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# Olfactory responses of the leafminer *Liriomyza cicerina* (Diptera: Agromyzidae) to chickpea plant volatiles

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**Introduction:** Chickpea (*Cicer arietinum* L.) is an essential pulse crop in many countries, but its productivity is severely constrained by the leafminer *Liriomyza cicerina* (Rondani), a major chickpea pest in the Mediterranean region and North Africa. Host location by *L. cicerina* is strongly affected by plant-emitted volatile organic compounds (VOCs), which mediate insect host selection and oviposition. Understanding these chemical signals is essential for developing sustainable pest management strategies.

**Methods:** Y-tube olfactometer bioassays were conducted to evaluate the olfactory responses of adult leafminers to VOC blends from healthy and infested chickpea plants, to selected individual volatile compounds, and to VOCs released by chickpea varieties with distinct levels of resistance toward *L. cicerina*.

**Results and discussion:** Adult leafminers were significantly more attracted to VOCs emitted by healthy plants than to those released by infested plants. Among individual volatile compounds tested, trans-2-hexen-1-ol elicited the highest attraction (80%), whereas linalyl acetate induced the strongest repellence (73.3%). Moreover, VOC emissions varied among chickpea genotypes, influencing the host preference of *L. cicerina*. The susceptible variety Arifi (FLIP98-50 C) release more attractive VOC blends compared to the less susceptible genotypes tested. These findings highlight the ecological role of chickpea VOCs in mediating insect-plant interactions, with plant condition, genotype, and specific compounds shaping insect preference and host selection. Identifying attractive and repellent VOCs provides insights into the mechanisms underlying susceptibility and supports the development of sustainable pest management strategies, including monitoring lures, push-pull strategies, and selective breeding of less attractive chickpea varieties.

## KEYWORDS

chickpea (*Cicer arietinum* L.), host selection, *Liriomyza cicerina*, olfactory responses, volatile organic compounds, Y-tube olfactometer

# 1 Introduction

Chickpea (*Cicer arietinum* L.) is a major pulse crop cultivated widely in the semi-arid regions of Asia, Africa, and South America. It is valued for its high nutritional content and its significant role in improving soil fertility (Soltani et al., 2020; Makhlouf et al., 2024a; Zhang et al., 2024). In 2023, around 14.10 million hectares of chickpeas were harvested worldwide, producing approximately 16.52 million tonnes (Food and Agriculture Organization, 2025), making it the third-largest pulse crop globally, after field peas and dry beans (Toker et al., 2010; Muehlbauer and Sarker, 2017). However, despite its potential, chickpea yields remain low and variable due to abiotic stresses like drought, and biotic stresses such as pests, diseases, and weeds (Toker et al., 2007; Erler et al., 2009). Among the biotic constraints affecting chickpea, the leaf miner, *Liriomyza cicerina* (Diptera: Agromyzidae), is one of the most damaging insect pests, particularly in the Mediterranean region, North Africa, West Asia, and Southern Europe. Yield losses due to this pest can reach 30–40% in these areas (Sabraoui et al., 2019; Soltani et al., 2021).

In Morocco, chickpea is the second most important grain legume after faba bean, covering approximately 45096 hectares with an estimated production of 25701.6 tonnes in 2023 (Food and Agriculture Organization, 2025). *L. cicerina* has been identified as the predominant insect pest in main chickpea growing areas, causing yield losses of up to 20% during winter and up to 40% in the spring cropping seasons (Sabraoui et al., 2019). The larvae of *L. cicerina* are primarily responsible for the most severe damage to chickpea plants, as they feed within the leaf tissues, whereas adult females cause minor damage through their feeding activity (El Bouhssini et al., 2008). The larvae feed inside the leaves, creating mines that reduce photosynthetic capacity, and lead to leaf drying, early defoliation, and considerable yield losses (Yildirim et al., 2010; Ceylan et al., 2018; Chrighui et al., 2021). With two to three overlapping generations during one growing season, infestations can spread rapidly, underscoring the need for effective and sustainable pest management approaches (Toker et al., 2010; Oubayoucef et al., 2022).

