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EDITED BY
Juergen Gross,
Julius Kühn-Institut, Germany

REVIEWED BY
Mokhtar Abdulsattar Arif,
Ministry of Agriculture, Iraq
Haichen Yin,
Huazhong Agricultural University, China

*CORRESPONDENCE
Yongjun Zhang
zhangyongjun@caas.cn

†These authors have contributed equally to this work and share first authorship

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# Plant volatiles drive *Spodoptera frugiperda* behavioral preference to sweet corn

Christian Neckie Natt[1†], Chaoqun Yi[1,2†], Longfei Shi[1], Ruonan Li[1,3], Adel Khashaveh[1], Wentao Liu[1,3] and Yongjun Zhang[1*]

[1]State Key Laboratory for Biology of Plant Diseases and Insect Pests, Institute of Plant Protection, Chinese Academy of Agricultural Sciences, Beijing, China, [2]Laboratory of Natural Products Pesticide, College of Plant Protection, Southwest University, Chongqing, China, [3]College of Plant Protection, Hebei Agricultural University, Baoding, China

The Fall Armyworm (FAW), *Spodoptera frugiperda*, is a globally significant invasive lepidopteran pest responsible for severe crop damage, particularly to maize (*Zea mays*). In this study, we investigated the preference of FAW larvae and adults for regular corn (RC) versus sweet corn (SC) using a two-choice behavioral assay. Potential semiochemicals underlying this preference were isolated and identified through headspace volatile collection coupled with Solid-Phase Microextraction–Gas Chromatography–Mass Spectrometry (SPME-GC-MS). The behavioral activity of identified differential volatile compounds was then comprehensively evaluated using electroantennography (EAG), a Y-tube olfactometer, and cage-based oviposition preference tests. Our results demonstrate that FAW larvae exhibit a significant feeding preference for SC leaves, while adult females show a marked oviposition preference for SC plants. Volatile profiling revealed four compounds consistently expressed at higher levels in SC compared to RC: hexanal, trans-2-hexen-1-ol, linalool, and β-caryophyllene. EAG recordings indicated that trans-2-hexen-1-ol elicited the strongest antennal response in FAW adults. In behavioral assays, FAW larvae showed significant attraction to all four volatiles at concentrations of 10 and 100 mg/mL. Similarly, adults exhibited significant preference for most compound-concentration combinations, with the exception of linalool at 100 mg/mL. The volatile compounds identified in SC present promising candidates for use in behavior-based disruption techniques, offering a more environmentally benign alternative to conventional insecticides for FAW control. These findings provide a scientific foundation for developing volatile-mediated strategies as part of integrated pest management programs against this invasive pest.

KEYWORDS
*Spodoptera frugiperda*, volatile organic compounds, electroantennogram recording, behavioral ecology, host preference

## 1 Introduction

The fall armyworm (FAW), *Spodoptera frugiperda*, is an invasive migratory pest native to tropical and subtropical regions of America. In recent years, it has spread to Africa and Asia. (Sparks, 1979; Martinelli et al., 2006; Goergen et al., 2016). FAW is a typical holometabolous insect with a short generation cycle, developing from egg to adult in approximately 30 days (Prasanna et al., 2018). It possesses exceptional reproductive and migratory abilities (Wu et al., 2019). FAW has a wide host range and a large appetite, and can pose a serious threat to host plants (Anega and Birhane, 2025). Studies have shown that corn is a more suitable food source for it (Nagoshi, 2010). Larvae can cause damage throughout the entire corn growth cycle. During the seedling stage, young larvae feed on the tender tissue of the heart leaves, leaving them translucent and film-like. Larvae feed increasingly with age, and in severe cases, they may consume all the leaves in the seedling stage. During the ear stage, larvae feed not only on leaves but also on tassels, silks, and kernels, severely impacting normal growth and yield (Kuate et al., 2019; Jing et al., 2020). The number of eggs laid by female FAW at a time ranges from a few hundred to thousands, which undoubtedly poses a serious threat to crops (Prasanna et al., 2018; Lu et al., 2019). Corn is not only one of the most important food crops in the world, but also one of the key crops necessary for livestock feed and industrial applications (Tran et al., 2019; Paradhipta et al., 2020; Amer et al., 2021). Therefore, effective prevention and control of FAW is of great significance to global food crop security.

Currently, chemical control is the primary method for FAW control. While agricultural production relies on the use of chemical pesticides, their long-term, irrational use poses a destructive threat to the agricultural ecosystem and can also cause FAW to develop resistance. Organophosphates, pyrethroids, and carbamate insecticides are highly effective against FAW, but with long-term use, FAW gradually develops significant resistance (Lira et al., 2020; Zhang et al., 2021). Studies have shown that FAW cultured indoors after 10 generations of resistance screening developed over 10-fold resistance to chlorantraniliprole, while wild FAW populations exhibit high resistance to chlorpyrifos and deltamethrin (Guo et al., 2024; Chen et al., 2025).

