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RESEARCH ARTICLE

Screening and evaluation of plant-derived attractants for *Loxostege sticticalis* adult management

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Highlights

- Linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol are attractants for *L. sticticalis*.
- Four compounds mixed at a ratio of 5:1:1:10 are recommended for managing *L. sticticalis*.
- The lure equipment with mixtures can be integrated into the “push–pull” strategy.

Abstract

The *Loxostege sticticalis* (Lepidoptera: Pyralidae) is a major migratory pest of agriculture and animal husbandry in Asia and Europe. Utilizing plant volatile organic compounds (pVOCs) as attractants for monitoring and controlling pests is considered an environmentally friendly and effective method. However, limited knowledge exists regarding applying pVOCs to manage *L. sticticalis*. Here, volatile compounds released by *Chenopodium album*, *Setaria viridis*, and *Medicago sativa*, the three preferred oviposition plants for *L. sticticalis* females, were collected using dynamic headspace sampling techniques. A total of 55 distinct compounds were identified through gas chromatography-mass spectrometry (GC-MS), and 16 compounds in the concentration range from 0.001 to 100 μg μL^{-1} elicited consistently enhanced electrophysiological responses in both male and female *L. sticticalis*. Subsequently, the attraction potential of four bioactive compounds — linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol — were further confirmed by indoor behavioral bioassays. The blends of linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol mixed at ratios of 5:1:5:10 (formulation No. 25) and 5:1:1:10 (formulation No. 21) were highly attractive to *L. sticticalis* adults. Field-trapping assays indicated that lure No. 2 baited with formulation 21 demonstrated superior efficacy in field trapping. These findings suggest that pVOC-based attractants can be effectively employed for monitoring and mass trapping *L. sticticalis* adults, providing insights into the development of botanical attractants.

Keywords: *Loxostege sticticalis*, plant volatile, gas chromatography-mass spectrometry (GC-MS), electrophysiological response, behavioral bioassay

1. Introduction

The beet webworm *Loxostege sticticalis* is widely recognized as a serious polyphagous pest that causes significant ecological and economic damage to various crops and pasture grasses (Yu *et al.* 2023). The larvae typically create holes, skeletonize, or entirely consume the leaf blades of plants (Cheng *et al.* 2023). The damaged plants exhibit stunted growth, potentially reducing yields by up to 60%, and causing complete destruction of the plants in severe cases (Malysh *et al.* 2021). The current predominant method

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of controlling *L. sticticalis* is the utilization of chemical insecticides such as endosulfan and triazophos; however, this approach has been linked to the emergence of insecticide resistance (Ji *et al.* 2024). Additionally, the characteristics of long-distance migration, periodicity, and large-scale sudden outbreaks further complicate the management of *L. sticticalis*, posing a serious challenge to traditional pest control methods using chemical pesticides (Huang *et al.* 2024). Therefore, efficient and environmentally friendly strategies for the control of *L. sticticalis* are urgently needed.

Currently, there is a growing emphasis on reducing dependence on chemical pesticides by adopting sustainable, natural, and eco-friendly solutions for effective pest control, such as harnessing the ecological and agronomic potential of plant volatile organic compounds (pVOCs) to protect crops (Brilli *et al.* 2019; Makhlouf *et al.* 2024). Owing to their attractive or repellent properties, pVOCs can significantly influence feeding behavior, reproductive processes, olfactory perception, and host selection of insect pests (Singh *et al.* 2021; Arimura and Uemura 2025). Therefore, pVOCs usually serve as traps to manage the population dynamics of pests and act as the 'push' or 'pull' stimuli in pest behavior-regulating strategies (Yan *et al.* 2023; Makhlouf *et al.* 2024). The key compounds in pVOCs could induce strong electrophysiological and behavioral responses in insects and function as links for communicating information between plants and insects (Keesey *et al.* 2019). Nevertheless, there is a wide variety of pVOCs in the natural environment, and different insects have their preferred odor compound signals. For example, the botanical volatiles dibutyl phthalate and phytol were effective mating signals for *Hyphantria cunea* (Bai *et al.* 2020). The kairomones of 3-carene, *β*-pinene, and *α*-pinene exhibited the highest attractiveness to *Monochamus saltuarius* in the field (Dong *et al.* 2024). Furthermore, the appropriate blends or combinations of bioactive compounds may elicit stronger behavioral responses in insects than individual compounds (Bruce and Pickett 2011). However, the key odor compound signals from pVOCs that effectively attract *L. sticticalis* have not been accurately identified, and the precise ratio of these compounds remains unknown.

In addition to pVOCs, sex pheromones can also attract pests and thus enrich pest management strategies, including mass trapping, monitoring, and disrupting the mating of targeted pests. Numerous studies have demonstrated that combining pVOCs with sex pheromones effectively increases the attractiveness to insects. For instance, adding plant volatile *trans*-2-hexenal resulted in a 38.8% increase in the capture rate of *Spodoptera exigua* compared to using the sex pheromone lure alone in field experiments (Deng *et al.* 2004). The sex pheromone-baited traps combined with two host plant volatiles, (*Z*)-3-hexenyl acetate and 1-undecanol, attracted more *Grapholita molesta* males than the traps baited with sex pheromone alone in pear orchards (Yu *et al.* 2014). The combination of the sex pheromone with a plant volatile, allyl isothiocyanate, significantly increased the attraction of the pheromone trap for *Plutella xylostella* (Chi *et al.* 2024). Thus, the pVOCs may potentially function similarly to sex pheromones in helping insects find mating partners (Zhang *et al.* 2023). Individual studies, however, have indicated that the proposed attractant plant volatiles unexpectedly reduced the capture rate of males or failed to effectively capture females. For instance, including *cis*-2-penten-1-ol diminished the effectiveness of sex pheromone lures in capturing male *H. cunea*, as demonstrated in a long-range field trapping experiment (Tang *et al.* 2012). After mixing with the host-plant blends, the number of male *G. molesta* captured by the sex pheromone trap decreased in peach orchards in Chile, and the antagonistic effect of plant volatiles became more pronounced as their proportion increased (Barros-Parada *et al.* 2018). At present, the primary sex pheromone components of *L. sticticalis* have been successfully identified, and the blend of E11-14:OAc, E11-14:Ald, and E11-14:OH at a ratio of 5:3:12 was proven effective in attracting and trapping *L. sticticalis* (Ando *et al.* 2004; Shakhmaev *et al.* 2009; Liu *et al.* 2011). By contrast, knowledge of the effective plant volatiles that attract *L. sticticalis* remains limited, and the synergistic or antagonistic effects of pVOCs on the trapping efficiency of sex pheromones have not been adequately evaluated, hindering the utilization and application of pVOCs as attractants for managing *L. sticticalis*.

This study used dynamic headspace extraction, gas chromatography-mass spectrometry (GC-MS) analysis, and electroantennography (EAG) assays to identify and screen compounds with high EAG activity against the *L. sticticalis* adults. Subsequently, we conducted indoor behavioral bioassays and field-trapping assays to evaluate the attraction effectiveness of these bioactive compounds at different ratios and combinations on *L. sticticalis*. Eventually, we identified the four strongest bioactive compounds and a mixture formulation suitable for field trapping. The present study developed a novel eco-friendly biological attractant for effectively monitoring and mass trapping *L. sticticalis* adults, thereby enriching our understanding of the behavioral regulation mediated by pVOCs in specialist herbivores.

2. Materials and methods

2.1. Insect rearing and reagents

Loxostege sticticalis (beet webworm) was reared in an artificial climate incubator at the Institute of Plant Protection, Chinese Academy of Agricultural Sciences. The incubator (Ningbo, China) was set at (22±1)°C, (75±5)% relative humidity, and a 16-h photoperiod. The larvae were provided with fresh *Chenopodium album* as food. Newly emerged males and females were placed separately in cylindrical glass containers (*Φ*=10 cm, H=20 cm) and sealed with gauze. The 10% aqueous honey solution was applied to the sponge and placed into the containers as the food source for the adults. To prevent colony decline resulting from inbreeding, field-collected individuals were periodically introduced into the colony. The *L. sticticalis* used in related experiments were all adults that were 2–3 days old. All tested compounds with purity≥98% were purchased from Sigma-Aldrich (St. Louis, MO, USA).

