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Floral volatile composition of *Vanilla planifolia* and behavioural response of the weevil *Montella* sp. (Coleoptera: Curculionidae)

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Abstract

Vanilla planifolia (Orchidaceae), commonly known as vanilla, is the only orchid species cultivated commercially for its edible pods and is one of the most economically important spices worldwide. In northeastern Brazil, populations of *Montella* sp. (Coleoptera: Curculionidae) have emerged as a significant pest of vanilla crops, with both larvae and adults causing damage. Notably, adults are frequently observed on the flowers, suggesting a potential role of floral volatile organic compounds (VOCs) in host localization. To investigate this, we analysed the floral VOC profile of *V. planifolia* using dynamic headspace collection followed by gas chromatography–mass spectrometry (GC-MS). Six compounds were identified: β-myrcene, (*R*)-limonene, (*Z*)-β-ocimene, eucalyptol, (*E*)-β-ocimene, and β-caryophyllene, with (*E*)-β-ocimene being the predominant component of the natural floral bouquet. In Y-tube olfactometer assays, *Montella* sp. adults were significantly attracted to fresh flowers, floral VOC extracts, and a β-ocimene isomer mixture (Z/E = 1:3), the latter eliciting responses comparable to the full floral extract. These findings indicate that β-ocimene contributes to the attraction of *Montella* sp. and may be involved in host location, with the (*E*)-isomer representing the predominant form in the natural floral blend. Behaviourally active floral VOCs may therefore be exploited as semiochemical-based tools to improve monitoring and support integrated pest management strategies in vanilla cultivation systems.

Keywords Orchid weevil · Vanilla · Semiochemicals · Floral attractant

Introduction

Among the 110 species of the genus *Vanilla* distributed across the Americas, Africa, Asia, and Oceania, *Vanilla planifolia* Andrews (Orchidaceae) is the only one of commercial importance (Koch et al. 2013). Its economic value derives from the production of aromatic and food-flavoring agents based on vanillin (4-hydroxy-3-methoxybenzaldehyde), an organic compound found in high concentrations in cured *V. planifolia* pods (Kahane et al. 2008). In Brazil, vanilla cultivation became established in southern Bahia, where it adapted well to local environmental conditions and has been commercially produced under organic farming practices (Fraife et al. 2015). In this region, *Montella* sp. has recently been recognized as the most significant biological constraint to vanilla production, with widespread infestations (≈56% of plants attacked) and an economic injury level of 0.06 insects per plant, indicating that even very low insect densities can substantially reduce yield (Jordão et al. 2020). There are no registered chemical control methods for this pest in Brazil, highlighting the need for more sustainable management strategies.

The weevil *Montella* Bondar, 1948 (Coleoptera: Curculionidae: Baridinae: Madopterini) comprises a small group of Neotropical orchid-associated weevils that remains taxonomically poorly resolved, with few species formally

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described. Consequently, most specimens are identified only at the genus level and treated as *Montella* sp. due to the lack of reliable diagnostic characters (Kuschel 1995; Alonso-Zarazaga and Lyal 1999; Oberprieler et al. 2007; Bouchard et al. 2011; Santos et al. 2025). Species of this genus have also been reported in association with orchids in the Atlantic Forest of southeastern Brazil, where they interact with different orchid species (Mickeliunas et al. 2006; Nunes et al. 2016, 2018).

In these systems, adults are commonly found on flowers, where they feed on floral tissues and may also act as pollinators, while females oviposit in floral tissues and larvae develop within fruits, consuming seeds or developing ovules (Mickeliunas et al. 2006; Nunes et al. 2018). In vanilla crops, both larval and adult stages cause damage to vegetative and reproductive structures, including stems, leaves, and flowers, negatively affecting plant development and productivity (Jordão et al. 2020). Because floral cues can mediate both pollination and herbivory in these interactions, they may generate an ecological conflict between attracting beneficial visitors and herbivores, thus making the identification of the chemical signals exploited by *Montella* sp. essential for understanding its ecological role and developing management strategies.