In order to avoid the negative effects of pesticides, based on insect chemical ecology, the use of VOCs (volatile organic compounds) to control FAW is one of the important green control measures (Cui et al., 2018). Many studies have revealed that VOCs play an important guiding role in the behavior of FAW. For example, *E*-2-Decenal released by coriander (*Coriandrum sativum*) can effectively repel FAW adults and larvae, and can also effectively repel female FAW from laying eggs. It can be used as a field repellent for FAW to protect crops (Zhong et al., 2025). (*Z*)-9-tetradecenyl acetate (Z9-14:Ac), one of the sex pheromone components released by female FAW insects, combined with (*Z*)-7-dodecenyl acetate (Z7-12:Ac) and (*Z*)-11-hexadecenyl acetate (Z11-16:Ac), has a very significant effect on attracting male FAW insects in the field (Tumlinson et al., 1986; Groot et al., 2008; Wakamura et al., 2021). Trans-$\beta$-farnesene and trans-2-hexenal, two of the herbivore-induced plant volatiles (HIPVs) induced by FAW larvae feeding on corn, have different effects on FAW. Trans-$\beta$-farnesene has an aversion effect on unmated FAW females, while trans-2-hexenal can significantly attract mated FAW females for oviposition (Yang et al., 2025). In addition, the amount of HIPVs released by different varieties of corn after being eaten by FAW varies greatly (Degen et al., 2004), and for different corn growth stages, female FAW preferentially oviposit on maize at the seedling stage (Li et al., 2025).

In a recent indoor study, sweet corn was found to be more effective for FAW pupation, mating, and egg laying than regular corn and artificial diets (Tian et al., 2025), and the corresponding outdoor study found that FAW had a significant preference for sweet corn (Azwana, 2021). Therefore, in order to explore the effects of regular corn and sweet corn on the behavioral selection of FAW, we used a behavioral choice experiment combined with indoor and outdoor experiments to evaluate the choice preferences of FAW and analyzed the key volatile organic compounds related to the induction of FAW behavior, which will help to develop new strategies to optimize the green control methods of FAW and provide a data basis for the biological control strategy of corn pests.

## 2 Materials and methods

### 2.1 Insects and plants

FAW eggs and corn seeds were obtained from the National Plant Protection Scientific Observation and Experiment Station, Langfang. FAW were reared on an artificial diet until pupation in the artificial climate box (RXZ-500B, Ningbo Jiangnan Technology Co., Ltd., Ningbo, China) under controlled conditions (26 ± 1 °C, 65 ± 5% relative humidity, 16:8 h light/dark cycle). Adults and fourth to fifth instar larvae were used in oviposition, feeding, EAG, and behavioral assays. Both regular corn (RC: Zhengdan 958) and sweet corn (SC: Jinguan 597) were grown in pot culture in a greenhouse (26 ± 1 °C, 65 ± 5% relative humidity, 16:8 h light/dark cycle), and plants at the seedling stage (20 days) were used for behavioral choice experiments and volatiles collection.

### 2.2 Chemical compounds

All analytical standards, including hexanal (≥ 98% purity), trans-2-hexen-1-ol (≥ 97%), linalool (≥ 97%, mixture of isomers), $\beta$-caryophyllene (≥ 98%), cis-3-hexen-1-ol (≥ 98%), and mineral oil (light, suitable for GC), were obtained from Shanghai Aladdin Biochemical Technology Co., Ltd. (Shanghai, China).

### 2.3 Oviposition bioassay

A cage experiment simulated a field environment to assess the oviposition preferences of FAW on two different maize varieties. Ten seedling-stage RC and SC plants, each 10 plants, were placed on either side of the cage (1.5 × 1.0 × 1.5 m) (Figure 1A). A cotton ball

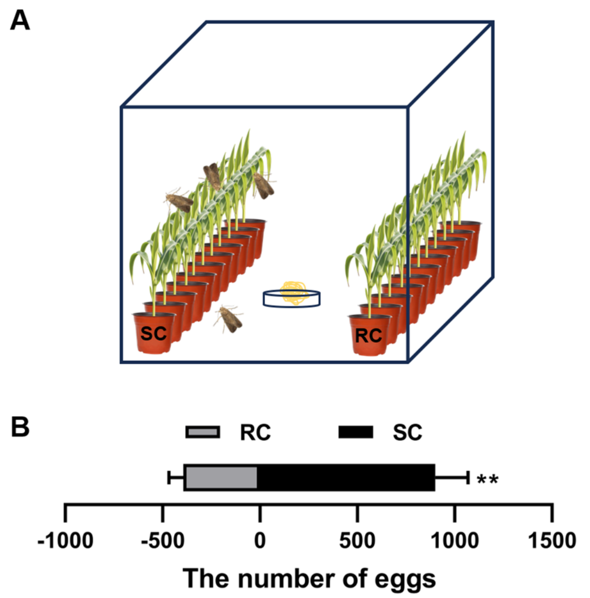


FIGURE 1
Oviposition preference of the FAW females between two different corn varieties. **(A)** Oviposition preference test diagram. **(B)** Results of oviposition preference behavior selection of the FAW female. The data are shown as mean ± SEM. Student's t-test analysis methods were used to analyze the significance of differences in the experimental data results. The FAW had a significantly higher oviposition preference for SC than for RC ($t$ = 4.772, $df$ = 4, $P$ = 0.009). Asterisks indicate a significant difference between the two groups at the 0.05 level ($P$ < 0.05).

soaked in a 10% honey solution was placed in the center of the cage for FAW to consume. Prior to testing, insects were sexed at the pupal stage. Upon emergence, males and females were paired and housed separately. Females exhibiting initial oviposition behavior were selected for the oviposition assays, with ten mated females used per replicate. Egg counts on leaves (excluding those on the cage walls) were counted 24 hours later. The oviposition preference experiment was conducted in a greenhouse (26 ± 1 °C, 65 ± 5% relative humidity, 16:8 h light/dark cycle) with 3 biological replicates.