2.2. Host plants

Experimental plants include *C. album*, *Setaria viridis*, and *Medicago sativa*, all of which are favored oviposition plants

for *L. sticticalis* females. In April 2022, the purchased seeds (Qingdao Haizhida Biotechnology Co., Ltd., China) were sown in seedling pots and placed in the greenhouse. They were watered appropriately according to soil moisture. No chemical agents were sprayed during the entire growth period of these plants.

2.3. Collection of volatiles

The headspace volatiles of *C. album*, *S. viridis*, and *M. sativa* were collected separately according to previously described methods with minor modifications (Yan *et al.* 2023). Before sampling, the glass instruments and rubber tubes were thoroughly washed with distilled water and *n*-hexane, after which they were dried at 70°C to eliminate any impurities. Then, healthy plants (20–25 cm high) removed from the greenhouse were carefully washed with distilled water, and the roots enclosed with soil were wrapped in zipper bags. The entire plant was then placed inside a gas sampling bottle. Afterward, the air was purified through activated charcoal (ANPEL) and humidified by a humidifier. The air was then guided through the inlet of an atmospheric sampler (QC-1B, Beijing Institute of Labor Protection Science, China). Then, the atmospheric sampler and gas sampling bottle were connected by a tube. Following this setup, the atmospheric sampler was turned on and allowed to run at a flow rate of 200 mL min^{-1} for 15 min to flush out any original gases present in the gas sampling bottle. After that, an adsorptive column containing Porapak™ Q (20 mg, 80–100 mesh, Waters, USA) was attached to the outlet of the gas sampling bottle. Following 4 hours of continuous sampling, the volatile compounds were eluted from the Porapak™ Q filter using 1 mL of n-hexane (≥99.5%) and stored in a light-free refrigerator at –20°C for subsequent analysis. The extraction of plant volatiles was conducted from 21:00 to 24:00 in the evening, with three replicates performed for each plant species. Control samples were obtained by collecting the air in the gas sampling bottle without any plants present.

2.4. GC-MS analysis

A Shimadzu single quadrupole gas chromatograph (GCMS-QP2010 SE, SKL-0108) equipped with an HP-5MS Ultra Inert column (30 m length, 0.25 mm inner diameter, and 0.25 μm film thickness; Agilent, USA) was used to analyze and identify the volatile compounds of each plant species. Here, the initial heating rate was set at 10°C min^{-1}, and then the subsequent heating process parameters were adjusted according to the GC-MS results from pre-experiments. Finally, the most suitable oven temperature schemes were obtained and are shown as follows:

Chenopodium album: 40°C (3 min) $\xrightarrow{5°C\ min^{-1}}$160°C (5 min) $\xrightarrow{10°C\ min^{-1}}$230°C (5 min)

Setaria viridis: 40°C (1 min) $\xrightarrow{5°C\ min^{-1}}$180°C (3 min)

Medicago sativa: 40°C (1 min) $\xrightarrow{4°C\ min^{-1}}$130°C (3 min) $\xrightarrow{10°C\ min^{-1}}$250°C (3 min)

Helium served as the carrier gas at a constant flow rate of 1 mL min^{-1}. The mass spectrometry parameters were configured as follows: the interface temperature was 250°C, the ionization energy was 70 eV, and the scanning speed was 5 times per second. A 1:5 split ratio was used when 1 μL of each sample was injected into the mass spectrometer. The pVOCs were identified by comparing their retention times and mass fragmentations with the NIST 2014 mass spectral library. Additionally, 16 compounds that elicited obvious EAG responses were further confirmed by injecting the corresponding standard compounds under the three oven temperature schemes.

2.5. EAG response assays

A constant dose of volatile chemicals was employed to determine the EAG (Syntech, IDAC-4, Germany) response of *L. sticticalis*, following the previously outlined methodology (Li *et al.* 2023). The intact antenna of *L. sticticalis* adult was excised using a surgical blade and mounted between two electrodes using conductive gel (SignaGen, USA). The compounds identified by GC-MS were diluted to 1 μg μL^{-1} with paraffin oil (Sigma-Aldrich, St. Louis, MO, USA). The 10 μL of each compound solution sample was dripped onto a filter paper strip (0.5 cm×3 cm) in a Pasteur pipette, which was then sealed with Parafilm® and kept for 5 min. The 10 μL paraffin oil was used as the control. During stimulus recordings, clean and moist gas carrying the test compound was delivered to the antenna at a flow rate of 500 mL min^{-1}. Stimulus recordings lasted for 0.5 s with an interval of more than 60 s between two stimuli. The order of compound stimulation was randomized. EAG responses of insects to each compound were indicated as EAG values relative to the paraffin oil control value. Here, a criterion for evaluating the intensity of the EAG response was established. A relative EAG response value≥1 mV indicated high EAG activity, a value between 0.5 and 1 mV denoted good EAG reactivity, a value between 0.3 and 0.5 mV indicated moderate EAG reactivity, and a value≤0.3 mV was interpreted as poor EAG activity (Li *et al.* 2022).

Subsequently, we selected 16 compounds that elicited obvious EAG responses in both males and females for subsequent concentration gradient experiments. These compounds were diluted to concentrations of 0.001, 0.01, 0.1, 1, 10, and 100 μg μL^{-1} using paraffin oil. The same antenna was utilized to evaluate various concentrations of the compound, with the concentrations being tested in ascending order. In the EAG experiments, each stimulus was tested with six individual male and female antennae, and each antenna was tested three times.

2.6. Indoor behavioral bioassays

The indoor behavior bioassays of *L. sticticalis* were conducted from 21:00 to 24:00 and detected using a self-made device, which was established following a previous method with minor modifications (Yin *et al.* 2004). The 16 compounds that elicited obvious EAG responses were diluted in paraffin oil to three suitable concentrations (0.1, 1, and 10 μg μL^{-1}) and used as odor sources for indoor behavioral assays. Prior to the bioassays, the atmospheric sampler was operated for 15 min to remove any residual odors. Then, the individual adult was introduced into the test chamber (60 cm×60 cm×60 cm) and acclimated for 15 min. Afterward,

a total of 50 μL compound or paraffin oil (control) was added to the lure, which was then placed in the small ball chamber adjacent to the test chamber. The atmospheric sampler was activated and operated at a flow rate of 1 L min^{-1}. Five minutes later, the number of adults on each side of the baffle (choice region) and in the no-choice region was recorded. The insect remaining in the choice region for more than one minute was considered selected, whereas those staying in the no-choice region were considered non-responsive. After 10 observations, all devices were cleaned with anhydrous ethanol, and the positions of the odor source and control were switched. Each concentration of these compounds was tested with a total of 90 insects. The selection rate (%)=(The number of insects selecting odor source chamber or control chamber/Total number of tested insects)×100. The effective selection rate (%)=(The number of insects in the odor source chamber–The number of insects in the control chamber)/(Total number of tested insects)×100.

To obtain the compound formulation with the most significant attraction effect on *L. sticticalis* adults, we used stepwise addition of compounds in combination with behavioral bioassays to screen the best compounds. Firstly, the four single compounds (linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol) with the best attraction effects were mixed with each other to form multiple binary formulations, and then other compounds were gradually added to these binary formulations to form ternary and quaternary formulations (Gregg *et al.* 2010). Additionally, these compounds were configured in different volume ratios within the formulations, and the final effective dose of compounds in all formulations was approximately 66 μg (Appendix A). These mixtures were then assessed using the behavioral device described above. The behavioral selection test comprised 60 male and 60 female subjects for each formulation, with paraffin oil (66 μL) serving as the control.

