



RESEARCH ARTICLE

Chemical profiling of maize volatiles based on retention characteristics and dependent emission patterns of healthy, oviposition-induced and herbivore-induced plant volatiles affected by fall armyworm *Spodoptera frugiperda* (J.E. Smith)

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Abstract

Maize (*Zea mays* L.) is a critically important global cereal crop, the productivity of which is increasingly threatened by the invasive fall armyworm, *Spodoptera frugiperda*. In response to herbivory, plants deploy indirect defences by emitting herbivore-induced plant volatiles (HIPVs), which can attract natural enemies of the pest. This study investigated the volatile organic compound (VOC) profile of maize plants under three conditions: healthy, oviposition-induced and herbivore-induced by *S. frugiperda*. Using gas chromatography mass spectrometry (GC-MS), we identified and quantified 11 key VOCs across 6 chemical classes. The results revealed significant qualitative and quantitative differences in the volatile profiles among the treatments. Key compounds included the aldehydes pentanal (2,2-dimethyl) and nonanal; the ketone 1-(3-ethyloxiranyl) ethanone; the alcohol 3-buten-2-ol; several esters, most prominently oxalic acid, cyclohexyl propyl ester; and the terpenes d-limonene and β -caryophyllene. The distinct emission patterns of these VOCs, particularly the significant changes in specific terpenes and green leaf volatiles (GLVs), provide crucial insights into the chemical ecology of maize defence against *S. frugiperda*. These findings suggest that induced volatile blends could play a role in tritrophic interactions and offer a foundation for developing sustainable pest management strategies based on plant signalling.

Keywords: cyclohexyl propyl ester; fall armyworm; gas chromatography-mass spectroscopy; herbivore induced plant volatiles; oxalic acid; pentanal, 2,2-dimethyl

Introduction

The introduction of exotic herbivores can disrupt native ecosystems by competing for resources and altering established trophic interactions (1). In this complex interplay, plants are not passive victims but active participants that emit herbivore-induced plant volatiles (HIPVs). These compounds serve as a sophisticated indirect defence mechanism by attracting the natural enemies of herbivorous insects (2).

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is a devastating polyphagous pest native to the Americas (3). With a reported host range of over 350 plant species, its rapid global spread since its 2016 introduction to Africa poses a significant threat to food security (4, 5). While the role of HIPVs in plant defence is well-established for many herbivores, the specific volatile profile elicited by *S. frugiperda* feeding and oviposition on maize, and its ecological implications-remains less

clear (6). Furthermore, plants also release Oviposition-Induced Plant Volatiles (OIPVs) in response to egg-laying, which can provide early cues for parasitoids, though this area is understudied in the maize *S. frugiperda* system (7).

Maize (*Zea mays*) emits a complex blend of volatile organic compounds (VOCs) that mediate its interactions with the environment (8). Previous research has shown that the composition of these blends is highly specific, varying with the herbivore species, its feeding guild and the plant cultivar (9, 10). Key HIPV classes include terpenoids, green leaf volatiles (GLVs) and fatty acid derivatives, which can function as within-plant signals, alerts to neighboring plants and foraging cues for predators and parasitoids (11, 12). For instance, compounds like (E)- β -caryophyllene and linalool have been identified as key attractants for natural enemies in other plant-herbivore systems (13).

However, a critical knowledge gap exists precisely characterising the VOC bouquet that defines the maize response to the dual stressors of *S. frugiperda* oviposition and subsequent herbivory. Many studies rely solely on library matching for compound identification, which can lead to contaminants being misidentified as plant-derived volatiles (14, 15). A more robust analysis, incorporating retention indices and mass spectral validation, is necessary for accurate profiling.

