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Role of herbivore-induced plant volatiles from *Cnaphalocrocis medinalis* infested rice genotypes in mediating host-location behaviour of the larval ectoparasitoid, *Habrobracon hebetor*

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Abstract

Herbivore-induced plant volatiles (HIPVs) are critical mediators of tritrophic interactions, providing parasitoids with reliable cues for host location and parasitisation. This study investigated whether HIPVs emitted by rice infested (I) with the rice leaffolder, *Cnaphalocrocis medinalis* (Guenee), affect the olfactory perception and behavioural responses of its larval parasitoid, *Habrobracon hebetor* (Say). Volatiles were collected from six rice genotypes (three resistant and three susceptible), each with three biological replicates. Gas chromatography–mass spectrometry (GC-MS) identified 37 volatile organic compounds (VOCs) in uninfested (U) and *C. medinalis*-I. plants across all genotypes. Uninfested plants served as the baseline for comparing infestation-related changes in volatile profiles. The antennal perception of female *H. hebetor* in response to VOCs from *C. medinalis*-I. rice plants was assessed using gas chromatography–electroantennographic detection (GC-EAD). Ten common VOCs consistently elicited antennal depolarisation across both resistant and susceptible genotypes. These compounds were subsequently evaluated for behavioural responses in female *H. hebetor* using a Y-tube olfactometer. β-ocimene, β-caryophyllene, 1,2,3,4-tetrahydronaphthalene, (R)-limonene, methyl jasmonate and methyl salicylate elicited positive orientation while xylene elicited significant avoidance in female *H. hebetor*. These findings demonstrate that individual HIPVs from *C. medinalis*-I. rice genotypes produce distinct behavioural effects on *H. hebetor* under controlled conditions. The study offers valuable insights into the identification of potential host-location cues for *H. hebetor*, which may contribute to the sustainable management of *C. medinalis*, warranting further validation in ecologically relevant volatile blends and field trials.

Keywords: biological control; herbivore-induced plant volatiles; semiochemicals; tritrophic interactions; volatile organic compounds

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1. Introduction

Rice (*Oryza sativa* L.) is the principal staple food crop for more than half of the global population and is fundamental to food security, particularly in Asia (1, 2). However, insect pests severely constrain rice productivity and the rice leaffolder, *Cnaphalocrocis medinalis* (Guenee) (Lepidoptera: Crambidae), is one of the most destructive defoliators (3). Larvae fold leaves longitudinally and scrape mesophyll tissues, resulting in reduced photosynthetic efficiency, impaired plant growth and significant yield losses under severe infestations (3, 4). Although chemical insecticides remain the principal method for controlling *C. medinalis*, their indiscriminate and repeated application has led to insecticide resistance, destruction of natural enemies, environmental contamination and ecological imbalance (5, 6). Consequently, biological control approaches that enhance natural enemy activity are an important component of sustainable *C. medinalis* management (7, 8).

Among the natural enemies associated with *C. medinalis*, the gregarious larval ectoparasitoid *Habrobracon hebetor* (Say) (Hymenoptera: Braconidae) is recognised as an efficient biological control agent due to its high reproductive potential and adaptability across diverse agroecosystems (9). For successful parasitisation, *H. hebetor* must first locate its larval host, *C. medinalis*, within the plant environment. This host-location process involves detecting chemical cues associated with herbivore

presence, including volatile signals emitted by plants following herbivory (10).

Plants respond to herbivore attack by activating sophisticated direct and indirect defence mechanisms, including the production of herbivore-induced plant volatiles (HIPVs) (11). In rice, herbivore feeding activates defence signalling pathways involving jasmonic acid (JA), salicylic acid (SA) and ethylene (ET). These signalling pathways regulate the biosynthesis and emission of volatile blends comprising green leaf volatiles, terpenoids, benzenoids and other defence-related metabolites (12). These HIPVs can function as long-range chemical signals, providing information about herbivore infestation and thereby contributing to interactions among rice, *C. medinalis* and its parasitoids (13, 14). For parasitoids, such plant-derived cues can facilitate to identify host-habitat location (15). Thus, the volatile signals emitted by rice following *C. medinalis* feeding may represent an important component of the chemical information available to *H. hebetor* during host location.

Despite the established role of HIPVs in plant–insect interactions, the volatile cues associated with *C. medinalis*-I. rice that are perceived and behaviourally relevant to *H. hebetor* remain poorly characterised. Chemical profiling alone cannot distinguish volatiles that are merely present from those detected by the parasitoid and capable of influencing its orientation. To address this knowledge gap, the present study integrated chemical profiling with electrophysiological and behavioural assays to elucidate the relationship between genotype-dependent volatile profiles and *H. hebetor* olfactory response. This approach delineates functionally active semiochemicals that modulate parasitoid orientation from those non-functional volatiles present in the headspace.

Therefore, the present study investigated volatile blends emitted by resistant and susceptible rice genotypes following *C. medinalis* infestation using gas chromatography–mass spectrometry (GC-MS). We identified electrophysiologically active compounds detected by female *H. hebetor* wasps using gas chromatography–electroantennographic detection (GC-EAD) and assessed their behavioural relevance using a Y-tube olfactometer bioassay. This integrated approach identified candidate rice volatile cues associated with the host-location behaviour of *H. hebetor* and evaluated their potential as semiochemicals for the sustainable management of *C. medinalis*.

2. Materials and Methods

Experimental site

The study was conducted at the Chemical Ecology Laboratory and Biocontrol Laboratory of the Division of Crop Protection, ICAR-Central Rice Research Institute (CRRI), Cuttack, India. The institute lies approximately between 85° 55′ 48″ E and 85° 56′ 48″ E and 20° 26′ 35″ N and 20° 27′ 35″ N.

Plant material

Fifty red rice accessions, together with the resistant check (TKM6) and susceptible check (TN1), were phenotypically screened for resistance to *C. medinalis* under field conditions using the rapid screening procedure against *C. medinalis* (16). Initial field screening across three seasons selected three highly resistant and three susceptible genotypes. These selected genotypes were subsequently subjected to volatile compound analysis and profiling to investigate potential differences in their chemical emissions. For field screening, the percentage of damaged leaves (Eq. 1) was converted into the adjusted damage leaf rating (ADLR) using the standard formula (Eq. 2). The resulting ADLR values were classified according to the standard evaluation system (SES) score (17) and the resistant category was assigned (Supplementary Table 1).

