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Behavioral and electrophysiological responses of fall armyworm larval parasitoid *Coccygidium luteum* to maize and companion plant volatiles

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Abstract Companion cropping and biological control are among the best agronomic practices recommended for ecologically sustainable management of the invasive fall armyworm (FAW), *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae). Companion plants may suppress the FAW population by repelling the pest, disrupting host-plant location and recruiting biocontrol agents such as parasitoids. These interactions are primarily mediated by plant-derived volatile organic compounds (VOCs). Understanding parasitoids' responses to VOCs emitted by companion plants enables selection of suitable cultivars to enhance biological control and design appropriate intercropping systems for effective FAW management. This study investigated behavioral and electrophysiological responses of a key FAW larval parasitoid, *Coccygidium luteum* Brullé (Hymenoptera: Braconidae), to odors from maize and different companion crops used in maize-based intercropping systems. In an olfactometer bioassay, gravid *C. luteum* were attracted to volatiles from FAW-damaged maize and intact companion plants (sweet potato, beans, groundnut) compared to control, but not to intact maize or cassava. Interestingly, females of *C. luteum* were equally attracted to volatiles from intact companion plants and FAW-damaged maize in multiple-treatment assays, suggesting that certain VOCs emitted by both plants may have ecological relevance. Chemical and electrophysiological analyses identified several bioactive compounds in the companion plant volatiles, including (*E*)-2-hexenal, (Z)-3-hexenyl acetate, nonanal, (*E*)-β-ocimene, (*E*)-4,8-dimethyl-1,3,7-nonatriene, decanal, (*E*)-nerolidol, and (*E*,*E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene, known to influence parasitoid foraging. These findings provide further insight into the companion plants-FAW-parasitoid interactions and support the development of effective, economical, and environmentally friendly FAW management strategies using companion cropping and biological control.

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Introduction

Plants naturally emit a wide range of volatile organic compounds (VOCs) from leaves, flowers, roots, etc. (Tamiru and Khan 2017; Kigathi et al. 2019; Malone et al. 2022). These VOCs serve crucial ecological functions, including shaping species-specific odor profiles and mediating interactions between plants, herbivores, and natural enemies (Vivaldo et al. 2017; Clavijo McCormick et al. 2023). The VOCs enable plants to defend themselves against pest attack by deterring herbivores and attracting pests' natural enemies such as parasitoids, which have evolved to use the chemical cues to enhance their foraging efficiency and improve their ecological fitness (Tamiru et al. 2015a,b; Ali et al. 2022).

The fall armyworm (FAW), *Spodoptera frugiperda* J.E. Smith (Lepidoptera: Noctuidae), is a highly adaptable, polyphagous pest that has spread from the Americas to Africa, Asia, the Middle East, and Oceania (Goergen et al. 2016; Guimapi et al. 2022). The pest causes significant damage, especially to maize, with economic losses in sub-Saharan Africa alone estimated at 13 million US$ annually (Day et al. 2017; Harrison et al. 2019). Although synthetic insecticides have traditionally been used to combat this threat (Kumela et al. 2018), mounting evidence of environmental and health risks (Kumela et al. 2018) and reports of pest's resistance development against various classes of insecticides (Zhang et al. 2021), have spurred growing interest in ecologically sustainable methods to manage the FAW.

Agroecological methods such as intercropping offer a sustainable alternative to synthetic insecticides by exploiting plant-derived VOCs to influence pests' behavior (Tamiru and Khan 2017; Schlaeger et al. 2018). Volatiles from some companion plants have been shown to disrupt FAW foraging behavior and attract its natural enemies, such as parasitoids and predators (Harrison et al. 2019; Sobhy et al. 2022; Peter et al. 2023, 2024). Attracting natural enemies with companion plants enhance biocontrol for ecological pest management (Sobhy et al. 2022; Huang et al. 2024). A solitary larval parasitoid, *Coccygidium luteum* (Brulle) (Hymenoptera: Braconidae), has recently been discovered forming a new association with FAW in Africa (Agboyi et al. 2020). Parasitism by *C. luteum* has been reported to range between 8.3 and 89.0% depending on the location (Sisay et al. 2019; Agboyi et al. 2020), showing the parasitoid's potential as an effective biological control agent against FAW pest.

Parasitoids navigating through diverse plant environments constantly encounter a rich array of plant-derived VOCs, but herbivore-induced plant volatile compounds (HIPVs) serve as a reliable cue for locating host habitats, helping parasitoids to distinguish between infested and intact plants (Pareja et al. 2007; Tamiru and Khan 2017; Kigathi et al. 2019). Some companion plants constitutively emit VOCs that mimic HIPVs, enhancing parasitoid recruitment (Khan et al. 2010; Sobhy et al. 2022). In this study, we hypothesized that the odors released by selected companion crops commonly grown in maize-based intercropping systems could potentially enhance the foraging efficiency of parasitoids and thereby contribute to the biological control of FAW. To validate this hypothesis, we (1) compared the responses of *C. luteum* to volatiles from FAW-infested maize, intact (undamaged) maize, and selected companion crops (cassava, sweet potato, groundnut, beans) in dual and multiple treatment combinations using a four-arm olfactometer, and (2) used chemical and electrophysiological analyses to detect, identify and compare bioactive volatiles capable of influencing the behavior of *C. luteum.*

Materials and methods

Plants and insects

Maize (SC Duma 43), beans (Punda), cassava, groundnut and sweet potatoes were procured from Simlaw Seeds Company, Kenya and grown in a 5 l pots (soil:organic manure, 2:1) inside a screenhouse protected from insects at the International Centre of Insect Physiology and Ecology (ICIPE), Duduville campus, Kasarani, Nairobi, Kenya (1° 13′ 25.6″ S, 36° 53′ 49.1″ E, 1616 m above sea level). All plants were maintained under natural conditions

[temperature: 25 ± 3 °C, RH: 65 ± 5%, and a L:D 12:12 photoperiod) and used in the study when four weeks old.

The larval parasitoid, *C. luteum*, was obtained from ICIPE's Animal Rearing and Quarantine Unit (ARQU) and reared on 2nd instar FAW larvae collected from infested maize fields in Mwea (0º 39′ 0.37″ S, 37º 22′4 8.1″ E, 1174 m above sea level). The insect cultures were maintained at 25 ± 3 °C, 50–70% RH, and a L:D 12:12 photoperiod, and regularly infused with a field-collected insect population to maintain desirable traits.

Volatile trapping

Headspace volatiles were collected from FAW infested maize, intact maize, companion plants, and blank controls, i.e., empty oven bags (polyethylene terephthalate; PET), using a dynamic push–pull technique for 24 h (Tamiru et al. 2011). Before the volatile collection, the aerial parts (leaves) of the study plants were carefully enclosed in preheated PET oven bags (volume 3.2 l, 12.5 µm film thickness), with charcoal-filtered air introduced through an inlet port at a 500 ml min^{-1} and volatiles trapped on Porapak Q filters (50 mg, 60/80 mesh; Supelco, Bellefonte, USA), which had been pre-conditioned with dichloromethane (DCM), at an outlet port with air drawn at a rate of 300 ml min^{-1} (Tamiru et al. 2011; 2020). For collecting volatiles from maize infested with FAW, the study plants were subjected to ten 2nd instar FAW larvae each and kept in a cage (80 × 40 × 40 cm) for 24 h to induce larval damage. After entrainment, volatiles were eluted with 0.5 ml of DCM into 2 ml sample vials and stored at -80 °C for later use in bioassay, chemical and electrophysiological analyses.