Therefore, this study aimed to identify and rigorously validated the specific VOC blends emitted by maize plants in response to *S. frugiperda* oviposition (OIPV) and herbivory (HIPVs) using retention indices and mass spectral libraries for accuracy, compare these profiles against those of healthy plants to pinpoint key quantitative and qualitative differences and hypothesise the ecological roles of the identified compounds based on their known functions in tritrophic interactions. We hypothesize that *S. frugiperda* infestation will trigger a distinct and quantifiable shift in the maize volatile profile, characterised by an increase in specific terpenes and GLVs known to attract natural enemies and that the oviposition and herbivory responses will be chemically distinct. The novelty of this work lies in its rigorous, comparative chemical profiling of both oviposition and herbivory-induced volatiles in a globally critical crop-pest system, providing a foundational dataset for developing sustainable monitoring and biocontrol strategies against *S. frugiperda*.

Materials and methods

Plant material and growth conditions

Maize plants were planted individually in pots within an insect-proof screen house. All plants were maintained under natural environmental conditions [25 ± 2 °C, 65 ± 5 % relative humidity (RH) and a 12:12 Light : Dark photoperiod].

Insect rearing

A laboratory colony of *S. frugiperda* was maintained on an artificial diet at 26 ± 2 °C, 75 ± 5 % RH and a 12:12 Light : Dark photoperiod. Pupae were sexed, and adults were held in cages for mating with a 10% honey solution provided as a food source (15).

Plant treatments

Three distinct plant treatments were prepared for the study. Healthy plants consisted of undamaged individuals of the same age as the treated plants. Oviposition-induced plants were obtained by exposing plants to ten gravid female moths for 24–48 hr in a net cage, with only those bearing confirmed egg masses selected for volatile collection (16). Herbivore-induced plants were prepared by placing two early-instar larvae on 2–3-week-old plants for 7 hr to simulate herbivore damage.

Volatile organic matter collection and analysis

Volatiles from each treatment, Healthy Maize Plant Volatiles (HMPVs), OIPVs, and HIPVs, were collected using a dynamic headspace sampling system (17). Five biological replicates were performed for each treatment. All glassware was cleaned with Teepol detergent, rinsed with distilled water and acetone, and oven-dried at 120 °C before use. Purified air was drawn over individual, bag-enclosed plants at a flow rate of 1 L min⁻¹ for 24 hr. Volatiles were trapped on Porapak Q adsorbent (50-80 mesh). After

collection, volatiles were eluted with 400 µL of HPLC-grade n-hexane and stored at -20 °C in GC-MS vials until analysis (18, 19).

Gas chromatography-mass spectrometry analysis

Volatile samples were analysed using an Agilent 7890B GC system coupled with a 5977B MSD. Separation was achieved on an HP-5 MS UI capillary column (30 m × 0.25 mm × 0.25 µm). The GC oven temperature was programmed as follows: initial hold at 60 °C for 2 min, ramped at 10 °C min⁻¹ to 300 °C, with a final hold of 5 min. Helium was used as the carrier gas at a constant flow of 0.5 mL min⁻¹. The injector temperature was 280 °C, and samples were injected in split mode (1:20). Mass spectra were acquired in electron impact (EI) mode at 70 eV, scanning from *m/z* 40 to 450.

Compound identification was conducted by comparing mass spectra with the NIST 14 library and by calculating Kovats retention indices using a C7-C30 n-alkane series. Compounds were tentatively identified based on a combination of spectral matches (similarity > 85 %) and RI comparisons (similarity > 85 %) and literature values. The volatile profiles of HMPVs, OIPVs, and HIPVs were compared based on the relative peak area percentage of tentatively identified compounds.

Statistical analysis

The relative abundance (area percentage) of volatile compounds across the three plant treatments (Healthy, OIPV, HIPV) was compared using a one-way Analysis of Variance (ANOVA). Data normality and homogeneity of variances were confirmed using Shapiro-Wilk and Levene's tests, respectively. Where ANOVA revealed significant differences ($p < 0.05$), post-hoc comparisons were performed using Tukey's HSD test. All analyses were conducted using SPSS Statistics version 16.0.

Results

Gas chromatography-mass spectrometry analysis

Gas chromatography linked to mass spectrometry results showed that a total of 11 similar compounds from 6 chemical groups, including aldehydes, ketones, alcohols, esters, terpenes and alkanes, were identified (Fig. 1, Table 1).