2.7. Field-trapping assays

The indoor behavioral bioassays demonstrated that formulation No. 25 exhibited the highest attractiveness towards *L. sticticalis*, thus earning its designation as lure No. 1. Formulation No. 21 displayed the second-best attractant properties and was designated as lure No. 2. The formulation No. 25 and formulation No. 21 were then combined to create the lure No. 3. Furthermore, a combination of formulation No. 25 with the sex pheromone of *L. sticticalis* [(E11-14:AC):(E11-14:AL):(14:OH)=5:3:12] at a volume ratio of 1:1 generated lure No. 4. Sex pheromones alone served as lure No. 5. The experimental controls included an automatic pest detection lamp (JD-CQ2) and a basic paraffin oil trap. The specific volumes of each compound in the different lures are presented in Appendix B. Field-trapping assays were conducted from July 26 to August 24, 2023, and 2024, in Kangbao County, Zhangjiakou City, Hebei Province, China (41°52′3.77′′N, 114°36′16.28′′E). The trapping efficacy of these lures on *L. sticticalis* adults in *Helianthus annuus* field, *Vicia faba* field, *Pisum sativum* and *Brassica napus* mixed field, *B. napus* field, and *Avena sativa* field were evaluated, respectively. Each crop field (3,600 m^2) was randomly divided into 15 treatment plots and 3 control plots, with a trap containing one type of lure placed in each plot, with 3 replicates of each type of lure. The traps were suspended on plastic brackets approximately 20–30 cm above the crop canopy and inserted into the center of the plots. Every morning from 6 a.m. to 9 a.m., the number of *L. sticticalis* adults in the traps was recorded, and then the adults were removed. The lure in the trap was replaced every 3 days.

2.8. Statistical analysis

All data are presented as mean±standard error (SE). Independent sample *t*-tests were used to compare the significant difference between male and female *L. sticticalis* regarding EAG response values. The one-way analysis of variance (ANOVA) followed by Tukey's multiple comparison test was employed to compare the EAG response differences among different compounds and different doses of the same compound, as well as to examine differences in the number of *L. sticticalis* adults attracted by different lures. The indoor behavioral bioassay data were determined by χ^2 test.

3. Results

3.1. Identification of host plant volatiles

The headspace volatile compounds of *C. album*, *S. viridis*, and *M. sativa* were collected and then analyzed by GC-MS, and a total of 55 distinct compounds were identified (Fig. 1-A; Table 1). Among these compounds, 26 were found in *C. album*, 23 in *S. viridis*, and 20 in *M. sativa* (Fig. 1-B–D). The volatile components of *C. album* were mainly composed of 1-octen-3-ol and geraniol. The *S. viridis* exhibited a higher abundance of *trans*-caryophyllene, *cis*-anethole, and linalool. Benzyl alcohol and phytantriol were the predominant components in *M. sativa*. Furthermore, the accuracy of 16 compounds that elicited obvious EAG responses was additionally confirmed through the analysis of standard compounds (Appendix C). Analysis of chemical types revealed that terpenes and alcohols constituted the major classes of these volatile compounds (Appendix D). The volatile components in *C. album* consisted of a relatively high number proportion of alcohols and aldehydes, both with similar numbers but significantly higher alcohol content compared to aldehydes. Among the volatile compounds in *S. viridis*, alcohols had the highest number, followed by terpenes, accounting for approximately half of the total content. *Medicago sativa* possessed the highest number of terpenes, but the content of terpenes was not as high, and alcohol content accounted for the highest proportion.

3.2. EAG responses of *L. sticticalis* to a fixed concentration of pVOCs

Of the 55 compounds tested, 33 compounds could evoke detectable electrophysiological responses in both male and female *L. sticticalis*, and the responses were stronger in males than in females for most of the compounds (Appendix E). Out of these 33 compounds, 16 showed obvious antennal electrophysiological responses in either males or females, suggesting a potential attraction effect (Fig. 2). Among

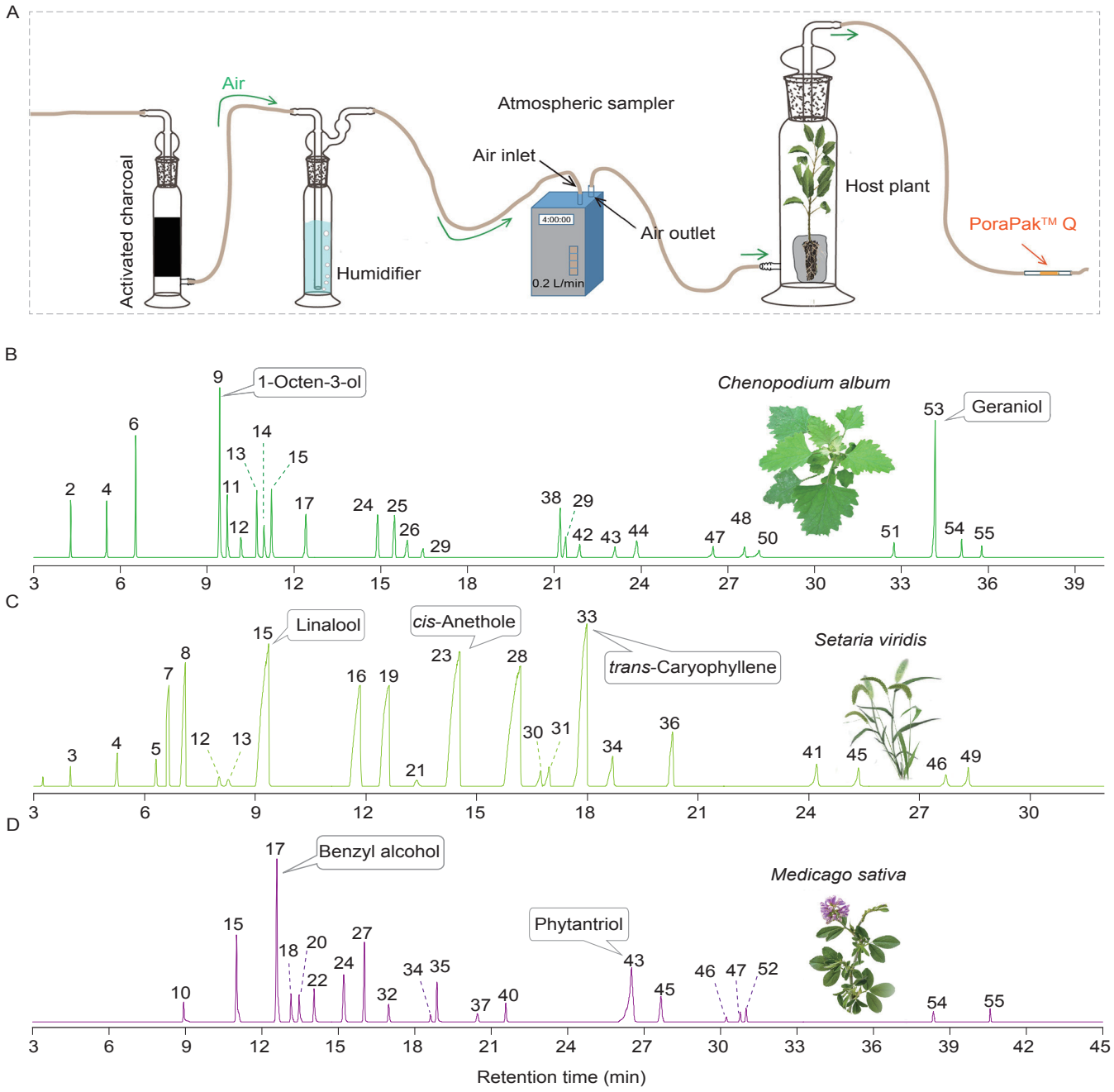


Fig. 1 Extraction and gas chromatography-mass spectrometry (GC-MS) analysis of plant volatile organic compounds. A, schematic drawing of collecting plant volatiles. B–D, GC-MS analysis of the crude extracts from *Chenopodium album* (B), *Setaria viridis* (C), and *Medicago sativa* (D), respectively. The numbers on the peaks indicate the compounds that were accurately detected.

them, hexanal elicited the highest electrophysiological response in males (F=32.13; df=32, 99; P=0.005), while nonanal resulted in the strongest response in females (F=26.84; df=32, 99; P=0.017). The response amplitudes of females to nonanal, linalool, and *cis*-3-hexene acetate were significantly higher than those of males (t=5.067, P=0.007; t=2.375, P=0.032; t=1.007, P=0.049), while there were no significant differences between males and females regarding their electrophysiological responses to benzaldehyde and *cis*-3-hexenyl isobutyrate (t=0.087, P=0.224; t=–2.994, P=0.317). The remaining compounds elicited a significantly greater male-biased antennal electrophysiological response compared to females (P<0.05).

