



Multidimensional characterisation of maize resistance to fall armyworm, *Spodoptera frugiperda* (J. E. Smith)

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Abstract

Fall armyworm (FAW, *Spodoptera frugiperda* (J. E. Smith)) is a major constraint in maize production and causes considerable yield loss. Although chemical control methods are being widely used for the management of FAW, there are increasing concerns regarding issues like pesticide resistance and ecological imbalance. Exploiting host plant resistance represents the eco-friendliest and most cost-effective approach. Cultivating resistant varieties is one of the eco-friendly approaches to FAW management. A key step in this line of research is the identification of resistant sources and the underlying mechanisms contributing towards resistance. The present study integrated field screening, ovipositional preference assays, volatile profiling and olfactory behavioural assays to characterise resistance in maize genotypes against FAW. Initial screening trials across two seasons revealed a dominance of susceptible genotypes, with DMRE 63 exhibiting resistance and CML 122 demonstrating moderate resistance. Leaf damage was most serious 14 days after infestation, corresponding to the late larval feeding stage. Ovipositional preference study revealed DMRE 63 had the lowest egg deposition under choice and no-choice conditions, indicating antixenosis. Induction of resistance is clearly evidenced through volatile profiling, showing distinct variation among genotypes in healthy, infested plants. Resistant genotype DMRE 63 produced biologically active aldehydes and inducible terpenoid–ketone compounds, whereas structural hydrocarbons dominated susceptible genotype CML 170. Olfactometer assays confirmed behavioural avoidance of infested plants in resistant, moderately resistant and susceptible genotypes. Principal component analysis explained 68.1 % of the total variability, separating resistant, moderately resistant and susceptible maize genotypes through volatile-mediated antixenosis, causing altered behaviour and ovipositional preference. This study highlights the need to integrate field screening with chemical ecology, ensuring sustainable pest management.

Keywords: behavioural response; leaf damage score; ovipositional assay; resistance; volatile profiling

Received: 21 May 2026. **Accepted:** 28 July 2026. **Published:** Version 1.0: 17 October 2026.

Cite this article: Feby A, Soundararajan RP, Murugan M, Srinivasan T, Ravikesavan R, Senthil N. Multidimensional characterisation of maize resistance to fall armyworm, *Spodoptera frugiperda* (J. E. Smith). Plant Science Today. 2026; 13(sp9): 1-20. <https://doi.org/10.14719/pst.15650>

1. Introduction

Fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), has emerged as one of the most destructive pests of maize worldwide over the past few years, causing severe yield reductions and imposing heavy economic burdens on producers (1). In response to this critical threat, although the rapid deployment of synthetic insecticides has been common, their overreliance has resulted in insecticide resistance, increased environmental contamination, non-target toxicity, human health risk and increased production costs for farmers (2, 3). Research attempts have been ongoing since the early 1980s to exploit the resistance and tolerance characteristics of the maize genotypes against FAW to counteract yield loss (4–7). Therefore, the sustainable management of

S. frugiperda necessitates the adoption of integrated pest management strategies, in which host plant resistance is always a critical component. Host plant resistance is a complex trait governed by genetic, biochemical and behavioural components (8).

In response to herbivory, maize plant deploys its defence strategies to counteract these intruders. In addition to constitutive morphological defences that provide preliminary protection, the plant also utilises direct and indirect biochemical defence compounds. It is also well established that herbivory induces the release of herbivore-induced plant volatiles (HIPVs), which influence members of the primary, secondary and tertiary trophic levels. The HIPVs function as indirect defence compounds through their roles in tritrophic interactions (9). Damaged plants release a

complex of volatile compounds belonging to different chemical classes like green leaf volatiles, phenylpropanoids, terpenoids, sulphur (S)-containing compounds and nitrogen (N)-containing compounds (10).

The present study combined a multidimensional approach with resistance screening, host-selection behaviour and chemical ecology to identify potential sources as well as to characterise resistance against FAW. Different maize genotypes were screened in the field with confirmatory screening experiments on the selected genotypes, followed by an oviposition assay to understand female adult preference for oviposition. The volatile profiles of healthy and FAW-infested plants were subsequently profiled, adult behavioural responses towards selected maize genotypes were evaluated by Y-tube olfactometry studies and all the parameters were utilised for principal component analysis.

2. Materials and Methods

Mass culturing of fall armyworm, *Spodoptera frugiperda*

Spodoptera frugiperda larvae were reared using a lablab-based artificial diet under controlled laboratory conditions (27 ± 2 °C, 70 ± 5 % RH and a 12 : 12 hr light-dark photoperiod) (11). Egg masses and adults were obtained from the FAW Laboratory, Department of Agricultural Entomology, Tamil Nadu Agricultural University, Coimbatore, India and all the lab experiments were conducted in the same laboratory. Neonates were reared in groups on artificial diet until the early stage of the third instar, which were then transferred to individual plastic containers with fresh diet for further development until pupation. After 5–6 days, pupae were collected, sexed and transferred to adult emergence cages (30 × 30 × 30 cm). Male and female moths emerging on the same day were paired in the ratio of 1 : 1 and released into oviposition cages provided with *Nerium oleander* L. shoots for oviposition. Emerged adults were supplied with sugar solution (10 %) as a food source.

Field screening of maize genotypes

A total of 48 maize genotypes suitable for the rabi season were raised during 2023–24 in the field at the Department of Millets, Tamil Nadu Agricultural College (TNAU), Coimbatore, Tamil Nadu, India. In the following season, 100 genotypes suitable for the kharif season were screened during 2024. Confirmatory field experiments with selected entries from both seasons were further carried out during rabi 2024–25 as well as kharif 2025. The experiments were conducted in randomised block design (RBD) with 2 replications for preliminary experiments and 3 replications for confirmatory experiments, each in a 2 m row with spacing of 75 × 20 cm. CML 170 was used as a susceptible check and CO (H) M 8 as a

local check in all four seasons. The source for maize genotypes was ICAR-Indian Institute of Maize Research, Hyderabad (12 entries) and the Department of Millets, TNAU, Coimbatore (122 entries). To ensure uniform infestation by fall armyworm in the field, an artificial larval infestation method was followed (12). After 10–12 days of germination, each plant was infested with 15–20 neonate larvae at the whorl region. Damage scoring was done on the 7, 14, 21 and 28 days after artificial infestation. The assessment of FAW infestation was done using 1–9 Davis scale for whorl injury (13).

Assessment of oviposition preference by fall armyworm adults in maize genotypes

The genotypes screened in the field confirmatory trials were further raised in the glasshouse for oviposition preference studies. Based on field screening and confirmatory experiments, 12 maize genotypes were selected to represent different categories of resistance for oviposition preference by fall armyworm adults in controlled conditions. Five seeds of each genotype were sown in pots of size 8.5 × 14 cm. Thinning was done three days after germination and 30-day-old individual plants were used for the assays. To understand the preference of female *S. frugiperda* towards maize genotype, oviposition assays were performed under laboratory conditions to investigate whether female moths display a preference for any particular genotype. The genotypes viz., CML 170, CML 108, CML 122, CML 121, CML 337, HKI 193-1, MIL 7-14-1, MIL 7-3-4, MIL 70-30-3-1, CO (H) M 8, CO (H) M 11, DMRE 63 were used for both the no-choice and choice test.

No choice assay on oviposition preference

The ovipositional preference of female *S. frugiperda* among different maize genotypes was determined by no-choice oviposition assay (14). The experiment was laid out in a completely randomized design with 3 replications for each genotype. A single plant of each genotype was maintained individually in pots. At the V5 phenological stage, each plant was enclosed individually in a cylindrical transparent nylon mesh cage. A single pair of newly emerged mated adults of *S. frugiperda* was released into each cage and allowed to oviposit for three days. Adults were provided with a 10 % honey solution soaked in cotton as a food source throughout the experimental period. The position of the cages was randomly rearranged daily to minimize positional bias (14). After three days, the egg masses laid on each genotype were collected and counted under a stereo zoom microscope. The mean number of egg masses and eggs laid per genotype was assessed to decide ovipositional preference.

Choice assay on oviposition preference

The preference of female *S. frugiperda* for oviposition among selected maize genotypes was determined by a choice oviposition assay (15). The experiment was laid



out in a completely randomized design with 3 replications for each genotype. A single plant of each genotype was maintained individually in pots. At the V5 phenological stage, the potted plants of the selected maize genotypes were arranged in a circular form equidistantly from each other and placed in a large rearing cage. A total of 12 pairs of newly emerged adults of *S. frugiperda* were released into the cage and allowed to oviposit for three days. Adults were provided with a 10 % honey solution soaked in cotton as a food source throughout the experimental period. The position of the cages was randomly rearranged daily, randomly, to minimise positional bias. After three days, the egg masses laid on each genotype were collected and counted under a stereo zoom microscope. The mean number of egg masses and eggs laid per genotype was used to assess ovipositional preference under multiple-choice conditions.