Esters

The esters were represented by the most abundant class with four compounds namely oxalic acid, butyl propyl ester, oxalic acid, cyclohexyl propyl ester, oxalic acid, cyclohexyl isobutyl ester and 1-butanol, 2-methyl propanoate were found with 0.65, 0.0, 0.0 and 0.02 area percentage, respectively, recorded in healthy maize plant while in oviposited induced plant the oxalic acid butyl propyl ester, oxalic acid, cyclohexyl propyl ester, oxalic acid, cyclohexyl isobutyl ester, 1-butanol, 2-methyl-, propanoate were recorded 0.00, 28.78, 3.73 and 0.04 %, respectively (Table 1). Oxalic acid, butyl propyl ester was not detected in OIPVs. Whereas in herbivore-induced plants, similar esters were significantly reduced from healthy plants, with 0.53, 3.88, 0.66 and 0.01 %, respectively (Fig. 1, Table 1).

Aldehydes

Pentanal, 2,2-dimethyl- and nonanal were detected as aldehydes with 21.55, 0.70 % in healthy maize plant, while 23.83 and 0.36 in oviposition induced plants, and 25.75 and 0.95 % in herbivore-induced plants, respectively (Fig. 1, Table 1).

Alkanes

The listed alkane compounds, such as undecane, 3,8-dimethyl, was detected in oviposited and damaged plants with 0.06 and 0.18 area percentage, respectively, while undecane, 3,8-dimethyl, was not detected in healthy plants (Fig. 1, Table 1).

Ketones

Ketone was represented by only one compound, such as ethanone,1-(3-ethyloxiranyl)- with 4.15, 4.69 and 5.29 % in healthy, oviposited, and damaged plants, respectively (Fig. 1, Table 1).

Alcohols

3-Buten-2-ol was detected as alcohol with 0.44 and 0.45 in

oviposited and damaged plants, respectively, while this was not detected from healthy plants (Fig. 1, Table 1).

Terpenes

d- Limonene and B- caryophyllene represented as terpene. The d- limonene was detected at 13.27, 0.0, and 0.06 % in healthy, oviposited and damaged plants, respectively, while the β - caryophyllene was recorded at 0.40, 0.31, and 0.42 % in healthy, oviposited, and damaged plants, respectively (Fig. 1, Table 1).

Paired t-tests comparing total volatile emissions across treatments revealed no statistically significant differences. The comparisons between HMPVs and OIPVs ($t = -1.052$, $p = 0.331$), OIPVs and HIPVs ($t = 1.475$, $p = 0.279$), and HMPVs and HIPVs

