



Characterization of antixenosis and antibiosis resistance to the fall armyworm, *Spodoptera frugiperda* (J.E. Smith) in maize

Lakshmi Soujanya Pamidi · J. C. Sekhar · K. R. Yathish · Chikkappa G Karjagi · K. Sankara Rao · S. B. Suby · Sujay Rakshit

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Abstract Fall armyworm (FAW) *Spodoptera frugiperda* (J.E. Smith) is an invasive insect pest that poses a severe threat to maize production affecting the livelihood and food security of small holder farmers in African and Asian countries. Host plant resistance is one of the potential methods for FAW management in a sustainable manner. Identification of genotypes with different categories of resistance is important to diversify the basis of resistance to FAW. This study aimed to characterize the antixenosis and antibiosis resistance through oviposition, developmental and survival parameters of FAW on 16 diverse maize genotypes. Antixenosis was assayed under no-choice and multi-choice conditions, while antibiosis was assayed in bioassays in which larvae were reared on leaf tissue. Genotype CML 336 showed strong antixenosis both under no-choice and multi-choice conditions while the genotypes DMRE 63, CML 59, CML 60, CML 70, and CML 501 exhibited antixenosis under multi-choice conditions. Genotypes CML 122, CML

330, CML 332 and CML 337 showed antibiosis characteristics and resulted in prolonged duration of the larval period. Further, the low larval survival (%), larval weight, and pupal weight when fed on DMRE 63 indicated that antibiosis could be conferring resistance to FAW. Based on GGE biplot analysis, the resistant genotypes (DMRE 63, CML 70, CML 337, and CML 122) were grouped along with group one parameters namely larval period and pupal period. The present study provides information on different categories of resistance in maize genotypes and results could be used in breeding programmes focusing on maize resistance to FAW.

Keywords Antixenosis · Antibiosis · Fall armyworm · Maize · Resistance categories · GGE biplot

Introduction

Maize (*Zea mays* L.) is a multifaceted cereal crop grown in diverse agroecological regions. It is used as food, feed, fodder, and raw material for industrial purposes. Among the pests that attack maize and affect its production, the fall armyworm (FAW), *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), native to the neotropics of the Americas (Sparks, 1979; Andrews, 1980;) is most economically important in African and Asian countries. Its first report outside the Americas was in Central

L. S. Pamidi (✉) · J. C. Sekhar · K. R. Yathish · K. S. Rao
Winter Nursery Centre, ICAR-Indian Institute of Maize Research, Rajendranagar, Hyderabad 500030, India
e-mail: soujanya.scientist@gmail.com

C. G. Karjagi · S. B. Suby
ICAR-Indian Institute of Maize Research, Delhi Unit, Pusa Campus, New Delhi 110 012, India

S. Rakshit
ICAR-Indian Institute of Agricultural Biotechnology, Garkhatanga, Ranchi 834 003, India

and West African countries in 2016 (Georgen et al. 2016). It later spread to almost all of the sub-Saharan African continent (Stokstad, 2017). Subsequently, FAW moved beyond Africa and invaded for the first time the Indian sub-continent in May 2018 and became the major insect in maize-growing ecologies within one year (Rakshit et al., 2019). FAW has since also been reported from Yemen, Bangladesh, China (Wu et al., 2019), and other Asia-Pacific countries by 2019 and to Queensland, Australia by February 2020 (Qi et al., 2021). FAW is a migratory pest and it is highly polyphagous, with a wide host range (> 350) plant species with a strong preference for maize (Montezano et al., 2018). The rapid dispersal of FAW indicates its threat in new habitats (Nagoshi et al., 2019) which poses a significant challenge to global food security.

FAW larvae damage maize at all crop growth stages and can cause 60% yield losses if not well managed (Farias et al., 2014). During the vegetative stage, it feeds on tender leaf whorls and young seedlings whereas, at the reproductive stage, it prefers developing ears. Although FAW can be managed with insecticides, the efficacy of chemical control is limited and inconsistent because larvae feed inside whorls of plants where contact insecticides do not reach (Cruz, 1995; Harrison et al., 2019). Furthermore, extensive use of insecticides may result in the development of resistant FAW populations, pest resurgence, and environmental hazards (Roubos et al., 2014). Therefore, under the present scenario, exploration and development of sustainable alternatives for FAW management is needed.

Host plant resistance (HPR) is one of the most important components of integrated pest management (IPM), and plays an important role in the development of environmentally friendly strategies for insect pest management (Smith, 2005; Stout, 2014). Deployment of resistant genotypes minimizes insecticide applications thereby reducing the cost of production and/or insect control. HPR, which results in reduced insecticide applications, also helps to maintain populations of natural enemies under field conditions (Abrol, 2013; Mohankumar & Ramasubramanian, 2014). Several maize germplasms have been evaluated to identify resistant sources against FAW (Wiseman et al., 1996; Ni et al., 2014; Abel et al., 2020; Prasanna et al., 2021, 2022; Lakshmi Soujanya et al., 2022). However, studies on the characterization

of resistance to FAW using diverse maize genotypes are limited.

Plants withstand herbivore attacks through morphological, biochemical, and molecular mechanisms (Womack et al., 2018). The known categories of resistance that impart HPR are non-preference, antibiosis, and tolerance (Painter, 1951). Antixenosis refers to plant traits affecting herbivore behaviour in ways that 'direct' herbivores away from a host plant and reduce the preference for, or acceptance of a plant as a host by a herbivore (Kogan & Ortman, 1978) whereas antibiosis refers to a reduction in the fitness of herbivores upon feeding resulting in mortality or reduced longevity and fecundity of insects (Horgan et al., 2021). The major category responsible for FAW resistance in maize is reported to be antibiosis (Wiseman et al., 1981; Wiseman & Widstrom, 1986; Williams & Davis, 1997; Paiva et al., 2016; Morales, 2021). Tolerance refers to the ability of a plant to withstand or compensate for herbivore injury such that damage (yield or fitness loss) per unit injury is reduced (Stout, 2019).