Olfactometer bioassay

Two sets of experiments were conducted using a Perspex four-arm olfactometer bioassay (Tamiru et al. 2011) to assess *C. luteum* responses to volatiles from infested maize, intact maize, companion crops (beans, groundnut, cassava, sweet potato), and a solvent control (DCM). In the first experiment, volatiles from individual plants were tested against the control (solvent only). Ten µl aliquots of headspace volatiles were placed in one arm, while the other three arms contained the same volume of solvent controls. The treatment stimulus was applied to a filter paper strip (4 × 25 mm) using a micropipette (Drummond Scientific, USA), allowed to dry solvent for 30 s, and then placed inside the inlet port of each olfactometer arm. Female *C. luteum* (aged 2–3 days), previously exposed to FAW damaged maize leaf odors (Sobhy et al. 2022), were individually introduced into the central chamber of the olfactometer using a custom-made glass tubing. Clean air was drawn through each olfactometer arm toward the center at 260 ml min^{-1}. Time spent and frequency of insect entry to the different arms of the olfactometer were observed and recorded using Olfa software (F. Nazzi, Udine, Italy) for 12 min (Tamiru et al. 2015a). To minimize positional bias, the olfactometer was rotated 90° clockwise every three minutes.

In the subsequent experiment, a similar setup was used for a choice test comparing insect responses to volatiles from infested maize, intact companion plants, and solvent control. Test stimuli (10 µl each) were placed in the two opposite arms, infested maize in one and companion plants in the other, with 10 µl of solvent (DCM) controls in the remaining arms. Each treatment was replicated 12 times, and each female *C. luteum* was tested once.

Volatile analysis

Two µl of headspace samples were analyzed using an Agilent 7890A gas chromatograph (GC) directly linked to a mass spectrometer (MS) (MSD 5975C triple-axis, Agilent Technologies, Palo Alto, USA). The GC–MS setup and method used were similar to those previously described by Peter et al. (2023). Compounds were identified by comparing their mass spectra data with authentic standards, using reference databases and retention indices (Peter et al. 2023). Quantification was based on external calibration curves using standard solutions (1–500 ng $µl^{-1}$), of representative alcohol [(*Z*)-3-hexen-1-ol], monoterpene (α-pinene), and sesquiterpene [(*E*)-β-caryophyllene], and results were expressed as ng $plant^{-1}$ h^{-1} (Peter et al. 2023). Mass spectrometry data, including peak detection

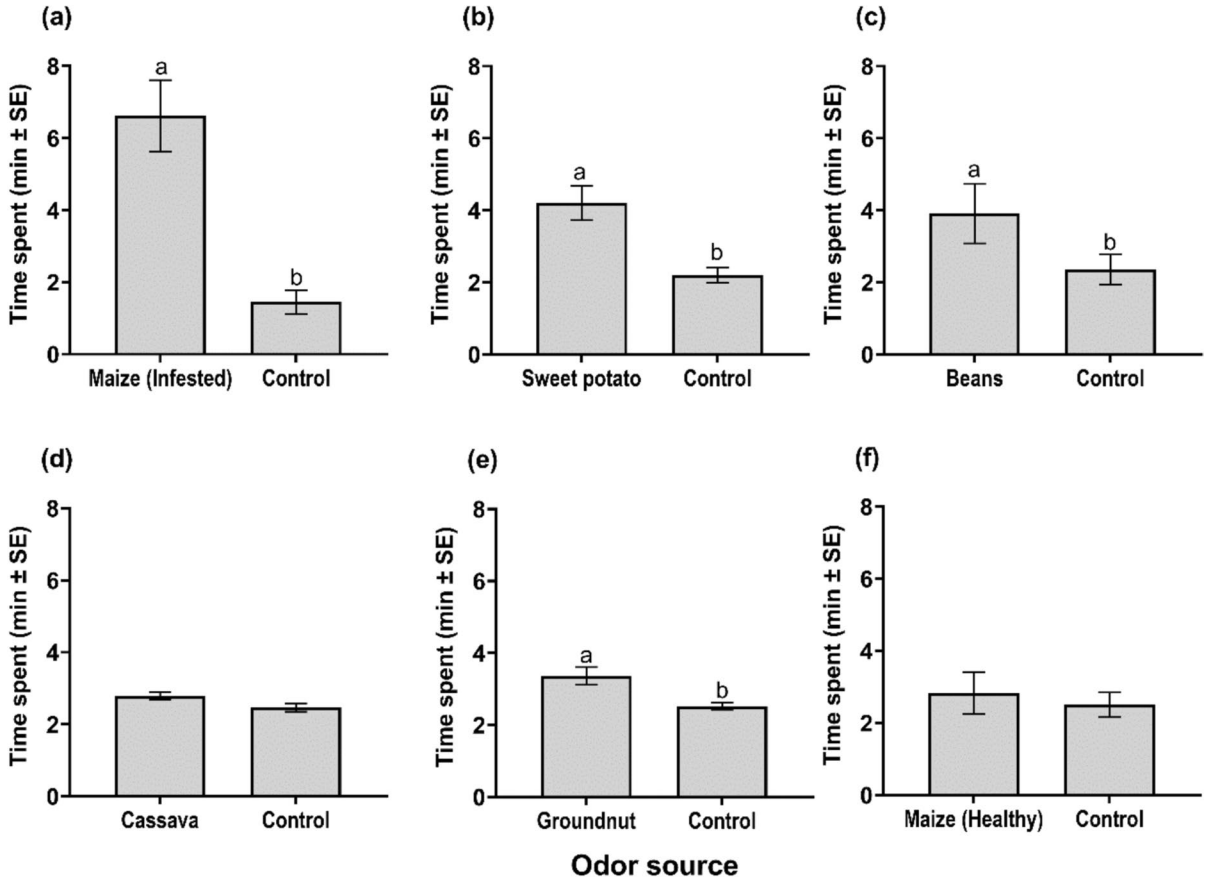


Fig. 1 Behavioral responses of *Coccygidium luteum* females to volatiles from the fall armyworm larvae infested maize **(a)**, intact sweet potato **(b)**, beans **(c)**, cassava **(d)**, groundnut **(e)**, maize **(f)**, and solvent control in a four-arm olfactometer. Observations were made for 12 min each (n = 12). Time spent by *C. luteum* in the treatment and control arms of the olfactometer are shown. Bars with different letters on top are significantly different (Newman-Keuls post-hoc test, $P < 0.05$). Bars with no letters are not significant difference

and visualization, were processed using MSD ChemStation software F.01.00.1903 (Agilent Technologies).

Electrophysiological recording

Electroantennogram (EAG) recordings were conducted using excised antenna from ice-chilled females. Antennae were mounted between two glass capillaries (1.5 mm inner diameter) filled with Ringer saline solution (Maddrell 1969), connected to silver-coated electrode wires of the probe (INR-II, Syntech, Hilversum, the Netherlands), with the base of the antenna linked to the reference electrode (Tamiru et al. 2011). A 2 µl headspace aliquot was injected into an HP7890 GC with a non-polar column (HP5-MSI, 30 m × 0.25 mm i.d. × 0.25 µm film thickness) and a flame ionization detector (FID) at an injection temperature of 280 °C. Oven temperature was programmed from 35 °C (held for 3 min) to 280 °C at a rate of 10 °C min^{-1}, with nitrogen serving as the carrier gas. Electroantennographic detection (EAD) software (GCEAD 2015 v1.2.6, Syntech) was used to record simultaneous EAD and FID responses across six replicates. Only FID peaks that elicited EAD activity in at least three of the six runs were considered physiologically active.