3.3. EAG responses of *L. sticticalis* to different concentrations of 16 bioactive compounds

The EAG concentration gradient experiments demonstrated that the electrophysiological responses of *L. sticticalis* to these 16 bioactive compounds exhibited an enhancement with increasing compound concentrations (Fig. 3). When the compound concentration increased from 0.001 to 0.01 μg μL^{-1}, most of the electrophysiological responses did not show a significant increase. Only hexanal and *trans*-2-octen-1-ol exhibited a noticeable augmentation in the

Table 1 Information on compounds identified by gas chromatography-mass spectrometry (GC-MS) analysis

No.	Compound name	CAS number	Molecular weight (g molL^{-1})	*Chenopodium album*		*Setaria viridis*		*Medicago sativa*	
				Peak time (min)	Peak area (%)	Peak time (min)	Peak area (%)	Peak time (min)	Peak area (%)
1	(*E*)-4-Hexen-1-ol	928-92-7	100.16	–	–	4.00	0.30	–	–
2	Hexanal	66-25-1	100.16	4.28	2.49	–	–	–	–
3	*trans*-2-Octen-1-ol	18409-17-1	128.22	–	–	5.26	0.69	–	–
4	*trans*-2-Hexenal	6728-26-3	98.14	5.53	2.97	6.25	0.14	–	–
5	1,2-Dichlorobenzene	95-50-1	147.00	–	–	6.32	0.57	–	–
6	3-Hexanol	623-37-0	102.18	6.53	6.76	–	–	–	–
7	*cis*-3-Hexenyl acetate	3681-71-8	142.20	–	–	6.66	4.60	–	–
8	Octan-2-ol	123-96-6	130.23	–	–	7.11	5.04	–	–
9	1-Octen-3-ol	3391-86-4	128.21	9.43	14.89	–	–	–	–
10	Naphthalene	91-20-3	128.17	–	–	–	–	8.93	1.97
11	Phenol	108-95-2	94.11	9.69	4.69	–	–	–	–
12	(+)-Limonene	5989-27-5	136.23	10.16	1.83	8.03	0.34	–	–
13	Heptan-1-ol	111-70-6	116.20	10.71	5.12	8.28	0.31	–	–
14	2-Ethylhexanol	104-76-7	130.23	10.96	3.75	–	–	–	–
15	Linalool	78-70-6	154.25	11.23	5.75	9.37	15.06	11.01	9.82
16	Methyl salicylate	119-36-8	100.16	–	–	11.83	8.83	–	–
17	Benzyl alcohol	100-51-6	108.14	12.41	5.57	–	–	13.35	15.64
18	1,8-Cineole	470-82-6	154.25	–	–	–	–	12.59	4.97
19	Nonanal	124-19-6	142.24	–	–	12.63	9.05	–	–
20	Octanal	124-13-0	128.21	–	–	–	–	13.14	4.55
21	(2,2-Dimethoxyethyl) benzene	101-48-4	166.22	–	–	13.38	0.29	–	–
22	*β*-Ionone	14901-07-6	192.30	–	–	–	–	14.05	5.89
23	*cis*-Anethole	104-46-1	148.20	–	–	14.54	16.10	–	–
24	*trans*-2-Hexenoic acid	13419-69-7	114.14	14.89	5.29	–	–	15.21	6.81
25	Heptanal	111-71-7	114.19	15.48	4.27	–	–	–	–
26	Benzaldehyde	100-52-7	106.12	15.92	2.31	–	–	–	–
27	3-Pentanone	96-22-0	86.13	–	–	–	–	16.03	8.64
28	*cis*-3-Hexen-1-ol	928-96-1	100.16	–	–	16.19	16.32	–	–
29	1,2,4-Trimethyl benzene	95-63-6	120.19	16.46	1.15	–	–	–	–
30	Phenyl acetaldehyde	122-78-1	120.15	–	–	16.74	0.54	–	–
31	Isolongifolene	1135-66-6	204.35	–	–	16.96	0.79	–	–
32	(+)-Camphor	464-49-3	152.23	–	–	–	–	16.97	1.49
33	*trans*-Caryophyllene	87-44-5	204.35	–	–	17.99	14.08	–	–
34	*α*-Caryophyllene	6753-98-6	204.35	–	–	18.69	1.34	18.77	1.02
35	Terpineol	98-55-5	154.25	–	–	–	–	18.87	6.37
36	*cis*-2-Nonen-1-ol	41453-56-9	142.24	–	–	20.31	3.75	–	–
37	(-)-*α*-Pinene	7785-26-4	136.23	–	–	–	–	20.46	1.44
38	*cis*-3-Hexenyl isobutyrate	41519-23-7	170.25	21.20	5.71	–	–	–	–
39	Lauryl aldehyde	112-54-9	184.32	21.39	2.53	–	–	–	–
40	Methyl palmitate	112-39-0	270.45	–	–	–	–	21.57	2.30
41	3-Methyl-1-hexanol	13231-81-7	116.20	–	–	21.86	0.52	–	–
42	*α*-Phellandrene	99-83-2	136.23	21.88	1.87	–	–	–	–
43	Phytantriol	74563-64-7	330.55	23.10	1.39	–	–	26.50	15.51
44	Hexadecane	544-76-3	226.44	23.84	2.63	–	–	–	–
45	Cinnamaldehyde	104-55-2	132.16	–	–	24.21	0.82	30.23	8.22
46	Caryophyllene oxide	1139-30-6	220.35	–	–	25.35	0.59	30.78	0.73
47	Undecanal	112-44-7	170.29	26.49	1.23	–	–	27.63	1.02
48	Dibutyl oxalate	2050-60-4	202.25	27.57	0.99	–	–	–	–
49	Benzothiazole	95-16-9	135.19	–	–	27.72	0.20	–	–
50	Triethyl citrate	77-93-0	276.28	28.08	0.71	–	–	–	–
51	Diisobutyl phthalate	84-69-5	278.34	34.17	13.09	–	–	–	–
52	Dermacrene B	15423-57-1	204.35	–	–	–	–	31.00	1.26
53	Geraniol	106-24-1	154.25	32.74	1.32	–	–	–	–
54	Pentadecyl acetate	629-58-3	270.46	35.08	1.01	–	–	38.55	1.10
55	Heneicosane	629-94-7	296.57	35.78	0.69	–	–	40.58	1.25