Based on the field screening data, a total of six genotypes, comprising three highly resistant and three susceptible genotypes, were selected for subsequent experiments.

$$\text{Damaged leaves (\%)} = \frac{\text{No. of damaged leaves observed in a hill}}{\text{Total number of leaves observed in a hill}} \times 100 \quad \text{Eq. (1)}$$

$$\text{Adjusted damage leaf rating (ADLR)} = \frac{\text{\% damage leaves in the test entry}}{\text{\% damage leaves in the susceptible check}} \times 100 \quad \text{Eq. (2)}$$

Plant preparation

Three 21-day-old seedlings of each of the six selected rice genotypes were transplanted individually into plastic pots and maintained inside insect-proof mesh cages to prevent unintended herbivore infestation. All plants were grown under uniform agronomic conditions, including the recommended fertiliser application rate (100 kg N, 80 kg P_2O_5 and 60 kg K_2O ha^{-1}), regular irrigation and standard crop management practices (18). At maximum tillering, the number of tillers was standardised to ten per pot to minimise variation in plant biomass among treatments. The VOCs were collected from rice plants at 45 days after transplanting (DAT). Before volatile collection, the potted plants were transferred to the laboratory and allowed to acclimatise for 1 hr under laboratory conditions to minimise any transient effects associated with handling and environmental changes (16). The experiment included three biological replicates per treatment.

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Collection of constitutive and herbivore-induced plant volatiles

Volatiles were collected from both uninfested (U) and *C. medinalis*-infested (I) plants of six selected rice genotypes using a standardised headspace sampling procedure (18). Constitutive volatiles were collected from pest-free 45-day-old plants to characterise the natural, uninduced volatile profile of each genotype, while herbivore-induced volatiles were collected to assess changes associated with herbivory. For herbivore-induced volatile collection, a fresh set of 45-day-old plants from each genotype was infested with three second-instar *C. medinalis* larvae that had been starved for 4 hr. Larvae were introduced onto each plant using a fine camel-hair brush and allowed to feed for 12 hr. Infestation commenced at 18:00 hr to align with the onset of nocturnal feeding. Each plant was individually enclosed in a transparent Mylar cage (50 cm in length and 18 cm in diameter) to prevent larval escape and external contamination. After 12 hr, herbivore-induced volatiles were collected from *C. medinalis*-I. rice plants.

Following the respective treatment, each plant from each genotype was transferred individually to a transparent 30 L borosilicate glass chamber for volatile collection (Supplementary Fig. 1). The soil surface of the pot was covered with moist absorbent cotton and the pot was tightly sealed with aluminium foil to minimise interference from soil-emitted volatiles (18). Charcoal-filtered air was continuously passed through the chamber and headspace volatiles were trapped on 200 mg of pre-conditioned Tenax TA (100–120 mesh; conditioned at 200 °C for 1 hr) for 4 hr at an airflow rate of 15 mL min^{-1}. The trapped volatiles were desorbed with 1 mL of analytical-grade *n*-hexane and the extracts were immediately sealed with parafilm and stored at −20 °C until GC-MS, GC-EAD and behavioural analyses. Blank controls consisting of soil-filled pots without plants were sampled under identical conditions to account for background volatile contamination (18). Each treatment (U and I) for each genotype had three independent biological replicates.

Rearing of *Habrobracon hebetor*

Habrobracon hebetor was reared in the Biocontrol Laboratory, Division of Crop Protection, ICAR–Central Rice Research Institute (CRRI), Cuttack, India, under controlled conditions of 25 ± 1 °C, 70 ± 5 % relative humidity and a 14:10 hr (L) photoperiod. The factitious host, *Corcyra cephalonica*, was obtained from the mass-rearing facility at ICAR-CRRI and was used as the host for rearing *H. hebetor* (19). Before being used as a host, *C. cephalonica* colony had been maintained for more than ten generations under these conditions.

Newly emerged *H. hebetor* adults were paired (one male and one female) in 1000 mL plastic containers and allowed to mate for 24 hr. Gravid females were separated and used for the behavioural bioassays and electrophysiological studies. For oviposition, fourth- and fifth-instar *C. cephalonica* larvae were exposed to the parasitoids using the sandwich method (20). Adult parasitoids were provided with a 50 % honey solution on cotton swabs as a carbohydrate source. After 48 hr of parasitisation, the parasitised *C. cephalonica* larvae were transferred to an insect growth chamber maintained at 25 ± 1 °C, 70 ± 5 % relative humidity and a 14:10 hr (L) photoperiod until *H. hebetor* adult emergence. The resulting *H. hebetor* colony was maintained for ten generations before using the parasitoids in both the GC-EAD and Y-Tube olfactometer experiments (9).

Metabolite profiling using gas chromatography-mass spectrometry

Samples of plant volatile collections were analysed using a GC-MS system (Trace 1300–TSQ 9000, Thermo Scientific, USA) equipped with an autosampler (TriPlus RSH) and a capillary column (TG-5MS; 30 m, i.d.: 0.25 mm, film thickness: 0.25 µm; Thermo Scientific, USA) The injector temperature was maintained at 260 °C. The GC oven was programmed with an initial hold at 40 °C for 5 min, followed by a temperature ramp to 200 °C at 8 °C min^{-1} with a 2 min hold and a final ramp to 260 °C at 6 °C min^{-1} with a 2 min hold. Helium (99.99 % purity) was used as the carrier gas at a constant flow rate of 1.0 mL min^{-1}. Mass spectrometric detection was performed in electron impact (EI) ionisation mode at 70 eV, with the ion source and transfer line temperatures maintained at 230 °C and mass spectra acquired over an m/z range of 50–550. Hexane was used as a solvent blank and peaks arising from column bleed or contamination were excluded. Volatile compounds were initially identified using the automated mass spectral deconvolution and identification system (AMDIS) software in combination with the National Institute of Standards and Technology (NIST) mass spectral library database. The compounds were identified by GC retention time, mass spectrum and retention index (RI). Compound identities were confirmed by comparison of experimental retention index values with published literature RI values. Kovats retention indices were calculated using the retention times of a homologous C7 to C30 n-alkane standard series analysed under identical chromatographic conditions (18).

Gas chromatograph-coupled electro antennographic detection

The response of *H. hebetor* antennae to the VOCs was studied by GC-EAD using an Agilent 7890 gas chromatograph (Agilent Technologies Inc., Santa Clara, CA, USA) coupled to a Syntech electroantennographic detection (EAD) system (Syntech, The Netherlands).

The study hypothesised that herbivory-induced changes in rice volatile emissions may provide chemical cues associated with the presence of *C. medinalis* and facilitate host location by *H. hebetor*. This hypothesis is supported by previous findings indicating that *H. hebetor* responds preferentially to host-associated volatiles, with odours from live moth larvae eliciting the strongest attraction compared with blank controls (21). Consequently, the present study analysed herbivore-induced volatiles from the selected

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rice genotypes by GC-EAD to identify compounds detected by *H. hebetor* which are potentially involved in host location behaviour.

