya [40]. They noted grain yield losses in the range of 53–54%. This is also in line with observations in a study in Nicaragua [33] where 15–73% yield losses from 55–100% infestation at mid to late whorl stages were reported. The same study noted that maize is more tolerant to FAW infestation at early vegetative growth stages. This differs from observations from the current study that hybrids and OPVs are more vulnerable at early growth stages, and they grow out of the FAW damage as they develop through mid to late whorl stages. Similarly, inbred lines were more vulnerable

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at early vegetative growth stages and without any control efforts, and unlike hybrids and OPVs, inbred lines showed a trend of increasing damage as they grew to maturity.

The different FAWD parameters which included FFAWD at 4 weeks, FFAWD at 8 weeks, FFAWD at 12 weeks and EFAWD, showed high positive correlations among them, suggesting that only one of these can be used for selection. For hybrids and OPVs, PH showed high and positive associations with GYD and AD. This shows that PH is a good indicator of yield under FAW infestation. The inbred lines showed high and positive associations of EFAWD with HC and ER. This suggested that genotypes with poor HC are likely to have high EFAWD and ER.

5. Conclusions

This study demonstrated that screening for FAW tolerance can be effectively performed under natural infestation conditions. Most cultivars currently in production have poor tolerance to FAW, with a few exceptions, which include PAN53, ZS242A, ZS246A, Mutsa MN521, Manajanja MN421, and ZAP61. Though most cultivars are susceptible to FAW, their vigor allows them to produce acceptable grain yield, as they tend to grow out of FAW damage over time. The commercial inbred lines SV1P and CML491 exhibited acceptable FAW resistance, and together with CML539, CLHP0005, CML304, and DPTY9 ... *9 they produced high grain yield under FAW infestation. These lines are recommended as potential sources for breeding for FAW resistance. HC, ER, AD, and PH were correlated with FAW resistance, hence they can be used for selecting genotypes resistant to FAW. FAW infestation in this study reduced grain yield by 49%–57%.

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