Collection of headspace volatiles from maize genotypes for gas chromatography–mass spectrometry analysis

Volatile profiling was carried out on 3 genotypes, viz., DMRE 63, CML 170 and CML 122, representing resistant, moderately resistant and susceptible categories of resistance from the present study. The plants were raised in pots in glasshouse and maintained up to 30 days after germination. Two treatments were set up for each genotype, with healthy plants having no FAW infestation and another set with FAW-infested plants. Two third-instar *S. frugiperda* larvae were introduced in each plant for 24 hr to obtain infested plants. After 24 hr, larvae were removed and plants were immediately used for volatile profiling in the herbivore-damaged and healthy genotypes.

Headspace volatiles from non-infested and herbivore-damaged maize plants were collected using an air entrainment chamber method (16). The volatile collection system consisted of a glass entrainment chamber with an inlet tube and an outflow silica tube. Air before reaching the entrainment chamber through the inlet tube is filtered and humidified. In the outlet tube to collect volatiles, a trapping tube with Porapak Q (50 mg, 60/80 mesh; Supelco, Sigma Aldrich, St Louis, United States) is used. The air flow is maintained at the rate of 500 mL min⁻¹. The experiment was run continuously for 9 hr during the photophase. At the end of the experiment, the trapped volatiles were eluted using high-performance liquid chromatography (HPLC)-grade hexane (500 µL) (purity >99.5 %, Merck) and stored at -20 °C until further analysis.

Volatile profiling of the eluted headspace plant volatiles was carried out using gas chromatography–mass spectrometry (GC-MS); an Agilent 7890B GC system equipped with mass spectrometry (MS) (Agilent 5977 MSD). Chromatographic separation of the volatile compounds was performed on HP-5 MS UI fused-

silica capillary column (30 m × 0.25 mm i.d., 0.25 µm film thickness). Helium gas of 99.999 % purity was used as carrier gas at a constant flow rate (0.5 mL min⁻¹). The injector temperature was maintained at 280 °C and samples were injected in split mode (1 : 20). The GC oven temperature is initial temperature of 60 °C (2 min), followed by a ramp-up temperature of 10 °C min⁻¹ to 300 °C (5 min). Mass spectrometric detection was performed using electron ionisation (EI) at 70 eV in full-scan mode over 40–450 m/z. Obtained volatile compounds were tentatively identified by comparing their mass spectra with the NIST 14 mass spectral library. Also, Kovats retention indices (RI) of the identified compounds were calculated using a homologous series of n-alkanes (C7–C30) under similar chromatographic conditions. Compound identification and confirmation were further carried out on agreement between the reported retention index (RI) values and the experimental values and the relevant published literature.

Y-tube olfactometer assay on orientation of adult fall armyworm to maize genotypes

The olfactory responses of gravid female *S. frugiperda* to healthy and infested volatiles from three different maize genotypes were studied using Y-tube olfactometer assay (17). Airflow into the olfactometer was provided by an aquarium pump, maintained at 4 L min⁻¹ using a flow meter and passed through a charcoal filter and humidifier before entering the system. Single gravid female *S. frugiperda*, which were 2–3 days old, were introduced through the 28.5 cm long stem. For the volatile sources, infested and healthy potted maize genotypes were placed inside two 10 L glass chambers connected to the two 11 cm long arms. A total of 30 moths were tested for each genotype. Each released moth was observed for 5 min. The response of the introduced moth was recorded as valid if the insect crossed the midpoint of either arm within 5 min of initiating the experiment. Moths that failed to move from the point of release or those that did not enter and reach the end of the arms within 5 min were recorded as non-responders. To minimise positional bias, the arm of the odour source was interchanged after every five adults. After each assay, the olfactometer and glass chambers were cleaned with 75 % ethanol, rinsed with distilled water and thoroughly dried to prevent odour carryover. The entire experiment was conducted at ambient atmospheric conditions with a room temperature at 27 ± 1 °C and relative humidity at 60–80 % under red light during scotophase.

Statistical analysis

The results of field screening were analysed using R software version (2024.12.0 + 467). Waffle charts and principal component analysis were prepared using the online platform, SRplot and heat maps were prepared using the platform MetaboAnalyst. The



percentage of FAW female moths responding to plant volatiles from healthy and infested genotypes was compared using a Chi-square test at a significance level of $\alpha = 0.05$.

3. Results and Discussion

Screening of maize genotypes for resistance to *Spodoptera frugiperda*

Forty-eight maize genotypes, comprising 9 quality protein maize and specialty corn entries, 29 inbreds, 2 hybrids, 6 late-maturity and 2 medium-maturity entries, were evaluated under artificial FAW infestation during rabi 2023–24 (Supplementary Table 1). Although resistance screening can be conducted under both natural and artificial infestation, natural infestation is usually conducted in hotspot areas where a predictable, high level of FAW infestation occurs. Host plant resistance screening against FAW primarily relies on artificial infestation as it ensures uniform pest pressure and synchronised infestation, thereby minimising environmental variation and enabling reliable discrimination among genotypes (5). Using the FAW damage rating score at 14 DAI, 41 lines were categorised as susceptible, five as moderately resistant and two as resistant (Fig. 1A). A total of 100 maize genetic materials were evaluated under field conditions with artificial infestation during kharif 2024 (Fig. 1B). Among them, 94 genotypes were found susceptible, five moderately resistant and one resistant (Supplementary Table 2). A total of 12 entries were selected covering different categories of resistance, viz., resistant, moderately resistant and susceptible, for further confirmatory field screening during rabi 2024–25 and kharif 2025. The results of the confirmatory experiment denoted that one resistant, four moderately resistant and seven susceptible genotypes were recorded. Significant variation in leaf damage rating (LDR) scores was observed among the genotypes in response to *S. frugiperda* infestation in both seasons (Tables 1 and 2). Across both rabi 2024–25 and kharif 2025, mean LDR increased from 7–14 days after infestation (DAI) and declined thereafter.

During rabi 2024–25, for the most susceptible genotype CO (H) M 11 at 7 and 14 DAI, the LDR rose from 3.90–6.50, then decreased to 2.90 and 2.00 at 21 and 28 DAI respectively. A comparable pattern was observed in kharif 2025 for susceptible genotype MIL 70-30-3-1, with LDR increasing from 2.80 at 7 DAI to 6.40 at 14 DAI and subsequently declining to 4.00 at 21 DAI and 2.10 at 28 DAI. A similar pattern of damage was also observed in the resistant and moderately resistant lines from the present study. The temporal assessment of leaf damage revealed that the peak damage occurred on 14 DAI. Earlier reports indicated that 14 DAI coincides with the peak feeding stage (4th, 5th and 6th instars) when larvae cause heavy defoliation, consuming 4.7 %, 16.3 % and 77.2 % of the total foliage consumed (18). Thus, categorisation of R, MR and S was also based on the

scoring results of 14 DAI ratings. Furthermore, the level of resistance recorded at 7 DAI was inadequate for reliable discrimination, as the early *S. frugiperda* instars (1st–3rd) exhibit limited feeding, contributing to only a small fraction (2 %) of total leaf consumption (18). During 21 DAI and after, the larvae begin their transition to the pupal stage and therefore no further leaf damage is observed. Additionally, the plant begins to recover from the inflicted damage (19, 20).

In both confirmatory experiments, DMRE 63 consistently exhibited a resistant (R) reaction, with LDR scores of 3.90 in rabi 2024–25 and 3.40 in kharif 2025, whereas CO (H) M 8 (5.90 in rabi 2024–25; 5.20 in kharif 2025), CML 337 (5.10 in rabi 2024–25; 4.10 in kharif 2025), CML 122 (4.60 in rabi 2024–25; 4.10 in kharif 2025) and CML 121 (4.70 in rabi 2024–25; 4.30 in kharif 2025) showed moderately resistant (MR) reactions. The genotypes CO (H) M 11, MIL 7-14-1, MIL 7-3-4, CML 170, CML 108, HKI 193-1 and MIL 70-30-3-1 showed susceptible (S) reactions with LDR ≥ 6.0 or above. The grain quality traits and plant yield of the selected genotypes from the experiment indicated that the resistant and moderately resistant entries had comparable yield parameters with medium grain type (Supplementary Table 3). All the 12 entries taken for confirmatory field trials were taken for the oviposition preference laboratory study.