Chemicals

External standards for compounds verification and quantification included (*E*)-2-hexenal,

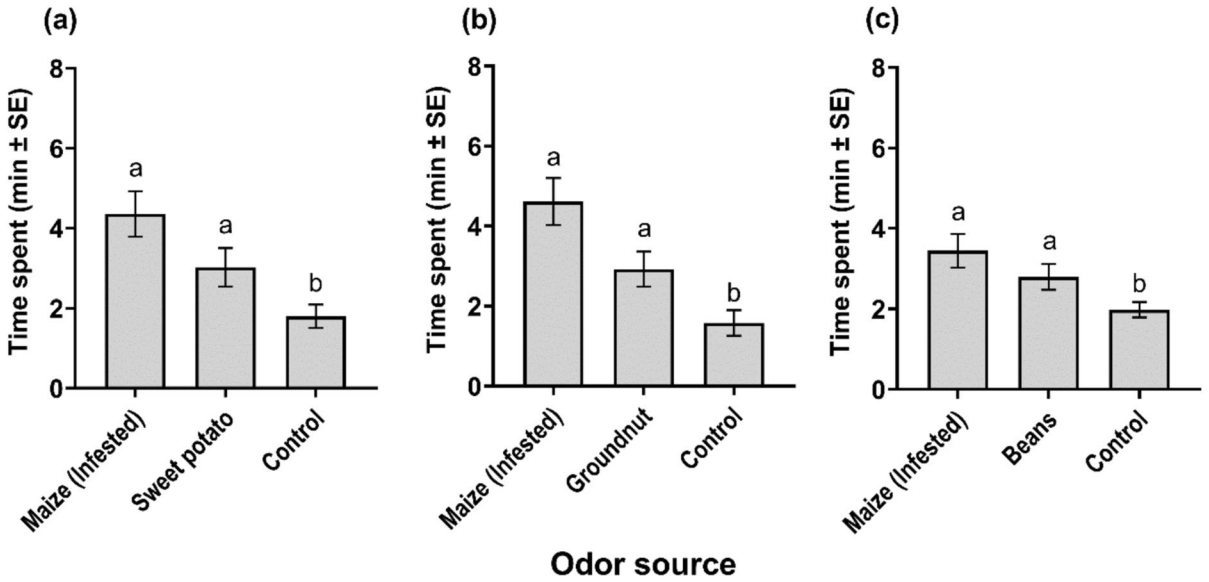


Fig. 2 Behavioral responses of *Coccygidium luteum* females to volatiles from the fall armyworm larvae infested maize, intact companion plants, namely sweet potato **(a)**, beans **(b),** groundnut **(c)**, and solvent control in a four-arm olfactometer. Observations were made for 12 min each (n = 12). Time spent by *C. luteum* in the treatment and control arms of the olfactometer are shown. Bars with different letters on top are significantly different (Newman-Keuls post-hoc test, $P < 0.05$)

(*Z*)-3-hexen-1-ol, 2-heptanone, 2-heptanol, α-pinene, β-pinene, 1-octen-3-ol, β-myrcene, ρ-cymene, limonene, β-phellandrene, (*E*)-β-ocimene, linalool, methyl salicylate (MeSA), β-elemene, and (*E*)-β-caryophyllene, all obtained from Sigma-Aldrich with > 95% purity. Dichloromethane (99.9% purity) was procured from Merck (Darmstadt, Germany).

Statistical analysis

To analyze *C. luteum* response data from the four-arm olfactometer assays, one-way ANOVA with R software (Supplementary Material S1) was used after converting time spent data into proportions to account for dependence of insect visiting time, followed by log10-ratio transformation to allow the analysis of compositional data (Aitchison 1982; Tamiru et al. 2011). Significant differences between means were determined using the Newman-Keuls post-hoc test ($P < 0.05$). For analysis of volatile compound concentrations emitted by the test plants, which exhibited non-normal distribution (Shapiro-Wilk test: $p < 0.05$), a non-parametric test; Mann-Whitney Wilcoxon [Treatment (T) = 2] and Kruskal-Wallis ($T \geq 3$) tests followed by Dunn's post-hoc test were applied. All data analyses was conducted using R statistical software version 4.0.4 (R Core Team 2021).

Results

Behavioral response of *C. luteum* to plant volatiles

In dual choice assays, females of *C. luteum* were significantly attracted to plant volatiles from FAW infested maize ($F_{1, 46} = 36.85$, $P < 0.05$, Fig. 1a), intact sweet potato ($F_{1, 46} = 14.59$, $P < 0.05$, Fig. 1b), beans ($F_{1, 46} = 7.04$, $P < 0.05$, Fig. 1c) and groundnut ($F_{1, 46} = 10.93$, $P < 0.05$, Fig. 1e) compared to solvent control (Fig. 1). However, *C. luteum* females could not discriminate between solvent control and volatiles from uninfested maize ($F_{1, 46} = 0.38$, $P > 0.05$, Fig. 1f) and cassava ($F_{1, 46} = 0.01$, $P > 0.05$, Fig. 1d). Interestingly, in multiple choice assays, *C. luteum* females were equally attracted to volatiles from FAW infested maize and intact companion plants but less attracted to the solvent control (sweet potato: $F_{2, 45} = 10.14$, $P < 0.05$, Fig. 2a; groundnut: $F_{2, 45} = 9.61$, $P < 0.05$, Fig. 2b; beans: $F_{2, 45} = 8.48$, $P < 0.05$, Fig. 2c) (Fig. 2).

Table 1 Volatile organic compounds (ng plant^{-1} h^{-1}) detected in the headspace samples collected from the experimental plants

Peak No	RT (min)[1]	Compound[2]	RI_{alk}[3]	RI_L[4]	Maize (infested)	Maize (undamaged)	Sweet potato	Groundnut	Cassava	Beans	*P* value[5]
1	8.05	(*E*)-2-hexenal#	861	846	63.68 ± 33.76^{a*}	nd	nd	nd	21.84 ± 0.49^{b}	nd	0.03
2	8.12	(*Z*)-3-hexen-1-ol#	863	858	57.57 ± 10.03^{a}	26.3 ± 1.28^{b}	27.4 ± 4.24^{b}	26.60 ± 2.10^{b}	23.66 ± 1.07^{b}	nd	0.04
3	8.93	2-heptanone#	894	895	nd	24.99 ± 2.62	nd	nd	nd	nd	–
4	9.16	2-heptanol#	904	903	nd	23.93 ± 1.44	nd	nd	nd	nd	–
5	9.82	α-pinene#	935	934	24.28 ± 2.35^{a}	24.44 ± 2.44^{a}	27.04 ± 1.69^{a}	23.09 ± 0.31^{a}	22.09 ± 0.41^{a}	24.34 ± 1.87^{a}	0.22
6	10.67	Sabinene	975	975	nd	nd	23.23 ± 1.82^{a}	22.06 ± 0.11^{a}	nd	nd	0.68
7	10.71	β-pinene#	977	981	nd	nd	23.75 ± 0.85^{a}	21.17 ± 0.13^{ab}	nd	19.28 ± 0.95^{b}	0.01
8	10.82	1-octen-3-ol#	982	983	nd	nd	nd	25.29 ± 1.61	nd	nd	–
9	11.03	β-myrcene#	992	992	57.49 ± 6.79^{a}	22.18 ± 0.37^{b}	23.47 ± 0.36^{ab}	nd	nd	nd	0.01
10	11.36	(*Z*)-3-hexenyl acetate	1009	1007	130.35 ± 0.84^{a}	26.67 ± 2.9^{b}	nd	60.68 ± 8.80^{ab}	nd	nd	0.009
11	11.66	ρ-cymene#	1026	1020	nd	nd	nd	24.19 ± 0.95^{a}	21.92 ± 0.30^{a}	nd	0.11
12	11.73	Limonene#	1029	1026	nd	31.33 ± 6.60^{bc}	41.04 ± 5.66^{ab}	25.06 ± 0.18^{bc}	21.80 ± 0.32^{c}	87.08 ± 11.63^{a}	0.004
13	11.78	1,8-cineole	1032	1036	nd	nd	nd	25.58 ± 1.27	nd	nd	–
14	12.09	(*E*)-β-ocimene#	1050	1050	nd	nd	23.90 ± 1.39^{a}	47.66 ± 3.62^{a}	30.50 ± 7.60^{a}	nd	0.08
15	12.65	Nonanal	1080	1083	nd	nd	nd	nd	nd	25.81 ± 3.41	–
16	12.80	Terpinolene#	1089	1090	nd	nd	21.08 ± 0.12	nd	nd	nd	–
17	12.99	Linalool#	1101	1101	51.76 ± 13.74^{a}	21.14 ± 0.13^{b}	nd	25.39 ± 2.76^{b}	nd	nd	0.02
18	13.26	DMNT	1117	1116	47.88 ± 7.65^{a}	21.07 ± 0.05^{b}	36.91 ± 5.27^{a}	34.52 ± 2.45^{a}	nd	nd	0.01
19	14.62	Methyl salicylate#	1202	1199	nd	nd	nd	51.36 ± 10.76	nd	nd	–
20	14.78	Decanal	1213	1206	23.02 ± 1.11	nd	nd	nd	nd	nd	–
21	15.93	Lavandulyl acetate	1293	1289	nd	33.11 ± 458.00	nd	nd	nd	nd	–
22	16.10	Indole	1305	1298	147.00 ± 43.01	nd	nd	nd	nd	nd	–
23	16.85	α-longipinene	1360	1352	nd	nd	nd	nd	21.85 ± 0.85	nd	–
24	17.07	Cyclosativene	1377	1369	26.85 ± 0.59^{b}	55.25 ± 8.02^{a}	nd	nd	nd	nd	0.03
25	17.15	Longicyclene	1382	1376	nd	nd	nd	nd	40.80 ± 5.40	nd	–
26	17.16	α-ylangene	1383	1382	nd	nd	23.61 ± 2.61	nd	nd	nd	–
27	17.17	α-copaene	1384	1384	25.44 ± 4.39^{b}	67.27 ± 10.88^{a}	22.73 ± 0.78^{b}	nd	nd	nd	0.01
28	17.37	β-elemene#	1398	1397	nd	28.84 ± 5.68^{a}	35.99 ± 2.89^{a}	nd	nd	nd	0.34
29	17.64	Longifolene	1419	1425	nd	nd	nd	nd	26.67 ± 0.95	nd	–
30	17 .73	α-cedrene	1426	1424	nd	nd	nd	nd	nd	16.06 ± 1.04	–
31	17.80	(*E*)-β-caryophyllene#	1432	1427	126.68 ± 11.06^{a}	83.37 ± 4.68^{b}	88.78 ± 20.99^{b}	nd	27.97 ± 2.99^{c}	nd	0.01
32	17.92	(*E*)-α-bergamotene	1442	1451	233.28 ± 32.51^{a}	25.33 ± 2.22^{b}	34.38 ± 2.44^{b}	28.96 ± 4.86^{b}	nd	nd	0.01
33	18.14	(*E*)-β-farnesene	1459	1461	265.59 ± 36.91	nd	nd	nd	nd	nd	–
34	18.22	α-humulene#	1466	1465	nd	32.04 ± 3.20^{a}	30.78 ± 3.55^{a}	nd	22.47 ± 1.11^{a}	nd	0.06
35	18.31	β-chemigrene	1473	1476	nd	nd	22.67 ± 0.84	nd	nd	nd	–
36	18.58	Germacrene D	1494	1490	41.48 ± 3.89^{a}	39.91 ± 8.55^{a}	48.35 ± 6.04^{a}	nd	26.37 ± 3.28^{a}	nd	0.10