Thus the resistance categories must be understood in the context of the relative importance of antixenosis/non-preference, antibiosis, and interaction among them concerning oviposition, survival, and developmental parameters of FAW to develop maize genotypes with high levels of resistance. Therefore, the present study was conducted with the following specific objectives: (i) to determine the preference of relative attractiveness of maize genotypes to FAW females for oviposition under multi-choice and no-choice conditions and (ii) to characterize the expression of antibiosis in diverse maize genotypes through detached leaf whorl assays under laboratory conditions.

Materials and methods

Maize genotypes

A set of 16 diverse maize genotypes were selected out of 94 lines based on leaf damage rating on a 1–9 scale to characterize the resistance against FAW (Lakshmi Soujanya et al., 2022). The genotypes selected for the study were previously screened against FAW under artificial infestation under net-house conditions. The genotypes included inbred lines of different kernel

colors and textures developed from diverse genetic backgrounds at ICAR-IIMR/AICRP centers (6) and CIMMYT (10) (Table 1).

Rearing of FAW

The initial population of FAW larvae was collected from infested plants in the experimental field at the Winter Nursery Centre, Hyderabad, India. The FAW larvae were reared on a chickpea flour-casein-based artificial diet (Singh & Rembold, 1992). The neonates were reared in groups of 50–100 in one-liter plastic jars containing a 2 to 3-mm layer of artificial diet on the bottom and sides for 5 days. Later, the larvae were transferred individually to 12-well plates (HiMedia) (each cell 2.5 cm in diameter and 2.3 cm in depth) to avoid cannibalism. The larvae were maintained in the laboratory at $28 \pm 1^\circ\text{C}$, $65 \pm 10\%$ RH under 16 h light/8 h dark in multi-well plates until pupation. The pupae were sterilized with 2% sodium hypochlorite solution and kept in groups of 25–50 in a one-liter plastic jar containing soil. After adult emergence, 10 pairs were released inside an oviposition cage (L=30 cm; D=23 cm). Adults were provided with a 10% honey solution in a cotton swab for feeding. The

blotting paper strips were hung inside the cage as an oviposition substrate. The strips were replaced daily and the eggs were sterilized with a 10% formalin solution. After egg hatching, the neonate larvae were transferred to plastic jars containing an artificial diet with a hairbrush, and the neonate larvae were used for all the experiments.

Assessing antixenosis resistance

The oviposition preference of female FAW adults, one of the antixenosis categories, was evaluated through no-choice and multi-choice conditions. As no-choice conditions are not adequate enough to test antixenosis, multi-choice conditions were also conducted. The no-choice and multi-choice tests were conducted in five replications by following a completely randomized design. For no-choice conditions, three seeds of each genotype were sown individually in five separate plastic pots (30 cm height, 30 cm top diameter, and 19 cm bottom diameter) filled with soil. Each plastic pot was covered with a cylindrical transparent nylon-mesh cage of 30 cm × 23 cm (length × diameter) dimension. The seed was allowed to germinate by watering the pots as per the requirement. The seedlings were thinned-out on

Table 1 The details of maize inbred lines used in the study

S.No	Genotype	Category	Grain colour/ texture	Source germplasm/Pedigree	Response of lines to FAW
1.	DMRE 63	Early	Orange, Flint	WNZPBTL 9	R
2.	CML 59	Medium	Yellow, Semi Flint	ANT11305-1-1-B11-2-3-B	MR
3.	CML 60	Medium	Yellow, Flint	ANTGP2-5-#-1-2-5-1-1-1-B	MR
4.	CML 70	Late	Flint	(ANTGP2-5-#-1/ANT38586-1)-6-B-2-3-1-B	MR
5.	CML 122	Medium	Yellow, Dent	(MP704/MP78-518)-8-3-4-B-4-2-3-B	MR
6.	CML 330	Early	White, Semi Dent	(SUWAN8422)/(P47/MP78-518)-#-7-1-1-1-1-1-B	MR
7.	CML 332	Early	White, Semi Dent	(SUWAN8422)/(P47/MP78-518)-#-183-1-7-3-1-2-B	MR
8.	CML 336	Early	Yellow, Dent	(TL8645)/(P47/MP78-518)-B-24-1-1-4-1-3-B	MR
9.	CML 337	Early	Yellow, Dent	(TL8645)/(P47/MP78-518)-B-24-1-3-2-1-2-B	R
10.	CML 405	Late	White, Flint	LAPOSTASEQ-C0-B*3-12-1-1-B	MR
11.	CML 501	Early	Yellow, Semi Flint	(CL02709/V)-B*3-1-1-B	MR
12.	CM 202	Late	Yellow, Dent	C121E	S
13.	CM 500	Early	Yellow, Flint	Antigua-Gr-I	S
14.	BML 6	Late	Yellow, Semi Dent	SRRL65-B96-1-1-2-#-2-2-1-X-1-1	S
15.	BML 7	Medium	Orange, Flint	[×2Y Pool × CML 226]-B 98 R-1-1-1-⊗ b -⊗ b -⊗ b -⊗ b	S
16.	WNZ Exoticpool	Early	Yellow, Flint	WNZPBTL1/2/3/4/5/6/7/8/9####	S