## 2.4 FAW larvae feeding test

The leaf disc test method established by Jermy (Jermy et al., 1968) was used to evaluate the feeding preference behavior of FAW larvae (Figure 2A). Before the test, the 4-5th instar FAW larvae used in the test were subjected to 12 hours of starvation, and the leaves of two types of maize at the seedling stage were trimmed to a length of about 5 cm. During the test, the prepared RC and SC leaves were placed in a 15 cm diameter culture dish, symmetrically arranged on both sides. During the test, a larva was placed in the center of the selection device, and the selection was recorded. 1 hour later, feeding preferences were assessed based on the area they ate. Leaves with larger feeding areas were considered to be preferred by FAW larvae, and this result was used to calculate the selection rate. The entire feeding choice test was completed in a greenhouse (26 ± 1 °C, 65 ± 5% relative humidity, 16:8 h light/dark cycle), and 80 biological replicates (n = 80 larvae) were performed.

## 2.5 Volatile collection and analysis

Volatile organic compounds (VOCs) were collected from RC and SC seedlings using solid-phase microextraction (SPME) coupled with a 50/30 µm polydimethylsiloxane (PDMS) fiber assembly. Twenty minutes before collection, cover the stems and leaves of the corn plant above ground with a polyethylene terephthalate (PET) sampling bag to avoid mechanical damage to the plant during the operation. SPME technology was used for adsorption and collection for 6 hours. During adsorption, the SPME fiber was suspended and fixed above the sample using a support. 5 biological replicates were performed (n = 5 adsorption collections). Agilent Technologies (China) Co., Ltd., used gas chromatography-mass spectrometry to separate and identify volatile compounds.

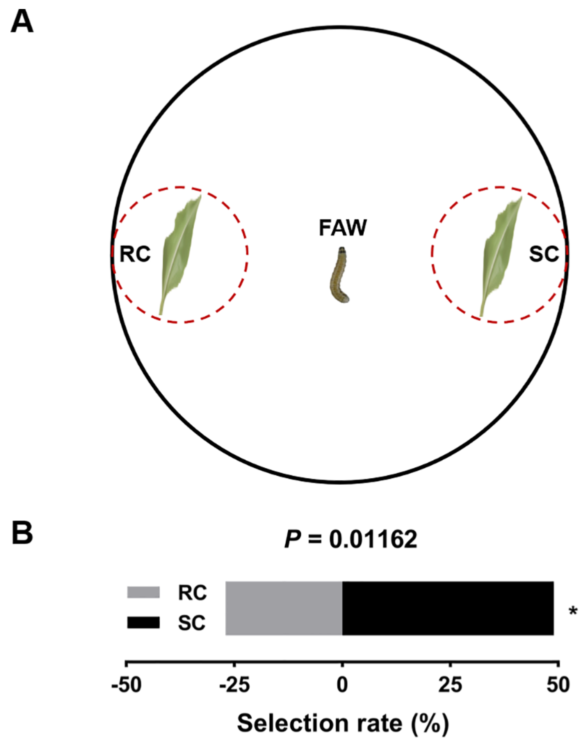


FIGURE 2
The feeding preferences of the FAW larvae for the leaves of two different varieties of corn. **(A)** Schematic diagram of the leaf disc behavior test. **(B)** Results of feeding behavior selection of FAW larvae. The leaf disc method was used to test the feeding preferences of FAW larvae for SC (sweet corn) and RC (regular corn). The results showed that the larvae had a significantly higher feeding preference for SC than for RC (Chi-square tests: $\chi^2$ = 6.3684, $df$ = 1, $P$ = 0.01162). Asterisks indicate a significant difference between the two groups at the 0.05 level.

Gas Chromatography (GC: 8890A) Conditions: Compound separation was performed on an HP-5MS capillary column (30 m × 0.25 mm × 0.25 μm) with the following temperature program: initial temperature of 40 °C (hold 1 min), ramped at 5 °C/min to 150 °C (hold 2 min), then increased at 8 °C/min to 250 °C (hold 52 min). The carrier gas (He) flow rate was maintained at 1.0 mL/min with constant pressure mode. The injection port temperature was set at 250 °C with splitless mode, and the septum purge flow rate was 3.0 mL/min.

Mass Spectrometry (MS: 5977B) Parameters: The GC effluent was directly introduced into the mass spectrometer with the following operating conditions: electron impact (EI) ionization mode at 70 eV; ion source temperature 230 °C; quadrupole temperature 150 °C; mass range 40–550 amu at 1562 amu/s scanning speed. Compounds identification was achieved by retention time matching with standards and comparing mass spectra with NIST 17 library (match threshold >85%), and the relative content of each substance was calculated using area normalization.

## 2.6 Electroantennogram recordings

Electroantennography (Tangshan Dinggan Technology Co., Ltd.) was used for recording the activity responses of the antennae of female FAW. Before the EAG recording, the odor source was prepared. The test substance was dissolved in mineral oil at various concentrations (0.1, 1, 10, and 100 mg/mL). The blank control (CK) consisted of mineral oil, and the positive control (CF) consisted of 100 mg/mL cis-3-hexen-1-ol. Before testing, 10 μL of each test substance was pipetted onto filter paper in a blue pipette tip (1 mL) and sealed with tin foil. During testing, both ends of the antenna were fixed to the electrodes using conductive adhesive, the test sequence for each group was CK, CF, test substance (0.1, 1, 10, and 100 mg/mL), and CF, CK. The test interval was 45 seconds, and each substance was repeated five times (n = 5 female antennae). The relative antennal response (%) induced by each test substance concentration was recorded.