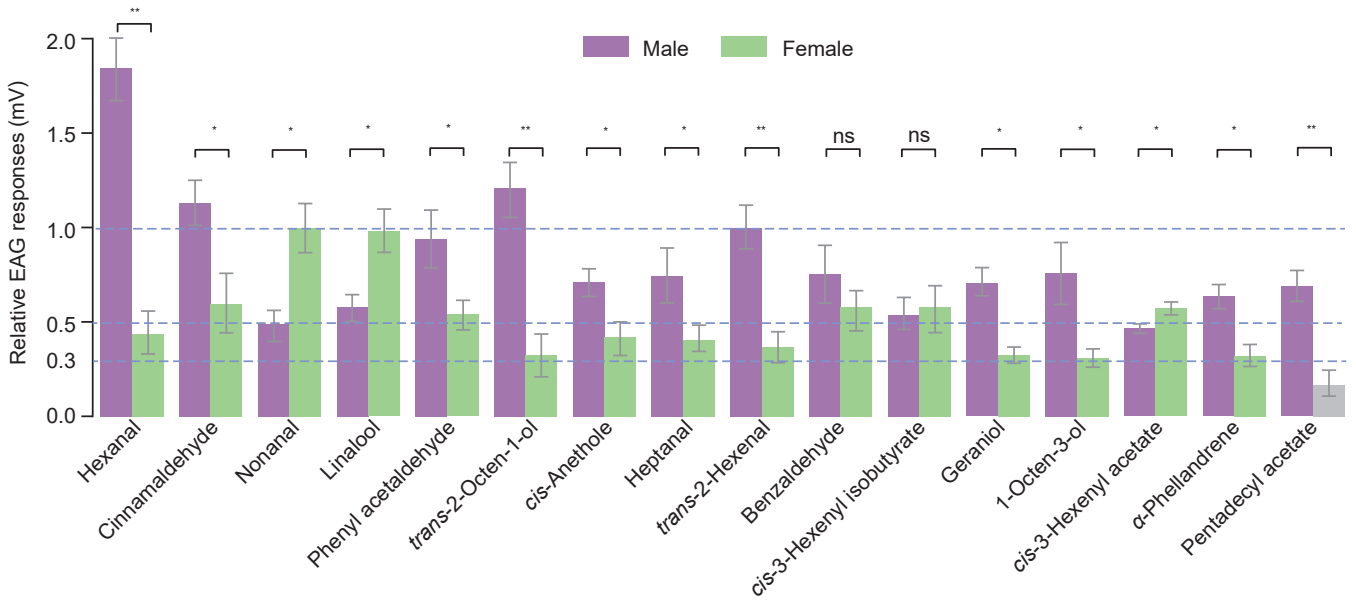


Fig. 2 Electroantennography (EAG) responses of *Loxostege sticticalis* to 16 bioactive compounds. The concentration of the compounds was 1 μg μL^{-1}. The values corresponding to the dotted lines in the figure are the criteria for judging the strength of the EAG responses. The relative EAG response values are presented as mean±SE of six replicates. Statistical differences were determined by independent sample *t*-tests at the significance levels set at *, P<0.05, **, P<0.01; ns, not significant.

electrophysiological response towards males (Fig. 4-A and F) and nonanal towards females (Fig. 4-C). When the compound concentration was increased to 0.1 μg μL^{-1}, the electrophysiological responses induced by pentadecyl acetate were significantly enhanced in males (Fig. 4-P). Upon increasing the compound concentration to 1 μg μL^{-1}, most of the electrophysiological responses of males and females exhibited significant improvement, and this reaction intensity further escalated when adjusting the compound concentration to 10 and 100 μg μL^{-1}. Overall, the *L. sticticalis* exhibited strong electrophysiological responses to hexanal, linalool, *trans*-2-octen-1-ol, heptanal, 1-octen-3-ol, and pentadecyl acetate, while displaying weak electrophysiological responses to nonanal, phenyl acetaldehyde, benzaldehyde, and *α*-phellandrene.

3.4. Behavioral responses of *L. sticticalis* to the 16 bioactive compounds

The behavioral responses of *L. sticticalis* to these 16 bioactive compounds at three concentrations were further observed in the laboratory using a self-designed behavioral observation device (Fig. 4-A). The results revealed that males consistently preferred linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol within the dose range of 0.1–10 μg μL^{-1}. At the high concentration of 10 μg μL^{-1}, other compounds such as *trans*-2-octen-1-ol and *cis*-3-hexenyl acetate significantly attracted males (χ^2=6.564, P=0.010; χ^2=7.367, P=0.007). However, at the low concentration of 0.1 μg μL^{-1}, hexanal could also attract males (χ^2=4.900, P=0.027). The females exhibited a distinct tropism to different concentrations of linalool, *trans*-2-hexenal, and 1-octen-3-ol. Only high concentrations of other compounds, such as hexanal and pentadecyl acetate, had attractive effects on females (χ^2=8.018, P=0.005; χ^2=4.738, P=0.030). Among all the tested compounds, linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol were the most effective attractant compounds for *L. sticticalis*.

3.5. Behavioral responses of *L. sticticalis* to the different formulations of bioactive compounds

The four attractant compounds, linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol, were further combined in different ratios to create a total of 25 binary, ternary, and quaternary formulations (Fig. 5-A). The behavioral results of these various formulations indicated that most of them showed significant efficacy in attracting *L. sticticalis* compared to the control group (Fig. 5-B). However, formulations of No. 2, No. 3, No. 11, and No. 12 did not exhibit such efficacy. The adults displayed selectivity towards the binary formulations with a range from 50.66 to 36.00%. Among these formulations, formulation No. 10 demonstrated the highest attraction to *L. sticticalis* with an efficacy of 50.66% (χ^2=8.963, P=0.003). The attractive effects of the ternary formulations on adults were more stable, and the ternary formulation No. 19 exhibited the greatest attraction to *L. sticticalis* among all ternary formulations with a selection rate of 56.00% (χ^2=11.655, P<0.001). The selectivity induced by the quaternary formulation was between 54.66% and 73.33%. In all compound mixtures, formulation No. 25 (linalool:*cis*-anethole:*trans*-2-hexenal:1-octen-3-ol=5:1:5:10) demonstrated the highest attractant activity towards *L. sticticalis* with an effective selection rate of 56.00%, followed by the formulation No. 21 (linalool:*cis*-anethole:*trans*-2-hexenal:1-octen-3-ol=5:1:1:10), which could effectively attract about 50.00% of *L. sticticalis*.

