Indian Journal of Agricultural Sciences **94** (4): 410–415, April 2024/Article
https://doi.org/10.56093/ijas.v94i4.142582

Electrophysiological and behavioural responses of fall armyworm *Spodoptera frugiperda*: A potential phytovolatile technology for its management

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Received: 17 September 2023; Accepted: 25 January 2024

ABSTRACT

The fall armyworm (FAW), scientifically known as *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera:Noctuidae), is an invasive and polyphagous pest associated with maize (*Zea mays* L.). An experiment was conducted during 2020–21 at South Eastern University of Sri Lanka, Oluvil, Sri Lanka and the Coconut Research Institute of Sri Lanka Lunuwila, Sri Lanka to investigate the olfactory perception of 22 host plant volatiles by electroantennogram (EAG) and behavioural assays for males, virgin and mated females of FAW. The findings indicated that trans-2-Hexen-1-ol, Benzaldehyde, Nonanoic acid, cis-3-Hexen-1-ol, and 4-Phenyl-2-butanone elicited elevated EAG responses in FAW antennae. Additionally, β-Citronellol and ethyl butyrate elicited amplified responses specifically in mated females and males, respectively. Dose-response study revealed that the observed responses remained statistically non-significant ($P>0.05$), regardless gender or physiological condition of females across the 1%, 5%, 10% and 15% dose intervals. In behavioural study, observed that 1% Benzaldehyde attracted a substantial number of moths to the treatment side for both virgin and mated females, whereas 1% β-Citronellol displayed repellent properties specifically for mated females of FAW. Therefore, these findings suggest that volatile plant compounds may serve as a theoretical basis for devising novel control strategies for FAW. This includes the potential development of attractants, repellents, and mass capture killers effective for both males and females of FAW, in addition to the currently used female sex pheromone.

Keywords: Attractants, Behavioural assays, Electroantennogram (EAG), Fall armyworm, Mass trapping, Repellents

Fall armyworm (FAW) *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera:Noctuidae) is a notorious pest of maize (*Zea mays* L.) cultivations, native to the tropical and subtropical regions of the Americas. In late 2018, the alien pest was reported in Sri Lanka and quickly spread to all maize-growing areas in the country, and over 50% of the *Maha* season cultivation (54,416 ha) was affected (DOA, 2019). Chemical pesticides are heavily used in Sri Lanka and other countries such as Brazil and Africa to control pests. According to Sharma *et al*. (2019) estimation around 2 million tonnes of pesticides are used globally each year reflecting a significant upward trend. Improper use of pesticides leads to serious environmental and health impacts in addition leads to the rapid development of resistant populations (Nicolopoulou-Stamati *et al*. 2016), reduction of natural enemy population, pest resurgence, and development of secondary pest outbreaks (Tabashnik *et al*. 2014). Therefore, strategies other than chemical pesticides need to be developed to control FAW by averting these issues. The FAW larvae are minimally mobile but still find the optimal food source. Therefore, it can be assumed that female moths play a key role in host plant selection (Rojas *et al*. 2018). Although the host plants are often hidden among a huge number of other plants, insects can locate their hosts. Various types of research have examined host plant selection behaviour for volatile chemical cues and their impact on olfactory sensory methods and behavioural studies (Dicke 2000, Knight *et al*. 2005 and Castrejon *et al*. 2006). The olfactory cues could identify a host plant using either species-specific compounds or specific ratios of ubiquitous compounds known as green leaf volatiles (GLVs) which are vital in the host localization process (Bruce *et al*. 2005). In this study, we examined the electroantennogram (EAG) and behavioural responses of both male and female *S. frugiperda* to a range of concentrations of 22 host plant volatiles to identify chemical compounds that can be used to attract or repel the FAW moths, finally use effectively in developing green pest management tactics.