The use of semiochemicals therefore represents a potential tool for managing *Montella* sp. infestations in vanilla crops. In particular, allelochemicals produced by *V. planifolia* flowers may act as kairomones, attracting insects to host plants and serving as feeding or oviposition stimulants (Yew and Chung 2015; Rodriguez et al. 2018). Flowers synthesize compounds with attractive properties for pollinators, functioning as a plant reproductive strategy. However, these volatile organic compounds (VOCs) can also play different roles in plant–insect interactions, including acting as attractants for pests (Dicke and Takken 2006). Recent studies have identified an aggregation-sex pheromone in *Montella* sp., highlighting the importance of chemical communication in this species (Santos et al. 2025). In this context, this study investigates the floral VOCs of *V. planifolia* that mediate the attraction of the pest insect *Montella* sp.

Materials and methods

Plants and insects

Vanilla planifolia flowers and *Montella* sp. insects were collected from Ilha Flora Farm (14°47′ 87.1″ S, 39°11′ 85.3″ W) in Ilhéus, Bahia, Brazil, and transported to the laboratory in plastic containers. Flowers and insects were transported separately to avoid contact between them. Based on morphological characteristics, the specimens were assigned to the genus *Montella* (Coleoptera: Curculionidae: Baridinae: Madopterini) through comparison with available descriptions and reference material previously examined by taxonomic specialists Dr Germano H. Rosado Neto (UFPR) and Dr Sérgio A. Vanin (USP). Representative specimens from this population are deposited in the Entomological Collection of the Federal University of Paraná (voucher 0145/2018-RN). Adults measured approximately 2.8–3.1 mm in body length (Santos et al. 2025). Species-level identification was not achieved, as the genus comprises few described species with overlapping morphological characters and lacks a modern taxonomic revision, as previously reported for this population (Santos et al. 2025). Fresh plant material was used for the experiments on the same day of collection. Flowers and insects were maintained under controlled conditions of temperature (26 ± 2 °C), relative humidity (60–80%), and a 12:12 h light–dark photoperiod. Adult insects were collected, sorted by sex, placed in plastic cages (500 mL) with small holes to allow air flow, and fed with fresh sugarcane pieces. Sex determination was based on external morphology: males of *Montella* sp. exhibited abdominal convexity in the first sternite and a rounded shape in the last tergite, which were not observed in females. These differences in abdominal tergites are consistent with those described for other weevil species (Sarro et al. 2004; Silva-Filho et al. 2007; Barreto and Rosado-Neto 2012). Food was replaced and cages were cleaned every three days. All individuals used in this study originated from a single field population associated with *V. planifolia*, ensuring consistency across experiments. Although all specimens were morphologically similar and assigned to *Montella* sp., the available evidence does not allow confirmation of whether they represent a single species or a species complex. Since it was not possible to rear these insects and establish their complete life cycle under laboratory conditions, field-collected adults were used for the bioassays.

VOC collection

The volatile organic compounds from *V. planifolia* flowers were collected using the dynamic headspace technique. A continuous airflow (0.5 L min^{-1}), generated by a vacuum pump and filtered through activated carbon, was passed through Erlenmeyer-shaped glass chambers (200 mL) containing ~ 130 mg of flowers (detached sepals and petals). The airflow carried the volatile compounds released from the plant material through a glass column containing 30 mg of adsorbent polymer (HayeSep-Q). The compounds adsorbed onto the polymer were eluted with 300 µL of HPLC-grade hexane, and the extracts were analysed directly without prior concentration. Volatile collection was performed in three independent biological replicates over a 24 h period.

The collected extracts were stored at −20 °C until further chemical analyses and bioassays.