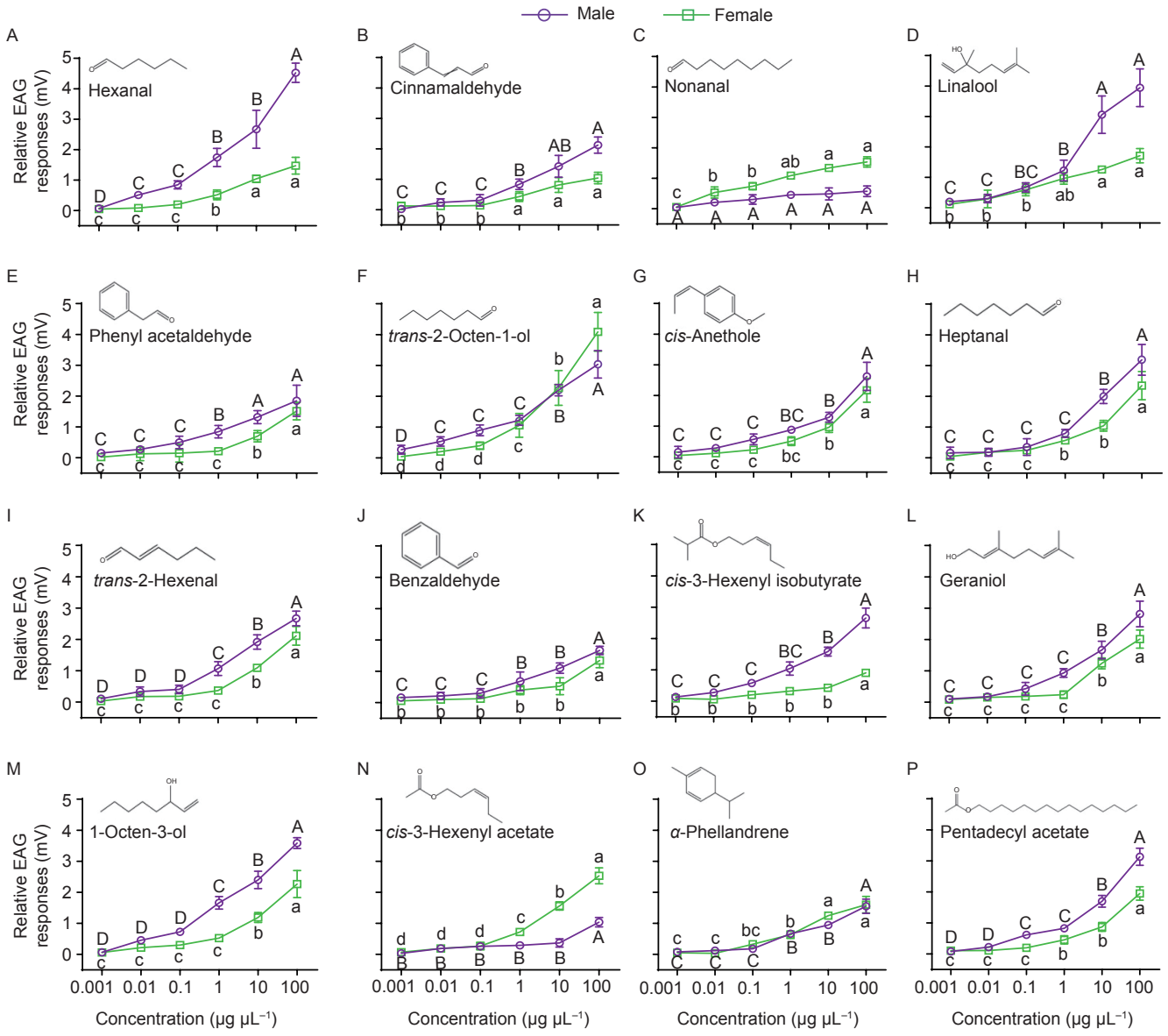


Fig. 3 Electroantennography (EAG) responses of *Loxostege sticticalis* to different concentrations of 16 bioactive compounds. The data are presented as mean±SE of six biological replicates. Different uppercase and lowercase letters indicate significant differences in the relative EAG response values of males and females to various doses of compounds, respectively (one-way ANOVA, Tukey's test, $P<0.05$).

3.6. Attractive effect of formulations on *L. sticticalis* in the field

The results of field-trapping assays (2023) showed that the lure No. 2, containing formulation No. 21 exhibited the most effective trapping effect on *L. sticticalis*, capturing 17.00±2.32, 25.00±5.84, 24.00±6.67, 33.00±4.71, and 38.00±3.16 adults from *H. annuus* field, *V. faba* field, *P. sativum* and *B. napus* mixed field, *B. napus* field, and *A. sativa* field, respectively, within 30 days (Fig. 6-A). Lure No. 1 loaded with formulation No. 25 caught a lower number of *L. sticticalis* compared to lure No. 2 but significantly higher than the other lures in *H. annuus* field, *V. faba* field, and *B. napus* field ($P<0.05$). Lure No. 1 and No. 3 were equally effective in trapping *L. sticticalis* in *P. sativum* and *B. napus* mixed field as well as *A. sativa* field. In these diverse fields, the pVOCs-based lures (lure No. 1 and No. 2) exhibited superior trapping effects compared to the sex pheromone lure (lure No. 5) alone, with no obvious difference observed in the number of male and female *L. sticticalis* attracted by the pVOCs-based lures. Moreover, the addition of formulation No. 25 to sex pheromone significantly diminished their trapping efficacy ($P<0.05$). To demonstrate the effectiveness of monitoring, we presented the total number of *L. sticticalis* adults captured by lure No. 1, No. 2, and No. 3 each day throughout the observation period (2023 and 2024) (Fig. 6-B and C). The results revealed that the three lures trapped more adults than the automatic pest detection lamp, and the peak occurrence of pests monitored by all three lures was almost consistent with that detected by the detection lamp, indicating accurate monitoring capability for *L. sticticalis*. In terms of monitoring sensitivity, lure No. 2 exhibited significantly higher sensitivity compared to lure No. 1 and No. 3. Therefore, lure No. 2

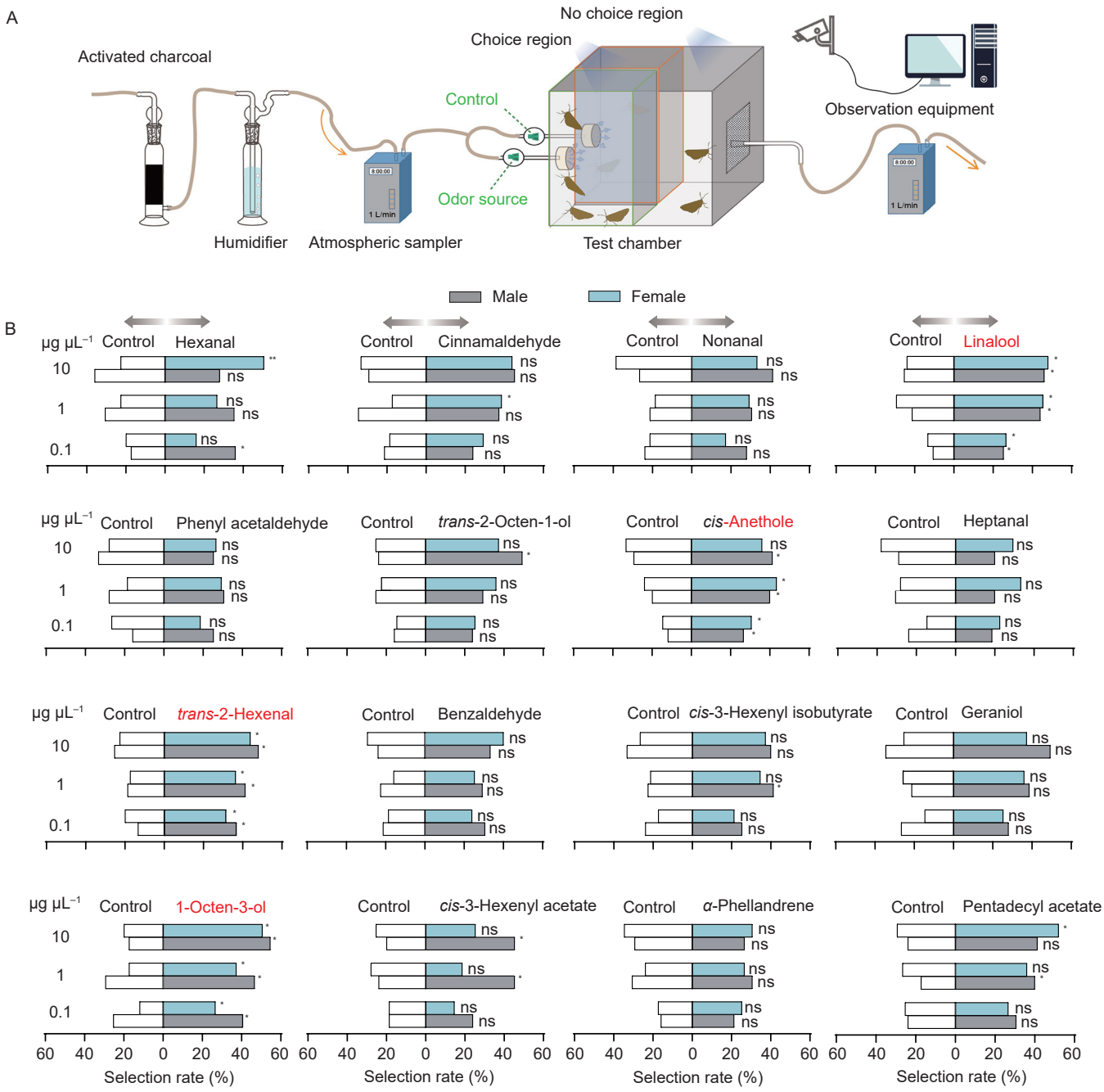


Fig. 4 The olfactory behavioral responses of *Loxostege sticticalis*. A, schematic drawing of the self-designed behavioral observation device for *L. sticticalis*. B, behavioral selection of *L. sticticalis* males and females to three concentrations of 16 bioactive compounds. The data are presented as means±SE. The χ^2 test was used to evaluate statistical differences in the number of adults choosing control and compound (ns, not significant; *, P<0.05, **, P<0.01).

can be utilized as an attractant for detecting and managing *L. sticticalis* in field conditions.

4. Discussion

The pVOCs function as the main olfactory cues for insects seeking hosts, playing pivotal roles in the co-evolutionary dynamics between plants and insects (Arimura and Uemura 2025). Insects depend on their highly advanced olfactory systems to detect and differentiate a broad spectrum of odor stimuli (Schmidt and Benton 2020). Therefore, pVOCs can serve as attractants or repellents to regulate the olfactory behavior of insects and aid in pest management.