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MATERIALS AND METHODS

Insect colony: The FAW larvae were initially collected from maize growing areas in Kandaketiya (N 7° 10' 33.0176"

E 80° 58' 58.2005", altitude 123 m amsl), Badulla District, Sri Lanka, during the 2020 *Yala* season (May to August). Subsequently they were reared in the laboratory of the Department of Bio Systems Technology at South Eastern University during 2020–21 and following bioassays were conducted. The rearing protocol followed was previously described by Du Plessis *et al*. (2020) and Muhandiram *et al.* (2022), which involved providing fresh maize leaves as the natural diet to the larvae in plastic containers until pupation. The laboratory was maintained under ambient conditions of temperature (27±1°C), relative humidity (70–75%), and photoperiod (12 h light:12 h dark). Pupae were sex-separated daily, following the procedure described by Sharanabasappa *et al*. (2018), and kept until adult emergence. The emerged adult moths were placed in oviposition chambers and provided with 10% sucrose solution everyday as feeding source and allowed to oviposition. The laid eggs were then carefully removed and kept on immature maize leaves until the first instar larvae hatched. This rearing protocol was repeated for several generations to obtain sufficient numbers of moths for each bioassay replacing them with natural populations.

Volatile phytochemicals: The study utilized synthetic standard volatile phytochemicals (Table 1) that were purchased from a commercial supplier. Hexane of HPLC grade was used as a solvent to prepare various concentrations (1%, 5%, 10%, and 15% v/v) of the phytochemicals and stored at -4°C until the bioassay.

Electroantennogram Studies: The electroantennogram (EAG) bioassay was conducted at the Electrophysiological Testing Laboratory in Coconut Research Institute, Lunuwila, Sri Lanka, using a commercially available EAG system (Syntec). One to two days old unmated males, females and mated females (24 h with males), were anesthetized by chilling at approximately 4°C for 20–30 sec. A micro scissor was used to remove an antenna from the anesthetized FAW at its base. The detached antennas were mounted between forked metal electrodes of the Universal EAG probe, using an electrical conductivity gel (Spectra 360). The distal end of the antennas was connected to an IDAC-2 signal acquisition controller and then connected to the EAG software (EAG 2000, version 2.7 Syntec). A filter paper (3 cm × 0.5 cm) containing 5 µL of 1% volatile solution was inserted into a glass Pasteur pipette (15 cm long, 12 mm diameter). The pipette tip containing the test compound was then inserted into the side hole located in the center of a glass tube, through which clean air was blown at 0.5 L/min to humidify the air. The air stimuli controller (CS-55) generated a stimulus that delivered 0.5 sec stimuli of carbon-filtered airflow (600 mL/s) that passed through a cartridge before entering the main airflow. The interval between the two stimuli was 1 min to allow the antennae to recover. Dose responsive EAG values were recorded after identifying the volatile compounds that showed higher EAG responses for a 1% concentration of each volatile. The dose-responsive EAG was performed at 1%, 5%, 10%, and 15% dose levels using 5 µL of the identified chemicals. All the bioassays were replicated five times using one antenna per replicate.

Behavioural assay: To investigate the behavioural response of virgin male and female FAW to highly responsive volatile compounds identified through the electrophysiological stimuli bioassay, a dual-choice olfactometer was employed as described in Kaushalya *et al*. (2021). The experiments were conducted in a dark room with controlled environmental conditions under the temperature of 27±1°C and relative humidity of 70–75%. A red fluorescent tube was used to provide uniform lighting for easy observation. Filter papers (2 cm diameter) containing 100 µL of 1% concentrated volatiles diluted in HPLC grade dichloromethane (DCM) were placed on one arm (treatment side) while the other arm served as a control (DCM only). The insects were simultaneously released into the middle chamber, and their movement was recorded during the active period in the scotophase. Each volatile was tested five times separately for males and females. After each trial, the olfactometer was cleaned with 70% ethanol (v/v) and rotated 180° out of position before the next trial.

Ovipositional bioassay: The ovipositional bioassay

Table 1 List of synthetic volatiles used for the EAG responsive and behavioural studies of *Spodoptera frugiperda*