Oviposition preference study

While field screening through artificial infestation identified the resistant genotypes and explained the interactions between larval biology and host, studying ovipositional preference is essential to understand the role of adult behaviour in sustaining the pest pressure (21). The host selected by the parents strongly influences offspring development (22). Ovipositional preference mediates the distribution of the larval populations and thereby influences the continuity and intensity of damage across generations (21). Understanding ovipositional preference is important to understand the period of peak crop damage. Genotype-dependent variation in the oviposition behaviour of *S. frugiperda* was observed in both the choice and no-choice assays (Table 3). Resistant genotype DMRE 63 consistently exhibited the lowest oviposition in both choice (25.67 eggs, 0.67 egg masses) and no-choice (24.00 eggs, 0.67 egg masses) assays. This suggests the presence of deterrent factors, absence of oviposition cues or essential nutrients, thereby reflecting an antixenosis-based resistance mechanism. A higher number of eggs were laid on susceptible genotypes MIL 70-30-3-1, HKI 193-1, CML 108, CML 170, CO (H) M 11, MIL 7-14-1 and MIL 7-3-1 in comparison to moderately resistant genotypes CO (H) M 8, CML 122, CML 121 and CML 337 (Table 3). A similar trait pattern has been documented in maize land races, where the least preferred accession for *S. frugiperda* oviposition also showed antibiosis towards larvae (22).





Table 1. Field screening of maize genotypes against *Spodoptera frugiperda* (rabi 2024–25)

Genotypes	Leaf damage rating				Level of resistance
	7 DAI	14 DAI	21 DAI	28 DAI	
CO (H) M 8	3.80	5.90	2.60	3.00	MR
CO (H) M 11	3.90	6.50	2.90	2.00	S
MIL 7-14-1	3.70	6.10	5.20	3.80	S
MIL 7-3-4	4.30	6.10	1.90	2.40	S
CML 170	3.90	6.00	2.50	2.40	S
HKI 193-1	3.20	6.10	3.00	2.20	S
CML 337	3.50	5.10	2.10	1.70	MR
CML 122	3.20	4.60	3.60	2.00	MR
MIL 70-30-3-1	4.00	6.00	2.60	1.70	S
CML 121	2.90	4.70	4.50	2.60	MR
CML 108	3.00	6.20	4.30	2.70	S
DMRE 63	3.20	3.90	3.60	2.00	R
Mean	3.55	5.58	3.07	2.38	
SEd	0.32	0.35	0.76	0.53	
CD ($p = 0.05$)	0.71	0.77	1.68	1.16	

R: resistant; MR: moderately resistant; S: susceptible; DAI: days after infestation.

Table 2. Field screening of maize genotypes against *Spodoptera frugiperda* (kharif 2025)

Genotypes	Leaf damage rating				Level of resistance
	7 DAI	14 DAI	21 DAI	28 DAI	
CO (H) M 8	3.30	5.20	5.00	2.50	MR
CO (H) M 11	2.00	6.00	3.70	1.90	S
MIL 7-14-1	2.80	6.20	2.70	2.0	S
MIL 7-3-4	3.00	6.20	4.5	2.20	S
CML 170	3.50	6.20	4.90	2.90	S
HKI 193-1	3.20	6.00	3.80	2.80	S
MIL 70-30-3-1	2.80	6.40	4.00	2.10	S
CML 337	3.50	4.10	3.70	2.20	MR
CML 122	3.10	4.10	3.80	1.90	MR
CML 121	3.40	4.30	3.70	2.20	MR
CML 108	2.50	6.00	2.80	2.40	S
DMRE 63	2.70	3.40	2.90	2.30	R
Mean	2.98	5.40	3.87	2.26	
SEd	0.35	0.50	0.72	0.69	
CD (P=0.05)	0.76	1.11	1.58	1.51	

R: resistant; MR: moderately resistant; S: susceptible; DAI: days after infestation.

Table 3. Oviposition preference of *Spodoptera frugiperda* females on different maize genotypes

Genotype	Resistance category	Choice assay		No choice assay	
		Mean no. of eggs	Mean no. of egg mass	Mean no. of eggs	Mean no. of egg mass
CO (H) M 8	MR	49.33	1.00	96.00	1.33
CO (H) M 11	S	360.67	2.00	250.33	2.33
MIL 7-14-1	S	474.00	3.33	144.00	1.67
MIL 7-3-4	S	163.00	2.33	93.00	1.00
CML 170	S	279.33	1.67	267.00	2.67
HKI 193-1	S	149.67	1.33	346.33	3.00
MIL 70-30-3-1	S	388.67	3.00	363.67	3.00
CML 337	MR	163.67	1.67	81.67	1.33
DMRE63	R	25.67	0.67	24.00	0.67
CML 121	MR	97.00	1.33	109.33	2.00
CML 108	S	397.000	2.667	359.667	2.667
CML 122	MR	159.333	2.000	109.000	1.667
Mean		225.611	1.917	187.000	1.944
SEd		72.6260	0.6086	48.9569	0.7328
CD (P=0.05)		149.8927	1.2560	101.0421	1.5125

MR: moderately resistant; S: susceptible.

Contrastingly, FAW females are also known to make suboptimal host plant choices, which the neonate larvae correct later to adapt by colonising suitable plants through dispersal mechanisms such as crawling and ballooning (23).

In this study, some genotypes exhibited differential responses under choice versus no-choice conditions, indicating that oviposition behaviour is influenced not only by a particular genotype but also by relative attractiveness in the presence of an

alternative host genotype. Oviposition preference is known to be driven by plant volatiles, which act as chemical cues for host selection. The HIPVs are used by pests for host recognition and identification of suitable oviposition sites (24, 25). Therefore, based on field screening and oviposition assay, volatile profiling of three genotypes belonging to three distinct resistance categories, DMRE 63 (resistant), CML 122 (moderately resistant) and CML 170 (susceptible) was conducted to identify the plant volatiles associated with host-selection behaviour and in turn influencing resistance and susceptibility.

Chemical profiling of maize volatiles

The GC-MS analysis of volatile profiles from maize entries with infested and healthy plants revealed significant variation in the chemical profile. A distinct difference in volatile profile was observed among the three genotypes studied, suggesting that volatile emission is strongly genotype dependent (26). Healthy DMRE 63 plants were characterised by the presence of aldehydes such as nonanal and decanal. Previous studies have identified these compounds as constituents of the volatile profile of healthy maize plants and have been reported as important host-location cues for gravid *Ostrinia nubilalis* females (27), whereas they were found to be repellent towards *Ostrinia furnacalis* larvae and adults (28). Their constitutive presence in DMRE 63 indicates that this genotype possesses a distinct basal volatile profile and this needs to be further validated for their bioactive role towards larvae and adults of *S. frugiperda*. Upon infestation with *S. frugiperda*, a marked shift in metabolite composition is observed (Fig. 2). A predominance of ketone compounds, including the branched ketone (3-n-Propyl-5-methylhexan-2-one) and β -diketones (3-n-Propyl-2,4-pentanedione, 2-Decanone), along with the appearance of terpenoid derivatives such as dihydro citronellyl angelate was detected (Fig. 2; Table 4). This indicates activation of herbivory-induced metabolic pathways in maize, synthesising more terpenoids (29, 30) and induction of ketones upon herbivory (31). Interestingly, aldehydes which were detected in the healthy plants were not observed after infestation. It denotes dynamic reprogramming of volatile biosynthesis in the infested and healthy plants. The results demonstrate that DMRE 63 employs an inducible defence mechanism, with a transition from aldehyde-based signalling to more ketone- and terpenoid-mediated responses following herbivore attack.

The volatile profile of the healthy plants of moderately resistant genotype CML 122 was characterised by the presence of cycloalkanes and ketone compounds, particularly substituted heptanones and hexanones (Table 5). In addition to ketones, hydrocarbons such as decane were detected (Fig. 2). Hydrocarbons such as decane, cyclohexane and pentane derivatives are components of cuticular wax and do not directly participate in volatile-mediated defence signalling. The absence of major green leaf volatiles such as

aldehydes suggests that the volatile mediated defence response in CML 122 under healthy conditions is moderate. The volatile profile of infested CML 122 showed changes with long-chain hydrocarbons such as pentacosane, heptacosane and octacosane detected in higher abundance as observed in the chemical composition of *Bessera elegans* Schult.f. (Asparagaceae) flower extracts exhibiting insecticidal effect against *Melanaphis sacchari* (32). The long-chain hydrocarbons are also major constituents of cuticular wax in eucalyptus and mediate physical defence towards *Austropuccinia psidii* (33). However, the absence of key herbivory-induced plant volatiles such as aldehydes and terpenoids indicates that the induced defence response in CML 122 is moderate and not strongly reliant on volatile-mediated signalling mechanisms.