Plant volatiles are synthesized *via* a series of biochemical pathways, producing a diverse array of compounds (Dudareva *et al.* 2013). Constitutively released pVOCs carry fingerprint information about the identity of the emitter and confer a unique chemical odor signature to each plant (Ninkovic *et al.* 2016). Insects, especially females, typically rely on volatile organic compounds emitted by plants to locate optimal food resources and suitable sites for oviposition (Carrasco *et al.* 2015). Thus, the three favored oviposition plants for *L. sticticalis* females were selected to extract the

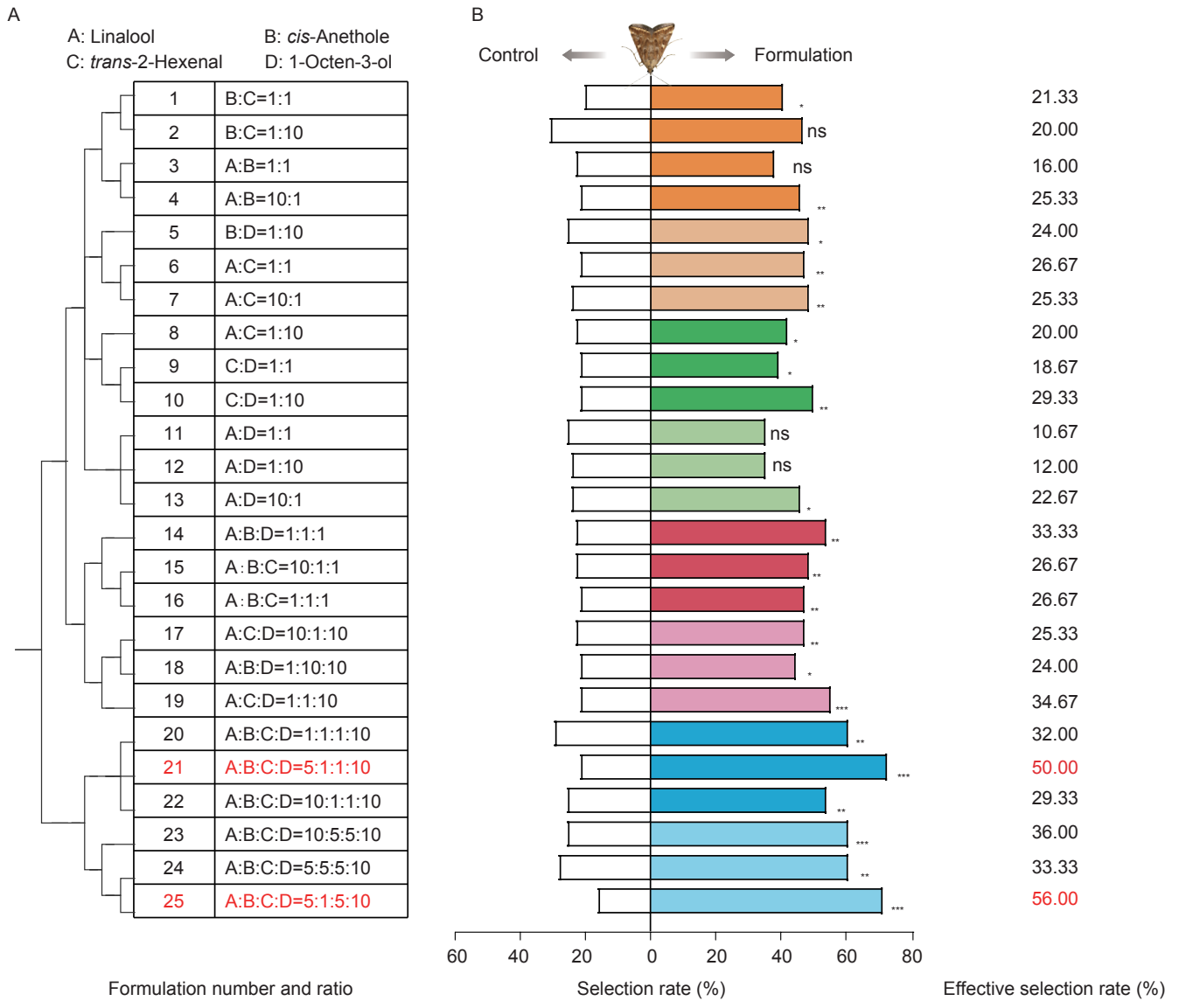


Fig. 5 The olfactory behavioral responses of *Loxostege sticticalis* to 25 attractant formulations. A, cluster plot based on the type and ratio of the compounds in each formulation. B, the selection rates and effective selection rates of *L. sticticalis* to the 25 different attractant formulations. The data are presented as mean±SE. Statistical differences in adult numbers between the control and formulation groups were evaluated using the χ^2 test (ns, not significant; *, $P<0.05$, **, $P<0.01$, ***, $P<0.001$).

headspace volatile compounds here (Fig. 1-A). Subsequent GC-MS analysis indicated that 55 different compounds were identified: 26 were found in *C. album*, 23 in *S. viridis*, and 20 in *M. sativa* (Table 1). Additionally, terpenes and alcohols constituted the major classes of these volatile compounds (Appendix D). The species and compositional data of these volatile compounds offer crucial insights for identifying the bioactive attractants of *L. sticticalis*.

The EAG technique thoroughly evaluates odorant reception at the peripheral level, facilitating the rapid and accurate identification of bioactive compounds (Park *et al.* 2002; Ngumbi *et al.* 2010; Liu *et al.* 2024). The EAG assay results showed that 33 compounds could evoke detectable EAG responses in both male and female *L. sticticalis* (Appendix E). The similar capability of both genders to detect plant volatiles is likely attributed to their shared habitat, which necessitates the utilization of analogous cues for locating host plants essential for survival and reproduction. It is worth noting that the EAG responses were stronger in males than in females for most of the compounds (Fig. 2). Similar results have been observed in previous research, which indicated that the green leaf volatile components elicited significantly greater EAG responses in *Iragoides fasciata* males than in females (Huang *et al.* 2012). However, there were also some reports pointing out that the EAG response profiles of *Phthorimaea operculella* and *Lobesia botrana* females to plant volatiles were generally higher than those of males (Das *et al.* 2007; Pérez-Aparicio *et al.* 2019). Therefore, the sensitivity of male and female moths to plant volatiles is not fixed, which may be related to the antennal structure, the number of antennal sensilla, the age of adults, and whether they have mated (Martel *et al.* 2009; Malo *et al.* 2020). Regarding *L. sticticalis*, the stronger EAG responses observed in males compared to females may be attributed