Volatile	Source	Purity	Volatile	Source	Purity
(S)-(-)Limonene	Sigma-Aldrich	96.0%	β-Citronellol	Sigma-Aldrich	95.0%
(R)-(+)-Limonene	Sigma-Aldrich	97.0%	(-)-Menthone	Sigma-Aldrich	90.0%
(-)-β-Pinene	Sigma-Aldrich	99.0%	Geraniol	Sigma-Aldrich	98.0%
α-Pinene	Sigma-Aldrich	98.0%	Camphor	Sigma-Aldrich	96.0%
Benzaldehyde	Sigma-Aldrich	99.9%	1-Octen 3-ol	Sigma-Aldrich	98.0%
Ethyl propionate	Sigma-Aldrich	99.0%	Myrcene	Sigma-Aldrich	99.9%
Nonanoic acid	Sigma-Aldrich	97.0%	3-Pentanol	Sigma-Aldrich	98.0%
4-phenyl-2-butanone	Sigma-Aldrich	98.0%	cis-3-Hexen-1-ol	Sigma-Aldrich	98.0%
Propyl butyrate	Sigma-Aldrich	99.0%	Thymol	Sigma-Aldrich	99.0%
Ethyl butyrate	Sigma-Aldrich	99.0%	Linalool	Sigma-Aldrich	97.0%
trans-2-Hexen-1-ol	Sigma-Aldrich	96.0%	Hexane	Sigma-Aldrich	97.0%

EAG, Electroantennogram.

investigated the behavioural reactions of gravid females of FAW to selected EAG-responsive volatiles using a dual-choice oviposition chamber made of transparent films described by Kumara *et al*. (2015). The chamber dimensions were 42 cm length × 10 cm diameter, and both sides of the chamber were covered with a muslin cloth. A 10% sucrose solution was provided as feeding material in the center of the chamber. For the study, 100 µL of 1% volatiles dissolved in DCM was placed on one side of the chamber, and the other side was the control (100 µL DCM only). The number of eggs laid on each side was counted daily until moth death, after releasing five mated females into the chamber. The bioassay was repeated five times for each volatile, and the test structures were kept far from a well-ventilated area inside the laboratory.

Data analysis: The study examined EAG responses to volatiles, comparing males, females, and gravid females, and analyzed dose-responsive EAG values with ANOVA and Tukey post-hoc test. Behavioural experiments used Pearson's chi-square to compare the number of moths and paired-sample t-test to evaluate oviposition preference. IBM SPSS (version 25) was used for all statistical tests at a 5% significance level.

RESULTS AND DISCUSSION

Insects depend on their olfactory systems throughout their life cycle to locate partners for reproduction and host plants for oviposition (Cardé and Willis 2008). In this study, we assessed the olfactory sensitivity of male and female fall armyworms to 22 common plant volatiles. According to the results, there were significant differences in the mean EAG responses of FAW males, females, and gravid females to the assessed phytochemical volatiles. Specifically, Benzaldehyde, tran-2-Hexen-1-ol, Nonanoic acid, cis-3-Hexen-1-ol, and β-Citronellol were found to elicit strong responses in gravid females. The trans-2-Hexen-1-ol, Benzaldehyde, 4-Phenyl-2-butanone, Nonanoic acid, and cis-3-Hexen-1-ol were found to elicit a stronger response against female antennae compared to male antennae (Table 2). Similarly, Malo *et al*. (2004) reported that Hexan-1-ol produced a stronger response than β-Pinene, Hexanal, (E)-3-Hexenol, 2-Carene, Phellandrene, Limonene, and Linalool in EAG studies of FAW. Another EAG study on *Spodoptera exigua* found that Linalool, Myrcene, and Benzaldehyde were among the plant volatiles with the strongest responses (Burguiere *et al*. 2001). There were no significant differences in mean EAG values for sex or female physiological state, however, the response values were greater in females compared to males (Table 2). The insects possess antennae and mouthparts, including olfactory receptor neurons (ORN) as advanced sensory systems. Plant signaling molecules enter through the skin pore of sensory organs and are then directed to the ORN membrane by odorant binding proteins (OBPs), eventually causing the generation of responsible actions (Kaissling 2014). The olfactory process for ephemeral reception includes important events such as the generation of electrical signals in the

Table 2 EAG responses of male, female, and mated females of *Spodoptera frugiperda* to volatile compounds diluted in Hexane