Response of lines to FAW was given based on leaf damage rating (1–9 scale) (Lakshmi Soujanya et al. 2022)

the third day after germination to maintain one seedling per pot. The seedlings of each genotype were grown separately by providing optimum growing conditions till the V5-6 stage. A pair of adult FAW moths (one male and one female) was introduced into each oviposition cage which consisted of a cylindrical transparent nylon-mesh cage in order to oviposit for two days. The adults were provided with a 10% honey solution soaked in cotton. For the multi-choice test, 16 pairs of FAW moths were introduced into oviposition cages in which pots were distributed circularly at equidistant and all test genotypes together covered by a cylindrical transparent nylon-mesh cage (Fig. 1). The oviposition preference was assessed at 48 h after the release of the pair of moths. In both no-choice and multi-choice tests, the number of eggs in egg batches was counted under a stereo-zoom microscope. A paintbrush with a fine tip was used to remove the egg scales. The number of egg layers were counted and the eggs from the outermost

layer were quantified and multiplied by the number of layers and the posterior eggs adjacent to the layer were also counted (Leuck & Perkins, 1972).

Assessing antibiosis resistance

Antibiosis was assessed by means of a leaf whorl assay. The experiment was conducted under laboratory conditions with 20 neonate larvae per replication by releasing each neonate larva into the leaf whorl of each genotype kept separately in the plastic rearing jars and covered with a muslin cloth. The bottom end of each maize stem was wrapped with a wet cotton swab to keep it in a turgid condition. The experiment was laid out in a completely randomized design with five replications. The leaf whorls of each genotype were changed once in two days until pupation. The insect feces and exuviae were removed at regular intervals to maintain aseptic conditions inside the jars. The observations



Fig. 1 Assessing antixenosis category of resistance through oviposition under no-choice (a) and multi-choice (b) conditions. c, d: Egg batch; e: Male adult; f: Female adult

were recorded on the number of larvae that survived at 10 days after release, larval weight at 10 days after release, larval period, pupal weight, pupal period, and percent adult emergence. The weights of larvae and pupae were determined with an analytical balance. The pupae were sexed by observing the abdomen morphology as described by Luginbill (1928).

Statistical analysis

The data generated on number of egg batches, number of eggs per egg batch, larval survival, larval period, larval weight, pupal period, pupal weight, and adult emergence were subjected to analysis of variance (ANOVA) by using a general linear model (PROC GLM), performed with SAS version 9.3 (SAS Institute, 2011). The Shapiro-Wilk normality test was performed before performing multiple comparisons and three out of the six parameters namely larval weight, pupal weight, adult emergence fulfilled the normality assumption, however, the remaining parameters were transformed to fulfill the normality assumption. The significance of differences between the genotype means was measured by *F*-test, while the treatment means were compared using Tukey HSD at $P=0.05$. To understand the interrelationship between different parameters of antibiosis, the mean values of different parameters of resistance mechanisms were further subjected to generate GGE biplot. The tester-centered (G+GE) biplot, which depicts the main effect of parameters and the interaction among the parameters together, was generated to visualize the interrelationship between different parameters of antibiosis and antixenosis (Yan & Holland, 2010). The genotype and genotype by environment biplot graphs were generated by using a graphical user interface package of R statistical software (R Core Team, 2015). The genotypes displaying the combination of different parameters determining antibiosis were identified using the genotype trait biplot.

Results

Antixenosis for oviposition in maize genotypes against FAW

The results of the egg load, a function of the total number of egg batches, and the total number of eggs

per batch under no-choice and multi-choice conditions are presented below.

No-choice conditions

The mean number of egg batches on different genotypes varied from 0.00 ± 0.00 (CML 336) to 1.80 ± 0.17 (WNZ Exoticpool). Significant differences were observed among the tested genotypes based on the mean number of egg batches (Table 2). No eggs were recorded on the genotype CML 336. The genotypes which recorded the lowest number of egg batches (0.80 ± 0.17) were CML 405 and CML 332. The other genotypes with a relatively higher numbers of egg batches were BML 6 (1.40 ± 0.21) and WNZ Exoticpool (1.80 ± 0.17).

The number of eggs per egg batch showed significant differences among genotypes. It varied from 0.00 ± 0.00 (CML 336) to 71.60 ± 1.63 (WNZ Exoticpool). Based on the number of eggs per egg batch test genotypes were classified into three groups: first group ≤ 30 eggs; second group: 31–50 eggs; third group: ≥ 50 eggs. Lower number of eggs per egg batch were represented by CML 59, CML 70, CML 122, CML 337, and DMRE 63 while the genotypes with a significantly higher number of eggs per egg batch were CML 405, WNZ Exoticpool, CML 501, BML 7, and CML 60. The remaining genotypes CML 330, CM 202, CML 332, CM 500, and BML 6 were numerically represented as intermediate between the groups.

Multi-choice conditions

The mean number of egg batches showed significant differences among genotypes (Table 2). The number of egg batches per plant varied from 0.00 ± 0.00 to 1.60 ± 0.21 . Six genotypes, namely, DMRE 63, CML 59, CML 60, CML 70, CML 336 and CML 501 recorded no egg batch under multi-choice conditions. The number of egg batches in the rest of the genotypes varied from 1.00 to 1.60. In two genotypes, namely, CML 330 and CML 337, the number of egg batches was intermediate (1.00 ± 0.28) whereas the highest number of egg batches was recorded on WNZ Exoticpool. In the remaining genotypes, the egg batches were higher with significant differences in CM 202, CM 500, BML 6, CML 122, CML 332, CML 405, and BML 7. The number of eggs per egg batch showed significant differences among genotypes, which varied

Table 2 The mean egg batches and mean total number of eggs of fall armyworm on different maize genotypes under no-choice and multi-choice conditions