Volatile extracts (1 µL) were injected in split mode (200 : 1) at an injector temperature of 260 °C. Helium was used as the carrier gas at a constant flow rate of 0.2 mL min^{-1}. The oven temperature programme consisted of an initial hold at 40 °C for 5 min, followed by heating to 200 °C at 8 °C min^{-1} with a 2 min hold and then to 260 °C at 6 °C min^{-1} with a final hold of 2 min. The GC effluent was split post-column with a split ratio of 1 : 1, with one stream directed to a flame ionisation detector (FID) maintained at 300 °C and the other to the EAD through a heated transfer line. Nitrogen was supplied as the make-up gas at a flow rate of 25 mL min^{-1}.

Gravid female *H. hebetor* were cold-anaesthetised for 2 min and one antenna from each individual was excised using fine scissors. Approximately 1 mm of the antennal tip was removed and the antenna was mounted between the reference and recording electrodes of a Syntech EAG combi probe using conductive gel (Parker Sigma, India). A continuous stream of humidified air was passed over the antenna throughout the recording period to maintain antennal viability. Electrophysiological responses were recorded using a Syntech IDAC-4 Intelligent Data Acquisition Controller and analysed with Syntech GcEad 2014 software. Antennal responses (depolarisations) were matched with the corresponding FID chromatographic peaks (polarisations) to identify GC-EAD active volatile compounds. Only peaks that elicited consistent antennal responses across all five biological replicates were considered olfactory-active volatile compounds (OAVCs) (22).

Chemicals

Authentic standards (> 96 % purity) of the selected VOCs, namely Xylene, α-Pinene, p-Cymene, R-Limonene, β-Ocimene, 1,2,3,4-Tetrahydronaphthalene, Methyl salicylate, β-Caryophyllene, 1-Dodecanol and Methyl jasmonate, identified through GC-EAD analysis, were procured from Sigma-Aldrich (Bangalore, India). Stock solutions of each compound were prepared in analytical-grade *n*-hexane and diluted to the required concentrations for electrophysiological and behavioural assays.

Y-tube olfactometer bioassay

Bioassays were conducted to evaluate the behavioural responses of gravid female *H. hebetor* to selected synthetic volatile compounds using a glass Y-tube olfactometer, with *n*-hexane as the solvent control (20). The olfactometer consisted of a central tube 15 cm long and 1 cm internal diameter (i.d.), with two lateral arms 5 cm long and 1 cm i.d. Each lateral arm was separately connected to an extending glass tube 10 cm long and 1 cm i.d. Humidified and purified air was supplied through the extending glass tubes at a flow rate of 150 mL min^{-1} using Teflon connections. The experiments were conducted in an isolated, darkened room maintained at 26 ± 2 °C and 70 ± 5 % relative humidity to minimise environmental disturbances and extraneous odours. Gravid female *H. hebetor* were transferred to the experimental room 30 min before the assays to allow acclimatisation to the test conditions. During the assays, a 20 W office lamp provided uniform illumination from a vertical position 50 cm above the olfactometer.

For each assay, 10 µL of the test solution (0.1 µg $µL^{-1}$ in *n*-hexane) was applied to a filter-paper strip (1 × 1 cm) and allowed to air-dry for 30 sec before being placed in one odour chamber connected to an arm of the Y-tube. An equal volume of *n*-hexane was applied to a similar filter-paper strip and placed in the opposite arm as the solvent control. Individual gravid female *H. hebetor* were released at the entrance of the common arm and allowed a maximum of 10 min to choose between the test odour and solvent control. For each volatile compound, the assay was conducted until 30 responsive gravid females of *H. hebetor* were obtained. A choice was recorded when a female entered either the treatment or control arm and remained in that arm for at least 30 sec. Females that entered the treatment arm and remained for at least 30 sec were classified as responders, while those that entered the control arm and remained for the same duration were classified as non-responders to the treatment odour. Females that remained in the common arm without entering either choice arm during the observation period were excluded from the preference analysis. The position of the treatment and control arms was alternated after every five insects to minimise positional bias. The Y-tube olfactometer was cleaned with ethanol followed by acetone, rinsed with distilled water and oven-dried before reuse.

Statistical analysis

For volatile collection and profiling, three independent biological replicates were analysed for each of the six rice genotypes under U and *C. medinalis* infestation conditions, resulting in 36 independent volatile samples in total (6 genotypes × 2 infestation states × 3 replications). For GC-MS profiling, raw peak-area data obtained after AMDIS processing were imported into MetaboAnalyst 6.0. For multivariate analysis and heat-map visualisation, VOC peak-area data were subjected to median normalisation, followed by log10 transformation and Pareto scaling. For each genotype–treatment combination, mean VOC peak areas across three biological replicates were calculated and used for multivariate analysis. Partial least squares discriminant analysis (PLS-DA) was performed to assess differences in volatile profiles among resistant and susceptible genotypes under I and U conditions. Variable importance in projection (VIP) scores was calculated to identify VOCs contributing to group discrimination, with VIP > 1.0 considered indicative of important variables. The robustness of the PLS-DA model was assessed by cross-validation and 1000-permutation testing to evaluate model performance and potential overfitting. For GC-EAD analysis, five independent biological replicates were analysed for

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each genotype using fresh antennae from five fresh gravid females of *H. hebetor*, resulting in 30 independent GC-EAD recordings (6 genotypes × 5 antennae). Compounds showing reproducible, coincident GC-EAD and GC-FID responses across all 6 genotypes were classified as common antennally active volatiles and selected for subsequent behavioural evaluation in the Y-tube olfactometer. The observed choices of female *H. hebetor* in the Y-tube olfactometer bioassays were analysed using the chi-square (χ^2) test in IBM SPSS Statistics version 25.0 (IBM Corp., Armonk, NY, USA). For each volatile compound, behavioural responses were recorded until 30 responsive gravid females of *H. hebetor* were obtained. Females that did not make a choice within 10 min excluded from the assay; therefore, the sample size of 30 reported for each compound represents responding parasitoids only. Statistical significance was considered at $p < 0.05$ and the results were expressed as χ^2 values and corresponding p values.