Chemical analysis

The extracts were analysed by gas chromatography–mass spectrometry (GC–MS) using a Shimadzu QP2010-Plus equipped with an electron impact ionization detector (70 eV) and an RTX-5 capillary column (30 m × 0.25 mm × 0.25 µm; Restek Chromatography Products USA). The extracts (1 µL) were analyzed in splitless mode (250 °C), and the oven temperature program started at 40 °C for 3 min, then increased at a rate of 7 °C min^{-1} until reaching 250 °C, which was held for 2 min. The ion source and transfer line temperatures were set at 200 °C and 250 °C, respectively. Helium was used as the carrier gas at a flow rate of 1 mL min^{-1}. GC analysis using an enantioselective stationary phase was performed in a Nexis GC-2030 chromatograph equipped with a βDex 325 capillary column (25% heptakis-2,3-di-O-methyl-6-O-TBDMS-β-cyclodextrin, 30 m × 0.25 mm × 0.25 µm, Supelco, USA) and a flame ionization detector. The temperature program started at 50 °C (held for 1 min), then increased at 1 °C min^{-1} to 150 °C, and maintained for 10 min. The analysis was performed in splitless mode with helium as the carrier gas at 1.5 mL min^{-1}. Retention indices were calculated relative to the retention times of C10-C26 *n*-alkane standards. The mass spectra obtained were analyzed and compared with NIST mass spectral libraries. Chemical structures were identified by comparing retention indices and mass spectra with NIST 27 and NIST 147 libraries and with the literature (Adams 2007), and were confirmed using synthetic standards [β-myrcene (≥90%), (R)-limonene (≥93%), and β-ocimene isomer mixture (1:3 Z/E, ≥ 90%); Sigma-Aldrich, Milwaukee, WI, USA] when available (Table 1). Quantification was performed using dodecane (20 µg mL^{-1}) as an internal standard added directly to each sample, based on relative peak area comparison.

Behavioural experiments

Insect behavioural responses to the extracts were evaluated using a Y-tube glass olfactometer (4.5 cm i.d.; 40 cm main tube length; two 20 cm arms). Individual bioassays were conducted for each treatment using 30 males and 30 females, totaling 60 individuals tested. Prior to the bioassays, insects were maintained without food for 1 h to standardise their behavioural state. The treatments consisted of: (I) ~ 130 mg of fresh flowers vs. blank air; (II) hexane extract of floral VOCs vs. hexane; (III) β-ocimene isomer mixture in hexane (100 µg mL^{-1}, 1:3 Z/E) vs. hexane; and (IV) β-ocimene isomer mixture in hexane (100 µg mL^{-1}, 1:3 Z/E) vs. hexane extract of floral VOCs. For treatments using extracts or synthetic compounds, 10 µL of the solution were applied to filter paper squares (1.0 × 1.0 cm), and the solvent was allowed to evaporate before the papers were placed at each end of the olfactometer arms. When the odor source consisted of fresh flowers, they were placed inside glass chambers identical to those used for volatile collections, directly connected to the olfactometer arms and outside the insects' line of sight. In all cases, the odor sources were supplied with a continuous airflow of 1.0 L min^{-1}, pushed through the system, and insect behavior was monitored for 5 min. A "response" was recorded when the insect crossed beyond 50% of the length of the arm containing the odor source and remained in that area for more than 2.5 min (Dos Santos Neta et al. 2021). The arm position was changed every three repetitions to control for directional bias.

Statistical analysis

The frequency distribution of Y-tube olfactometer bioassay count data was analysed using *Chi-square* tests (x^2), with the BioEstat program (version 5.0), to determine significant differences in *Montella* sp. responses between tested odors (fresh flowers, hexane extract of floral VOCs, β-ocimene isomer mixture) and controls. For each bioassay, the number

Table 1 Volatile Organic Compounds (VOCs) identified in the volatile extracts of *Vanilla planifolia* flowers (fresh floral tissues). Quantities and relative abundances are presented as means ± SD

Peak[a]	RT (min)	RI[b]cal	RI[c]lit	Compound	Quantity (µg.g^{-1} flower)	Relative Abundance (%)
1	10.22	988	991	β-Myrcene[d]	2.21 ± 0.08	2.77 ± 0.10
2	11.15	1031	1031	(*R*)-Limonene[d]	0.71 ± 0.10	0.89 ± 0.13
3	11.40	1036	1037	(*Z*)-β-Ocimene[d]	0.68 ± 0.08	0.85 ± 0.10
4	11.43	1038	1039	Eucalyptol	4.89 ± 0.22	6.12 ± 0.28
5	11.60	1048	1050	(*E*)-β-Ocimene[d]	70.60 ± 0.21	88.40 ± 0.26
6	13.90	1425	1419	β-Caryophyllene	0.77 ± 0.13	0.96 ± 0.16