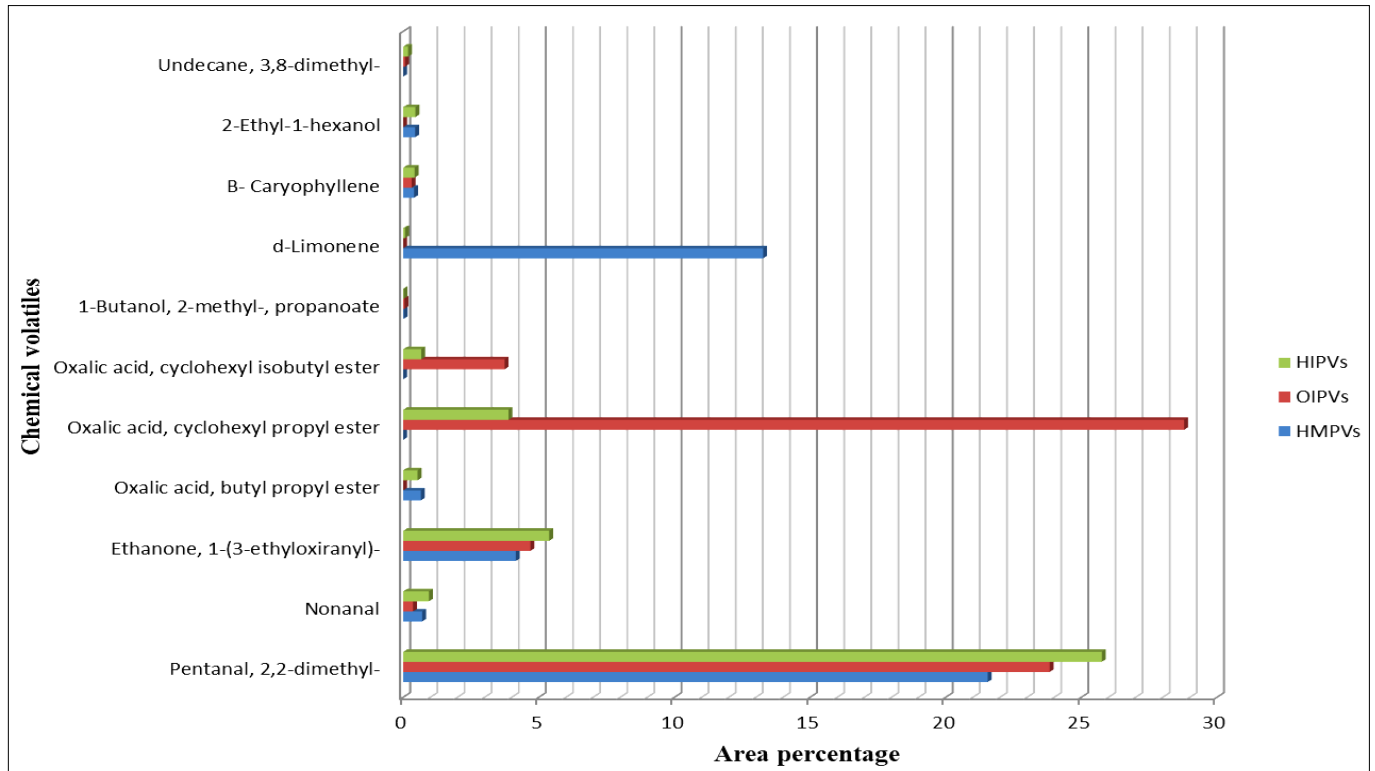


Fig. 1. Representative GC-MS volatile blends from healthy, oviposition-induced and herbivore-induced maize plants.

Table 1. Chemical profile of volatile compounds from healthy, oviposition-induced, and herbivore-induced maize plants

Chemical group	Compound name	Retention Time	Area percentage			Chemical Formula
			Healthy	Oviposition-induced	Herbivore-induced	
Aldehydes						
1.	Pentanal, 2,2-dimethyl-	4.3605	21.55	23.8328	25.7541	C ₇ H ₁₄ O
2.	Nonanal	7.2062	0.701	0.3638	0.9517	C ₉ H ₁₈ O
Ketones						
3.	Ethanone, 1-(3-ethyloxiranyl)-	4.6828	4.157	4.69	5.3848	C ₆ H ₁₀ O ₂
Esters						
4.	Oxalic acid, butyl propyl ester	4.5920	0.652	-	0.5317	C ₉ H ₁₆ O ₄
5.	Oxalic acid, cyclohexyl propyl ester	5.4271	-	28.7886	3.8810	C ₁₁ H ₁₈ O ₄
6.	Oxalic acid, cyclohexyl isobutyl ester	5.5944	-	3.7396	0.6674	C ₁₂ H ₂₀ O ₄
7.	1-Butanol, 2-methyl-, propanoate	15.0816	0.023	0.0493	0.0153	C ₈ H ₁₆ O ₂
Terpenes						
8.	d-Limonene	6.0292	13.27	-	0.0666	C ₁₀ H ₁₆
9.	B- Caryophyllene	11.8811	0.409	0.3135	0.4232	C ₁₅ H ₂₄
Alcohols						
10.	2-Ethyl-1-hexanol	5.9900	0.449	-	0.4530	C ₈ H ₁₈ O
Alkanes						
11.	Undecane, 3,8-dimethyl-	12.7431	-	0.0696	0.1815	C ₁₃ H ₂₈

volatiles ($t = 0.636, p = 0.486$) all yielded p -values greater than the 0.05 significance level (Table 2).