Genotypes	No-Choice assay		Multi-Choice assay	
	Number of egg batches	Number of eggs in egg batch	Number of egg batches	Number of eggs in egg batch
DMRE 63	1.2±0.17 ^a	29.2±1.46 ^{efd}	0.0±0.00 ^b	0.0±0.00 ^g
CML 59	1.0±0.00 ^{ab}	10.4±1.75 ^{gf}	0.0±0.00 ^b	0.0±0.00 ^g
CML 60	1.0±0.00 ^{ab}	60.2±1.11 ^{ab}	0.0±0.00 ^b	0.0±0.00 ^g
CML 70	1.0±0.28 ^{ab}	23.6±6.25 ^{ef}	0.0±0.00 ^b	0.0±0.00 ^g
CML 122	1.2±0.17 ^a	23.4±1.21 ^{ef}	1.4±0.21 ^a	43.2±0.97 ^c
CML 330	1.0±0.28 ^{ab}	34.4±8.84 ^{cde}	1.0±0.28 ^a	31.4±1.43 ^d
CML 332	0.8±0.17 ^{ab}	38.6±9.73 ^{cde}	1.4±0.21 ^a	29.0±1.0 ^{de}
CML 336	0.0±0.00 ^b	0.0±0.00 ^g	0.0±0.00 ^b	0.0±0.00 ^g
CML 337	1.0±0.00 ^{ab}	28.0±1.0 ^{ef}	1.0±0.28 ^a	13.0±3.9 ^f
CML 405	0.8±0.17 ^{ab}	72.2±1.77 ^a	1.4±0.21 ^a	20.0±1.58 ^{ef}
CML 501	1.2±0.17 ^a	62.0±1.22 ^{ab}	0.0±0.00 ^b	0.0±0.00 ^g
CM 202	1.2±0.17 ^a	37.2±0.8 ^{cde}	1.2±0.17 ^a	127.8±1.65 ^b
CM 500	1.2±0.17 ^a	40.4±1.6 ^{bc}	1.2±0.17 ^a	138.6±2.89 ^a
BML 6	1.4±0.21 ^a	48.4±1.29 ^{bcd}	1.2±0.17 ^a	123.6±2.32 ^b
BML 7	1.2±0.17 ^a	66.6±1.29 ^{ab}	1.4±0.21 ^a	120.0±1.39 ^b
WNZ Exoticpool	1.8±0.17 ^a	71.6±1.63 ^a	1.6±0.21 ^a	126.4±3.39 ^b
Mean	1.06	40.38	0.8	40.32
F	3.35	32.15	13.84	896.51
P	0.0004	0.0001	0.0001	0.0001
Tukey	1.02	19.45	0.88	9.57

Each value represents the mean ± SEM of 5 replications. Means within a column followed by different letters are significantly different (Tukey HSD Test $p=0.05$)

from 0.00 ± 0 to 138.60 ± 2.89 . Apart from the genotypes DMRE 63, CML 59, CML 60, CML 70, CML 336, CML 501 with zero egg batches, a significantly lower number of eggs/egg batches were observed on CML 337, CML 405, CML 332, CML 330 and CML 122 while in the rest of the genotypes, the number of eggs/egg batches was significantly higher. In BML 6, WNZ Exoticpool, CM 202, BML 7, and CM 500 significantly higher number of eggs per batch was observed. The genotype CM 500 with the highest number of eggs per batch has differed significantly from the other genotypes.

Antibiosis test

Larval survival ranged from 41.0% (DMRE 63) to 77.0% (BML 6) and showed significant differences between test genotypes ($F=58.97$; $P<0.0001$; Tukey HSD=7.07) (Figs. 2 and 3). The larval

survival rates on DMRE 63, CML 122, CML 337, CML 70, CML 59, CML 336, CML 330, and CML 60 were significantly lower as compared to survival observed on CML 405, CML 501, CM 202, CM 500, BML 6, BML 7, and WNZ Exoticpool. The larval weight ranged from 63.03 mg in DMRE 63 to 118.16 mg in BML 6 among the test genotypes. The larval weights, when fed on DMRE 63, CML 70, CML 122, and CML 337, were significantly lower as compared to the other genotypes ($F=495.94$; $P<0.0001$; Tukey HSD=3.48).

The larval period ranged from 15.10 days (BML 6) to 17.32 days (CML 330) on the different maize genotypes. The larval periods on BML 6, BML 7, and WNZ Exoticpool were significantly shorter than on CML 122, CML 330, CML 337, CML 60, and CML 332 ($F=115.24$; $P<0.0001$; Tukey HSD=0.33). The larval period of the remaining genotypes was intermediate and showed significant

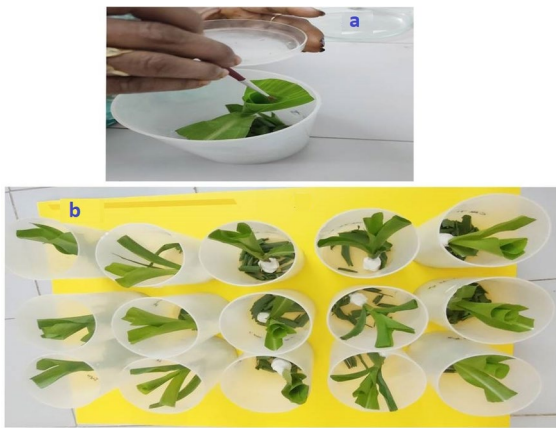


Fig. 2 Assessing antibiosis category of resistance using the detached leaf-whorl assay **a:** Release of neonate larvae into the whorl of the plant; **b:** Larvae feeding in the leaf whorl