Table 1 (continued)

Peak No	RT (min)[1]	Compound[2]	RI_{alk}[3]	RI_L[4]	Maize (infested)	Maize (undamaged)	Sweet potato	Groundnut	Cassava	Beans	*P* value[5]
37	18.62	α-selinene	1498	1498	nd	nd	34.81 ± 1.48	nd	nd	nd	–
38	18.79	Isodaucene	1512	1500	nd	nd	42.95 ± 8.09	nd	nd	nd	–
39	18.82	α-muurolene	1514	1502	nd	25.74 ± 3.79	nd	nd	nd	nd	–
40	18.84	β-bisabolene	1515	1508	37.74 ± 3.19	nd	nd	nd	nd	nd	–
41	18.96	γ-cadinene	1525	1513	nd	23.21 ± 1.15[a]	nd	24.41 ± 0.82[a]	nd	nd	0.48
42	19.05	β-sesquiphellandrene	1533	1521	58.94 ± 4.90	nd	nd	nd	nd	nd	–
43	19.09	δ-cadinene	1536	1525	30.87 ± 2.12[a]	46.66 ± 9.97[a]	33.19 ± 1.33[a]	nd	nd	nd	0.50
44	19.46	(*E*)-nerolidol	1567	1564	32.01 ± 8.90	nd	nd	nd	nd	nd	–
45	19.52	Unknown	1574	–	nd	38.34 ± 7.28[a]	27.42 ± 2.55[a]	35.43 ± 5.59[a]	nd	nd	0.59
46	19.67	TMTT	1585	1584	28.43 ± 4.27[b]	nd	35.51 ± 5.18[b]	58.54 ± 8.03[a]	nd	nd	0.02

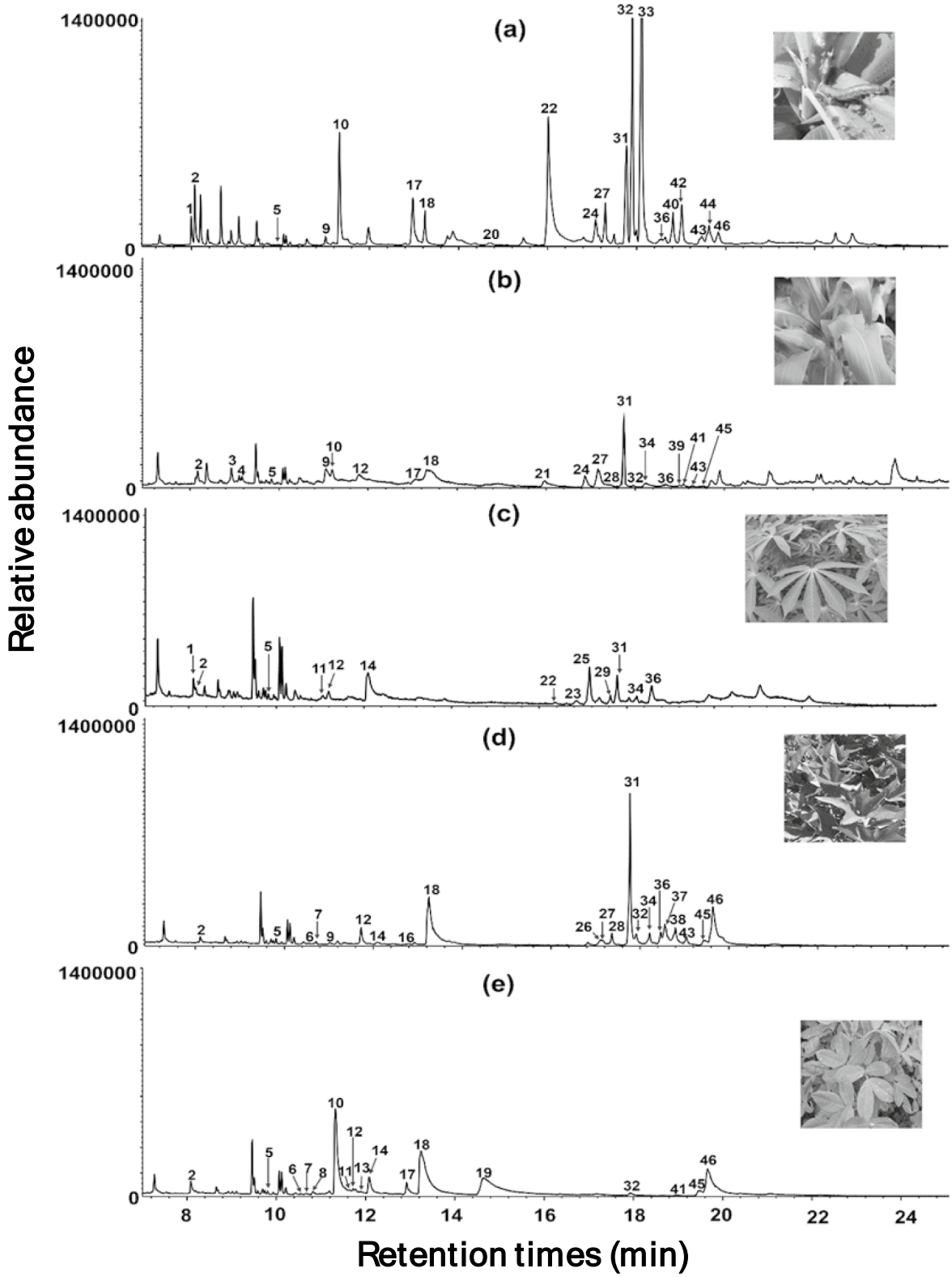
[1]Compounds are listed according to increasing retention time.[2]Volatile organic compounds were identified by comparing their mass spectra with those from authentic external standards (compounds marked with[#]), mass spectra databases such as Adams2, Chemecol, and NIST11, online NIST Chemistry Webbook and retention index (KI).[3]Retention index determined relative to C_8-C_{23} n-alkanes on an HP-5MS capillary column.[4]Retention index referenced from literature (Khan et al. 2012).[5]P-value obtained from non-parametric Kruskal–Wallis and two-sample Wilcoxon tests to compare the amounts of volatile organic compounds among the test plants (n = 4). *Means (±SE) with different superscript letters within a row indicate significant differences (Dunn's post-hoc test, $P < 0.05$). "nd" signifies compounds that were not detected. DMNT stands for (*E*)-4,8-Dimethyl-1,3,7-nonatriene, while TMTT for (*E, E*)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene

Chemical analysis of plant volatiles

A total of 46 VOCs were identified across the test plants, with terpenes being the most dominant, followed by aldehydes, esters, alcohols, an alkaloid, and a ketone (Table 1; Fig. 3). The sesquiterpene (*E*)-β-farnesene was the most abundant VOC emitted by maize plants exposed to FAW larval feeding, followed by (*E*)-α-bergamotene, indole, (*Z*)-3-hexenyl acetate and (*E*)-β-caryophyllene (Table 1). These compounds were also detected in the companion plant volatiles except indole and (*E*)-β-farnesene (Table 1; Fig. 3). Other bioactive compounds significantly induced in maize plants infested with FAW larvae, compared to intact maize, include (*Z*)-3-hexen-1-ol, β-myrcene, linalool, (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and (*E, E*)-4,8,12-Trimethyl-1,3,7,11-tridecatetraene (TMTT). Some of these compounds were also present in intact companion plant volatiles, though in relatively lower concentrations. For example, the concentrations of β-myrcene and linalool were more than two-fold in FAW infested maize compared to companion plants (sweet potato, groundnut) volatiles (Table 1). Interestingly, the emission rate of key bioactive compounds DMNT and TMTT by FAW infested maize were on a par with companion plants sweet potato and groundnut while significantly lower or absent in intact maize and cassava plant volatiles (Table 1). Furthermore, VOC emissions varied significantly among companion plants. For example, groundnut emitted more TMTT than sweet potato (KW $\chi^2 = 7.73$, df = 2, $P < 0.05$), with none detected in cassava. Octen-3-ol, (*Z*)-3-hexenyl acetate, linalool, and methyl salicylate (MeSA) were unique to groundnut while nonanal and α-cedrene appeared only in beans (Table 1).

Electrophysiological responses of C. luteum

Coupled GC-electroantennographic detection (GC-EAD) analysis using female *C. luteum* antennae revealed 14 bioactive compounds emitted by FAW infested maize and intact companion plants (Fig. 4) with potential biological relevance. Female *C. luteum* antennae detected nine VOCs from FAW-infested maize volatiles namely, (*E*)-2-hexenal, (*Z*)-3-hexenyl acetate, DMNT, decanal, (*E*)-nerolidol, TMTT and three unidentified compounds (Fig. 4a). In groundnut, four volatile compounds [(*E*)-β-ocimene, DMNT,


(a)
(b)
(c)
(d)
(e)
1400000
0
Relative abundance
8
10
12
14
16
18
20
22
24
Retention times (min)

◂**Fig. 3** Representative GC–MS profiles of volatiles from the experimental plants. (**a**) the fall armyworm larvae infested maize, (**b**) intact maize, **(c)** cassava, **(d)** sweet potato, **(e)** groundnut. Identities and emission rates (ng plant^{-1} h^{-1}) of the compounds (peaks) are shown in Table 1

TMTT and an unidentified compound] showed consistent electrophysiological activity (Fig. 4b), whereas, in beans, nonanal and three unidentified compounds elicited steady EAD responses (Fig. 4c).

Discussion

Plants have evolved intricate defense strategies against herbivores, including the emission of volatile organic compounds (VOCs) which attract herbivore's natural enemies such as parasitoids. While most defense VOCs are induced after herbivore attack (Dicke and Bald win 2010; Tamiru et al. 2012; Turlings and Erb 2018), some plants produce them constitutively (Pichersky et al. 2006; Pickett et al. 2006). On the other hand, parasitoids have co-evolved to exploit these chemical cues to locate suitable herbivorous hosts (Gohole et al. 2003; Clavijo McCormick et al. 2023). Attraction of parasitoid wasps to bioactive VOCs has been shown to enhance their foraging efficiency eventually improving their ecological fitness (Tamiru et al. 2015b).

Our findings revealed that the FAW larval parasitoid *C. luteum* was strongly attracted to volatiles from FAW infested maize and some intact companion plants such as sweet potato, beans and groundnut. In contrast, *C. luteum* females did not show preference to volatiles from intact (uninfested) maize and cassava compared to the solvent control (DCM). This demonstrates the parasitoid's differential response to plant volatiles and highlights the role of certain companion crops in boosting parasitoid attraction. Parasitoids primarily rely on plant-emitted volatile cues for locating their herbivore hosts. Volatiles from undamaged companion plant species have been shown to increase parasitoid efficiency and parasitism rates (Glinwood et al. 2009; Sobhy et al. 2022; Montagné 2024). Therefore, identification of companion plants that release appropriate VOCs to attract natural enemies greatly enhance biological control for ecologically pest management (Pickett et al. 2006; Khan et al. 2010).

Our results also showed that female *C. luteum* were equally attracted to both infested maize and intact companion plants (groundnut, beans and sweet potato) suggesting ecologically relevance of constitutive VOCs from these companion plants. While there is selection pressure on the parasitoids to detect and respond to herbivore-induced signaling chemicals, evolutionary processes may enable intact plants to protect themselves from potential pest attack by producing defense VOCs that are attractive to natural enemies of pests (Heil et al. 2004; Dicke and Baldwin 2010; Maffei 2010). Several studies have shown that parasitoid wasps, such as *Cotesia* spp. and *Chelonus* spp., are attracted to VOCs induced by herbivore feeding (HIPVs) (Tamiru and Khan 2017; Turlings and Erb 2018; Onjura et al. 2025; Tepa-Yotto et al. 2025). Though HIPVs serve as reliable cues for host presence (Melo Machado et al. 2014), growing evidence indicates the parasitoids also exploit volatiles from intact companion plants to locate their hosts (Sobhy et al. 2022; Peter et al. 2023; Huang et al. 2024; Tepa-Yotto et al. 2025).