3. Results

Phenotyping screening

Screening of the rice genotypes revealed distinct responses to *C. medinalis*. Among the resistant genotypes, TKM6 recorded the lowest pooled ADLR (9.56 %) with an SES score of 1, followed by Asophol (ADLR 11.84 %, SES score 1) and Kaali Bank (ADLR 15.81 %, SES score 1). The SES scores of 1–3 indicates resistance. In contrast, TN1 exhibited the highest susceptibility, with a pooled ADLR of 100.00 % and an SES score of 9, followed by Kouka Kh–16 (ADLR 89.31 %, SES score 9) and Kalobhat (ADLR 88.89 %, SES score 9). An SES score of 9 indicates susceptibility. Based on these screening responses, TKM6, Asophol and Kaali Bank were selected as resistant genotypes, while TN1, Kouka Kh–16 and Kalobhat were selected as susceptible genotypes for subsequent volatile profiling and analysis (Supplementary Table 2).

Metabolomics

For each genotype, the mean peak area of VOCs for each genotype was calculated across biological replicates and these averages were used for PLS-DA analysis. A total of 37 VOCs were identified among the genotypes evaluated (Supplementary Table 3). Partial least squares discriminant analysis was conducted to assess differences in VOC profiles between resistant and susceptible rice genotypes under both *C. medinalis*-I. and U conditions. The resulting PLS-DA score plot revealed a clear separation among the four treatment groups: infested resistant (IR), infested susceptible (IS), uninfested resistant (UR) and uninfested susceptible (US) plants (Fig. 1A).

The first component explained 85 % of the total variation, while the second component accounted for 9.90 %, together representing 94.90 % of the variation in the VOC dataset. The IR samples were distinctly separated from the other groups along the first two components and the US samples were positioned apart from the UR and IS groups. These observations suggest that both genotype and herbivore infestation status are critical factors influencing the VOC composition in rice plants.

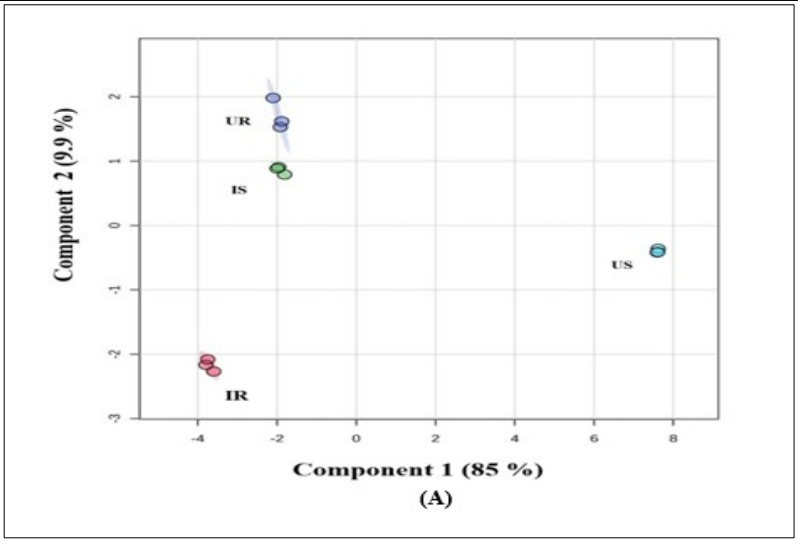
To identify the VOCs contributing most significantly to the discrimination among the four treatment groups, variable importance in projection (VIP) analysis was performed (Fig. 1B). The highest VIP scores were observed for (Z)-3-hexenyl acetate (1.98), β-caryophyllene (1.96), (R)-limonene (1.93), methyl jasmonate (1.87), methyl salicylate (1.83), (E)-β-farnesene (1.80), xylene (1.79), α-pinene (1.77), linalool (1.73) and β-ocimene (1.70). Additional VOCs with VIP scores above 1.0, including (E)-2-octenal (1.67), nerol (1.66), 1-octen-3-ol (1.42) and 1,2,3,4-tetrahydronaphthalene (1.05), were also found to contribute to the observed separation among the treatment groups. The results indicate that specific VOCs are associated with the distinct VOC profiles characteristic of each group.

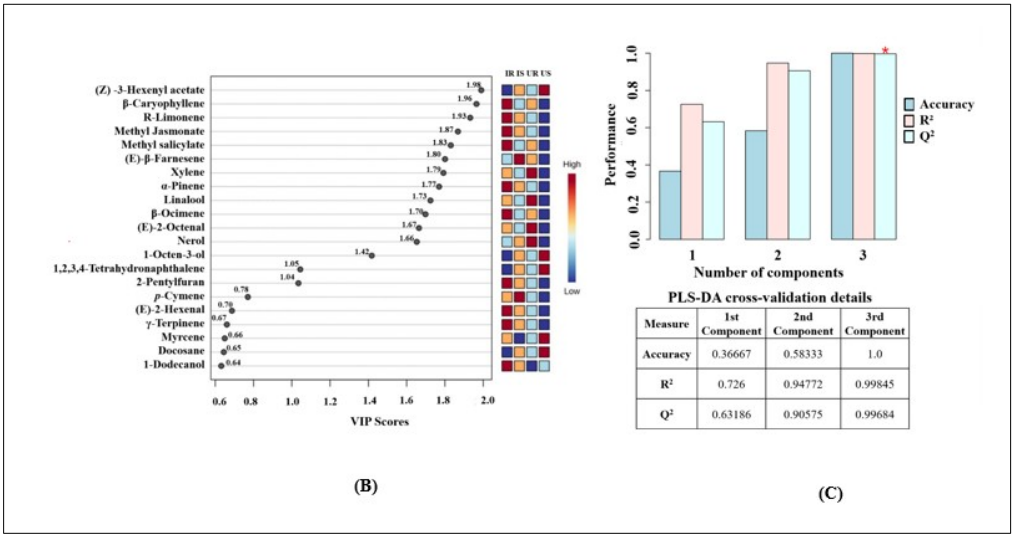
Cross-validation analysis revealed that model performance improved with the inclusion of additional components. The three-component model, constructed using three biological replicates per treatment group, achieved the highest classification accuracy (1.00), with R^2 and Q^2 values of 0.99845 and 0.99684, respectively (Fig. 1C). The perfect classification accuracy indicated that all samples were correctly assigned during cross-validation, while the high R^2 and Q^2 values reflected a strong model fit and robust predictive performance. To further confirm the robustness of the group separation, a permutation test was performed using 1000 random permutations of the class labels (Fig. 1D). None of the permuted models produced a separation statistic greater than that of the original model ($p < 0.001$; 0/1000 permutations), providing strong statistical support for the observed separation among the four VOC groups.