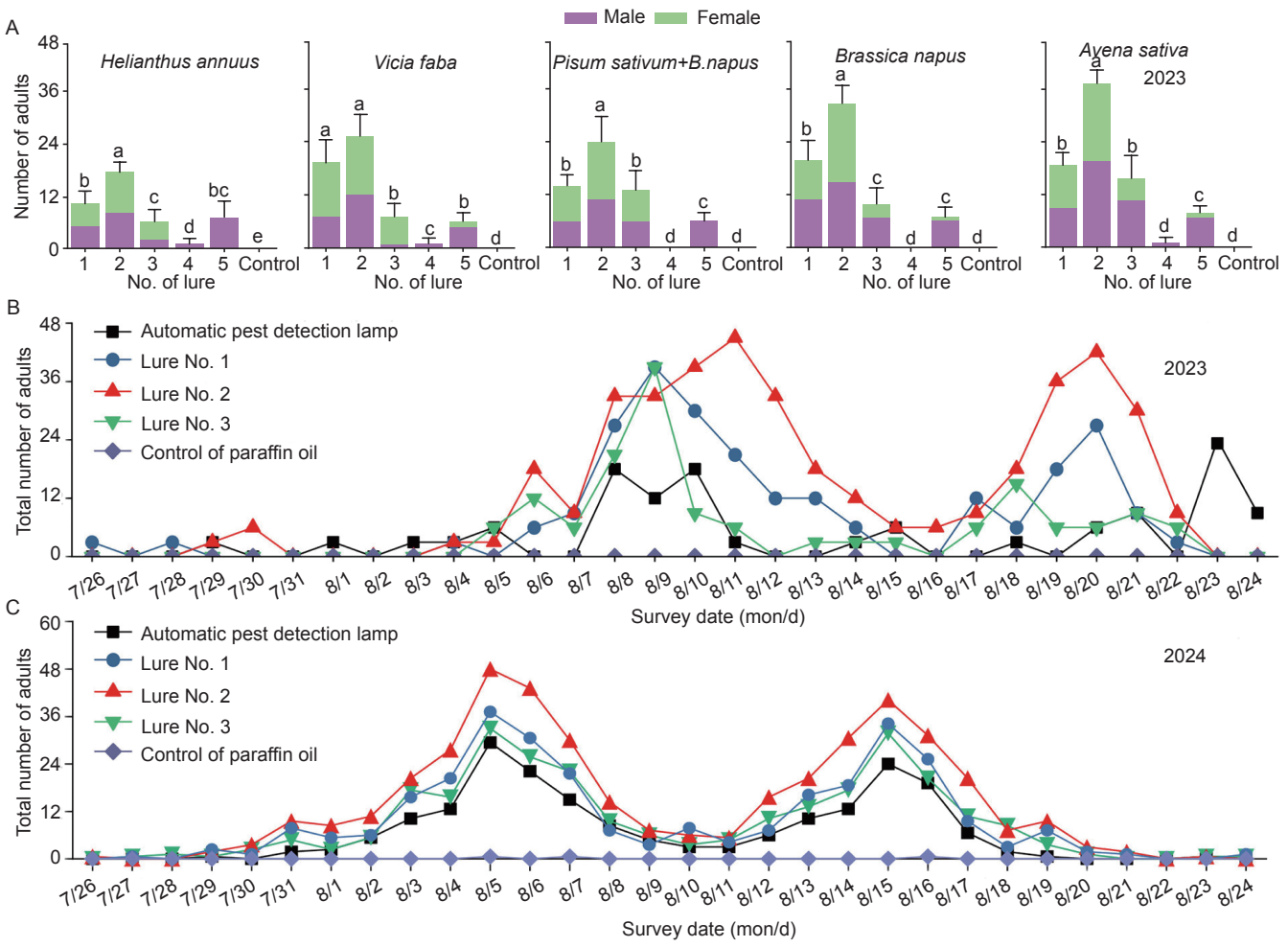


Fig. 6 The trapping effect of lures baited with different formulations on *Loxostege sticticalis* in the field. A, number of *L. sticticalis* captured within different fields for each type of lure during 30 days in 2023. Data are means±SE of three lure replicates. Different letters above the bars indicate significant differences at $P<0.05$ (one-way ANOVA, Tukey's test). B and C, total number of *L. sticticalis* trapped by lure No. 1, No. 2, and No. 3 per day from July 26 (B) to August 24, 2023 and 2024 (C). The lure containing paraffin oil was used as the negative control.

to the necessity for males to employ a heightened sensitivity in their olfactory system, which increases the likelihood of encountering females, thereby providing an advantage in resource competition and mate location (Hansson and Stensmyr 2011). Previous research has demonstrated that compounds with shorter carbon chains are more likely to diffuse into insects' olfactory organs than those with longer carbon chains, thereby increasing the likelihood of detection and eliciting a subsequent response (Pophof 1997). Here, we observed a similar result, where the EAG responses of male *L. sticticalis* to *trans*-2-hexenal (1.01±0.13 mV), heptanal (0.76±0.14 mV), nonanal (0.49±0.11 mV), and lauryl aldehyde (0.29±0.14 mV) progressively diminished as the carbon chain length of these aldehydes increased (Appendix E). Notably, there were significant differences in the EAG responses between males and females to the different compounds at various doses, indicating sexual dimorphism in *L. sticticalis* (Fig. 3) (Huang *et al.* 2012).

Indoor behavioral bioassays indicated that linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol were the most effective attractant compounds for *L. sticticalis* (Fig. 4-B). Previous studies showed that *trans*-2-hexenal and 1-octen-3-ol may participate in the oviposition preference of *L. sticticalis* (Yin *et al.* 2005). The plant volatile compounds released by green manure can directly influence the oviposition site selection and egg hatchability of *L. sticticalis* (Ma *et al.* 2023). The host plant volatiles linalool, *trans*-2-hexenal, and 1-octen-3-ol could be detected by the general odorant binding protein 2 of *L. sticticalis* (Yin *et al.* 2012). Based on these previous findings, we hypothesized that the four bioactive compounds identified in our study may primarily function as oviposition cues and interact with key olfactory recognition proteins in *L. sticticalis* females, thereby eliciting tropism behavioral responses. Interestingly, all four compounds also elicited strong attraction to *L. sticticalis* males (Fig. 4-B). Considering that *L. sticticalis* males tested in this experiment recently emerged, we speculate that the unmated males may possess a stronger olfactory identification ability, which allows them to effectively search for females (Johnson *et al.* 2022).

A previous study has pointed out that mixing different volatile compounds in their natural proportions in the

host plant can produce a strong attraction to insects (van Wijk *et al.* 2008). However, the strong green leaf odor background in the field might interfere with the synergistic effect of these compounds (Borrero-Echeverry *et al.* 2015; Cai *et al.* 2017). Consequently, a super-blending method was adopted, which is more appropriate for compound mixing experiments (Gregg *et al.* 2010, 2018). After testing these compounds using behavioral devices, we ultimately identified two quaternary formulations (Formulation No. 25 and No. 21) with optimal attraction (Fig. 5-B). In the field-trapping assays, the pVOCs-based lures baited with formulations No. 25 and No. 21 demonstrated superior trapping performance compared to the sex pheromone lure alone. Similarly, a plant volatiles mixture containing (*Z*)-3-hexenyl acetate and 1-undecanol increased the capture rate of *G*. *molesta* by 2.4 times compared to the pheromone-only controls (Yu *et al.* 2014). Integrating plant volatiles and insect sex pheromones into trapping devices can enhance the efficacy of large-scale pest management (Dudareva *et al.* 2004; Chi *et al.* 2024). Nonetheless, adding pVOCs (formulation No. 25) to the sex pheromone significantly reduced the trapping efficacy for *L*. *sticticalis* (Fig. 6-A). The dosage of plant volatile compounds and their ratio to the sex pheromone are critical factors in certain instances (Xiang *et al.* 2019). In our experiment, the ratio of plant volatiles to sex pheromones was set at 1:1, which did not exhibit a synergistic effect, suggesting that additional ratios need to be tested. Moreover, factors such as trap design, lure type, target species, blend complexity, and insect habitat may also impact the trap effectiveness of combined lures (Cai *et al.* 2017; Gregg *et al.* 2018). Therefore, further experiments are required to elucidate the complex interactions between pVOCs and the sex pheromones of *L*. *sticticalis*.

5. Conclusion

Our study identified 55 volatile compounds with potential attractiveness to *L*. *sticticalis* from their three preferred oviposition plants. Among these compounds, four bioactive compounds — linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol — mixed at a ratio of 5:1:1:10 could significantly attract both male and female *L*. *sticticalis* indoors and demonstrated superior efficacy in field trapping. These results suggest that volatiles derived from the oviposition preference plants of *L*. *sticticalis* can be used to develop targeted attractants for monitoring and mass trapping. Compounds such as linalool, *cis*-anethole, *trans*-2-hexenal, and 1-octen-3-ol are promising candidates to be incorporated into a ‘push–pull’ strategy to control *L*. *sticticalis*.

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Declaration of competing interest

The authors declare that they have no conflict of interest.

Declaration of generative AI and AI-assisted technologies in the writing process

The authors declare that they did not use AI in the preparation and writing of this manuscript.

Ethical statements

All applicable international, national, and institutional guidelines for the care and use of animals were followed.

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