Volatile	EAG Response ± SE (µV)		
	Male	Female	Gravid female
(S)-(-)Limonene	1.454 ± 0.140^{bcd}	1.765 ± 0.279^{bcdef}	1.628 ± 0.156^{cde}
(R)-(+)-Limonene	1.556 ± 0.188^{bcd}	1.711 ± 0.236^{cdef}	1.498 ± 0.134^{de}
(-)-β-Pinene	1.523 ± 0.156^{bcd}	1.594 ± 0.205^{cdef}	1.490 ± 0.120^{de}
α-Pinene	1.691 ± 0.183^{abcd}	1.823 ± 0.217^{bcdef}	1.640 ± 0.130^{cde}
Benzaldehyde	1.815 ± 0.121^{abcd}	2.344 ± 0.203^{ab}	2.323 ± 0.183^{a}
Ethyl propionate	1.562 ± 0.205^{bcd}	1.905 ± 0.126^{abcdef}	1.532 ± 0.111^{de}
Nonanoic acid	1.828 ± 0.210^{abcd}	2.218 ± 0.150^{abc}	2.109 ± 0.151^{ab}
4-phenyl-2-butanone	1.871 ± 0.192^{abc}	2.246 ± 0.266^{abc}	1.855 ± 0.138^{bcd}
Propyl butyrate	1.693 ± 0.254^{abcd}	1.709 ± 0.203^{cdef}	1.547 ± 0.109^{de}
Ethyl butyrate	1.690 ± 0.202^{abcd}	1.706 ± 0.138^{cdef}	1.647 ± 0.128^{cde}
trans-2-Hexen-1-ol	2.252 ± 0.143^{a}	2.448 ± 0.148^{a}	2.282 ± 0.152^{a}
β-Citronellol	1.620 ± 0.199^{abcd}	2.020 ± 0.166^{abcde}	1.875 ± 0.138^{bcd}
(-)-Menthone	1.246 ± 0.168^{cde}	1.554 ± 0.164^{def}	1.524 ± 0.138d^{e}
Geraniol	1.327 ± 0.146^{cd}	1.456 ± 0.189^{def}	1.431 ± 0.123d^{e}
Camphor	1.369 ± 0.205^{bcd}	2.062 ± 0.162^{abcde}	1.716 ± 0.13bc^{d}
1-Octen 3-ol	1.627 ± 0.203^{abcd}	1.843 ± 0.218b^{cdef}	1.647 ± 0.133^{cde}
Myrcene	1.579 ± 0.188^{bcd}	1.765 ± 0.066^{bcdef}	1.639 ± 0.099^{cde}
3-Pentanol	1.509 ± 0.255^{bcd}	1.893 ± 0.136^{abcdef}	1.719 ± 0.085^{bcd}
cis-3-Hexen-1-ol	2.012 ± 0.302^{ab}	2.145 ± 0.162^{abcd}	2.009 ± 0.42^{abc}
Thymol	0.667 ± 0.260^{e}	0.789 ± 0.024^{g}	0.737 ± 0.167^{f}
Linalool	1.197 ± 0.123^{de}	1.564 ± 0.163^{def}	1.488 ± 0.171^{de}
Hexane	1.239 ± 140^{cde}	1.340 ± 0.164^{g}	1.246 ± 0.099^{e}
F	4.273	5.519	5.039
Df	(22,91)	(22,88)	(22,137)
P	P<0.01	P<0.01	P<0.01

The superscript letters within the column indicate the significant differences among the volatiles at 0.01 significant level and NS indicates the non-significant difference within rows (among sex and physiological states of FAW) at P=0.05 significant level on Tukey's post hoc test. EAG, Electroantennogram.

antennae after ephemeral and transmission to the brain, after integration and generation of behavioral signals (Leal 2013). Monophagous species have distinct receptors that are unique and specialized to specific plant stimuli from host plants, while polyphagous insects have a limited range of receptors (Raguso *et al.* 1996). ORNs are covered with different types of antennal sensilla (Anton *et al*. 2003). According to an earlier study by Malo *et al*. (2004), seven types of sensilla were found in the flagellum of FAW known Trichodea, Chaetica, Coeloconica, Styloconica, Auricilica, Squamiformia, and Basiconica, while Trichodea was found in both sexes. However, these sensilla were more common in males than in females. This ORN activity can be measured by electroantennogram (EAG) recording using different types of compounds (Morawo *et al*. 2016). Hence these results are in line with Fraser *et al.* (2003) and Ramachandran *et al.* (1990) who reported that female antennae are more sensitive to signals from host plants than males. In contrast, Malo *et al.* (2004) found that males of FAW exhibit a greater response to pheromone compounds. This is owing to the results of Anderson *et al*. (1995) and Luis *et al*. (2010) who reported males having significantly more trichoid sensilla covered with neurons that respond to pheromone compounds than females. Since males of FAW have no biological need to locate host plants, their primary goal is to find and mate with females to maximize reproductive success. This could explain the lower EAG levels in males for the green volatile compounds. Females, on the other hand, may rely primarily on volatile components of the host plant to locate suitable oviposition sites, which could explain their stronger reactions to the volatiles tested. The EAG responses for the highly-responsive volatiles dose-dependent study tested at four different doses (1%, 5%, 10%, and 15%). However, no significant differences (P>0.05) were found in the responses of the tested males, virgin and gravid females. Nevertheless, significant differences (P<0.05) were observed in the EAG values among the volatiles. This could be attributed to the polyphagous nature of the fall armyworm, which is sensitive to a wide range of doses. Additionally, the dose range used for synthetic volatiles varied from 1 to 15% with 5-time intervals, but a possible reason would be the active dose range may be lower than 1% with slight variation.