Gas chromatograph-coupled electroantennographic detection analysis

The GC-EAD profile of volatile extracts from *C. medinalis*-I. rice plants showed distinct antennal responses corresponding to gas chromatography–flame ionisation detection (GC-FID) peaks (Fig. 2). Across the analysed samples, GC–EAD analysis revealed 10 volatile compounds that elicited antennal responses in female *H. hebetor*. The EAD responses coincided with the corresponding GC-FID peaks and were identified as xylene (RT 6.55 min), α-pinene (8.67 min), *p*-cymene (11.15 min), (R)-limonene (11.27 min), β-ocimene (11.45 min), 1,2,3,4-tetrahydronaphthalene (14.16 min), methyl salicylate (14.80 min), β-caryophyllene (18.91 min), 1-dodecanol (19.71 min) and methyl jasmonate (22.26 min) (Table 1). A total of ten volatile compounds consistently elicited reproducible antennal responses in female *H. hebetor* across all six rice genotypes. These compounds were subsequently considered for further behavioural evaluation via Y–tube olfactometer assay.

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Measure	1st Component	2nd Component	3rd Component
Accuracy	0.36667	0.58333	1.0
R^2	0.726	0.94772	0.99845
Q^2	0.63186	0.90575	0.99684

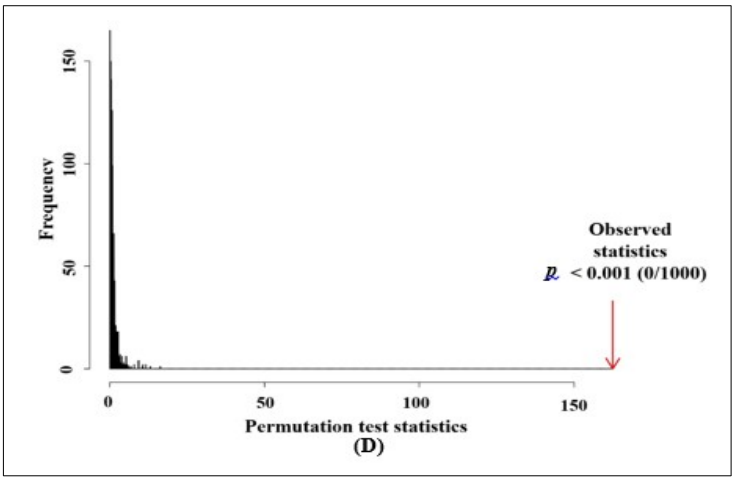


Fig. 1. Partial least squares discriminant analysis (PLS-DA) of volatile organic compounds (VOCs) profiles in resistant (R) and susceptible (S) rice genotypes under *Cnaphalocrocis medinalis-infested* (I) and uninfested (U) conditions. A: PLS-DA score; B: Variable importance in projection (VIP) scores. The dots represent individual VOCs and the numbers adjacent to the dots indicate their corresponding VIP scores; C: Cross-validation results of the PLS-DA model showing accuracy, R^2 and Q^2 values. The asterisk (*) denotes the optimal number of components yielding the highest predictive performance; D: Permutation test of the PLS-DA model based on separation distance (between-group/within-group ratio, B/W) using 1000 permutations.

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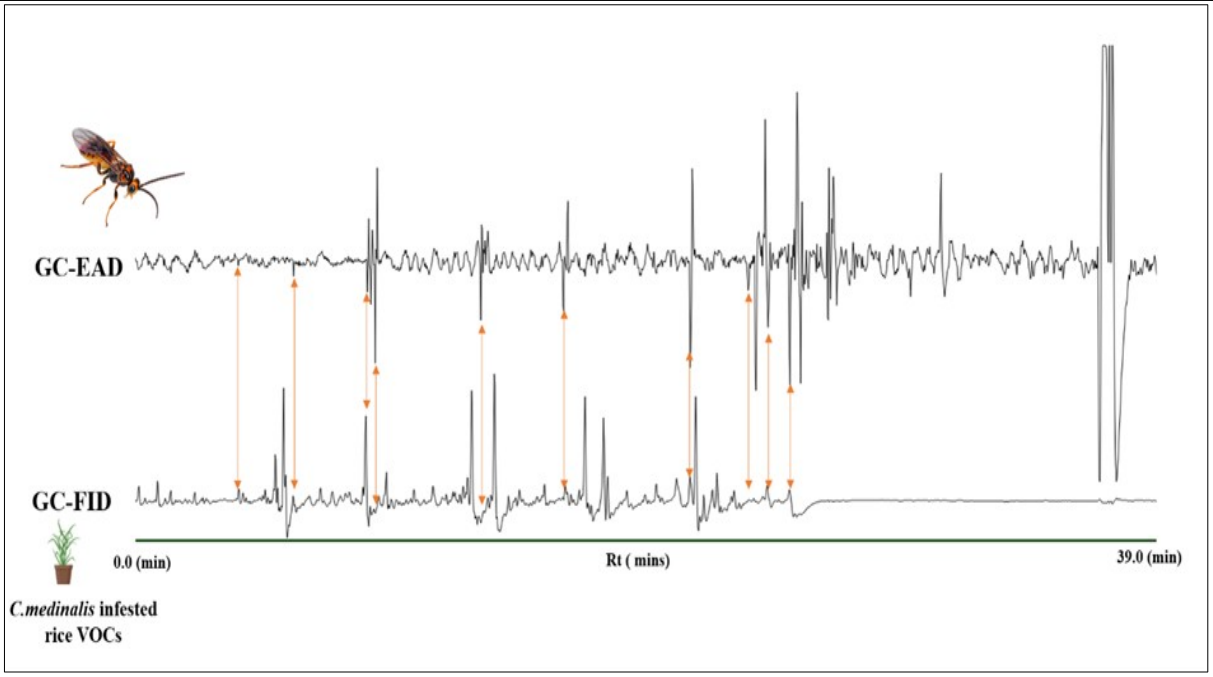


Fig. 2. Gas chromatography–electroantennographic detection (GC–EAD) response of female *Habrobracon hebetor* to volatiles emitted from *Cnaphalocrocis medinalis* infested rice plants.

Y–tube olfactometer assay

Y-tube olfactometer bioassays revealed that female *H. hebetor* were significantly attracted to β-ocimene (χ^2 = 13.33; p < 0.001), β-caryophyllene (χ^2 = 8.53; p = 0.003), 1,2,3,4-tetrahydronaphthalene (χ^2 = 6.53; p = 0.011), methyl jasmonate (χ^2 = 6.53; p = 0.011), methyl salicylate (χ^2 = 4.80; p = 0.028) and (R)-limonene (χ^2 = 4.80; p = 0.028) (Fig. 3). In contrast, significantly more number *H. hebetor* females responded towards the control arm than the xylene arm (χ^2 = 6.53; p = 0.011). The remaining compounds, viz., α-pinene (χ^2 = 3.33; p = 0.068), p-cymene (χ^2 = 2.13; p = 0.144) and 1-dodecanol (χ^2 = 0.53; p = 0.465) did not exhibit any significant response towards the respective volatiles compared with the control (Fig. 3, Supplementary Table 4). Among the tested compounds, β-ocimene elicited the strongest positive orientation response of *H. hebetor*, whereas xylene was the only volatile associated with a significant negative orientation response in female *H. hebetor*.