Host location by *L. cicerina* is largely mediated by volatile organic compounds (VOCs) emitted by chickpea plants, which act as kairomones, olfactory cues that guide insect feeding and oviposition behavior, over medium to long distances (Zhao and Kang, 2002; Kessler et al., 2023; Makhlouf et al., 2024b). The behavioral responses of insects to VOCs are influenced by multiple factors, including plant health status (healthy or herbivore-infested), the chemical nature and concentration of specific compounds (whether attractive or repellent), and plant genotype. Healthy chickpea plants release VOC blends that may attract adult leafminers, while infestation alters these emissions, potentially making the plant more or less attractive to herbivores (Wei et al., 2006). Additionally, VOC profiles vary across chickpea genotypes, with some producing compounds that deter insects and others releasing compounds that attract them. Studies have shown that *L. cicerina* exhibits clear oviposition preferences among chickpea genotypes, with susceptible varieties receiving higher egg loads and supporting better insect performance than resistant ones

(Oubayoucef et al., 2022). This genotype-dependent variation suggests that plant genetic background significantly influences VOC emission and herbivore behavior. Recent research has highlighted the potential of VOCs, particularly green leaf volatiles (GLV) and terpenoids such as trans-2-hexen-1-ol and linalool, as tools for sustainable pest management (Yan et al., 2023; Makhlouf et al., 2024a). Depending on context, these compounds can function as attractants or repellents, making them valuable for strategies such as selective breeding, monitoring, mass trapping, or push-pull systems. As environmentally friendly alternatives to synthetic insecticides, VOCs offer advantages including reduced harm to non-target organisms and lower production costs.

The present study investigates the role of individual VOCs and complex mixtures, emitted by chickpea plants of varying genotypes and health statuses, in shaping the host-selection behavior of *L. cicerina*. The work focuses on determining which VOCs act as attractants or repellents and how these emissions vary according to genotype and plant health. This finding aims to inform the development of VOC-based strategies for more effective integrated pest management in chickpea farming systems.

# 2 Materials and methods

## 2.1 Leafminer collections

Adults of male and female *L. cicerina* were collected during April and May 2025 from several spring-planted chickpea fields (cv. Arifi) at the vegetative growth stage in Marchouch (33°46'35" N, 6°32'52" W), Morocco. Collections were conducted early in the morning using a manual aspirator equipped with aerated plastic tubes to capture and temporarily hold the insects. The collected adults were maintained under suitable temperature and humidity until use in Y-tube olfactometer bioassays. The required number of adults was collected daily, and Y-tube olfactometer tests were performed on the same day of collection.

## 2.2 Chickpea planting and infestation

Three chickpea genotypes, the released variety Arifi (FLIP98–50 C) and two accessions (ILC86 and ILC93), were selected from ICARDA genebank for this study based on their reactions to Leafminer under field infestation (Table 1). The genotypes were planted on March 17, 2025, at Marchouch experimental station, in a randomized complete block design with four replications. Seeds were sown in 12-cm-diameter plastic pots filled with field soil and

TABLE 1 Characteristics of the studied chickpea genotypes.

| Genotypes           | Leaf type    | Leaflet size | Susceptibility to leafminer |
|---------------------|--------------|--------------|-----------------------------|
| Arifi (FLIP98–50 C) | Normal       | Intermediate | Susceptible                 |
| ILC 86              | Normal       | Intermediate | Moderate resistant          |
| ILC 93              | Multipennate | Very small   | Resistant                   |

maintained under field conditions. Irrigation was applied once weekly. Chickpea plants were placed in protective cages (5×5×3.6m) covered by mosquito netting, in the field to prevent natural infestation by leaf miners and other pests. Upon reaching the vegetative stage, the plants were evenly divided: 50% were maintained as healthy controls in one cage, while the remaining 50% were transferred to a second cage of the same dimension, where the field-collected insects were released to initiate infestation. Plant assessment was conducted 24 hours later to check for leafminer punctures indicative of oviposition. Once eggs were detected on the leaves, the egg-infested plants, along with their corresponding non-infested controls, were collected and transferred to the laboratory for Volatile Organic Compounds (VOCs) collection. The remaining plants were monitored daily to assess leafminer infestation and track development from egg deposition through successive larval stages. When larvae reached the second instar, each infested plant, along with its corresponding control, was collected and processed in the laboratory for VOCs extraction. Each variety included both egg-infested plants (in a range between 5 and 50 eggs per plant) and plants with developing larvae, and the infestation rates were recorded at both stages.