The susceptible genotype CML 170 in the healthy stage showed a volatile profile dominated by long-chain hydrocarbons with very low levels of biologically active aldehydes (Table 6). Many of the detected hydrocarbons are mainly associated with cuticular wax and have limited ecological signalling function (33). These cuticular wax compounds are primarily structural and do not play a direct role in volatile-mediated defence signalling. Young *Pieris rapae* larvae were susceptible to feeding on cabbage leaf with higher content of *n*-nonacosane in leaf epicuticular wax (34). However, tricosane, octacosane and docosane are documented as a potential kairomone in attracting natural enemy *Trichogramma chilonis* (35). Among the detected compounds, only a few ketones, such as 2-heptanone derivatives and substituted hexanones, were identified as potential plant-derived volatiles. Their low abundance suggests a weak constitutive defence response. The absence of the key HIPVs, such as aldehydes and terpenoids, indicates that CML 170 lacks a strong basal volatile defence system. This may contribute to its susceptibility to insect herbivory. Overall, the results suggest that the volatile emission profile of CML 170 is dominated by structural hydrocarbons rather than biologically active signalling compounds, highlighting its limited defensive capacity under healthy conditions. The volatile profile of infested CML 170 was characterised by ketones together with branched alkanes and cycloalkanes (Fig. 2).

A terpenoid-derived compound, dihydro citronellyl angelate, was also detected, suggesting a limited induction of herbivory-associated pathways. Dihydro citronellyl angelate was detected in both infested DMRE 63 and CML 170. However, its component area was lower in CML 170 (23555.4) than in DMRE 63 (28742.9), indicating a comparatively weaker induction of herbivory-associated terpenoid metabolism in the susceptible genotype. Key green leaf volatiles such as aldehydes were absent, indicating a weak volatile-mediated defence response.

In the resistant genotype DMRE 63, the chemical profile is characterised by the presence of aldehydes such as nonanal and decanal under healthy conditions and a shift toward herbivory-induced metabolic pathways, synthesising more terpenoids and ketones. In contrast, the susceptible genotype CML 170 showed a volatile profile dominated by long-chain hydrocarbons with minimal

biologically active signalling compounds, indicating a weak and ineffective defence system. The moderately resistant genotype CML 122 displayed a moderate response with a transition from cycloalkane and ketone-dominated profiles to long-chain hydrocarbons following herbivory. This shift in metabolites suggests a reliance on structural and cuticular defences rather than volatile-mediated signalling.

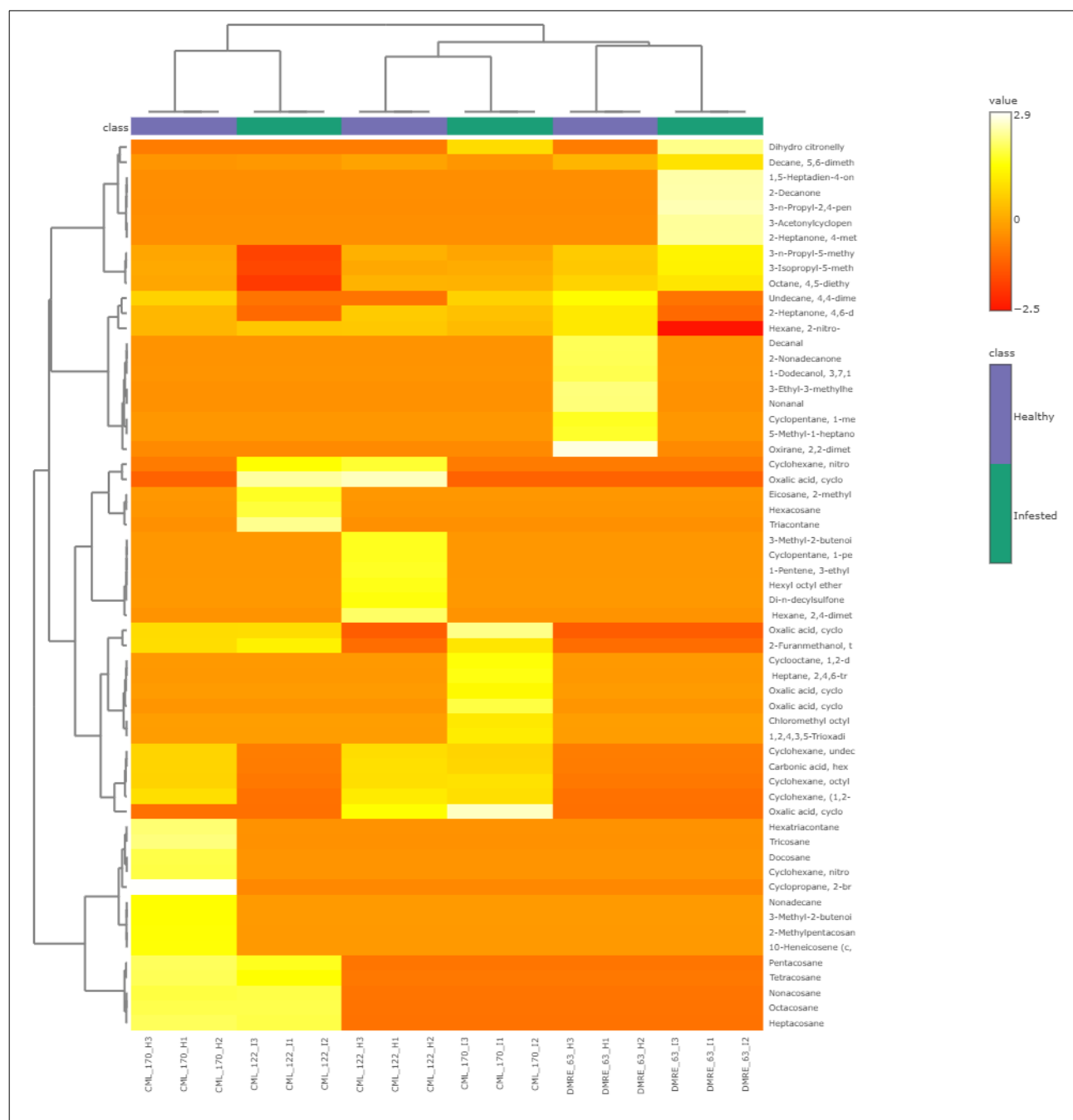


Fig. 2. Heat maps comparing the volatile profile in healthy and infested plants of selected maize genotypes.

Table 4. Volatiles identified from healthy and infested resistant DMRE 63 maize plants

Major volatile compounds detected in gas chromatography–mass spectrometry (GC-MS)					
Healthy			Infested		
Compound name	Component area	Chemical class	Compound name	Component area	Chemical class
1-Dodecanol, 3,7,11-trimethyl-	52238.4	Terpenoid alcohol (isoprenoid alcohol)	Dihydro citronellyl angelate	28742.9	Terpenoid ester (monoterpene derivative)
Octane, 4,5-diethyl-Alkane	52231.1	Branched hydrocarbon	3-n-Propyl-5-methylhexan-2-one	28217.7	Branched ketone
3-Ethyl-3-methylheptane Alkane	51126.2	Branched hydrocarbon	3-n-Propyl-2,4-pentanedione	26650.2	β-diketone
Nonanal	48929.0	Aldehyde (aliphatic, GLV)	2-Decanone	22631.5	Diketone (β-diketone)
Decanal	28592.1	Aldehyde (aliphatic, GLV)	1,5-Heptadien-4-one, 3,3,6-trimethyl-	21912.2	Terpenoid-related ketone
2-Heptanone, 4,6-dimethyl-	19107.6	Ketone	3-Isopropyl-5-methylhexan-2-one	18731.4	Terpenoid ester (monoterpene derivative)
5-Methyl-1-heptanol	14354.7	Alcohol	2-Heptanone, 4-methyl-	18441.3	Terpenoid-related ketone
			3-Acetyl-cyclopentanone	17694.9	Cyclic ketone

Table 5. Volatiles identified from healthy and infested moderately resistant CML 122 maize plants

Major volatile compounds detected in gas chromatography–mass spectrometry (GC-MS)					
Healthy			Infested		
Compound name	Component area	Chemical class	Compound name	Component area	Chemical class
2-Heptanone, 4,6-dimethyl-	19776.8	Ketone	Octane, 4,5-diethyl-	121897.8	Branched hydrocarbon
3-Isopropyl-5-methylhexan-2-one	19954.5	Ketone			Branched hydrocarbon
3-n-Propyl-5-methylhexan-2-one	32356.0	Ketone	Decane, 5,6-dimethyl-	51243.2	Branched hydrocarbon
1-Pentene, 3-ethyl-3-methyl-	43699.6	Minor alkene (Branched hydrocarbon)			Branched hydrocarbon
Decane, 5,6-dimethyl-	52735.9	Branched hydrocarbon	Pentacosane	230798.6	Straight chain hydrocarbon
Octane, 4,5-diethyl-	25564.1	Alkane (Branched hydrocarbon)	Tetracosane	131964.9	Straight chain hydrocarbon
Cyclopentane derivative	39812.2		Heptacosane	451111.9	Straight chain hydrocarbon
			Octacosane	471996.9	Straight chain hydrocarbon
			Nonacosane	427403.3	Straight chain hydrocarbon
Cyclohexane derivative	51650.2	Cycloalkane (alicyclic hydrocarbon)	Hexacosane	97992.4	Straight chain hydrocarbon
			triacontane	363070.3	Straight chain hydrocarbon