## 2.7 Behavioral assay

To assess the behavioral responses of FAW larvae and adults to target volatile standards, tests were conducted using a Y-tube olfactometer and a three-chamber olfactometer, respectively. The Y-tube glass olfactometer (2.5 cm in diameter) comprises a 20 cm main tube and two 20 cm side tubes forming a 45-degree angle, and is housed in a steel chamber (1.0 × 0.8 × 0.8 m) equipped with a camera and a 40 W fluorescent lamp that delivers uniform illumination (~2000 lux) (Yi et al., 2023). The three-chamber olfactometer consists of two outer odor chambers and a central insect chamber. Compressed gas is introduced into the two outer chambers, and a common outlet at the top of the central chamber facilitates airflow. All experiments were conducted in a behavioral laboratory (26 ± 1 °C, 65 ± 5% relative humidity).

For larval behavioral testing (12-hour-starved 4-5th instar larvae), 20 μL of the volatile stimulus and 20 μL of mineral oil (CK) as a control were placed as the two odor sources in the Y-tube olfactometer. Individual larvae were placed in the olfactometer for behavioral choice testing. A choice was scored when the larva entered more than one-third of either arm and remained there for at least 30 seconds. 50 independent biological replicates (n = 50 larvae) were performed for each test substance. To mitigate positional bias, the left and right arms were swapped following every third test. The airflow was filtered through activated carbon and water before being delivered into the two side arms of the olfactometer at 300 mL/min, proceeding toward the central main arm.

For adult behavioral testing, 20 μL of each test substance and mineral oil (CK) were placed as odor sources in the olfactory chambers on either side of the three-chamber olfactometer (Figure 3A). 1 female moth were placed in the central compartment, 50 independent biological replicates (n = 50) were performed for each test substance. Purified air entered the two side chambers of the olfactometer simultaneously. An air pump then directed the odor from these chambers into the central compartment at a flow rate of 300 mL/min. Following each test, the chambers were thoroughly cleaned, and the left and right odor sources were swapped for the next trial to control for any positional effects. The experiment lasted from 9 pm to 5 am the following morning, which corresponds to the nocturnal activity period of FAW.

## 2.8 Data analysis

All data were analyzed using IBM SPSS Statistics v31 (SPSS Inc., Chicago, IL, USA). Student's t-test was used to analyze significant differences in the oviposition preference test ($P < 0.05$). Chi-square tests were used to analyze significant differences in disk feeding and indoor olfactometer tests ($P < 0.05$). The significance of the difference in the relative content of the same volatile compound between the two corn varieties was analyzed using Student's t-test ($P < 0.05$). The significance of the difference between the relative response of EAG was analyzed using one-way ANOVA and Tukey's test ($P < 0.05$). EAG relative responses (%) = [(Treatment - CK)/(CF - CK)] × 100%. GraphPad Prism 9 software was used to plot these data.

# 3 Result

## 3.1 Oviposition preference

Statistical analysis shows that in the oviposition preference test (Figure 1, Supplementary Table S1), mated FAW females preferred to lay eggs on SC maize plants, with the number of eggs on SC leaves being significantly higher than on RC leaves ($t = 4.772$, $P < 0.001$).