## 2.3 Volatile organic compounds extraction from chickpea plants

A dynamic headspace sampling method was employed to collect volatiles emitted from healthy and infested chickpea plants (egg- and larva-infested plants). Individual potted plants were enclosed in pre-cleaned plastic oven bags made of polyethylene terephthalate (PET), which had been baked in an oven at 150 °C for 2 h for decontamination, and sealed near the base of the pot with rubber bands. The soil surface in the pot was covered with a layer of aluminum foil, previously rinsed with acetone and baked at 150 °C for 2h. The compressed air (Atlas Copco GA 7 VSD) was purified and humidified using an inline Clean Air Filter ICVAF-2.5x10 (Sigma Scientific LLC, Micanopy, FL) prior to entering the enclosure. Filtered air was pumped into the plastic bag through an inlet tube at a rate of 1.5 L.min<sup>-1</sup>, while VOCs were simultaneously drawn out through an outlet of the same diameter, maintaining a continuous airflow. The outlet was connected in series to a 20 mg Porapak-Q adsorbent trap (Analytical Research Systems, Gainesville, FL, USA), a flowmeter set to 1 L.min<sup>-1</sup> (KNF Diaphragm Vacuum Pumps), and a vacuum pump. This push-pull airflow setup prevented ambient air contamination during the extraction time. The dynamic headspace collection lasted for 7 h, usually from 10:00 am to 5 pm. Volatile compounds extracted from chickpea plants were eluted from the volatile collector trap filled with 20 mg Porapak-Q (VCT - 1/4 - 3 - POR-Q) using 300 µL of dichloromethane and stored in 2 mL glass vials at -20 °C until Y-tube olfactometer assays. After each sampling session, the oven bags were washed with hexane or acetone and re-sterilized by baking at 120 °C for 2h, while Super Q traps were cleaned with dichloromethane, then heated at 132 °C for 2 h to remove residual contaminants.

For the individual VOCs, we referred to the literature to select volatile compounds previously identified in chickpea using GC-MS

analysis (Rembold et al., 1989; Cruz et al., 2012; Khrisanapant et al., 2019; Karolkowski et al., 2021; Gasiński et al., 2025), which were subsequently purchased for use in bioassays. Chemical standards included trans-2-hexen-1-al (98%); trans-2-hexen-1-ol (97%); 1-hexanol (99.9%); linalool (99.0%); 1-Penten-3-ol (99%); 3-méthyl-1-butanol (99%); linalyl acetate (97%); and 2-hydroxy-3-methylbenzaldehyde (98%), were purchased from Sigma-Aldrich Inc. (Steinheim, Germany).

## 2.4 Y-tube olfactometer bioassay

A glass Y-tube olfactometer (4.1 cm inner diameter) was employed to investigate the host selection behavior of *L. cicerina* adults in response to headspace volatiles collected from chickpea plants as well as 8 common synthetic volatile compounds, under laboratory conditions (24 ± 1 °C temperature; 60% – 70% RH). The olfactometer consisted of a Y-shaped glass tube with a 19 cm main arm and two lateral arms (each 10 cm, 45° angle) (YT 4035, Sigma Scientific LLC, Micanopy, FL) connected to odor sources placed in sealed glass chambers. Charcoal-filtered, humidified air was continuously delivered through each arm at a rate of 1 L.min<sup>-1</sup> using two inline 150-mm flow meters (Cole-Parmer).