[a]Peak number corresponding to the peaks indicated in Fig. 1

[b]Calculated retention indices

[c]Retention indices reported in the literature

[d]Chemical structures confirmed with authentic standards

of responding insects (n) was recorded, and non-responders were excluded from the analysis. The χ^2 statistic was calculated from observed and expected counts for each test and compared with the critical χ^2 value for 1 degree of freedom (χ^2 *critical* = 3.84, $p = 0.05$); if χ^2 calculated > χ^2 critical, the null hypothesis was rejected. Each olfactometry bioassay was analyzed separately, comparing only two factors at a time.

Results

Gas chromatographic analysis of *Vanilla planifolia* floral VOC extracts (Fig. 1) revealed six distinct compounds. GC–MS analyses revealed spectra (Figures S1–S6) indicating the presence of five monoterpenes and one sesquiterpene. The characteristic terpene fragment, *m/z* 93—resulting from double bond isomerization followed by allylic cleavage—was present in all compounds, appearing as the base peak for compounds **1**, **3**, and **5**, identified as β-myrcene, (*Z*)-β-ocimene, and (*E*)-β-ocimene. Compound **2** exhibited a base peak at *m/z* 68, consistent with retro Diels-Alder fragmentation typical of cyclic alkenes, and was identified as (*R*)-limonene based on mass spectra and chiral GC analysis (Figure S7). Compound **4** showed a base peak at *m/z* 43 and was identified as eucalyptol. Compound **6**, tentatively identified as β-caryophyllene, showed *m/z* 41 as its base peak, which is also very common for terpenes and was present in the mass spectra of all compounds identified in this study. The quantitative and relative abundance data for each compound are summarized in Table 1, which allows direct comparison among the identified VOCs. The major component was (*E*)-β-ocimene, accounting for 88.40% of the mixture, followed by eucalyptol (6.12%) and β-myrcene (2.77%). The remaining components accounted for 2.70% of the mixture (Table 1). Considering the average floral mass used for volatile collections (~130 mg), this represents approximately 9.180 µg of (*E*)-β-ocimene per sampled floral set, highlighting its high emission in *V. planifolia* flowers.

Dual-choice bioassays (Fig. 2) revealed that fresh *V. planifolia* flowers were highly attractive to *Montella* sp. adults ($N = 59$; $\chi^2 = 23.20$, $p < 0.001$). No significant differences were observed between males and females across treatments; therefore, responses were pooled for analysis.