Our study revealed significant variations in the composition and proportions of volatile compounds between the various experimental plants. Several VOCs were released in significantly higher amounts in maize infested by FAW larvae compared to intact (uninfested) plants. Typically, undamaged plants emit minimal amounts of volatile compounds (Pichersky et al. 2006; Tamiru and Khan 2017; Turlings and Erb 2018). However, VOCs emission from plants undergoes significant changes in quantity and composition upon herbivore feeding (Clavijo McCormick et al. 2012; Kigathi et al. 2019; Onjura et al. 2025). Some of the strongly induced VOCs from maize plants damaged by FAW larvae in our study include (*E*)-β-farnesene, (*E*)-α-bergamotene, indole, (*Z*)-3-hexenyl acetate, linalool, (*E*)-β-caryophyllene, β-myrcene, DMNT, TMTT, (*E*)-2-hexenal and (*Z*)-3-hexen-1-ol. These VOCs have previously been reported to have ecological relevance in recruiting pest natural enemies such as parasitoids (Khan et al. 1997; Melo Machado et al. 2014; Turlings and Erb 2018). Interestingly, we detected several of these bioactive compounds including (*E*)-α-bergamotene, (*Z*)-3-hexenyl acetate, (*E*)-β-caryophyllene, DMNT, TMTT, (*E*)-2-hexenal and (*Z*)-3-hexen-1-ol in

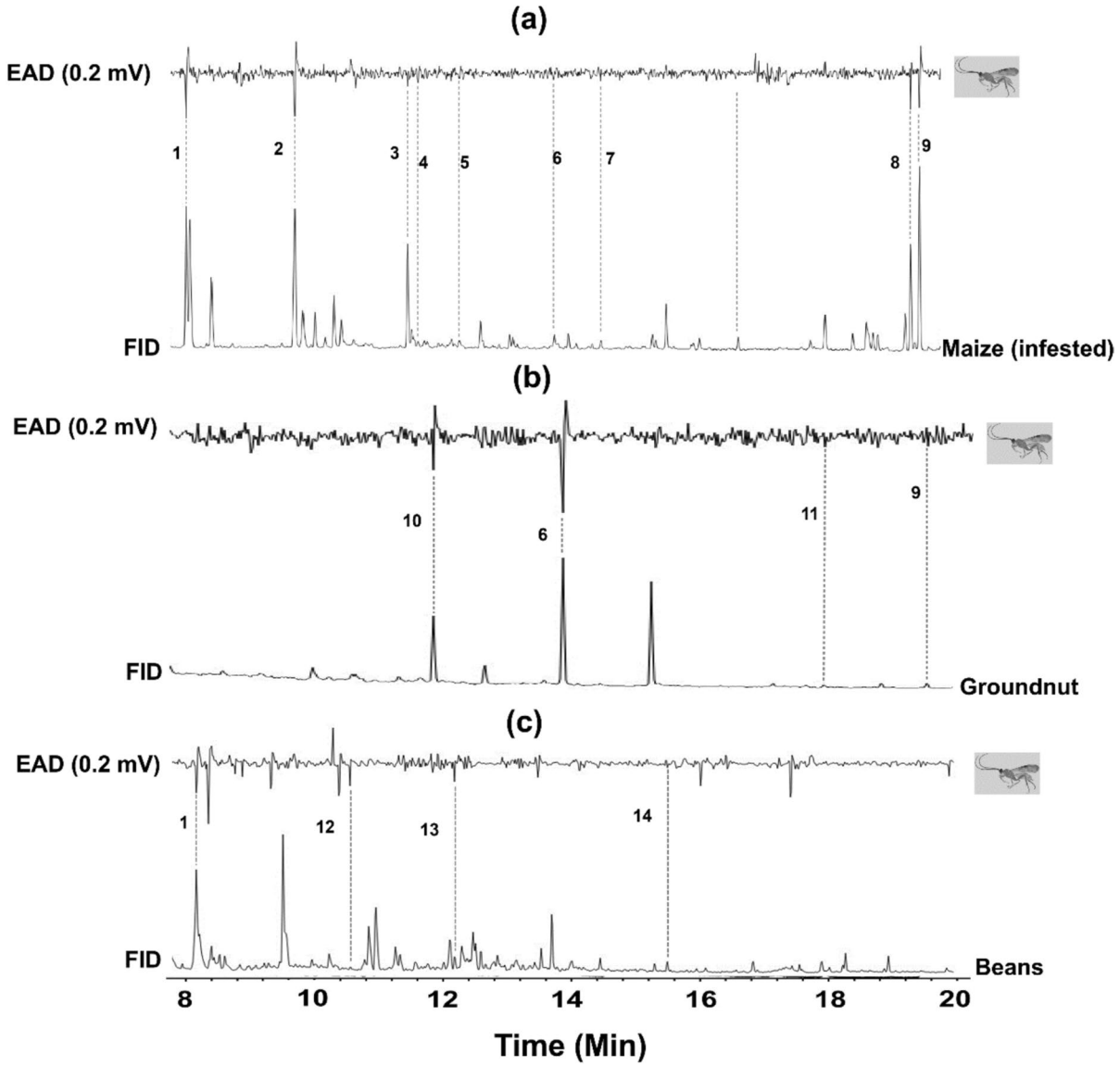


Fig. 4 Representative GC-EAD recordings of female *Coccygidium luteum* responses to different volatiles in headspace samples of **(a)** the fall armyworm larvae infested maize, **(b)** intact groundnut, and **(c)** beans. The upper trace represents EAD responses of the *C. luteum* antenna, whereas the lower traces represent the GC–flame ionization detector (GC–FID) responses of headspace volatile samples. Identities of the electrophysiologically active volatiles are as follows: (1) unidentified, (2) (*E*)-2-hexenal, (3) unidentified (4) unidentified, (5) (*Z*)-3-hexenyl acetate, (6) (*E*)-4,8-Dimethyl-1,3,7-nonatriene, (7) Decanal, (8) (*E*)-nerolidol, (9) (*E, E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (10) (*E*)-β-ocimene, (11) unidentified, (12) unidentified (13) nonanal, (14) unidentified

the intact companion plant volatiles, elucidating the underpinning chemical mechanisms for their attractiveness to the parasitoid. Some of the bioactive compounds were detected in relatively lower concentrations in the companion plants compared to FAW infested maize, whereas others were detected in similar or higher quantities. Previous studies have shown that even lower emissions of bioactive volatiles can trigger a significant behavioral response in insects when the VOCs are present in the correct combination (Bruce et al. 2010; Bruce and Pickett 2011). Furthermore, the bioactive compounds such

as (*E*)-2-hexenal, (*Z*)-3-hexen-1-ol, (*E*)-β-ocimene, (*E*)-β-caryophyllene, DMNT and TMTT, which were detected in the intact companion plant volatiles, have been reported to recruit crop pest natural enemies, such as parasitoids and predatory lacewings (Pickett et al. 2006; Tamiru et al. 2015a; Huang et al. 2024).

We also observed that the companion plants, i.e., groundnut, beans and sweet potato, which were attractive to the parasitoid *C. luteum,* emitted bioactive VOCs such as 1-octen-3-ol, limonene, (*E*)-β-ocimene, nonanal, MeSA, and TMTT, which were absent or present in trace amounts in intact cassava and undamaged maize plants. The presence of these compounds exclusively or in higher concentrations in attractive companion plants suggests their key role in mediating parasitoid attraction. The strong attractiveness of bean volatiles to *C. luteum,* despite the absence of some of bioactive VOCs, can be attributed to beans unique volatile profile, notably the presence of nonanal and high concentrations of limonene which are known to mediate insect–plant interactions and parasitoid attraction (Xiang et al. 2017; Mohammed et al. 2020)**.** In contrast, the unattractiveness of cassava to *C. luteum* is likely due to the absence of key bioactive compounds such as 1-octen-3-ol, nonanal, DMNT, MeSA, and TMTT detected in other attractive companion plants. This also suggests *C. luteum*'s host-location behavior is influenced, not by ubiquitous plant volatiles, but rather by specific VOCs that vary among plant species. Recent studies have identified key bioactive VOCs detected in our study such as 1-octen-3-ol, (*E*)-β-ocimene, MeSA, and TMTT, in non-edible companion plants like *Desmodium intortum*, *D. uncinatum*, and Brachiaria Mulato II (Sobhy et al. 2022; Odermatt et al. 2025). This demonstrates the potential for developing pest resilient cropping systems that utilize edible companion plants emitting ecologically relevant signaling chemicals for ecological sustainable pest management in agricultural settings (Harrison et al. 2019; Librán-Embid et al. 2023; Huang et al. 2024).