Three sets of behavioral assays were performed to evaluate the olfactory response of *L. cicerina* to chickpea volatiles:

1. Synthetic volatile attraction: The behavioral response of *L. cicerina* to eight individual synthetic volatile compounds commonly found in chickpea headspace was assessed.
2. Plant health status preference: Leafminer adults were given a choice between volatile blends collected from healthy plants and those from leafminer-infested plants (egg-infested or larva-infested) to evaluate their olfactory attraction.
3. Effect of plant resistance: The influence of plant resistance on insect preference was evaluated by exposing leafminer adults to volatile blends from chickpea genotypes with different resistance levels (susceptible, moderately resistant, and resistant), tested in pairwise combinations.

For each treatment, a total of 30 field-collected leafminer adults were tested individually. A single adult *L. cicerina* (male or female) was randomly selected and introduced at the base of the Y-tube (stem inlet). Each insect was given up to 10 minutes to make a choice between the two odor sources. A choice was recorded if the insect moved at least halfway into one of the Y-tube arms. If no choice was made within 15 minutes, the assay was terminated. A 10 µL headspace of volatiles collected from either healthy or infested plants and 10 µL of solvent (dichloromethane) as a control were applied to a cut piece of filter paper (6 mm x 15 mm, Whatmann No. 1) and placed in the odor source chambers. Dichloromethane was placed in both arms of the olfactometer as a control treatment to assess solvent effects. To eliminate positional bias, the orientation of the Y-tube and the position of odor sources were alternated after every five replicates. Additionally, the Y-tube was thoroughly cleaned with acetone and air-dried on the laboratory bench between replicates to prevent cross-contamination. A new insect was used for each replicate, and no individual was tested more than once.

## 2.5 Statistical analysis and data visualization

Behavioral data from Y-tube olfactometer assays were analyzed using XLSTAT (version 2024.4.0). Choice distributions were assessed with chi-square goodness-of-fit tests ( $df = 1$ ), while choice latencies were compared using Mann–Whitney U tests, as the data did not meet the assumptions of normality. Statistical significance was determined at the  $\alpha = 0.05$  level. Data visualization was performed in R (version 4.4.1) using the *tidyverse* package. Diverging bar plots were generated to represent the number of insects selecting each option, with bars extending symmetrically in opposite directions from a central axis.

## 3 Results

### 3.1 Infestation level assessment

Significant differences in *L. cicerina* infestation were observed among chickpea genotypes for both eggs and larvae (Figure 1). The analysis of variance revealed a significant effect of genotype on egg infestation ( $F(2, 9) = 8.61$ ,  $p = 0.008$ ,  $R^2 = 0.657$ ) and on larval infestation ( $F(2, 9) = 12.13$ ,  $p = 0.003$ ,  $R^2 = 0.729$ ). Chickpea variety *Arifi* showed the highest levels of infestation, with mean proportions of 0.338 for eggs and 0.500 for larvae. In contrast, ILC 93 exhibited the lowest infestation (0.138 for eggs and 0.263 for larvae), while ILC 86 presented intermediate values (0.200 for eggs and 0.338 for larvae).

*Post-hoc* comparisons indicated that *Arifi* was significantly more infested than ILC 93 for both egg and larval stages, whereas ILC 86 did not differ significantly from either genotype in egg infestation level but grouped with ILC 93 for larval infestation. These results indicate that *Arifi* is the most susceptible genotype, while ILC 93 exhibits the highest resistance, and ILC 86 shows an intermediate level of resistance.