differences. The pupal weight varied from 97.54 mg (DMRE 63) to 151.22 mg (BML 6) mg among the tested genotypes. The pupal weights on DMRE 63, CML 60 and CML 122 were significantly lower as compared to the WNZ Exotic pool, BML 7, CM 500 and BML 6 ($F=321.66$; $P<0.0001$; Tukey HSD=4.48). The pupal period varied from 7.22 days in BML 7 to 8.10 days in CML 70. The pupal period on BML 7, BML 6 and WNZ Exoticpool were significantly shorter than those of larvae feeding on other genotypes ($F=13.21$; $P<0.0001$; Tukey HSD=0.33). The adult emergence from the test genotypes varied from 40.71% (CML 60) to 74.35% (WNZ Exoticpool). However, the percentage adult emergence was significantly lower on CML 60, CML 70, CML 59, CML 337, DMRE 63, CML 330, CML 336, CML 122, and CML 332 as compared to rest of the genotypes ($F=17.01$; $P<0.0001$; Tukey HSD = 15.57).

Trait genotype relation

The interrelationship between different parameters of resistance categories was visualized graphically in the GGE biplot (Fig. 4). The first two principal components captured 75.93% of the total variation. All the parameters of the categories of resistance were classified into two groups in the biplot. The first group is comprised of larval period (LP) and pupal period (PP) with a strong correlation between them.

Similarly, the second group is comprised of rest of the parameters namely the number of egg batches (nEM) and number of eggs/egg batches (NoE) in both no-choice and multi-choice conditions, larval weight (LW), pupal weight (PW), percent larval survival (PIs) and adult emergence (AE) with a strong correlation between them. Further, there was a strong negative correlation between the groups comprising different parameters. The genotypes with strong resistance reactions namely DMRE 63, CML 70, CML 337, and CML 122 to FAW were grouped along with antibiosis indicative factor group having larval period (LP) and pupal period (PP). Similarly, the genotypes with susceptible reactions to FAW namely CM 500, BML 6, BML 7, and WNZ Exoticpool grouped along with the parameters of the second group.

Discussion

Host plant resistance to FAW is a complex phenomenon. Many traits either independently or in combination determine the level of resistance through various mechanisms. Globally several efforts have been made to identify resistant sources against FAW in maize (Widstrom et al., 1975; Prasanna et al., 2018; Badji et al., 2018; Rwumoshana et al., 2018; Kasoma et al., 2020). The CML lines selected in the present study were earlier developed through classical plant breeding efforts over the years by researchers of USDA-ARS. These breeding programs used germplasm of Caribbean origin, particularly from the Antigua Group, and yielded some temperate maize inbred lines with resistance to both FAW and southwestern corn borer (*Diatraea grandiosella* Dyar) (Lepidoptera: Crambidae) (Prasanna et al., 2022). The genotype DMRE 63 from ICAR-Indian Institute of Maize Research was found resistant to FAW, pink stem borer *Sesamia inferens* (Walker) (Lepidoptera: Noctuidae) which was developed from CM 500. The genotype CM 500 was derived from Antigua group-1 population which was previously used as a source of resistant to stem borers.

Upon the invasion of FAW into India in 2018 (Rakshit et al., 2019; Suby et al., 2020a), efforts were made to develop a visual leaf damage rating (LDR) on a 1–9 scale which can be used for objective identification of resistant germplasm (Lakshmi Soujanya et al., 2022). In this rating scale, the descriptive part of each damage rating (1– 9 scale) was modified