The behavioural responses found that Nonanoic acid attracted male moths significantly ($\chi2$ = 24.00, df = 1, P<0.01), while Ethyl butyrate, 4-phenyl-2-butanone, and Hexane had a repellent effect on them ($\chi2$ = 7.00, df = 1, P<0.01; $\chi2$ = 13.63, df = 1, P<0.01; $\chi2$ = 21.42, df = 1, P<0.01, respectively). Benzaldehyde, trans-2-Hexen-1-ol, and cis-3-Hexen-1-ol had no effect on male behaviour. Similarly, female moths were significantly attracted to Benzaldehyde and 4-phenyl-2-butanone ($\chi2$=18.00, df=1, P<0.01; $\chi2$ = 40.00, df = 1, P<0.01, respectively), while cis-3-Hexen-1-ol, trans-2-Hexen-1-ol, and nonanoic acid had a repellent effect ($\chi2$=50.00, df=1, P<0.01; $\chi2$ = 25.57, df=1, P<0.01; $\chi2$=13.63, df=1, P<0.01, respectively). Hexane and Ethyl butyrate had no significant effect on female behaviour (Fig. 1 and 2).

The dual-choice oviposition bioassay conducted for highly EAG responsive volatiles in gravid females showed that Benzaldehyde-treated chambers had significantly more eggs laid on the treatment side (108.4±5.06) compared to the control side (93.20±2.76). However, when the oviposition chambers were treated with 1-Octen-3-ol, cis-3-Hexen-1-ol, β-Citronellol, and 4-Phenyl-2-butanone, significantly higher numbers of eggs were found on the control side (101.33±10.39), (142.16±11.63), (112.90±8.19), and (160.75±7.63), respectively, compared to the volatile side. Nonanoic acid and trans-2-Hexen-1-ol exhibited a neutral response to oviposition (Table 3).

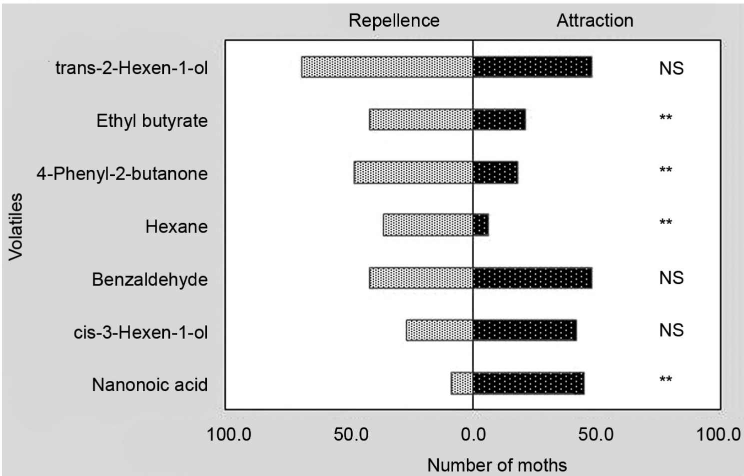

Fig. 1 Mean behavioural responses of FAW male moths to synthetic plant volatiles in the dual-choice olfactometer. ** Indicate the significant responses between repellence and attraction from the volatiles at P< 0.01 and NS = non-significant.