Table 6. Volatiles identified from healthy and infested susceptible CML 170 maize plants

Major volatile compounds detected in gas chromatography–mass spectrometry (GC-MS)					
Healthy			Infested		
Compound name	Component area	Chemical class	Compound name	Component area	Chemical class
2-Heptanone, 4,6-dimethyl-	21400.3	Ketones	2-Heptanone, 4,6-dimethyl-	16656.0	Ketones
3-Isopropyl-5-methylhexan-2-one	31692.6	Ketones	3-Isopropyl-5-methylhexan-2-one	29027.5	Ketones
3-n-Propyl-5-methylhexan-2-one	49650.8	Ketones	3-n-Propyl-5-methylhexan-2-one	24714.3	Ketones
2-Furanmethanol, tetrahydro-5-methyl-	82000.8	Minor oxygenated compound (Alcohol)	Dihydro citronellyl angelate	23555.4	Terpenoid-related compound
Nonadecane	52572.9	Straight chain hydrocarbons	Decane, 5,6-dimethyl-	25101.6	Alkane (branched hydrocarbon)
Docosane	180699.7	Straight chain hydrocarbons	Undecane, 4,4-dimethyl-	21169.7	
Tricosane	419599.9	Straight chain hydrocarbons	Cyclooctane, 1,2-diethyl-	32981.8	Cyclo alkane
Tetracosane	655509.2	Straight chain hydrocarbons	Cyclohexane, (1,2-dimethylbutyl)-	39616.1	Cyclo alkane
Pentacosane	810374.4	Straight chain hydrocarbons	Cyclohexane, undecyl-	16923.7	Cyclo alkane
Heptacosane	832588.3	Straight chain hydrocarbons	Cyclohexane, octyl-	33251.5	Cyclo alkane
Octacosane	723564.7	Straight chain hydrocarbons			
Nonacosane	591790.9	Straight chain hydrocarbons			
Hexatriacontane	351345.9	Straight chain hydrocarbons			

These findings suggest that resistance to *S. frugiperda* is associated with an ability to synthesise chemically active defence responses, whereas susceptibility is linked to passive metabolite profiles lacking effective signalling compounds. Across all 3 genotypes, the total volatile emission of potential compounds was lower in the infested volatile profile than in the healthy profile. Although leaf feeding by herbivores generally enhances the release of plant volatiles, under specific plant-herbivore interactions, suppression of volatile emission post-herbivory has also been reported. Following root herbivory in maize, a reduction in emission of herbivore-induced root volatiles was observed (36).

Previous studies reveal that *S. frugiperda* feeding suppresses HIPV emissions in maize relative to those elicited by other chewing herbivores (37). Similarly, the reduction in volatile abundance post herbivory indicates that feeding by fall armyworm might reduce the synthesis of maize volatiles while promoting accumulation of other defence compounds and this requires further investigation.

Environmental conditions are known to influence both the production and composition of HIPVs. Temperature, relative humidity, light intensity and plant developmental stage regulate energy allocation, stress responses, photosynthetic efficiency and ultimately affect the accumulation of volatiles and other secondary metabolites (38, 39). The variation in the above factors

may cause small but significant changes in the relative proportion of different volatile compounds. However, in the present study, all maize genotypes were evaluated at the same developmental stage under identical greenhouse conditions and subjected to uniform herbivory treatment. Standard experimental conditions adopted in the study minimised the environmental variations, enabling reliable comparison of genotype-dependent volatile profiles. Validation under multiple environments and seasons must be carried out to determine the stability of these volatile-mediated resistance traits under field conditions.

Behavioural assay with olfactometer

Host selection behaviour of *S. frugiperda* female moths towards three different maize genotypes was analysed using a Y-tube olfactometer. The gravid females preferred healthy maize plants over herbivory-damaged plants in all the three genotypes tested. In the susceptible genotype CML 170, female moths exhibited a greater attraction to healthy plants by 75 % compared to 25 % attraction towards infested plants. Similarly, female moths responded to healthy plants over infested plants in moderately resistant genotype CML 122 (68 % and 32 %). A similar pattern of response was observed in resistant genotype DMRE 63 (Table 7). However, the strongest preference for volatiles from healthy plants was observed in the susceptible genotype CML 170 ($\chi^2 = 6.00$, p -value = 0.014), as indicated by the greatest difference in female response (75 % vs. 25 %) and the



lowest p-value. The results are consistent with previous findings, where females preferred volatiles from healthy plants over herbivore-induced plants (40). Preference for healthy plant volatiles is assumed to be an adaptive

behaviour of female moths to choose oviposition sites free from previous invaders so as to avoid competition for food for their offspring.

Table 7. Behavioural response of *Spodoptera frugiperda* females to maize genotypes in Y-tube olfactometer

Genotypes	Mean females responded (%)		Chi-square	p-value
	Arm A (Infested plant)	Arm B (Healthy plant)		
DMRE 63	35.0	65.0	1.80	0.035*
CML 122	32.0	68.0	3.24	0.042*
CML 170	25.0	75.0	6.00	0.014*

*Significant at 5 % level.

Besides this, HIPVs attract natural enemies, causing egg, larval predation and parasitism (40). Insect herbivory is often known to induce the synthesis of repellent compounds and suppress the emission of attractive compounds (41). This explains the enhanced attractiveness of FAW moths towards healthy plants compared to infested plants. Among the healthy plants, susceptible genotype CML 170 exhibited the highest percentage of attraction (75 %) in comparison to resistant DMRE 63 (65 %) and moderately resistant genotype CML 122 (68 %). The sucking pest, mirid bug *Apolygus lucorum*, was found to prefer volatile organic compounds from susceptible cotton cultivar in comparison to volatiles from resistant cultivar (42). Likewise, there might be a greater emission of attractive volatile compounds by healthy plants of CML 170, which requires further validation using the individual synthetic volatile compounds identified based on GC-MS results and their blends.

Principal component analysis

Principal component analysis (PCA) was performed using leaf damage score (LDS), behavioural response (BR), oviposition and seven groups of volatile compounds (aldehydes, alcohols, branched hydrocarbons, cycloalkanes, ketones, straight-chain hydrocarbons and terpenoids) to understand their association with resistance responses in three maize genotypes under healthy and FAW-infested conditions. For leaf damage score, mean damage rating at 14 DAI during rabi 2024–25 and kharif 2025 were used for the analysis and volatile emission of each chemical group was expressed as the sum of GC–MS component peak area. The first two principal components summarised the major variation among volatile groups, behavioural response and ovipositional preference. The two principal components (PC1, PC2) jointly explained 68.1 % of total variability, indicating that in response to insect feeding, activation of metabolic pathways causes a change in plant volatile profile and subsequent influence on insect behaviour (30, 43, 44). PC1 accounted for 46.0 % (eigenvalue = 5.52) and PC2 accounted for 22.1 % (eigenvalue = 2.65) (Fig. 3, 4; Table 8).

The loading matrix revealed that PC1 was primarily influenced by ovipositional preference (0.449), alcohols (0.443), straight-chain hydrocarbons (0.391),

ketones (0.364), behavioural response (0.355) and leaf damage score (–0.305). Thus, PC1 separates the maize genotypes based on host plant attractiveness and preference for oviposition. Contrastingly, PC2 was influenced by aldehydes (0.549), branched hydrocarbons (0.398), behavioural response (0.355), leaf damage score (–0.466) and ketones (–0.344), indicating that this component primarily described variation related to volatile composition and herbivory response to volatiles from healthy and infested plants. The PCA differentiated DMRE 63 (resistant), CML 122 (moderately resistant) and CML 170 (susceptible) maize genotypes, indicating that antixenosis-mediated resistance separates the three genotypes.

Considering the susceptible genotype CML 170, in its healthy state the position within the biplot corresponds to high oviposition, behavioural response and high abundance of alcohols, ketones and straight-chain hydrocarbons. This suggests a preferential attraction of female FAW moths, resulting in a higher preference for oviposition (45). Following infestation, CML 170 shifted towards the negative side of both PC1 (–1.82) and PC2 (–1.87), reflecting an extensive modification of HIPV in comparison to the healthy volatile profile. CML170 being a susceptible genotype, the induced changes in the volatile profile likely represent a response to herbivory rather than influencing the plant defence mechanism.