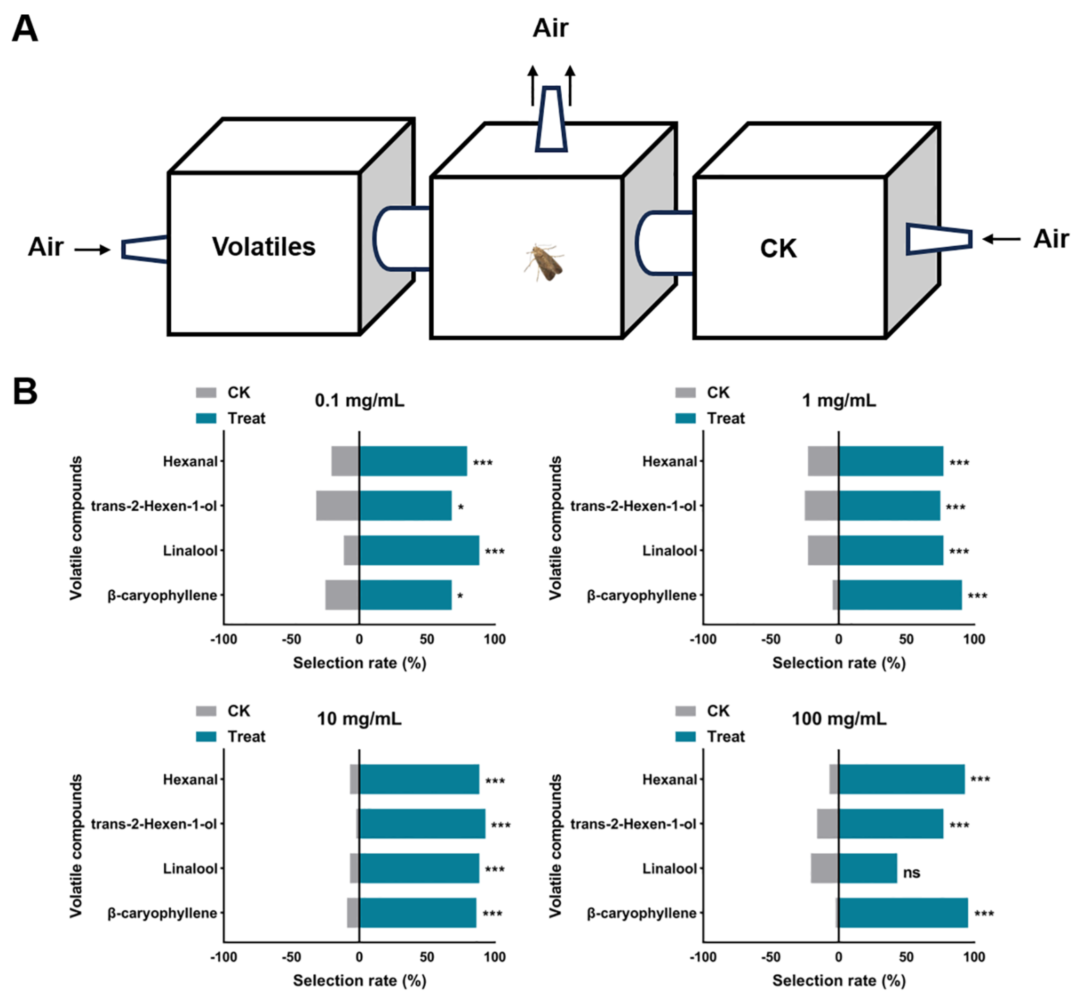


FIGURE 3
The behavioral responses of FAW females to volatiles. **(A)** Schematic diagram of the behavioral selection experiment. **(B)** The chi-square test was used to analyze the significance of the behavioral choices between the treatment group (Treat) and the control group (CK). Asterisks indicate significant differences between test and control groups at the 0.05 level (ns: $P \geq 0.05$, *: $P < 0.05$, ***: $P < 0.001$).

## 3.2 FAW larvae feeding test

In this experiment, we recorded that 49 larvae chose to feed on sweet corn leaves, and 27 chose to feed on regular corn leaves. The results show that FAW larvae have a significant preference for feeding on sweet corn ($\chi^2 = 6.368$, $P = 0.01$) (Figure 2).

## 3.3 Collection and identification of volatile substances from corn

Volatile compounds from the two corn varieties were collected by solid-phase microextraction (SPME) and separated and identified by gas chromatography-mass spectrometry (GC-MS). Qualitative analysis revealed no significant differences between SC and RC, with 21 compounds identified in both. However, quantitative analysis revealed significantly higher levels of four volatile compounds in SC compared to RC (Table 1). The specific compounds that differed were hexanal ($t = -9.468$, $P < 0.001$), trans-2-hexen-1-ol ($t = -13.894$, $P < 0.001$), linalool ($t = -35.608$, $P < 0.001$), and $\beta$-caryophyllene ($t = -29.664$, $P < 0.001$).

## 3.4 EAG recordings

Mass spectrometry analysis revealed that four volatiles with significantly higher relative concentrations in SC than in RC were tested in mated and unmated female FAW insects. The results showed that the relative EAG responses of female corn borers to these four substances increased with increasing concentration. The EAG responses were lowest at 0.1 mg/mL and highest at 100 mg/mL (Figure 4). Specifically, at 100 mg/mL of hexanal and $\beta$-caryophyllene, mated females exhibited significantly higher EAG responses than unmated females. Furthermore, at 10 mg/mL of trans-2-hexen-1-ol, mated females exhibited significantly higher EAG responses than unmated females. At the same concentration of the other substances, no significant differences in EAG responses were observed between mated and unmated females (Table 2S).

TABLE 1 Volatile organic compounds (VOCs) of the seedling stage of two different corn varieties.

| CAS | Compound | Relative content (%) | | Statistical analysis | | | |
|---|---|---|---|---|---|---|---|
| | | SC | RC | *t* | *df* | *P* | Significance |
| **66-25-1** | **Hexanal** | **0.14 ± 0.01** | **0.06 ± 0.01** | **-9.468** | **8** | **< 0.001** | *** |
| 928-96-1 | cis-Hex-3-en-1-ol | 1.06 ± 0.04 | 1.10 ± 0.04 | 0.724 | 8 | 0.49 | NS |
| 111-71-7 | Heptanal | 1.39 ± 0.05 | 1.49 ± 0.05 | 1.249 | 8 | 0.247 | NS |
| 110-93-0 | 6-Methyl-5-hepten-2-one | 0.12 ± 0.00 | 0.13 ± 0.00 | 1.507 | 8 | 0.17 | NS |
| 3681-71-8 | cis-3-Hexenyl acetate | 34.70 ± 0.10 | 35.18 ± 0.22 | 1.957 | 8 | 0.086 | NS |
| **928-95-0** | **trans-2-Hexen-1-ol** | **0.15 ± 0.00** | **0.06 ± 0.01** | **-13.894** | **8** | **< 0.001** | *** |
| 3779-61-1 | (*E*)-B-Ocimene | 2.21 ± 0.03 | 2.23 ± 0.04 | 2.173 | 8 | 0.061 | NS |
| **78-70-6** | **Linalool** | **3.51 ± 0.04** | **1.74 ± 0.03** | **-35.608** | **8** | **< 0.001** | *** |
| 124-19-6 | Nonanal | 0.56 ± 0.03 | 0.57 ± 0.02 | 0.316 | 8 | 0.76 | NS |
| 119-36-8 | Methyl salicylate | 38.34 ± 0.22 | 39.00 ± 0.18 | 2.311 | 8 | 0.051 | NS |
| 112-40-3 | Dodecane | 1.32 ± 0.02 | 1.38 ± 0.03 | 1.832 | 8 | 0.104 | NS |
| 112-31-2 | Decanal | 1.30 ± 0.03 | 1.34 ± 0.03 | 0.989 | 8 | 0.351 | NS |
| 2801-84-5 | 2,4-Dimethyldecane | 0.92 ± 0.02 | 0.95 ± 0.03 | 0.825 | 8 | 0.433 | NS |
| 4418-61-5 | 5-Aminotetrazolyl | 0.10 ± 0.00 | 0.11 ± 0.00 | 1.172 | 8 | 0.275 | NS |
| 112-30-1 | 1-Decanol | 1.22 ± 0.03 | 1.29 ± 0.03 | 1.491 | 8 | 0.174 | NS |
| 629-59-4 | Tetradecane | 11.79 ± 0.18 | 12.19 ± 0.08 | 2.046 | 8 | 0.075 | NS |
| **87-44-5** | ***β*-Caryophyllene** | **0.16 ± 0.00** | **0.05 ± 0.00** | **-29.664** | **8** | **< 0.001** | *** |
| 3796-70-1 | Geranylacetone | 0.13 ± 0.00 | 0.13 ± 0.00 | 0.966 | 8 | 0.362 | NS |
| 128-37-0 | Antioxidant 264 | 0.43 ± 0.02 | 0.45 ± 0.01 | 1.153 | 8 | 0.282 | NS |
| 629-73-2 | 1-Hexadecene | 0.20 ± 0.00 | 0.21 ± 0.00 | 1.601 | 8 | 0.148 | NS |
| 544-76-3 | n-Hexadecane | 0.33 ± 0.01 | 0.34 ± 0.00 | 1.401 | 8 | 0.198 | NS |