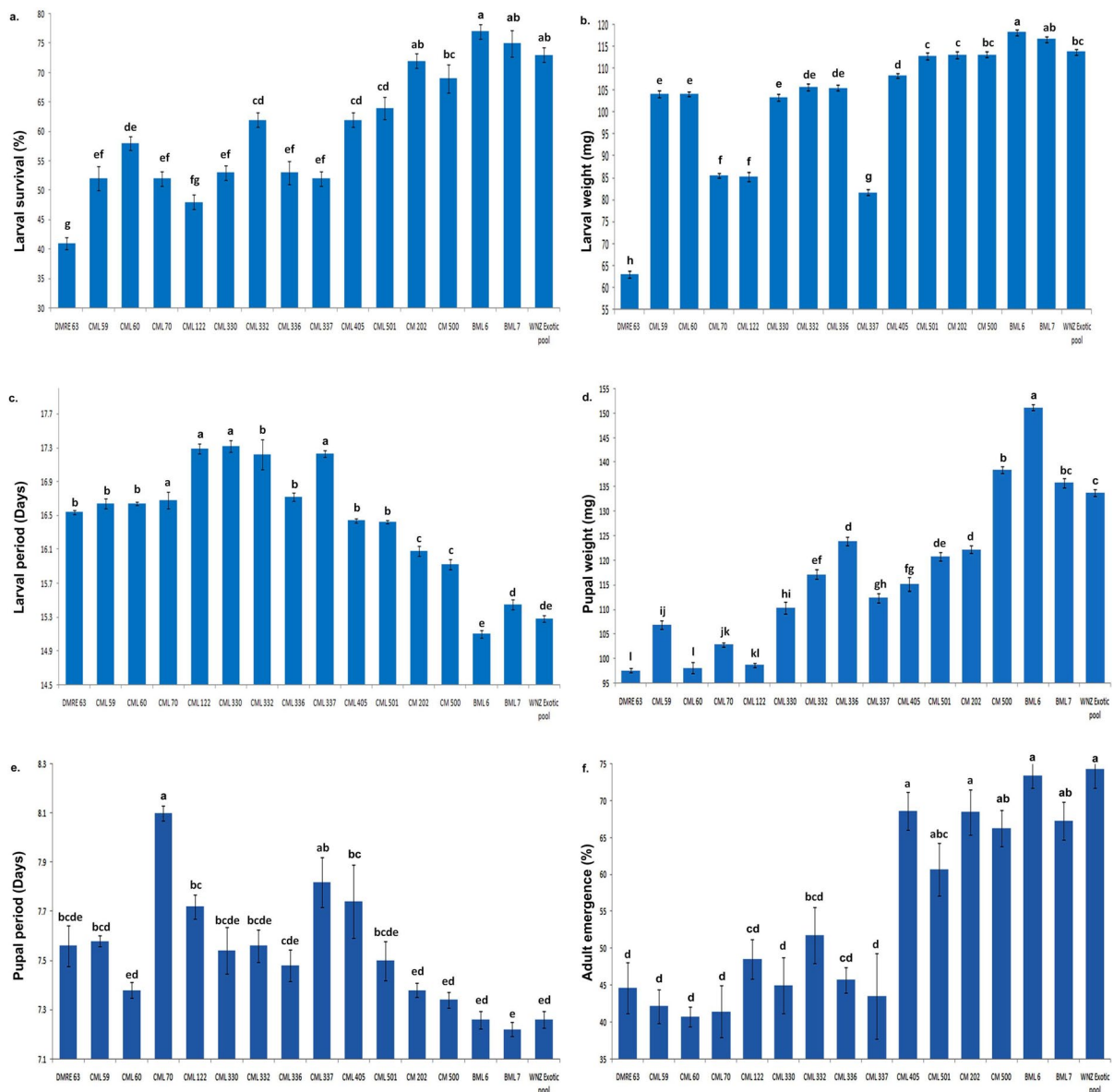


Fig. 3 Expression of antibiosis category of resistance to FAW in different maize genotypes **a:** Effect on larval survival (%); **b:** Effect on larval weight (mg); **c:** Effect on the larval period (days); **d:** Effect on pupal weight (mg); **e:** Effect on the pupal

period (days); **f:** Effect on Adult emergence (%) Error bar indicates mean \pm SEM of five replications. Different letters represent statistically significant differences (Tukey HSD Test $p=0.05$)

based on the visual assessment of foliage damage on the whole plant. 1- Healthy plant/No damage/Visible symptoms; 2- Few short /pin size holes/scraping on few leaves (1–2); 3- Short/pin size holes/scraping on several leaves (3–4); 4- Short/pin size holes/scraping on several leaves (5–6) and a few long elongated lesions (1–3 Nos) up to 2.0 cm length present on

whorl and or adjacent fully opened leaves; 5- Several holes with elongated lesions (4–5 Nos) up to 4.0 cm length and uniform/ irregular shaped holes present on whorl and or adjacent fully opened leaves. The description of lesion length particularly at 6, 7, and 8 ratings is precise and provides the information about degree of susceptibility of the tested genotype.

Scaled (Divided by): Standard Deviation (SD)
Centered by: Tester-Centered G+GE
Singular Value Decomposition (S.V.P.): HJ=Dual Metric
Preserving

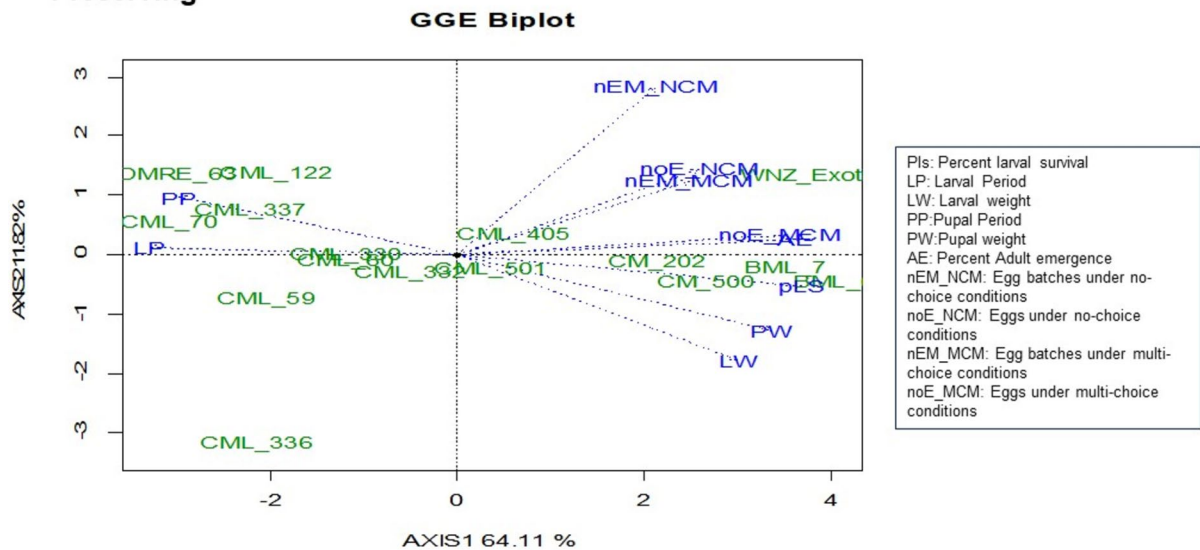


Fig. 4 The genotype trait biplot shows the relationship between genotypes and antixenosis and antibiosis traits. pLS=per cent larval survival; LP=Larval period; PP=Pupal period; LW=Larval weight; PW=Pupal weight; AE=Adult emergence; nem_NCM=Number of egg batches under no-

choice conditions; noE_NCM=Number of eggs/egg batches under no-choice conditions; nem_MCM=Number of egg batches under multi-choice conditions; noE_MCM=Number of eggs/egg batches under multi-choice conditions

The scores between 6, 7, and 8 were described based on the length of elongated lesions as up to 6.0 cm, 10.0 cm, and > 10 cm, respectively. This rating scale describes the proportion of damaged leaves and elongated lesions so that fine differences in damage levels can be estimated. Based on the LDR scale the genotypes were grouped into resistant (1–4), moderately resistant (4.1–6), and susceptible (6.1–9). The study reported that DMRE 63 (3.70) and CML 337 (3.59) as resistant; CML 59 (5.46), CML 60 (4.42), CML 70 (5.26), CML 122 (4.58), CML 330 (4.79), CML 332 (4.42), CML 336 (4.14), CML 405 (4.95), CML 501 (4.77) (LDR: 4.1–6) as moderately resistant; and CM 500 (7.38), BML 6 (7.43) and BML 7 (6.93) as susceptible to FAW in maize.