Healthy DMRE 63 showed a negative PC1 score (–0.65) and the highest positive PC2 score (2.91), characterised by aldehydes and branched hydrocarbons. These volatile groups might represent characteristic features of volatiles from the resistant genotype. After infestation, the genotype shifted towards negative PC (PC1 = –1.18; PC2 = –0.57). Terpenoids, ketones and leaf damage exhibited the highest contributions, suggesting that the change in volatile profile compared to the healthy plant is characteristic of the HIPV profile in the resistant genotype.

Unlike the resistant (DMRE 63) and susceptible (CML 170) genotypes, the moderately resistant genotype (CML 122) occupied an intermediate position closer to the origin in healthy (PC1 = 0.23; PC2 = 0.30) and infested state (PC1 = –1.17; PC2 = 0.15). The position in the biplot indicates that no single volatile

class or behavioural trait exerted a greater influence in the PCA distribution.

Table 8. Principal component analysis (PCA) of fall armyworm, damage, adult behavioural response, oviposition preference with maize plant volatiles

Genotype	LDS	BR (%)	Oviposition (eggs laid)	ALD	ALC	KET	TER	SCH	BHC	CYC	PC1 score	PC2 score	Level of resistance
DMRE 63 (H)	0.00	65.0	24.835	77521.1	114354.7	19107.6	52238.4	0	103357.3	0	-0.65	2.91	R
DMRE 63 (I)	3.65	35.0	12.000	0	0	95194.3	87827.8	0	0	0	-1.18	-0.57	
CML 122 (H)	0.00	68.0	134.167	0	0	72087.3	0	0	121999.6	91462.4	0.23	0.30	MR
CML 122 (I)	4.35	32.0	60.244	0	0	0	0	2174338.3	173141	0	-1.17	-0.15	
CML 170 (H)	0.00	75.0	273.165	0	82000.8	184744.5	0	4618045.9	0	0	4.59	-0.55	S
CML 170 (I)	6.1	25.0	30.400	0	0	70397.8	23555.4	0	46271.3	122773.1	-1.82	-1.94	

H: healthy; I: infested; LDS: leaf damage score; BR: behavioural response; ALD: aldehyde; ALC: alcohol; KET: ketone; TER: terpenoid; SCH: straight chain hydrocarbon; BHC: branched hydrocarbon; CYC: cycloalkane.

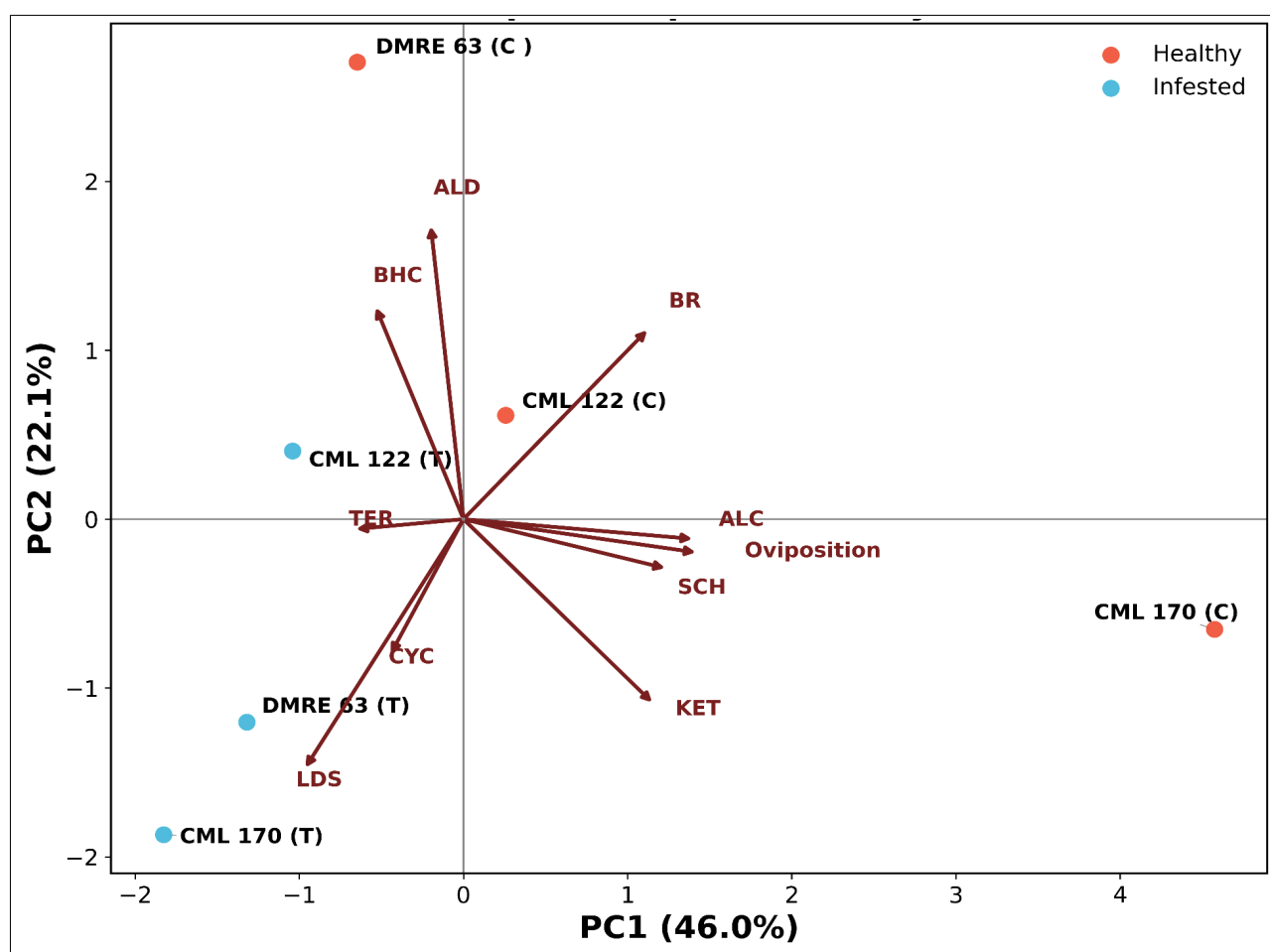


Fig. 3. Principal component analysis (PCA) biplot showing the distribution of maize genotypes under healthy and infested conditions based on resistance-associated traits. LDS: leaf damage score; BR: behavioural response; ALD: aldehyde; ALC:

alcohol; KET: ketone; TER: terpenoid; SCH: straight chain hydrocarbon; BHC: branched hydrocarbon; CYC: Cycloalkane.

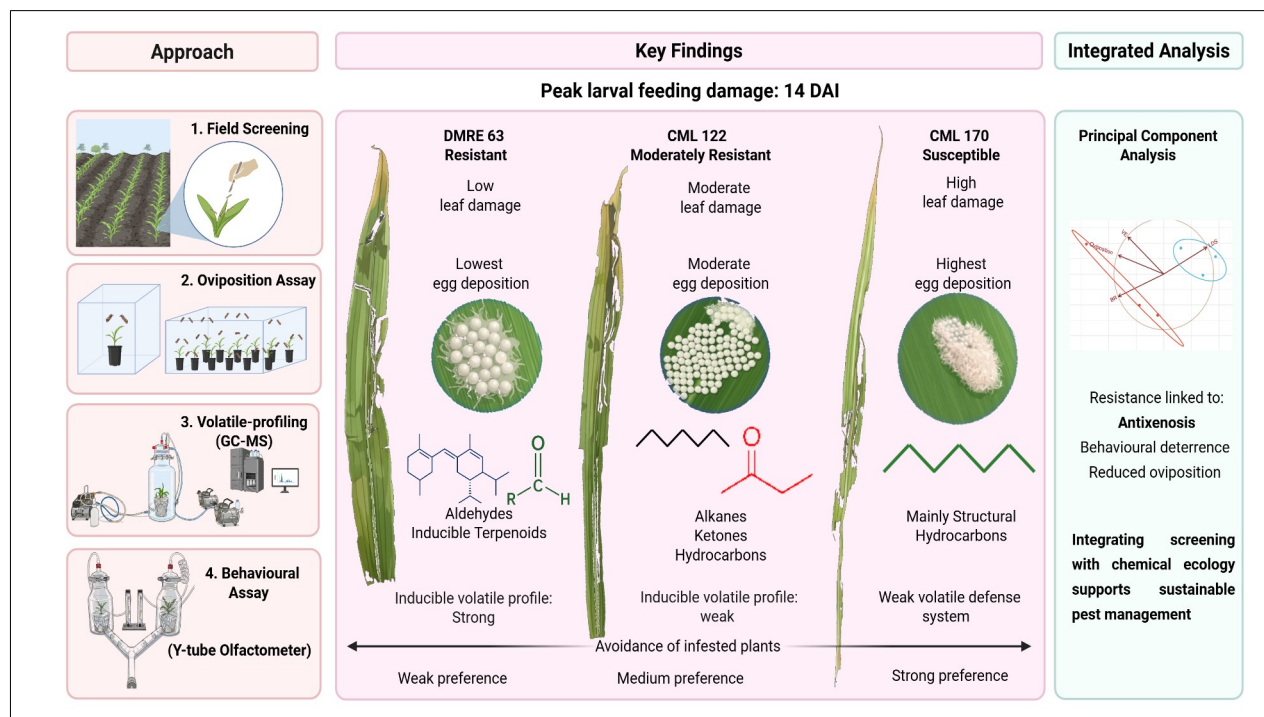


Fig. 4. Multidimensional characterisation of maize resistance to *Spodoptera frugiperda*.