The data are shown as mean ± SEM. Student's t-test analysis methods were used to analyze the significance of differences in the experimental data results. Asterisks indicate a significant difference between the two groups at the 0.05 level ($P < 0.05$).
The compounds marked in bold represent those that showed statistically significant differences in relative content between the two maize varieties.

## 3.5 The Y-tube olfactometer assays

Behavioral results obtained using a Y-tube olfactometer showed that hexanal, trans-2-hexen-1-ol, linalool, and $\beta$-caryophyllene all exhibited varying degrees of attraction to FAW larvae (Figure 5, Supplementary Table S3). Specifically, hexanal, trans-2-hexen-1-ol, and linalool were attractive to FAW larvae at all four concentrations. However, $\beta$-caryophyllene exhibited the most significant attraction only at 10 mg/mL and 100 mg/mL. In contrast, 0.1 mg/mL linalool ($\chi^2$ = 37.098, $P$ < 0.001) and 100 mg/mL hexanal ($\chi^2$ = 39.093, $P$ < 0.001) exhibited the most significant attraction.

## 3.6 Three-chambers olfactometer trial

Behavioral selection tests of FAW adults for volatile standards revealed that the four volatiles elicited behavioral responses that differed from those of larvae (Figure 3, Supplementary Table S4). All four volatiles exhibited significant attraction to adults at both 1 mg/mL and 10 mg/mL concentrations. At 0.1 mg/mL, trans-2-hexen-1-ol ($\chi^2$ = 5.818, $P$ = 0.016), and $\beta$-caryophyllene ($\chi^2$ = 8.805, $P$ = 0.003) exhibited weaker attraction than hexanal ($\chi^2$ = 15.364, $P$ < 0.001), linalool ($\chi^2$ = 26.273, $P$ < 0.001), but all significantly attracted FAW females. At a concentration of 100 mg/mL, hexanal ($\chi^2$ = 32.818, $P$ < 0.001), trans-2-hexen-1-ol ($\chi^2$ = 17.780, $P$ < 0.001), and $\beta$-caryophyllene ($\chi^2$ = 39.093, $P$ < 0.001) had a significant attraction effect on FAW females, while Linalool ($\chi^2$ =3.571, $P$ = 0.059) had no significant attraction effect.

# 4 Discussion

Complex nutritional relationships exist between herbivorous insects and their host plants. Corn is one of the most important hosts for FAW, and FAW exhibits varying preferences for different corn varieties. Previous studies have shown that FAW prefer sweet corn outdoors (Azwana, 2021). Correspondingly, using different