4. Discussion

Insect herbivory can alter plant volatile emissions, generating chemical signals that shape interactions among plants, herbivores and their natural enemies (11). These HIPVs are particularly important in tritrophic interactions because parasitoids can use them as host-location cues (23). Herbivore-induced volatile emissions can vary substantially among plant genotypes, altering the chemical cues available to parasitoids during host searching (23). Previous work in maize has shown that volatile defence signalling induced by fall armyworm (*Spodoptera frugiperda*) differs among maize genotypes and affects the foraging behaviour of the egg parasitoid, *Telenomus remus*. *Telenomus remus* exhibits preferential responses to herbivore-induced volatiles from certain maize genotypes and chemical analyses indicate that volatile blends with elevated levels of mono-, homo-, or sesquiterpenes in combination with green leaf volatiles (GLVs) are more attractive than GLVs alone (24). In the present study, volatile profiles of resistant and susceptible rice genotypes were compared under both U and *C. medinalis*-I. conditions to determine whether genotype-dependent variation and infestation-induced changes observed in maize are also present in the rice–rice leaffolder (*C. medinalis*)–*H. hebetor* system. The PLS-DA distinguished four groups: UR, US, IR and IS plants. The observed patterns suggest that genotype determines the baseline volatile profile and that herbivory alters volatile composition in a genotype-dependent manner (Fig. 1A). These findings align with previous reports indicating that plant genotype influences volatile defence responses following herbivore attack (24). The most prominent feature of the volatile profiles observed from PLS-DA score plot (Fig. 1A) was the distinct positioning of IR plants away from the other treatment–genotype groups, suggesting that resistant genotypes undergo a unique reconfiguration of volatile metabolism following herbivory (25). Furthermore, infestation-dependent differences between resistant and susceptible plants suggest that the volatile response to herbivory is genotype-dependent (23). Thus, following herbivore attack, resistant and susceptible plants exhibited distinct changes in their volatile profiles.

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Table 1. Gas chromatography–mass spectrometry (GC-MS identification, retention indices and mean peak areas of gas chromatography–electroantennographic detection (GC–EAD)-active volatiles from *Cnaphalocrocis medinalis*-infested rice detected by *Habrobracon hebetor*

Sl. No.	Compound name	RT (min)	MW	Similarity (%)	IR (Mean peak area ± SD)	IS (Mean peak area ± SD)	UR (Mean peak area ± SD)	US (Mean peak area ± SD)	RI	
									Ex.	Lit.
1	Xylene	6.55	106.17	97 %	$1.80 \times 10^8 \pm 5.00 \times 10^6$	$5.25 \times 10^7 \pm 1.70 \times 10^6$	$2.35 \times 10^8 \pm 6.20 \times 10^6$	$1.65 \times 10^7 \pm 7.10 \times 10^5$	869	865
2	α-Pinene	8.67	136.23	96 %	$6.38 \times 10^7 \pm 1.87 \times 10^6$	$2.61 \times 10^7 \pm 9.85 \times 10^5$	$2.09 \times 10^7 \pm 1.14 \times 10^6$	$1.52 \times 10^7 \pm 6.50 \times 10^5$	933	934
3	p-Cymene	11.15	134.22	87 %	$1.69 \times 10^7 \pm 5.13 \times 10^5$	$1.18 \times 10^8 \pm 5.13 \times 10^5$	$1.36 \times 10^7 \pm 5.20 \times 10^5$	$8.90 \times 10^6 \pm 3.70 \times 10^5$	1027	1027
4	R-Limonene	11.27	136.23	96 %	$6.83 \times 10^7 \pm 6.81 \times 10^5$	$2.74 \times 10^7 \pm 1.14 \times 10^6$	$2.67 \times 10^7 \pm 1.32 \times 10^6$	$1.12 \times 10^7 \pm 4.80 \times 10^5$	1032	1036
5	β-Ocimene	11.45	136.23	95 %	$9.44 \times 10^7 \pm 1.82 \times 10^6$	$7.52 \times 10^7 \pm 2.91 \times 10^6$	$8.81 \times 10^7 \pm 2.08 \times 10^6$	$1.63 \times 10^7 \pm 7.10 \times 10^5$	1040	1043
6	1,2,3,4-Tetrahydronaphthalene	14.16	132.2	97 %	$3.87 \times 10^7 \pm 1.21 \times 10^6$	$6.53 \times 10^7 \pm 1.46 \times 10^6$	$4.84 \times 10^7 \pm 1.02 \times 10^6$	$7.96 \times 10^7 \pm 2.86 \times 10^6$	1162	1160
7	Methyl salicylate	14.8	152.15	97 %	$5.14 \times 10^7 \pm 9.45 \times 10^5$	$8.36 \times 10^6 \pm 1.67 \times 10^5$	$4.36 \times 10^7 \pm 1.72 \times 10^6$	$1.18 \times 10^6 \pm 5.20 \times 10^5$	1193	1192
8	β-Caryophyllene	18.91	204.35	96 %	$1.52 \times 10^8 \pm 4.73 \times 10^6$	$7.32 \times 10^7 \pm 1.66 \times 10^6$	$1.21 \times 10^8 \pm 3.80 \times 10^6$	$2.91 \times 10^7 \pm 1.10 \times 10^6$	1425	1428
9	1-Dodecanol	19.71	186.33	97 %	$8.13 \times 10^7 \pm 2.25 \times 10^6$	$7.40 \times 10^7 \pm 2.72 \times 10^6$	$2.94 \times 10^7 \pm 1.11 \times 10^6$	$5.82 \times 10^7 \pm 2.04 \times 10^6$	1475	1473
10	Methyl jasmonate	22.26	224.3	93 %	$3.15 \times 10^7 \pm 1.23 \times 10^6$	$1.91 \times 10^7 \pm 1.17 \times 10^6$	$1.36 \times 10^7 \pm 6.10 \times 10^5$	$8.20 \times 10^6 \pm 3.60 \times 10^5$	1649	1647

IS: *C. medinalis*-infested susceptible rice genotypes (Kalobhat, Kouka–Kh–16 and TN1); IR: *C. medinalis*-infested resistant rice genotypes (Asophol, Kaali Bank and TKM6). RT: retention time; MW.: molecular weight; RI: retention index; Ex.: experimental RI; Lit.: literature RI. Mean peak area values are presented as mean ± SD, calculated from three susceptible genotypes for IS and three resistant genotypes for IR, with three biological replicates per genotype.