## 3.2 Behavioral responses of *Liriomyza cicerina* adults to chickpea plant VOCs

### 3.2.1 Olfactory preference of *L. cicerina* adults for VOC blends emitted from healthy and infested chickpea plant

Across all tested genotypes and both infestation stages, adults of *L. cicerina* exhibited a stronger attraction to VOCs emitted from healthy plants compared to those released by infested plants (Figure 2). In ILC 86, *L. cicerina* adults exhibited a significantly stronger attraction to VOCs collected from healthy plants, with 80% preferring the healthy-plant blend, compared to 20% attracted to the egg-infested blend ( $df=1$ ,  $p = 0.001$ ). A similar pattern was observed at the larval infestation stage, where 73.33% of adults were attracted to VOCs from healthy plants, compared to 26.67% responding to VOCs from larva-infested plants ( $df=1$ ,  $p = 0.011$ ). For *Arifi* and ILC93, significant attraction was observed at the larval infestation stage ( $p < 0.005$ ). In *Arifi*, 76.67% of adults were attracted to VOCs from healthy plants, compared to 23.33% attracted to VOCs from larva-infested plants ( $p = 0.003$ ). Likewise, in ILC 93, 83.33% of adults responded to VOCs from healthy plants, whereas only 16.67% were attracted to VOCs from larva-infested plants ( $p < 0.001$ ). However, at the egg-infestation stage, the attraction of adults to VOCs from healthy versus egg-infested plants was not statistically significant. No significant differences in preference or decision time were detected across all varieties and infestation stage ( $p > 0.05$ ), except for the *Arifi* variety at the larval infestation stage ( $p < 0.05$ ).

### 3.2.2 Behavioral response of *L. cicerina* adults to VOC blends extracted from resistant and susceptible chickpea genotypes

In both comparisons, a slightly higher number of leafminer adults were attracted to the VOCs emitted by the susceptible variety *Arifi* compared to the two other genotypes. However, these differences in the attraction of adult insects between the two odor sources of the

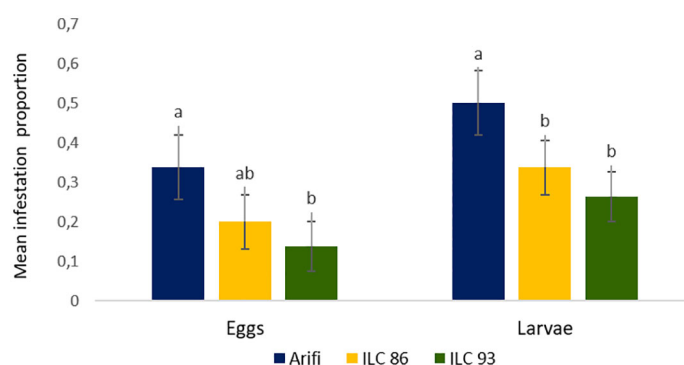


FIGURE 1

Mean infestation proportion caused by *L. cicerina* on chickpea genotypes (means followed by a different letter(s) are significantly different based on Newman–Keuls test ( $p < 0.05$ )).

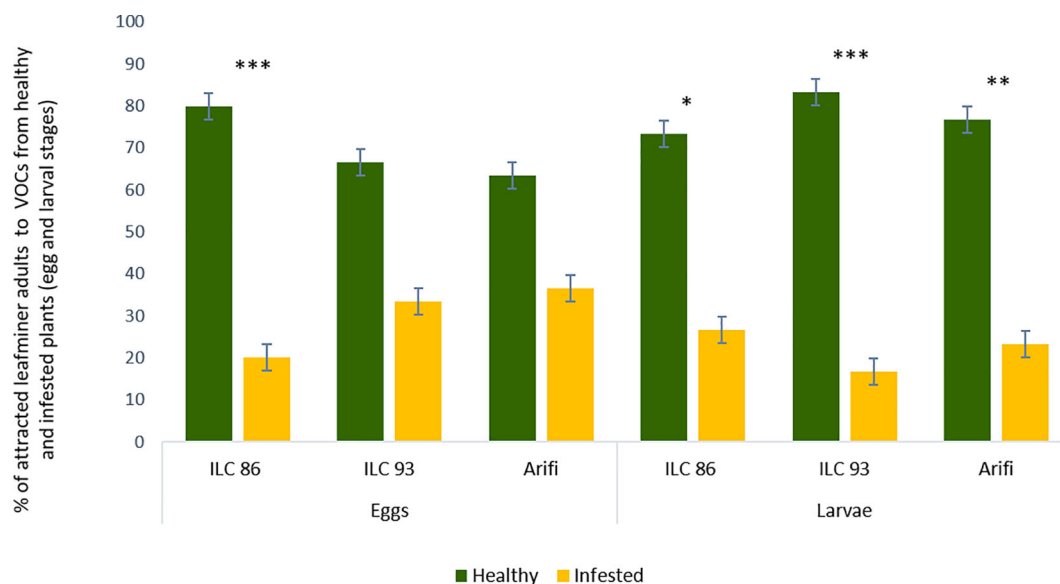


FIGURE 2

Behavioral responses of *L. cicerina* adults to VOC blends (from healthy and infested plants) and solvent (control) (mean  $\pm$  SE) in a Y-tube olfactometer. The asterisks indicate the significance levels ( $p < 0.05 = *$ ,  $p < 0.01 = **$ ,  $p < 0.001 = ***$ ; ns, not significant).