Table 2. Statistical comparison (paired t-test) of total volatile emissions between plant treatments ($p < 0.05$)

Volatiles	t value	p-value (>0.05)
HMPVs/ OIPVs	-1.052	0.331
OIPVs/HIPVs	1.475	0.279
HMPVs/HIPVs	0.636	0.486

Discussions

Plants activate sophisticated biochemical defences against herbivores, primarily through the production of secondary metabolites and VOCs. This defence cascade is initiated by the plant's ability to perceive both mechanical wounding and herbivore-specific chemical cues, such as oral secretions. This recognition triggers rapid changes in plasma membrane potential, driven by ion fluxes, which in turn activate complex intracellular signal transduction networks. Key phytohormones, including jasmonic acid, salicylic acid, and ethylene systemically coordinate these pathways. The interplay of these signals ultimately orchestrates the biosynthesis and release of specific VOCs for indirect defence and the accumulation of defensive secondary metabolites for direct resistance (20). These VOCs mediate critical ecological interactions, attracting natural enemies of the herbivore and priming defence responses in neighboring plants (21).

The timing and composition of these induced volatiles can vary between plant genotypes. For instance, comparative studies on maize cultivars 'Ioana Sweet Corn' and 'LG11' revealed that, while GLVs were released immediately after damage, 'LG11' emitted a distinct set of compounds not found in 'Ioana', with indole being a key differential (11).

The specific herbivore species also critically shapes the volatile response. Maize plants infested with the specialist *S. frugiperda* emit a significantly weaker bouquet of HIPVs compared to plants attacked by generalist noctuid larvae like *S. littoralis*, *S. exigua*, and *Helicoverpa armigera*. This suggests that *S. frugiperda* may actively suppress HIPV emissions to reduce the attraction of its natural enemies (22, 23). Furthermore, plants activate sophisticated biochemical defences against herbivores, primarily through the production of secondary metabolites and VOCs. This defence cascade is initiated by the plant's ability to perceive both mechanical wounding and herbivore-specific chemical cues, such as oral secretions. This recognition triggers rapid changes in plasma membrane potential, driven by ion fluxes, which in turn activate complex intracellular signal transduction networks. Key phytohormones, including jasmonic acid, salicylic acid, and ethylene systemically coordinate these pathways. The interplay of these signals ultimately orchestrates the biosynthesis and release of specific VOCs for indirect defense and the accumulation of defensive secondary metabolites for direct resistance (24).

Finally, multiple abiotic and biotic stressors can interact to modulate VOC emission. While individual stressors like flooding and herbivory induce VOC release in maize, their combination can result in a synergistic effect, triggering significantly greater amounts of volatiles than either stressor alone (25, 26).

Conclusion

This study provides a comparative chemical profile of the VOCs emitted by maize plants under healthy, oviposition-induced and herbivore-induced states. The identification of 11 key volatiles across six chemical classes reveals that maize undergoes a dynamic reprogramming of its volatile bouquet in response to different ecological stimuli. A critical finding was a significant shift in the dominant compound, oxalic acid cyclohexyl propyl ester, which was most abundant in healthy and oviposited plants but was markedly reduced in herbivore-damaged plants. This suggests a potential reallocation of metabolic resources from the production of constitutive volatiles towards the activation of direct or indirect defence pathways following herbivory.

These results have important practical implications. The distinct volatile signatures, particularly the suppression of specific compounds after damage, could serve as biochemical markers for early pest detection and monitoring. Furthermore, the identified HIPV blend provides a foundation for developing sustainable management strategies, such as using these volatile cues to enhance the foraging efficiency of natural enemies against *S. frugiperda*. Future research should focus on validating the ecological function of these key volatiles, particularly their role in tritrophic interactions, to harness their full potential in integrated pest management programmes.

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Authors' contributions

AK and RBS conceptualised and designed the study. AK, BS, RBS, MM, RAR and AP performed the experiments. ST, RAR and SM provided guidance on volatile collection. RBS, ST, RAR and SA supervised the experiments. AK, MV, RAR and SA conducted the GC-MS analysis. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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