Using GC-EAD recordings, we identified bioactive VOCs that could play a role in mediating the observed behavioral response of *C. luteum* to constitutive companion plants and FAW-infested maize plant volatile cues. Several VOCs such as (*E*)-2-hexenal, (*Z*)-3-hexenyl acetate, nonanal, (*E*)-β-ocimene, DMNT, decanal, (*E*)-nerolidol and TMTT elicited consistent response from female *C. luteum* antennae. Our results corroborate with previous findings which reported these compounds in eliciting EAD-responses from *C. luteum* (Sobhy et al. 2022) and other natural enemies (parasitoids) (Gouinguené et al. 2005; Clavijo McCormick et al. 2012; Melo Machado et al. 2014; Wang et al. 2020). Interestingly, predominant FAW-infested maize volatiles like (*E*)-β-farnesene and indole did not elicit responses in *C. luteum*, possibly due to concentration-dependent effects (Rosenkranz and Schnitzler 2016; Ali et al. 2022). In contrast, minor compounds triggered significant EAD-responses from *C. luteum.* Parasitoid antennae are highly sensitive to subtle VOC cues that may not be easily detected using chemical analysis methods but are behaviorally relevant (Bruce and Pickett 2011; Tamiru et al. 2015a).

In summary, our findings demonstrated that *C. luteum* parasitoids are attracted to the VOCs emitted by maize plants attacked by FAW larvae and selected companion plants (sweet potato, beans, groundnut). Moreover, chemical and electrophysiology analyses detected key bioactive VOCs from the headspace samples of the attractive companion plants with the potential to influence the foraging behavior of *C. luteum*. The low preference of *C. luteum* to intact (uninfested) maize and cassava volatiles demonstrates parasitoid's differential responses and role of specific bioactive VOCs that vary among plant species. Our findings provide valuable insights into the underpinning chemical ecology mechanisms of companion plants-FAW-*C. luteum* tritrophic interactions and pave the way for the development of effective, economical, and ecologically sustainable FAW management strategies by exploiting edible companion crop to enhance biological control. Moreover, our research results provide new knowledge to deepen our understanding about the intricate ecological interactions between plants, herbivores, and their natural enemies mediated by plant derived volatile organic compounds.

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Declarations

Conflicts of interest The authors have no relevant financial or non-financial interests to disclose.

Research involving human participants and/or animals Our research does not involve human participants or animals. The study was carried out in adherence to all ethical research practices, environmental responsibility, and responsible data and material handling.

Informed consent The authors affirm that the research adheres to all ethical guidelines.

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References

Agboyi LK, Goergen G, Beseh P, Mensah SA, Clottey VA, Glikpo R, Buddie A, Cafà G, Offord L, Day R, Rwomushana I, Kenis M (2020) Parasitoid complex of fall armyworm, *Spodoptera frugiperda*, in Ghana and Benin. Insects 11(2):68

Aitchison J (1982) The statistical analysis of compositional data. JR Statist Soc B 44:139–177

Ali MY, Naseem T, Zhang J, Pan M, Zhang F, Liu T-X (2022) Plant volatiles and herbivore induced plant volatiles from chili pepper act as attractant of the aphid parasitoid *Aphelinus varipes* (Hymenoptera: Aphelinidae). Plants 11(10):1350

Bruce TJ, Pickett JA (2011) Perception of plant volatile blends by herbivorous insects–finding the right mix. Phytochemistry 72(13):1605–1611

Bruce TJA, Midega CAO, Birkett MA, Pickett JA, Khan ZR (2010) Is quality more important than quantity? Insect behavioural responses to changes in a volatile blend after stemborer oviposition on an African grass. Biol Lett 6(3):314–317

Clavijo McCormick A, Unsicker SB, Gershenzon J (2012) The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. Trends Plant Sci 17(5):303–310

Clavijo McCormick A, Effah E, Najar-Rodriguez A (2023) Ecological aspects of volatile organic compounds emitted by exotic invasive plants. Front Ecol Evol 11:1059125

Day R, Abrahams P, Bateman M, Beale T, Clottey V, Cock M, Colmenarez Y, Corniani N, Early R, Godwin J, Gomez J, Moreno PG, Murphy ST, Oppong-Mensah B, Phiri N, Pratt C, Silvestri S, Witt A (2017) Fall armyworm: impacts and implications for Africa. Outlooks Pest Manag 28(5):196–201

Dicke M, Baldwin IT (2010) The evolutionary context for herbivore-induced plant volatiles: beyond the 'cry for help.' Trends Plant Sci 15(3):167–175

Glinwood R, Ahmed E, Qvarfordt E, Ninkovic V, Pettersson J (2009) Airborne interactions between undamaged plants of different cultivars affect insect herbivores and natural enemies. Arthropod Plant Interact 3:215–224

Goergen G, Kumar PL, Sankung SB, Togola A, Tamò M (2016) First report of outbreaks of the fall armyworm *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), a new alien invasive pest in West and Central Africa. PLoS ONE 11(10):e0165632

Gohole LS, Overholt WA, Khan ZR, Vet LEM (2003) Role of volatiles emitted by host and non-host plants in the foraging behaviour of *Dentichasmias busseolae*, a pupal parasitoid of the spotted stemborer *Chilo partellus*. Entomol Exp Appl 107(1):1–9

Gouinguené S, Pickett JA, Wadhams LJ, Birkett MA, Turlings TCJ (2005) Antennal electrophysiological responses of three parasitic wasps to caterpillar-induced volatiles from maize (*Zea mays*), cotton (*Gossypium herbaceum*), and cowpea (*Vigna unguiculata*). J Chem Ecol 31(5):1023–1038

Guimapi RA, Niassy S, Mudereri BT, Abdel-Rahman EM, Tepa-Yotto GT, Subramanian S, Mohamed SA, Thunes KH, Kimathi E, Agboka KM, Tamo` M, Rwaburindi JC, Hadi B, Elkahky M, Sæthre M, Belayneh Y, Ekesi S, Kelemu S, Tonnang HEZ (2022) Harnessing data science to improve integrated management of invasive pest species across Africa: an application to fall armyworm (*Spodoptera frugiperda*) (J.E. Smith) (Lepidoptera: Noctuidae). Glob Ecol Conserv 35:e02056

Harrison RD, Thierfelder C, Baudron F, Chinwada P, Midega C, Scha U, van den Berg J (2019) Agro-ecological options for fall armyworm (*Spodoptera frugiperda* J.E. Smith) management: providing low-cost, smallholder friendly solutions to an invasive pest. J Environ Manag 243:318–330

Heil M, Greiner S, Meimberg H, Kruger R, Noyer JL, Heubl G, Linsenmair KE, Boland W (2004) Evolutionary change