In continuation of our earlier work, the present study aimed to assess the antixenosis and antibiosis categories of resistance to FAW in diverse maize genotypes. In the present study, maize genotypes exhibited resistance to FAW by either negatively affecting oviposition (antixenosis) or interfering with growth or

survival (antibiosis). In the no-choice assay, it is more difficult or almost not possible to determine antixenosis resistance. However, CML 336 stood distinct among all genotypes as no egg masses were observed under both no-choice and multi-choice assays. In general, plant morphological traits and secondary metabolites influence host plant selection behaviour which are part of direct defenses of the plant. The non-preference towards the CML 336 genotype for egg laying could be due to higher trichome density. Gowda et al. (2023) evaluated maize germplasm for physico-morphological traits against fall armyworm in maize and observed a higher trichome density of 119.07 per cm² of leaf area in CML 336. Furthermore, a few researchers also reported that genotype CML 336 was found promising against FAW at the seedling stage of maize based on leaf injury rating (Ni et al., 2008; Prasanna et al., 2022).

In general, the genotypes that are less preferred in free-choice tests are not rejected in no-choice assays due to the survival strategy for the species offspring,

and females prefer to lay eggs even if survival is low (Singer & Stireman, 2001; Refsnider & Janzen, 2010). The genotypes, namely, DMRE 63, CML 59, CML 60, and CML 70 recorded no egg masses under the multi-choice test. However, under no-choice conditions, FAW females laid eggs on the genotypes as well. Nonetheless, the genotypes except CML 60 showed significant differences with CML 405, CML 501, BML 7, and WNZ Exoticpool in the number of egg batches. Nogueira et al. (2018) tested antibiosis/antixenosis resistance against FAW in Brazilian landraces and found that the FAW resistant landrace, Perola and cultivar, BRS-Caatingueiro were least preferred by FAW for oviposition. Further, reduced oviposition was observed under the free-choice test compared to the no-choice test. Studies by several authors reported that phytophagous insects prefer to lay eggs in genotypes that provide better performance for their offspring (Thompson, 1988; Schoonhoven et al., 2005; Gripenberg et al., 2010). Takahashi et al. (2012) reported a higher infestation of FAW in the Tuxpeno landrace (*Zea mays* ssp. *mays*) due to preferential host selection of FAW females compared to Balsas Teosinte (*Zea mays* ssp. *parviglumis*). The larval development was adversely affected when the larva was fed with Balsas Teosinte under laboratory conditions which indicates that FAW females laid more eggs on the best larval host. In the present study, the gravid females of FAW prefer oviposition on susceptible genotypes compared to resistant and moderately resistant genotypes. It can be inferred that the gravid FAW females recognized the most or least suitable maize genotypes for the development of their progeny concerning clues/signals in terms of volatiles present in these genotypes which attract or deter the FAW female for oviposition. This indicated the presence of the antixenosis category of resistance to FAW which prevents or limits oviposition. Seong et al. (1990) studied the ovipositional preference of FAW and observed significantly fewer eggs by FAW females on resistant hybrids compared to susceptible genotype SC229 X Tx601. The results of oviposition on different genotypes suggest the role of the genetic makeup of the genotype for non-preference. Smith (2005) reported that oviposition is influenced by the morphological and chemical cues present on the surface of maize genotypes. Several studies have shown that the ovipositional preference of female adults depends on varietal characteristics, age, size,

leaf damage, reproductive capacity, nutrient availability of plants (Latheef & Irwin, 1979; Thompson, 1988; Berdegue & Trumble, 1996), and also on volatile compounds (Ongaratto et al., 2021).

The survival and development of insects on genotypes could be related to the presence of morphological and biochemical traits of host plants. Smith (2005) reported that antibiosis occurs when the negative factors for larval growth in plant affect the biology of the insect. The present study also assessed antibiosis in maize against FAW by restricting FAW larvae to feed only on a single genotype. The larval growth and development parameters like larval and pupal weight showed significant differences between genotypes (Fig. 3). Furthermore, percentage survival, larval period, pupal period, and percentage adult emergence, which affect and influence the population dynamics of FAW also showed significant differences between genotypes. The genotypes, viz., DMRE 63, CML 59, CML 60, CML 330, CML 122, CML 337, and CML 332 had a significant adverse effect on the life cycle of FAW, i.e., prolonged larval duration by 1.14 fold when fed on CML 122, CML 330, CML 332 and CML 337, whereas in DMRE 63 the larval survival (%), larval weight, and pupal weight were lowered by 1.87, 1.87 and 1.55 fold, respectively in comparison to BML 6. Rajapakse and Walter (2007) reported that the extended life cycle duration directly affects population dynamics and fewer insect generations per year may occur.