Overall, the PCA differentiated DMRE 63 (resistant), CML 122 (moderately resistant) and CML 170 (susceptible) maize genotypes, indicating that antixenosis-mediated resistance separates the three genotypes. Here, antixenosis is associated with volatile-mediated defence mechanisms, behavioural deterrence and reduced ovipositional preference. Antixenosis is the first line of defence, deterring host plant selection for feeding and oviposition, whereas antibiosis constitutes the second line of defence by adversely affecting insect survival, growth and development (46).

Resistance in genotype DMRE 63 and CIMMYT genotypes CML 60, CML 59 and CML 71 revealed antibiosis and antixenosis as promising parameters reflected through prolonged larval duration, reduced survival and low feeding efficiency (7, 46). Contrastingly, CIMMYT genotypes CML 122, CML 330, CML 332, CML 337 primarily exhibited antibiosis while Perola cultivar, BRS-Caatingueiro exhibited antixenosis (22, 46). The resistant maize genotype Mp708, developed through conventional breeding, has been extensively characterised as a source of resistance to *S. frugiperda*. Multiple constitutive and inducible defence mechanisms, including elevated basal jasmonic acid levels and constitutive emission of (E)- β -caryophyllene, contribute to herbivore deterrence and indirect defence (4). Although the genetic and molecular mechanisms governing resistance in DMRE 63

remain largely unresolved, previous studies have consistently identified it as a stable source of resistance across seasons (46, 47). Resistance in DMRE 63 has been associated with favourable morpho-biochemical traits, including higher trichome density, greater leaf thickness and elevated defensive biochemical constituents, all of which are negatively correlated with leaf damage (47). Furthermore, DMRE 63 has been shown to express both antibiosis and antixenosis, resulting in reduced oviposition, lower larval survival and reduced larval and pupal weights (46).

The present study supplements the concept of plant volatiles in behavioural and non-preference in FAW attraction towards the host plants and subsequent oviposition. The gravid females recognise the suitable genotypes for the development of their progeny by recognising the volatile attractant or deterrent cues present in maize genotypes inducing oviposition. This indicated the presence of the antixenosis category of resistance to FAW which prevents or limits oviposition. While the present study identified antixenosis as the mechanism of resistance, exhibiting non-preference for oviposition and volatile-mediated behavioural deterrence, the contribution of antibiosis to the overall resistance mechanism cannot be overlooked. Long-chain hydrocarbons (docosane, heptacosane, nonacosane, octacosane, pentacosane, tricosane) identified from the volatile profile of the maize genotypes are

constituents of cuticular wax, which besides acting as physical defence, may also interfere with larval feeding and growth, thereby exerting antibiosis. Studies of rice wild genotypes indicated an antibiosis effect on FAW larvae by reduced larval weight gain compared with wax deficit mutants (48).

Similar antibiosis mechanism of resistance imparted by epicuticular wax was also observed in groundnut against FAW (49). Cabbage leaf with higher epicuticle wax (*n*-nonacosane) reduced *Pieris rapae* larval feeding (35). In addition to structural defences, biochemical traits also influence the survival and development of insects (46, 50).

The findings on DMRE 63 highlight its potential as a donor genotype for developing FAW-resistant maize cultivars. Resistance to FAW is a quantitative polygenic trait characterised by antixenosis, antibiosis and tolerance (8). Incorporating DMRE 63 into conventional breeding programmes, together with the development of molecular markers linked to resistance loci, are promising strategies to develop durable FAW-resistant cultivars. Advances in metabolomics, genomics and metabolic engineering may further facilitate the enhancement of defence-related metabolites associated with resistance (51). However, the ecological and agronomic consequences of modifying plants for resistance traits require careful evaluation. The constitutive expression of *Tps* gene in maize resulted not only in the continuous emission of HIPVs (*E*)- β -caryophyllene and α -humulene but also reduced plant growth and yield, together with increased attraction of both larval and adult *S. frugiperda* (52). Therefore, genome-editing and metabolic engineering approaches should be carefully evaluated to ensure that enhanced resistance is achieved without compromising agronomic performance, ecological fitness, or interactions with natural enemies.

4. Conclusion

The present study reveals the multifaceted nature of maize resistance to *Spodoptera frugiperda* involving both plant defence traits and insect behavioural response. Among the genotypes evaluated, DMRE 63 exhibited stable resistance, whereas CML 121 and CML 122 displayed moderate resistance across seasons. Resistance was characterised by reduced leaf damage, lower oviposition and a stronger behavioural deterrence to fall armyworm (FAW) adults. The resistant genotype DMRE 63 showed a noticeable change in the volatile composition. DMRE 63 presented a dynamic volatile defence system, shifting from aldehydes to terpenoid compounds upon herbivory. The consistent expression of resistance by DMRE 63 across field screening along with reduced oviposition, behavioural deterrence and a distinct volatile profile highlights its potential as a valuable donor genotype for the development of FAW-resistant genotypes. These findings highlight the importance of integrating field screening with chemical

ecology to identify resistant germplasms and also to improve our understanding of antixenosis-mediated resistance. Future research should focus on elucidating the functional roles of key volatile compounds like nonanal, decanal and inducible terpenoids. These compounds are potential semiochemical candidates for behavioral manipulation in the field. It is also essential to validate their ecological significance and identify the genetic and molecular mechanisms regulating their synthesis. Integrating metabolomics with genomics will facilitate the development of environmentally sustainable FAW-resistant maize cultivars.

Acknowledgements

The authors acknowledge the support of Tamil Nadu Agricultural University, Coimbatore.

Authors' contributions

All authors contributed to the study conception, design and manuscript preparation. FA carried out the experiments, recorded and analysed the data and wrote the manuscript. SRP structured and supervised the experiments and edited the manuscript. MM, ST, RR, SN critically reviewed the manuscript. All authors have read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

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Additional information

Peer review: Publisher thanks the Sectional Editor and anonymous reviewers for their contribution to the peer review of this work.

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Supplementary Files

Supplementary Table 1. Field screening of maize genotypes against *Spodoptera frugiperda* during rabi 2023–24

Sl. No	Genotype	Leaf damage rating				Score
		7 DAI	14 DAI	21 DAI	28 DAI	
1.	QPM23015	1.600	6.800	4.600	2.100	S
2.	QPM23016	2.800	6.400	4.100	2.600	S
3.	CO (H) M 8	3.400	5.400	4.500	2.100	MR
4.	QPM23021	2.500	6.500	4.200	3.100	S
5.	QPM23018	3.100	6.200	4.400	2.800	S
6.	CML 337	2.100	6.100	4.900	1.800	S
7.	QPM23017	5.500	6.100	4.500	2.200	S
8.	QPM23012	6.600	6.500	5.000	2.200	S
9.	DMRE 63	3.000	5.000	3.300	1.400	MR
10.	QPM23011	6.500	6.000	6.200	2.300	S
11.	QPM23007	2.200	6.200	4.700	1.900	S
12.	MIL 7-3-4	4.600	4.300	2.700	1.700	MR
13.	QPM23001	5.400	6.200	5.000	2.200	S
14.	CML 170	2.600	6.300	2.800	1.200	S
15.	L21016	3.400	6.700	5.500	2.000	S
16.	MIL 7-14-1	2.200	6.400	3.900	1.700	S
17.	L21006	2.500	6.200	4.300	2.300	S
18.	CML 330	1.400	2.100	3.600	1.000	R
19.	L21007	4.100	6.200	5.100	2.400	S
20.	L21015	2.500	6.500	4.300	2.100	S
21.	L21011	4.200	6.700	5.200	2.900	S
22.	L21017	4.100	6.100	5.000	2.200	S
23.	HKI 193-1	2.700	6.400	4.600	1.700	S
24.	CML 121	4.700	4.600	2.900	1.800	MR
25.	M22004	6.200	6.100	5.800	2.300	S
26.	M22010	4.900	6.300	5.400	2.200	S
27.	CML 108	2.900	6.700	5.200	1.800	S
28.	I2	2.800	6.700	4.400	1.750	S
29.	I17	2.200	6.100	4.400	1.611	S
30.	I23	2.500	6.400	5.100	1.450	S
31.	I4	3.400	6.900	4.800	1.417	S
32.	I10	5.000	6.500	5.000	1.350	S
33.	I1	5.000	6.400	5.000	1.625	S
34.	CML 122	3.600	4.300	3.000	1.800	MR
35.	I18	3.500	6.200	4.900	1.769	S
36.	I14	3.000	6.100	2.500	1.615	S
37.	I3	4.100	6.600	4.000	1.773	S
38.	I28	5.400	6.700	4.500	1.714	S
39.	I30	5.300	6.500	2.400	1.500	S
40.	I29	2.900	6.500	2.900	1.250	S
41.	I9	2.900	6.600	3.200	1.722	S
42.	I24	2.700	6.700	2.800	1.682	S
43.	I11	3.600	6.300	5.400	2.042	S
44.	I16	3.500	6.200	3.300	1.375	S
45.	I6	4.300	6.700	4.200	1.615	S
46.	CML 346	1.200	3.400	3.000	1.500	R
47.	I13	3.200	6.600	2.700	1.313	S
48.	I5	4.400	6.100	4.600	1.750	S
	Mean	3.588	6.090	4.246	1.867	
	SEd	0.53	0.37	0.43	0.28	
	CD (P=0.05)	1.07	0.74	0.86	0.56	