from induced to constitutive expression of an indirect plant resistance. Nature 430(6996):205–208
Huang S, Zhang W, Zhang Y, Jia H, Zhang X, Li H, Zhang J, Ge F, Cai Z (2024) Volatile chemical cues emitted by an agricultural companion plant (*Cnidium monnieri*) attract predatory lacewings (*Chrysoperla sinica*). Biol Control 192:105516
Khan ZR, Ampong-Nyarko K, Chiliswa P, Hassanali A, Kimani S, Lwande W, Overholt WA, Pickett JA, Smart LE, Wadhams LJ, Woodcock CM (1997) Intercropping increases parasitism of pests. Nature 388:631–632
Khan ZR, Midega CAO, Bruce TJA, Hooper AM, Pickett JA (2010) Exploiting phytochemicals for developing a "push-pull" crop protection strategy for cereal farmers in Africa. J Exp Bot 61(15):4185–4196
Khan M, Mousa AA, Syamasundar KV, Alkhathlan HZ (2012) Determination of chemical constituents of leaf and stem essential oils of *Artemisia monosperma* from central Saudi Arabia. Nat Prod Commun 7(8):1079–1082
Kigathi RN, Weisser WW, Reichelt M, Gershenzon J, Unsicker SB (2019) Plant volatile emission depends on the species composition of the neighbouring plant community. BMC Plant Biol 19(1):58
Kumela T, Simiyu J, Sisay B, Likhayo P, Gohole L, Tefera T (2018) Farmers' knowledge, perceptions and management practices of the new invasive pest, fall armyworm (*Spodoptera frugiperda*) in Ethiopia and Kenya. Int J Pest Manag 65(1):1–9
Librán-Embid F, Olagoke A, Martin EA (2023) Combining *Milpa* and push-pull technology for sustainable food production in smallholder agriculture. A review. Agron Sustain Dev 43:45
Maddrell SHP (1969) Secretion by the malphigian tubules of *Rhodnius*. The movement of ions and water. J Exp Biol 51:71–97
Maffei ME (2010) Sites of synthesis, biochemistry and functional role of plant volatiles. S Afr J Bot 76(4):612–631
Malone SC, Menalled FD, Weaver DK, Seipel TF, Hofland ML, Runyon JB, Bourgault M, Boss DL, Trowbridge AM (2022) Cropping systems alter plant volatile emissions in the field through soil legacy effects. Renew Agric Food Syst 37(5):375–381
Melo Machado RC, Sant'Ana J, Blassioli-Moraes MC, Laumann RA, Borges M (2014) Herbivory-induced plant volatiles from *Oryza sativa* and their influence on chemotaxis behaviour of *Tibraca limbativentris* Stal. (Hemiptera: Pentatomidae) and egg parasitoids. Bull Entomol Res 104(3):347–356
Mohammed K, Agarwal M, Li B, Newman J, Liu T, Ren Y (2020) Evaluation of *D*-limonene and β-ocimene as attractants of *Aphytis melinus* (Hymenoptera: Aphelinidae), a parasitoid of *Aonidiella aurantii* (Hemiptera: Diaspididae) on *Citrus* spp. Insects 11(1):44
Montagné N (2024) The role of volatile organic compounds in plant-insect communication. Biol Aujourd'hui 218(3–4):141–144
Odermatt DM, Chidawanyika F, Mutyambai DM, Schmid B, Domeignoz Horta LA, Onjura CO, Tamiru A, Schuman MC (2025) *Desmodium* volatiles in "push-pull" agriculture and protection against the fall armyworm *Spodoptera frugiperda*. Elife 13:RP100981
Onjura CO, Peter E, Asudi GO, Gicheru MM, Mohamed SA, Bruce TJA, Tamiru A (2025) Differential responses of the egg-larval parasitoid *Chelonus bifoveolatus* to fall armyworm-induced and constitutive volatiles of diverse maize genotypes. J Chem Ecol 51:34
Pareja M, Moraes MCB, Clark SJ, Birkett MA, Powell W (2007) Response of the aphid parasitoid *Aphidius funebris* to volatiles from undamaged and aphid-infested *Centaurea nigra*. J Chem Ecol 33:695–710
Peter E, Tamiru A, Subramanian S, Dubois T, Kelemu S, Kruger K, Torto B, Yusuf A (2023) Companion crops alter olfactory responses of the fall armyworm (*Spodoptera frugiperda*) and its larval endoparasitoid (*Cotesia icipe*). Chem Biol Tech Agric 10:61
Peter E, Yusuf A, Subramanian S, Kruger K, Green KK, Anderson P, Torto B, Tamiru A (2024) Crop mixtures influence fall armyworm infestation and natural enemy abundance in maize-based intercropping systems. J Crop Health 76:1491–1505
Pichersky E, Noel JP, Dudareva N (2006) Biosynthesis of plant volatile: nature's diversity and ingenuity. Science 311:808–818
Pickett JA, Bruce TJA, Chamberlain K, Hassanali A, Khan ZR, Matthes MC, Napier JA, Smart LE, Wadhams LJ, Woodcook CM (2006) Plant volatiles yielding new ways to exploit plant defence. In: Dicke M, Takken W (eds) Chemical ecology: from gene to ecosystem. Springer, Netherlands, pp 161–173
R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.r-project.org/
Rosenkranz M, Schnitzler J (2016) Plant volatiles. Encyclopedia of life sciences (eLS). Wiley, Chichester, pp 1–9
Schlaeger S, Pickett JA, Birkett MA (2018) Prospects for management of whitefly using plant semiochemicals, compared with related pests. Pest Manag Sci 74(11):2405–2411
Sisay B, Simiyu J, Mendesil E, Likhayo P, Ayalew G, Mohamed S, Subramanian S, Tefera T (2019) Fall armyworm, *Spodoptera frugiperda* infestations in East Africa: assessment of damage and parasitism. Insects 10(7):195
Sobhy IS, Tamiru A, Chiriboga Morales X, Nyagol D, Cheruiyot D, Chidawanyika F, Subramanian S, Midega CAO, Bruce TJA, Khan ZR (2022) Bioactive volatiles from push-pull companion crops repel fall armyworm and attract its parasitoids. Front Ecol Evol 10:883020
Tamiru A, Khan ZR (2017) Volatile semiochemical mediated plant defence in cereals: a novel strategy for crop protection. Agronomy 7(3):58
Tamiru A, Bruce TJA, Woodcock CM, Caulfield JC, Midega CA, Ogol CK, Mayon P, Birkett MA, Pickett JA, Khan ZR (2011) Maize landraces recruit egg and larval parasitoids in response to egg deposition by a herbivore. Ecol Lett 14(11):1075–1083
Tamiru A, Bruce TJ, Midega CA, Woodcock CM, Birkett MA, Pickett JA, Khan ZR (2012) Oviposition induced volatile emissions from African smallholder farmers' maize varieties. J Chem Ecol 38:231–234
Tamiru A, Bruce TJA, Woodcock CM, Birkett MA, Midega CA, Pickett JA, Khan ZR (2015a) Chemical cues

modulating electrophysiological and behavioural responses in the parasitic wasp *Cotesia sesamiae*. Can J Zool 93:281–287

Tamiru A, Khan ZR, Bruce TJ (2015b) New directions for improving crop resistance to insects by breeding for egg induced defence. Curr Opin Insect Sci 9:51–55

Tamiru A, Paliwal R, Manthi SJ, Odeny DA, Midega CA, Khan ZR, Pickett JA, Bruce TJA (2020) Genome wide association analysis of a stemborer egg induced "call-for-help" defence trait in maize. Sci Rep 10(1):11205

Tepa-Yotto GT, Kpongbe H, Winsou JK, Agossadou AH, Tamò M (2025) Plant signaling mediates interactions between fall and southern armyworms (Lepidoptera: Noctuidae) and their shared parasitoid *Cotesia icipe* (Hymenoptera: Braconidae). Insects 16(6):580

Turlings TCJ, Erb M (2018) Tritrophic interactions mediated by herbivore-induced plant volatiles: mechanisms, ecological relevance, and application potential. Annu Rev Entomol 63:433–452

Vivaldo G, Masi E, Taiti C, Caldarelli G, Mancuso S (2017) The network of plants volatile organic compounds. Sci Rep 7(1):11050

Wang C, Li G, Miao C, Zhao M, Wang B, Guo X (2020) Nonanal modulates oviposition preference in female *Helicoverpa assulta* (Lepidoptera: Noctuidae) via the activation of peripheral neurons. Pest Manag Sci 76(9):3159–3167

Xiang H, Ma R, Diao H, Li X, He X, Guo F (2017) Peach-specific aldehyde nonanal attracts female Oriental fruit moths, *Grapholita molesta* (Lepidoptera: Tortricidae). J Asia Pac Entomol 20:1419–1424

Zhang DD, Xiao YT, Xu PJ, Yang XM, Wu Q, Wu K (2021) Insecticide resistance monitoring for the invasive populations of fall armyworm, *Spodoptera frugiperda* in China. J Integr Agric 20(3):783–791

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