In the present study, DMRE 63 was found to provide resistance by reducing larval survival, and larval and pupal weights. The findings are in agreement with Wiseman and Widstrom (1986) who observed a longer life cycle of FAW, as well as smaller larvae and pupae when fed with silks of Zapalote Chico, a resistant cultivar, as compared to Stowell's Evergreen sweet corn, a FAW susceptible cultivar. Furthermore, a high degree of non-preference to silks of Zapalote Chico was observed by FAW larvae compared to Stowell's Evergreen. Wiseman (1997) also reported antibiosis in terms of the reduced size of larvae, prolonged length of both the larval and pupal periods, reduced pupal weight and fecundity, increased number of instars, and decreased head capsule size when FAW were reared on resistant maize genotypes. Antibiosis was also observed when FAW fed on MP 704 × MP 707 (R) compared to Ab24E (S) (Davis et al., 1998). In a similar kind of study, testing the influence

of different transgenic maize genotypes, Paiva et al. (2016) observed antibiosis in NS90 PRO 2, Maximus VIP 3, Feroz VIP 3, and Maximus VIP 3 which affected the larval weight and viability of pupae. In another study, larvae fed with Perola exhibited longer development times and lower survival rates (Nogueira et al., 2018). Morales et al. (2021) also reported reduced pupal weight and the lowest growth index when FAW fed with leaves of resistant genotype 'SC Duma 43' compared to susceptible genotypes (Rachar, Nyamula).

On the other hand, the genotypes BML 6 and WNZ Exoticpool favored the development of FAW with shorter larval periods and higher adult emergence. The present results corroborate our previous results, in which BML 6 was found susceptible to FAW and recorded the highest leaf damage rating under artificial infestation in net house conditions (Lakshmi Soujanya et al., 2022). The present results confirm that the genotypes namely DMRE 63, CML 59, and CML 60 showed antibiosis to FAW. It is ascribed to the reduction in larval and pupal weights is due to low reserves deposited during the larval period which might be due to a reduction in the food's nutritional value (Ongaratto et al., 2021). Lower adult emergence in these genotypes could be due to low nutritional quality which can influence insect development. Furthermore, these effects also reduce the oviposition and fertility of insects (Smith & Chuang, 2014). In addition, minimum oviposition was also observed in these lines, indicating that these genotypes exhibited both antixenosis and antibiosis as categories of resistance to FAW. The genotypes CML 70, CML 336, and CML 501 showed antixenosis while CML 122, CML 330, CML 332, and CML 337 possess antibiosis as the category of resistance to FAW. Antibiosis to FAW in maize genotypes was attributed to the thickness of cuticle and epidermal cell wall (Davis et al., 1995), high fiber content, and lower total protein content (Williams & Davis, 1997), high levels of hemicellulose (Hedin et al., 1996), chemical, physical, and anatomical leaf characteristics (Smith, 2005; Smith & Clement, 2012). The biochemical traits such as the presence of phenolic compounds, alkaloids, proteases (Pechan et al., 2002), protease inhibitors (Chen et al., 2009), maysin, chlorogenic acid (Wiseman et al., 1992; Snook et al., 1993; Brooks et al., 2007), caffeoylquinic acid, luteolin derivatives (Gueldner et al., 1992), flavonoids, polyphenols (Davis et al., 1995) may also inhibit the development of FAW larvae.

The GGE biplot method can be used to visualize complex relationships between several parameters. The GGE biplot helps identify the key and most important factors for imparting resistance. Since interaction among the parameters and their interrelationship together determine the overall resistance response. The GGE biplot effectively captures both the main effects of the parameters and their interaction simultaneously. Several researchers in different crops applied similar research to understand complex interactions (Rakshit et al., 2012; Chaudhary et al., 2019; Suby et al., 2020b). Through the graphical presentation, the complexity of the data was simplified. The graphical visualization has indicated that two parameters namely the larval period and pupal period are distinct and highly correlated. The larval period and pupal period are negatively correlated with the other parameters studied. Therefore, to determine the resistance genotypes, these two parameters are effective in identifying the resistant genotypes. All the parameters studied were found relevant to differentiate resistant and susceptible genotypes. Based on the GGE biplot, the genotypes DMRE 63, CML 70, and CML 337 had the lowest percent larval survival, prolonging the FAW larval and pupal period. On the contrary, genotypes BML 6, BML 7, and WNZ Exoticpool located on the far right side of the graph were highly susceptible to FAW compared to the remaining genotypes. This was attributable to the highest larval survival, larval, pupal weights, and percentage adult emergence of FAW when reared on these genotypes.

Conclusion

Antixenosis is the first line of defense while antibiosis is the second line of defense which imparts resistance to FAW in maize. The oviposition behavior towards different genotypes and the effect of different genotypes on larval growth and developmental parameters determine the level HPR. The genotype CML 336 was unique, on which no-egg laying was recorded under no-choice and multi-choice conditions indicating the strong antixenotic resistance. DMRE 63, CML 59, and CML 60 exhibited both antixenosis and antibiosis categories of resistance; CML 70, CML 336, and CML 501 showed antixenosis while CML 122, CML 330, CML 332, and CML 337 exhibited antibiosis to FAW. The information obtained through this study is

valuable to maize breeding-programs aimed at development of FAW-resistant maize genotypes.

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Author contributions P.L.S. conceived and designed the work, conducted the experiments and wrote the manuscript. J.C.S. was responsible for project administration, supervision and manuscript review. K.R.Y. was responsible for germplasm maintenance and ensuring seed availability. C.G.K. helped with statistical analysis and interpretation of the data. C.G.K., K.R.Y., K.S.R., and S.B.S. reviewed the manuscript. S.R. helped in the planning, interpretation of results and review of the manuscript. All authors read, corrected, and approved the manuscript.

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Data availability The authors confirm that the data that supports the findings of the study are available upon request.

Declarations

Competing interests The authors declare no competing interests.

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