tested chickpea genotypes were not statistically significant ( $DF = 1$ ,  $p > 0.05$ ). When Arifi was tested against ILC 93, 53.33% of adults were oriented toward the susceptible variety Arifi, while 46.67% were attracted to ILC 93 ( $p = 0.715$ ). Similarly, in the comparison between Arifi and ILC 86, about 56.67% of leafminer adults chose Arifi, whereas 43.33% oriented toward ILC 86 ( $p = 0.465$ ) (Figure 3). When comparing the time taken for insects to make a choice in the olfactometer, a shorter response time was consistently observed for individuals choosing the VOCs emitted by the susceptible variety

Arifi in both experiments. The analysis of time elapsed to respond to different stimuli in the olfactometer tests, revealed a significant difference in decision-making time between VOCs of Arifi variety and those of ILC86 ( $p = 0.048$ ). Insects that oriented toward VOCs blend emitted by Arifi made their choice more rapidly (median = 65.75 s) compared to those that chose VOCs blend of ILC86 (median = 130.33 s). In the Arifi vs. ILC93 test, although insects also showed a faster response to Arifi volatiles, the difference was not statistically significant (Figure 4).

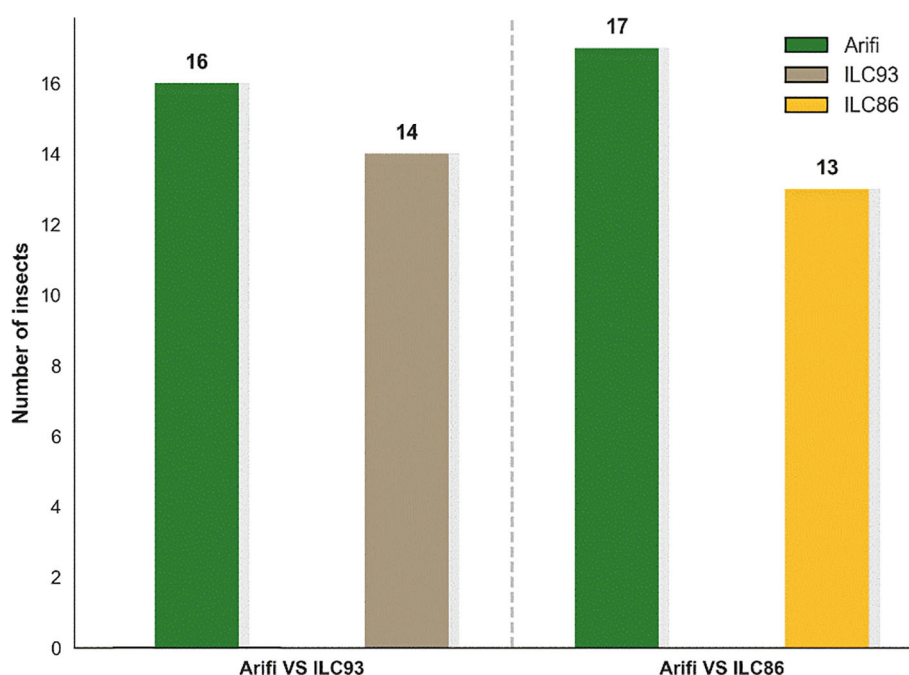
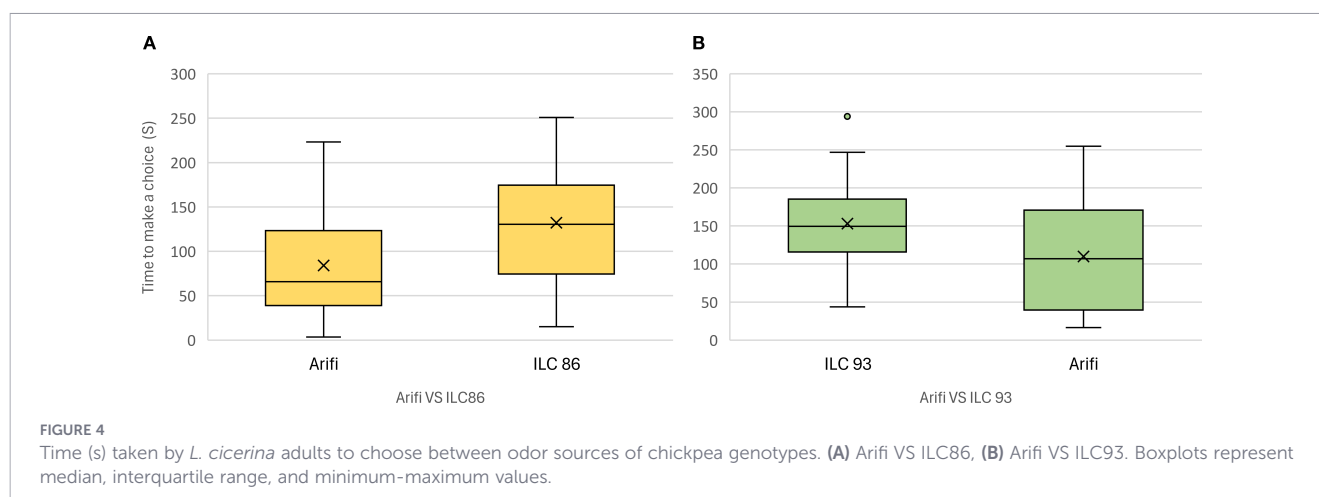