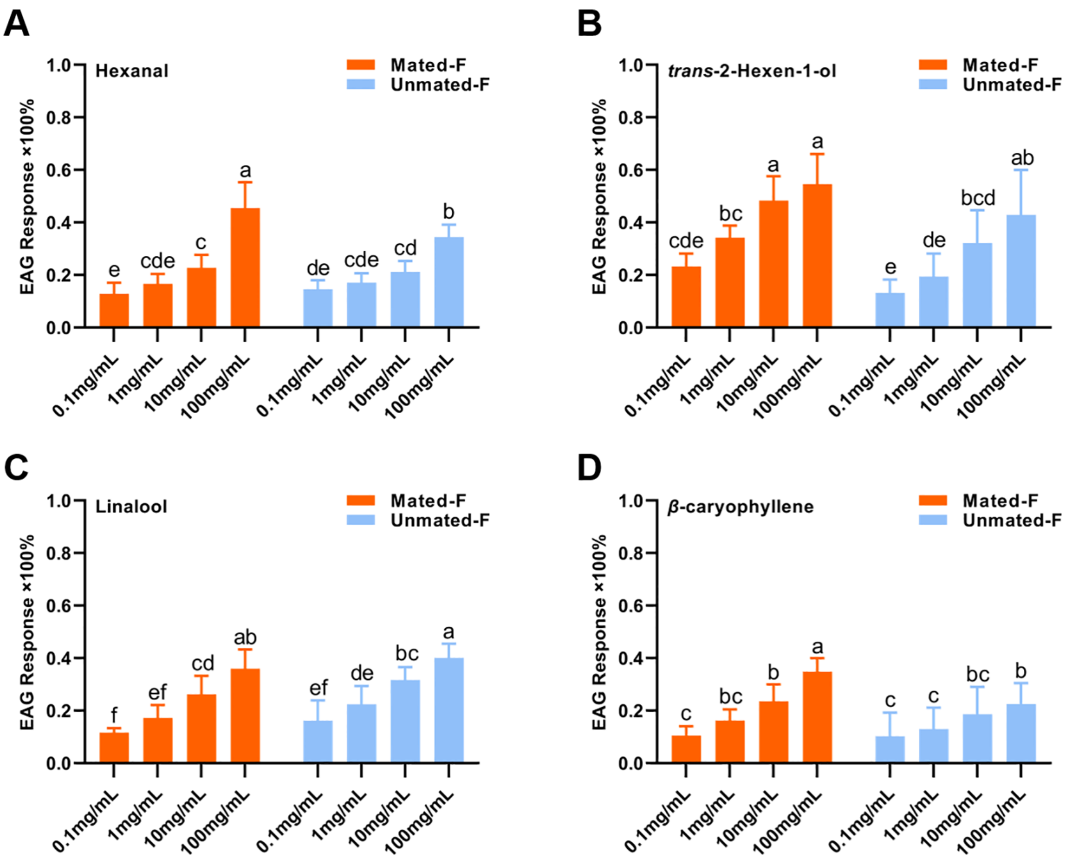


FIGURE 4
The EAG responses of the FAW females to volatiles. **(A)** Hexanal. **(B)** trans-2-Hexen-1-ol. **(C)** Linalool. **(D)** $\beta$-caryophyllene. Error bars represent the standard error of the mean (SEM). Tukey's analysis methods were used to analyze the significance of differences in the experimental data results. Different letters on the columns indicate significant differences at the 0.05 level ($P < 0.05$).

feeding methods indoors, sweet corn has been found to be more conducive to FAW pupation, mating, and oviposition (Tian et al., 2025). To clarify the basis for FAW's preference for sweet corn, we first investigated the corn varieties favored by FAW, leveraging the insect's sensitive olfactory system. In the two corn varieties SC and RC, it was found that FAW adults' egg-laying behavior was more significant on SC (Figure 1), and the larvae also preferred to feed on SC leaves (Figure 2), which is similar to the results of previous studies.

This host preference behavior also exists in other herbivorous insects. The pea aphid, *Acyrthosiphon pisum*, exhibits pronounced feeding preference for *Lupinus luteus* L., while demonstrating complete physiological incompatibility with *L. angustifolius* L., as evidenced by failed feeding attempts, arrested development, and reproductive failure. Phytochemical profiling reveals significant interspecific variation in both alkaloid composition (qualitative differences) and soluble sugar content (quantitative differences) between these lupine species, which directly mediates aphid host selection behavior and determines subsequent fitness outcomes (Kordan et al., 2008). Studies have found that the pink bollworm, *Pectinophora gossypiella* (Lepidoptera: Gelechiidae), revealed distinct oviposition preferences for four cotton cultivars (Lachata, Macnair-220, Midas, and Sandra), with gravid females significantly favoring Midas plants. Oviposition sites were predominantly localized on newly emerged, unexpanded leaves of seedlings and the subcalyx region of developing bolls (Chatzigeorgiou et al., 2010). In addition, in a study on the egg-laying preference of *Epilachna paenulata* on *Cucurbita maxima* and *Cucurbita moschata*, regardless of whether the larvae of *E. paenulata* were fed by *C. maxima* or *C. moschata*, the adults preferred to lay eggs on *C. maxima*. When analyzing the volatiles of the two hosts, it was found that the volatiles released by the two hosts had significant differences. *C. moschata* plants emit more aromatic compounds, monoterpenes, esters, linear hydrocarbons, and indole, *C. maxima* plants emit more aldehydes, ketones, sesquiterpenes, and sulfur compounds. These chemical differences may be important clues for *E. paenulata* to distinguish between the two host plants (Burgueño et al., 2024).

In this study, gas chromatography-mass spectrometry (GC-MS) analysis of volatile organic compounds between the two corn varieties revealed that four key plant volatiles, specifically hexanal, trans-2-hexen-1-ol, linalool, and $\beta$-caryophyllene, were significantly more abundant in volatile samples of SC compared to RC. EAG recordings revealed that all four volatiles elicited antennal responses in FAW adults. Indoor behavioral experiments revealed that both adults and larvae exhibited significant preferences for these identified compounds, suggesting