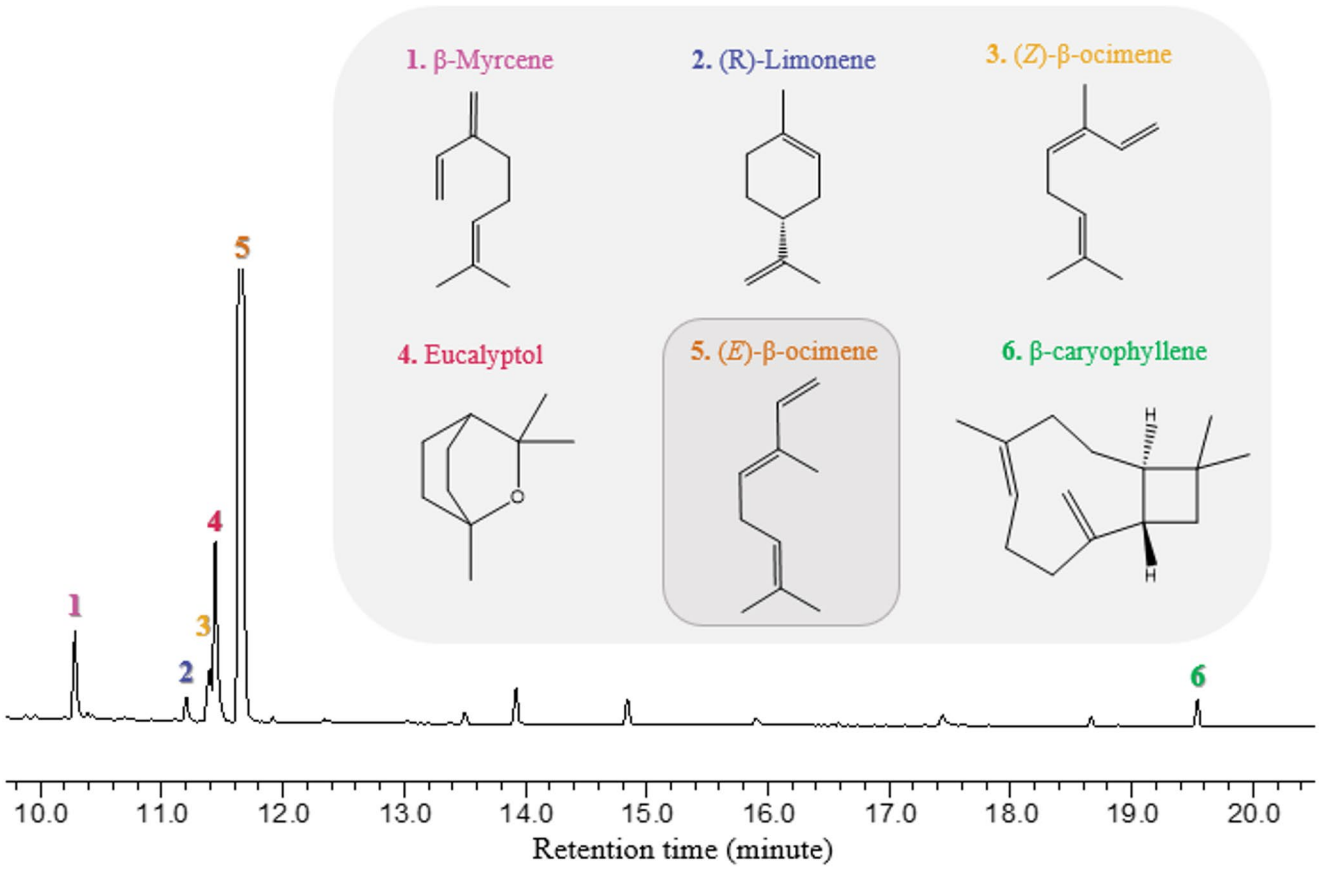


Fig. 1 Gas chromatogram of volatile extracts from *Vanilla planifolia* (Orchidaceae) flowers (fresh floral tissues). Chemical structures of the identified compounds are shown above the chromatogram for reference, and numbered peaks correspond to these structures. The unlabeled peaks correspond to contaminants and chromatographic column bleed