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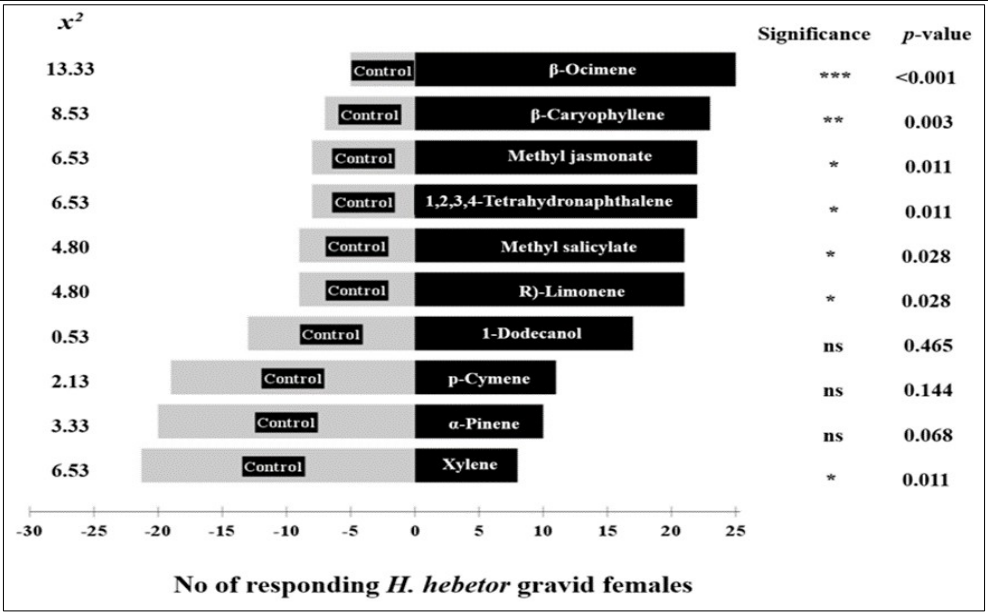


Fig. 3. Behavioural responses of gravid female *Habrobracon hebetor* to gas chromatography–electroantennographic detection (GC–EAD)-active compounds in a Y-tube olfactometer assay. Positive values on the X-axis indicate the number of gravid female *H. hebetor* responding to the test VOCs while negative values indicate the number responding to the solvent control (n-hexane) arm.

This has been further demonstrated by VIP scores indicating that multiple volatile compounds contributed to the separation of genotype–treatment groups (Fig. 1B). After infestation by *C. medinalis*, the volatile profile of resistant plants changed markedly in both composition and relative abundance. Infestation led to increased levels of β-caryophyllene, (R)-limonene, methyl jasmonate, methyl salicylate, α-pinene, β-ocimene, 2-pentylfuran, (E)-2-hexenal, γ-terpinene and 1-dodecanol, while xylene, linalool, (E)-2-octenal and nerol were more abundant in UR plants. Thus, herbivory did not simply increase the emission of pre-existing volatiles in resistant plants; it altered the relative proportions of individual compounds and generated a distinct infestation-associated volatile profile. This shift demonstrates considerable plasticity in volatile emission following herbivory and suggests that *C. medinalis* feeding may modify the chemical information available to parasitoids, potentially influencing their foraging behaviour (26). Similar coordinated changes in volatile emissions after *C. medinalis* feeding have been reported in rice, along with activation of jasmonic acid- and salicylic acid-associated defence responses (27). Comparable genotype-dependent variation in herbivore-induced volatile profiles has also been observed in maize following *Chilo partellus* infestation (28), supporting the role of plant genetic background in shaping both the magnitude and composition of chemical responses to herbivory (29). While resistant plants emit higher levels of defence-related VOCs, this increase does not necessarily indicate enhanced parasitoid attraction. The attraction of parasitoids depends on the ability of *H. hebetor* to detect and respond to these VOCs. Elevated terpenoid and benzenoid concentrations may serve as potential infestation signals. To identify which VOCs are detected or elicit responses from *H. hebetor*, GC-EAD and Y-tube olfactometer assays were conducted.

The GC-EAD analysis elucidated how *H. hebetor* interprets the complex volatile signals emitted by *C. medinalis*-I. rice. Gravid females of *H. hebetor* consistently responded to ten volatile compounds across six rice genotypes, despite the presence of numerous other VOCs in the plant headspace. However, antennal detection alone does not necessarily imply behavioural relevance. Among the electrophysiologically active compounds tested in the Y-tube assay, β-caryophyllene, β-ocimene, (R)-limonene, 1,2,3,4-tetrahydronaphthalene, methyl jasmonate and methyl salicylate elicited significant positive orientation responses from gravid female *H. hebetor*. The behavioural responses observed in the Y-tube assay require consideration of the experimental design, in which individual synthetic volatiles were tested against a control. The positive orientation responses to β-caryophyllene, β-ocimene, (R)-limonene, 1,2,3,4-tetrahydronaphthalene, methyl jasmonate and methyl salicylate indicate that these compounds elicit behavioural activity when presented individually under the tested conditions.

The positive orientation response of gravid female *H. hebetor* to β-caryophyllene is consistent with previous studies implicating this compound in herbivore-induced plant signalling and plant–parasitoid interactions. In maize, (E)-β-caryophyllene is a principal product of the herbivore-induced terpene synthase TPS23 and is associated with volatile signalling and the attraction of natural enemies to lepidopteran herbivores (30). However, this positive response contrasts with the avoidance observed in *Bracon nigricans*, which detected (E)-β-caryophyllene by GC-EAD and avoided *Trialeurodes vaporariorum*-I tomato plants when β-caryophyllene was present in the induced volatile blend (31). These findings indicate that the behavioural response to β-caryophyllene is species-specific and may be influenced by the composition and relative abundance of co-occurring volatiles. The positive orientation

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responses of *H. hebetor* to (R)-limonene and β-ocimene align with previous research demonstrating that monoterpenes can influence the responses of *B. nigricans* to volatiles from *Phthorimaea absoluta*-I tomato plants (32). Comparable responses have been reported in *Agathis bishopi* to D-limonene and ocimene emitted from *Thaumatotibia leucotreta*-I citrus fruit (33). The significant positive orientation towards 1,2,3,4-tetrahydronaphthalene is particularly notable, as its role in parasitoid-mediated tritrophic interactions remains poorly characterised. Detection by GC-EAD, together with the positive response in the Y-tube assay, indicates that this compound may contribute to the olfactory response of *H. hebetor* and merits further investigation.