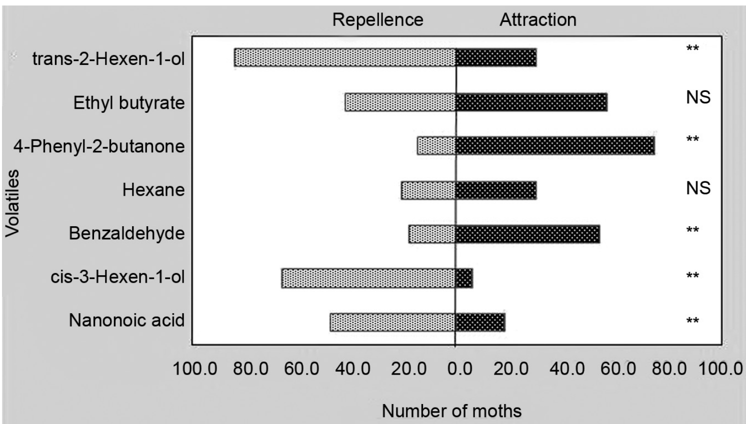

Fig. 2 Mean behavioural responses of FAW female moths to synthetic plant volatiles in the dual-choice olfactometer. ** indicate the significant responses between repellence and attraction from the volatiles at P<0.01 and NS = non-significant.

Table 3 Eggs laid by gravid females on dual choice oviposition choice assay

Volatile	Mean number of eggs ± SE		df	T value	Significant
	Treatment	Control			
1-Octane-3-ol	64.83 ± 3.46	101.33 ± 10.39	77	2.93	**
Benzaldehyde	108.40 ± 5.06	93.20 ± 2.76	129	2.43	*
Cis-3-Hexen -1- ol	130.66 ± 11.24	142.16 ± 11.63	77	0.72	**
β-Citronellol	58.50 ± 3.90	112.90 ± 8.19	129	6.50	**
Nonanoic acid	100.62 ± 6.75	114.87 ± 9.99	103	1.09	NS
4 –Phenyl-2- butanone	132.72 ± 6.55	160.75 ± 7.63	142	2.43	*
trans-2 -Hexen -1-ol	163.75 ± 13.61	147.50 ± 9.06	51	0.81	NS

Each cell represents the mean number of eggs between treatment and control sides; NS-non significant; and ** and * were significantly different at 0.01 and 0.05 by paired sample t-test.

In our study, Ethyl Butyrate had no preference in the dual-choice olfactometer despite a high EAG response in female antennae. Rojas (1999) found similar results for *Mamestra brassicae*, where the largest EAG response was for Hexan-1-ol, but females were not attracted in a wind tunnel bioassay. This shows that a high EAG response does not always lead to a behavioural response. Ren *et al.* (2017) reported that female beetles *Dastarcus helophoroides* showed a behavioural response to 3-Hexanol at different doses and the insects were repellent at a dose of 0.1% and attractive at a dose of 0.001%. Polyphagous insects, such as fall armyworm, face high pressure in selecting their hosts, and gravid females play a vital role in host finding (Gripenberg *et al.* 2010), as per the "mother knows best" hypothesis proposed by Jaenike (1978). This study provides valuable insights into fall armyworm moth's olfactory responses to green leaf volatiles and their potential use in pest management. Further research is needed to investigate the optimal ratios and combinations of these volatiles to attract or repel the moths effectively. Benzaldehyde could be used in trap and kill strategies as an attractive volatile, while β-Citronellol could be used as a repellent to prevent oviposition and reduce crop damage.

Through present study it can be concluded that FAW antennae showed stronger EAG responses to the volatiles of trans-2-Hexen-1-ol, Benzaldehyde, Nonanoic acid, cis-3-Hexen-1-ol, and 4-Phenyl-2-butanone. Behavioural studies have demonstrated that 1% Benzaldehyde attracts large numbers of both virgin and gravid female moths, while 1% β-Citronellol showed repellency for gravid FAW moths. Further studies are needed to develop effective formulations for each compound and to evaluate their persistence and reactivity with atmospheric factors. Based on these results, semiochemical-based pest management strategies that target female moths, such as trap and kill or repellent techniques, could be developed. Overall, these findings provide valuable insights for managing fall armyworm populations in maize cultivations. However, further detailed studies, including dose-response and formulation studies, are necessary to develop practical and cost-effective pest management strategies using green leaf volatiles.

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