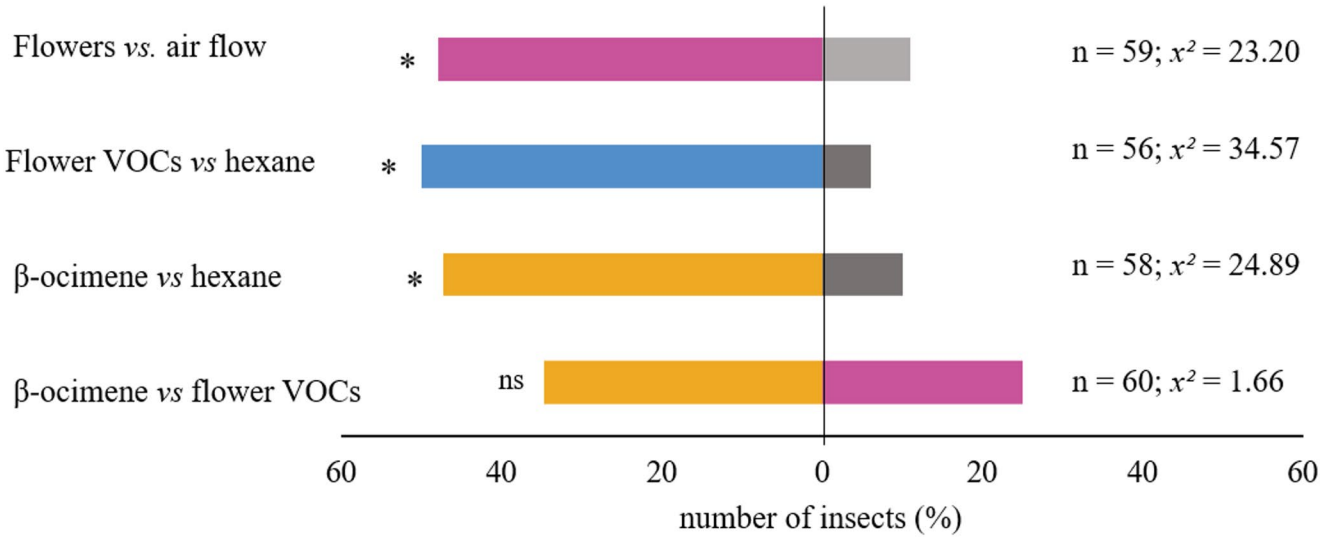


Fig. 2 Olfactory responses of *Montella* sp. (Coleoptera: Curculionidae) adults in dual-choice bioassays to fresh *Vanilla planifolia* flowers, floral volatile extracts, and a β-ocimene isomer mixture (1:3 Z/E). (*) Significant difference between treatments ($p \leq 0.05$), (^{ns}) not significant according to the *Chi-square* test

Bioassays with floral volatile extracts also resulted in significant attraction ($N=56$; $\chi^2 = 34.57$, $p<0.001$) compared to the hexane control. In Fig. 2, the graphical representation of choice responses highlights the strong preference for floral stimuli in both cases. When tested individually, the β-ocimene isomer mixture (1:3 Z/E) in hexane, representing a synthetic stimulus based on the major floral component, significantly attracted insects compared to hexane alone ($N=58$; $\chi^2 = 24.89$, $p<0.001$). However, comparisons between the β-ocimene isomer mixture and the floral volatile extract showed no significant difference in attractiveness ($N=60$; $\chi^2 = 1.66$, $p=0.197$), indicating that minor floral components did not appear to enhance attraction under the tested conditions.

Discussion

In our study, we demonstrate that the floral bouquet of *Vanilla planifolia* is dominated by (*E*)-β-ocimene (natural Z/E ≈ 1:99), and that the orchid weevil *Montella* sp. displays strong attraction to floral odours. Behavioural assays using a β-ocimene isomer mixture (Z/E = 1:3), though not identical to the natural isomeric ratio, indicate that β-ocimene is associated with host location. As this synthetic mixture differs from the natural isomeric ratio, the specific contribution of individual isomers to the observed behavioural response cannot be determined. However, the synthetic mixture elicited attraction similar to that produced by the full floral VOC extract, indicating that β-ocimene elicited a behavioural response under the tested conditions, supporting its ecological relevance in this interaction.

As a Baridinae weevil, *Montella* sp. commonly visits orchids in the genera *Dichaea*, *Grobya* and *Vanilla*, and is recognized as a florivore, significantly impacting both commercial and non-commercial orchids (Mickeliunas et al. 2006; Nunes et al. 2017, 2018; Jordão et al. 2020). Its exploitation of orchid-pollinator scent cues, especially those evolved to attract Euglossini bees (Nunes et al. 2016), aligns with its attraction to β-ocimene. Comparable behavior has been observed in other Curculionidae: *Rhyssomatus nigerrimus* attracted to soybean floral volatiles (González-Domínguez et al. 2024), *Anthonomus rubi* responding to flowering strawberry scent (Mozūraitis et al. 2020), A. *eugenii* responding to pepper volatiles with male-biased pheromone synergism (Muñiz-Merino et al. 2014) and *A. grandis* showing preference for cotton VOCs containing β-ocimene (notably the (*E*)-isomer), especially when coupled with aggregation pheromones (Magalhães et al. 2012).