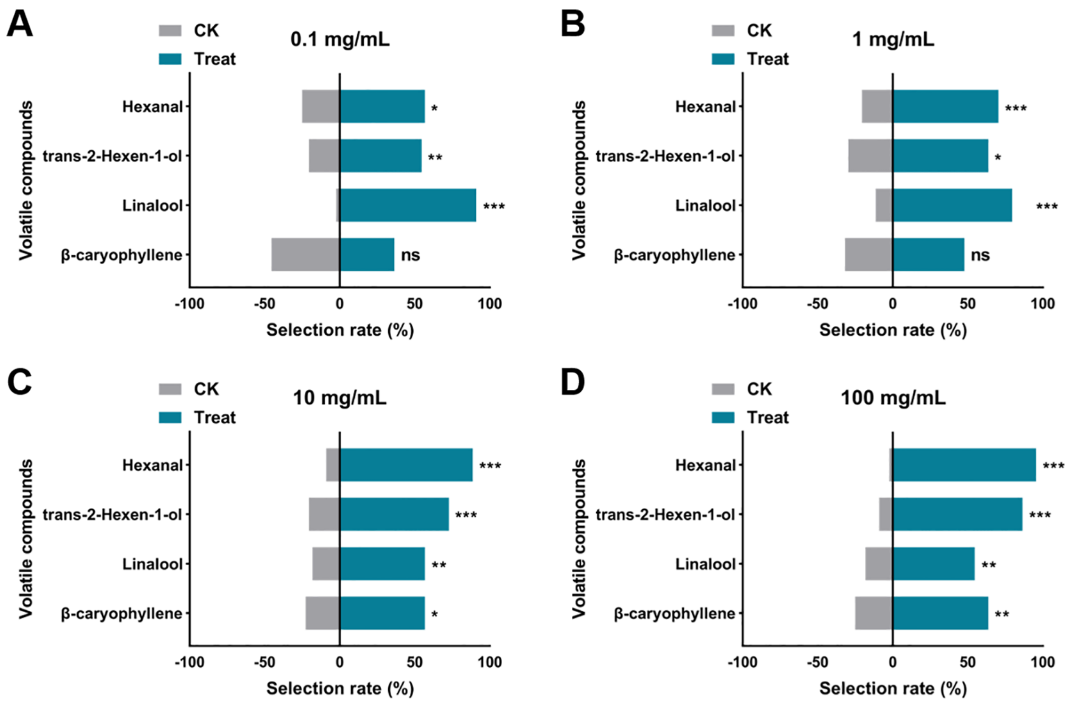


FIGURE 5
The behavioral responses of FAW larvae to volatiles. **(A)** Concentration 0.1 mg/mL. **(B)** Concentration 1 mg/mL. **(C)** Concentration 10 mg/mL. **(D)** Concentration 100 mg/mL. The chi-square test was used to analyze the significance of the behavioral choices between the treatment group (Treat) and the control group (CK). Asterisks indicate significant differences between test and control groups at the 0.05 level (ns: $P \geq 0.05$, *: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$).

that these four plant volatiles play an important role in insect chemical communication.

In a similar study, *Halyomorpha halys* was found to be significantly more oriented and attracted to fresh peanut seeds than to old peanut seeds. Chemical analysis determined that the primary volatile compound released by fresh seeds was hexanal. Subsequent behavioral experiments demonstrated that hexanal strongly attracted *H. halys* (Noge, 2019). *Spodoptera littoralis* is also a pest that harms corn and has a dose-dependent preference for hexanal (Rharrabe et al., 2014).

In the behavioral study of *Anthonomus grandis*, it was found that trans-2-hexen-1-ol not only increased the capture quantity of its pheromone trap but also prolonged the duration of the attractiveness of the pheromone lure trap (Dickens, 1989). Using the EAG technique, it was found that *Choristoneura rosaceana* and *Argyrotaenia velutinana*, when exposed to a mixture of several plant volatiles containing trans-2-hexen-1-ol, could significantly enhance their response to sex attractants through EAG (Stelinski et al., 2003).

Linalool is also a common volatile compound continuously released from leaves. The release increases when the host is fed by pests. *Tetranychus urticae* mites parasitizing tomatoes induce the host to release linalool (van Schie et al., 2007), while FAW larvae feeding on rice also induce the release of linalool, which significantly attracts the rice planthopper's parasitic wasp, *Cotesia marginiventris* (Yuan et al., 2008a, Yuan et al., 2008b).

*β*-Caryophyllene is an important secondary metabolite of plants. Many plants can release it, such as *Arabidopsis thaliana* and *Mikania micrantha* etc. However, usually, plants release more *β*-caryophyllene when they encounter stress, for example, red light irradiation can enhance the biosynthesis of *β*-caryophyllene in *A. thaliana* (Cheng et al., 2022). When the concentration of carbon dioxide increases, it will induce the production of *β*-caryophyllene synthase and alter the release ability of *β*-caryophyllene (Wang et al., 2010).

In summary, the above research results, based on the preference selection behavior of FAW, clarified the behavioral guidance role of four key volatiles on FAW larval feeding and adult oviposition from the perspective of chemical ecology, providing reliable data support for the development of FAW attractants and a theoretical basis for integrated pest management programs.

## Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding author.

## Author contributions

CN: Writing – original draft, Writing – review & editing. CY: Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – review & editing. LS: Investigation, Methodology, Writing – review & editing. RL: Investigation, Methodology, Writing – review & editing. AK: Investigation, Methodology, Writing – review & editing. WL: Formal analysis, Software, Visualization, Writing – review & editing. YZ: Conceptualization, Funding acquisition, Supervision, Validation, Writing – original draft, Writing – review & editing.

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## Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

## Generative AI statement

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## Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2025.1729374/full#supplementary-material

SUPPLEMENTARY TABLE 1
Oviposition preference of the FAW females between two different corn varieties.

SUPPLEMENTARY TABLE 2
EAG values of the FAW females to volatiles.

SUPPLEMENTARY TABLE 3
Behavioral choice of the FAW larvae towards volatiles.

SUPPLEMENTARY TABLE 4
Behavioral choice of FAW females towards volatiles.

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