R: resistant; MR: moderately resistant; S: susceptible; DAI: days after infestation.



Supplementary Table 2. Field screening of maize genotypes against *Spodoptera frugiperda* during kharif 2024

Sl. No	Genotype	Lead damage rating				SCORE
		7 DAI	14 DAI	21 DAI	28 DAI	
1.	SD200019	3.60	7.100	6.200	3.100	S
2.	SD200010	3.10	6.100	5.800	3.400	S
3.	SD200016	3.40	6.700	6.500	3.200	S
4.	SD200018	3.00	6.100	6.500	3.200	S
5.	SD200025	2.80	6.800	6.300	3.300	S
6.	SD200029	2.70	6.900	6.700	2.700	S
7.	SD200020	2.70	7.200	6.800	2.900	S
8.	SD200023	3.00	7.000	6.500	3.300	S
9.	SD200003	3.20	7.100	6.400	2.600	S
10.	MIL 7-14-1	4.90	6.300	3.500	2.700	S
11.	SD200030	4.10	6.600	5.300	3.200	S
12.	SD200031	3.30	6.800	6.400	3.300	S
13.	SD200005	3.50	6.30	7.00	3.400	S
14.	SD200007	3.40	6.100	5.700	2.900	S
15.	SD200017	3.20	7.300	6.400	3.400	S
16.	MIL 7-3-4	3.40	6.100	3.700	1.700	S
17.	SD200014	3.80	6.500	6.200	4.600	S
18.	SD200001	2.90	6.300	5.100	2.900	S
19.	SD200015	4.00	7.600	6.000	3.100	S
20.	SD200004	3.50	6.100	5.600	3.000	S
21.	CML 170	3.90	6.200	3.900	2.400	S
22.	SD200022	3.30	6.900	6.900	3.100	S
23.	SD200013	3.60	6.500	6.800	2.800	S
24.	LD221029	3.40	6.100	6.000	3.300	S
25.	CML 330	2.0	4.400	3.000	2.700	MR
26.	LD221005	3.80	6.100	6.400	3.400	S
27.	LD221042	3.10	6.800	6.100	3.600	S
28.	HKI 193-1	3.70	6.300	4.100	1.700	S
29.	LD221012	3.30	6.000	6.000	3.000	S
30.	LD221026	4.30	6.400	6.100	3.300	S
31.	CML 346	3.20	6.100	2.9	1.800	S
32.	LD221035	3.90	6.200	6.300	3.800	S
33.	LD221010	3.60	6.000	5.700	3.500	S
34.	CML 337	3.60	3.800	3.20	2.10	R
35.	LD221018	4.10	6.000	6.600	3.700	S
36.	LD221022	3.70	6.100	6.800	3.500	S
37.	LD221025	3.70	6.100	6.100	3.000	S
38.	LD221008	4.20	6.100	6.300	3.100	S
39.	DMRE 63	3.60	4.400	3.300	1.80	MR
40.	MD210003	3.30	6.300	6.300	3.800	S
41.	MD210021	3.20	6.100	6.200	3.700	S

42.	MD210037	3.50	6.100	6.100	3.100	S
43.	MD210039	2.80	6.100	6.200	3.700	S
44.	MD210028	3.00	6.100	6.400	3.600	S
45.	MD210020	3.60	6.800	6.700	3.400	S
46.	MD210029	3.00	6.100	6.400	3.400	S
47.	MD210013	3.20	6.700	6.900	3.900	S
48.	MD210014	3.60	6.400	6.700	3.600	S
49.	MD210026	3.50	6.500	6.600	3.700	S
50.	MD210017	3.40	6.300	6.200	4.100	S
51.	MD210034	3.30	6.200	6.300	3.700	S
52.	MD210015	3.50	6.100	6.300	3.400	S
53.	MD210036	3.30	6.000	6.100	3.900	S
54.	MD210007	3.10	6.600	6.200	3.200	S
55.	MD210004	3.10	6.400	6.600	3.200	S
56.	CML 108	4.40	6.8	6.2	1.90	S
57.	MD210008	3.50	6.500	6.600	2.900	S
58.	MD210000	3.10	6.200	6.300	3.300	S
59.	MD210023	3.30	6.200	6.500	2.800	S
60.	QPM230022	4.20	6.600	6.800	3.400	S
61.	MIL 70-30-3-1	3.20	6.500	4.50	2.10	S
62.	QPM230045	3.40	6.300	6.100	4.000	S
63.	QPM230020	3.20	6.100	6.000	3.400	S
64.	CML 121	5.50	4.9	4.90	2.20	MR
65.	QPM230021	3.30	6.100	6.400	3.600	S
66.	QPM230035	3.70	6.100	6.300	3.500	S
67.	QPM230006	3.40	6.400	6.200	3.900	S
68.	QPM230023	3.80	6.100	6.300	3.200	S
69.	QPM230047	2.90	6.100	6.200	3.300	S
70.	QPM230050	3.70	5.600	5.800	3.600	S
71.	QPM230013	3.50	6.200	5.900	3.600	S
72.	QPM230019	3.50	6.200	6.500	3.600	S
73.	QPM230016	3.40	6.000	6.200	3.100	S
74.	QPM230030	3.60	6.700	6.500	3.500	S
75.	CML 122	2.60	4.30	2.60	1.60	MR
76.	QPM230044	2.80	6.100	6.300	3.800	S
77.	QPM230009	3.30	6.000	5.700	3.400	S
78.	QPM230002	2.60	6.300	6.500	3.600	S
79.	QPM230007	3.40	6.200	6.100	3.700	S
80.	19003	6.20	6.500	6.600	3.700	S
81.	19005	2.70	6.100	6.600	3.600	S
82.	22010	4.10	6.900	7.500	3.500	S
83.	22011	4.50	7.000	7.300	3.300	S
84.	CO (H) M 8	4.00	4.40	3.20	2.10	MR
85.	22034	3.70	6.900	7.300	3.500	S
86.	705.15.1.22.2.3	3.30	6.300	6.800	2.800	S

87.	707.9.4.1.4.2	3.60	6.200	6.900	2.800	S
88.	711.13.1.4.5.59	3.40	6.600	7.400	3.600	S
89.	52099	4.00	6.700	7.300	3.900	S
90.	21028	3.70	6.300	6.800	3.600	S
91.	21039	6.10	6.100	6.900	3.200	S
92.	PAC 751 Elite	5.00	6.400	6.900	3.600	S
93.	DH-17	5.60	6.500	7.300	3.500	S
94.	DH-19	5.20	6.300	6.900	2.900	S
95.	CO (H) M 11	3.40	6.100	3.40	2.40	S
96.	DH-30	3.50	6.300	7.200	3.600	S
97.	DH-32	4.80	6.400	7.200	3.800	S
98.	DH-33	3.70	6.600	7.300	3.400	S
99.	DH-36	4.90	6.100	6.800	3.800	S
100.	DH-39	3.30	6.600	7.200	3.100	S
	Mean	3.60	6.255	6.069	3.216	
	SEd	0.81	0.70	0.91	0.53	
	CD (P=0.05)	1.62	1.39	1.82	1.04	

R: resistant; MR: moderately resistant; S: susceptible; DAI: days after infestation.