While β-ocimene is a well-known attractant for pollinators like Euglossini bees (Gerlach and Schill 1991; Pemberton et al. 2023), our findings underscore its role in attracting a florivorous pest. However, floral scent is a complex and context-dependent signal, and the information conveyed by individual compounds depends on the overall blend and its composition (Raguso 2008). Euglossophilous orchids produce a suite of monoterpenes—α-pinene, thujene, β-pinene, sabinene, β-myrcene, limonene, eucalyptol (1,8-cineole), (*Z*)- and (*E*)-β-ocimene, α-terpineol—that facilitate pollinator attraction (Gerlach and Schill 1991; Cancino and Damon 2006). In our analysis, *V. planifolia* produced five of these compounds, with (*E*)-β-ocimene as the predominant VOC, whereas pest-oriented studies report β-ocimene as attractive to species such as *A. grandis* (Magalhães et al. 2012)

and *Myllocerinus aurolineatus* (Sun et al. 2010). Thus, floral volatiles useful in pollination can also be co-opted by herbivores. Such compounds may simultaneously attract mutualists and antagonists, reflecting a trade-off in floral signalling (Nunes et al. 2016). Accordingly, β-ocimene alone is unlikely to function as a species-specific cue for host location. Whether the population studied here exhibits a broader host range remains to be determined.

The volatile profile of *V. planifolia* in our study, dominated by monoterpenes and sesquiterpenes, corresponds to results from studies on *V. pompona* and *V. planifolia* (Williams and Whitten 1983; Pemberton et al. 2023), although the dominant compounds differed—Pemberton et al. (2023) identified eucalyptol (1,8-cineole) as the major VOC, followed by β-ocimene, while our samples showed a predominance of (*E*)-β-ocimene. Methodological differences—SPME in Pemberton et al. (2023), in situ Tenax aeration in Williams and Whitten (1983), and dynamic headspace aeration on detached flowers in our study—may account for these variations, especially since β-ocimene emissions are known to increase following tissue damage in many plant species (Farré-Armengol et al. 2017; Gurr et al. 2023), which may have contributed to the high proportion of this compound in our samples. Geographic variation and deceptive floral strategies in Orchidaceae also likely contribute, reflecting conflicting selective pressures from pollinators, herbivores, and environmental conditions (Gross et al. 2016; Dormont et al. 2019; Strauss and Whittall 2006; Schemske and Bierzychudek 2007; Coberly and Rausher 2008).

Taken together, our results highlight the role of β-ocimene, particularly the (*E*)-isomer, as an attractive component involved in host location by *Montella* sp., and suggest its potential utility in semiochemical-based monitoring and management of vanilla pests. Although the synthetic mixture elicited strong attraction, the functional significance of other floral VOCs and of individual β-ocimene isomers remains unclear. Given that plant volatiles often synergize with pheromones (Reddy and Guerrero 2004), and that such synergy has been demonstrated for other curculionids (e.g., *A. eugenii*) (Muñiz-Merino et al. 2014), combining β-ocimene with *Montella*-specific pheromones, recently identified for this species (Santos et al. 2025), could improve control strategies.

In conclusion, this study clarifies the chemical basis of the *Montella—V. planifolia* interaction, identifying β-ocimene, particularly the predominant (*E*)-isomer in the natural blend, as an attractive component. It also provides a foundation for incorporating floral VOCs into pest monitoring and integrated management in vanilla cultivation. By bridging ecological insight with applied pest control, these findings offer tools to mitigate damage from florivorous pests that exploit signals traditionally associated with pollination.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11829-026-10250-9.

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Author contributions D.S.B., A.M.L.S and C.F.F. designed the study. D.S.B. and J.P.J. performed the experiments. J.P.J. and M.D.A.C. performed data analysis and discussion. All authors wrote the manuscript.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Competing interests The authors declare no competing interests.

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