In contrast, 1-dodecanol, α-pinene and p-cymene were detected by the parasitoid antennae but did not elicit significant orientation responses when tested individually. Xylene further illustrates the distinction between antennal detection and behavioural response. Although xylene (p = 0.72) was detected electrophysiologically by female *H. hebetor* in a previous study without eliciting a significant behavioural preference (18), it induced significant avoidance in the present study (p = 0.011). These discrepancies may be attributable to differences in chemical identity, concentration, parasitoid physiological state, or the composition of accompanying volatiles. A similar distinction has been observed in *Cotesia sesamiae*, where only a subset of antennally active compounds elicited behavioural responses individually, while a synthetic blend elicited attraction (34).

The behavioural activity observed for individual VOCs in this study does not provide evidence that these compounds function independently as semiochemicals under natural conditions. Parasitoids encounter complex mixtures of plant- and herbivore-derived volatiles, where interactions among components can alter the behavioural effects of individual compounds. These interactions may be additive, synergistic, or antagonistic (10). For example, the HIPV blend associated with *Lytopylus rufipes*, consisting of (Z)-3-hexenyl acetate, linalool, (E)-β-ocimene, (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT) and (E,E)-α-farnesene, elicited a stronger response than individual components (35). In *Cotesia vestalis*, individual HIPVs did not elicit significant preference, whereas a four-component blend of n-heptanal, α-pinene, sabinene and (Z)-3-hexenyl acetate induced significant preference, demonstrating that the behavioural effect of a blend can arise from the combined volatile signal rather than from its individual constituents. Notably, adding myrcene, camphor, or limonene to this active blend did not further increase attraction, indicating that the addition of compounds does not necessarily strengthen the response. Both the presence of particular components and changes in blend composition can modify the behavioural information conveyed by HIPV emissions (35). Conversely, combinations of HIPVs can also reduce or mask the activity of individual components (36). For instance, (E)-β-farnesene alone did not attract *Closterocerus ruforum*, but a combination containing β-phellandrene, (E)-β-ocimene, (Z)-β-ocimene, (E)-β-caryophyllene and α-humulene elicited attraction when presented at natural ratios (37). Therefore, the compounds identified in this study are best regarded as potential behaviourally active components rather than independently validated semiochemicals. Their contribution to parasitoid responses within the complete herbivore-induced volatile blend remains to be determined, including whether their effects are additive, synergistic, or antagonistic when combined at ecologically relevant concentrations and ratios.

The potential influence of population background, rearing conditions and prior odour experience on parasitoid olfactory responses should also be considered. The antennal responses observed in this study confirm that the laboratory-reared *H. hebetor* colony can detect the identified compounds, but do not establish whether wild or geographically distinct populations would exhibit similar response magnitudes. Evidence from other parasitoid species indicates that olfactory responses can vary among populations and may have a genetic basis. For example, in *Cotesia glomerata*, strains selected for divergent responses to plant–host odours differed in flight orientation and landing success and differences in responses to herbivore-I plants have been reported among laboratory-derived families and field-derived strains, indicating population-level variation in odour-guided behaviour (38). Rearing history and previous odour experience can further modify these responses. *Microplitis croceipes*, for instance, showed stronger orientation towards plant–host odours when hosts were reared on cowpea foliage rather than an artificial diet and adult exposure to an attractive plant–host combination further enhanced orientation (39). Similarly, *C. vestalis* altered its preference for volatile blends following oviposition or starvation, demonstrating that physiological state and prior experience can influence odour-guided behaviour (40). Thus, responses of *H. hebetor* to compounds such as β-ocimene may also be influenced by population origin, rearing history, physiological state and odour experience. However, these factors were not directly evaluated in this study. Comparative experiments involving geographically distinct, field-collected and laboratory-reared populations under standardised rearing and experience conditions are required to determine the extent to which the observed responses are conserved or context-dependent.

Collectively, these findings suggest that behavioural responses to individual VOCs are shaped by their chemical context, including their combination and relative abundance within a volatile blend. The EAD-active VOCs identified in this study should be considered as potential behaviourally active components of the odour signal associated with *C. medinalis*-I. rice, rather than as independently validated semiochemicals. This study did not determine how these compounds interact within the complete volatile blend or establish their optimal ratios. Further research using defined combinations of β-caryophyllene, β-ocimene, (R)-limonene and 1,2,3,4-tetrahydronaphthalene at ecologically relevant concentrations and ratios is required to assess whether their combined behavioural effects are additive, synergistic, or antagonistic.

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5. Conclusion

The present study highlights the role of herbivore-induced plant volatiles (HIPVs) in mediating the olfactory responses of gravid female *Habrobracon hebetor* to *Cnaphalocrocis medinalis*-infested (I) rice. Comparative volatile profiling demonstrated genotype- and infestation-dependent variation in rice volatile organic compounds (VOCs) emissions, while gas chromatography–electroantennographic detection (GC-EAD) analysis identified ten compounds consistently detected by the parasitoid antennae across the six rice genotypes. Among these, β-caryophyllene, β-ocimene, (R)-limonene, 1,2,3,4-tetrahydronaphthalene, methyl jasmonate and methyl salicylate elicited significant positive orientation responses, whereas xylene elicited avoidance under the laboratory conditions tested. However, responses to individual compounds may differ within natural volatile blends and parasitoid olfactory responses may also vary depending on population background, rearing conditions and prior odour experience. Consequently, these compounds should be regarded as potential behaviourally active compounds rather than definitive stand-alone attractants. Future research should evaluate combinations of these compounds at ecologically relevant ratios and concentrations using different populations of *H. hebetor*, followed by semi-field and field validation, to determine their potential contribution to *H. hebetor*-mediated biological control of *C. medinalis*.

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Authors' contributions

PB conducted the experiments, collected data and prepared the initial draft. SDM, TA and AS designed the study, supervised the research and provided critical inputs for data analysis and manuscript revision. PB, SDM and TA performed statistical analysis, interpreted the results and assisted in writing, editing and critically revising the manuscript. GB also critically revised the manuscript. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest

Authors do not have any conflict of interests to declare.

Ethical issues

None

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

The authors declare that ChatGPT, an AI-assisted language tool, was used solely to support language editing, improve clarity and refine the presentation of the manuscript.

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