FIGURE 3

Olfactory preference of *Liriomyza cicerina* adults for VOC blends extracted from different chickpea genotypes. Bars represent the number of adults choosing each genotype. Number above bars indicate the number of responding insects.



### 3.2.3 Olfactory response of leafminer adults to eight synthetic chickpea-derived volatiles

Y-tube olfactometer assays revealed that individual VOCs elicited distinct behavioral responses in adult leafminers (Figure 5). Among the eight compounds tested, five exhibited attractive effects, with linalool ( $df = 1$ ;  $p = 0.003$ ), 2-hydroxy-3-methylbenzaldehyde ( $df = 1$ ;  $p = 0.028$ ), and trans-2-hexen-1-ol ( $df = 1$ ;  $p = 0.001$ ) showing significant attraction. Trans-2-hexen-1-ol elicited the strongest response, with 80% of adults choosing this compound over the solvent. Linalool and 2-hydroxy-3-methylbenzaldehyde also attracted 76.7% and 70% of adults, respectively, confirming their role as potent attractants. In contrast, linalyl acetate was significantly avoided ( $df = 1$ ;  $p = 0.011$ ), with only 26.7% of adults orienting toward the compound compared to 73.3% choosing the solvent, indicating a strong repellent effect. The remaining compounds, including 1-penten-3-ol ( $df = 1$ ;  $p = 0.05$ ) and 3-methyl-1-butanol ( $df = 1$ ;  $p = 0.144$ ), elicited weak and non-significant repellency. The solvent control confirmed the absence of positional bias ( $p = 0.715$ ).

Analysis of insect response times revealed that trans-2-hexen-1-ol elicited the fastest median choice ( $\approx 90$  s), confirming its role as the most effective attractant and a strong behavioral cue. The volatile 2-hydroxy-3-methylbenzaldehyde also induced relatively rapid decisions ( $\approx 120$  s), indicating consistent but lower efficacy compared to trans-2-hexen-1-ol. Linalool showed higher variability among individuals, yet its median response time ( $\approx 130$  s) supported its attractiveness. Overall, leafminer adults responded preferentially to alcohols, aldehydes, and terpenoids, with trans-2-hexen-1-ol emerging as the most potent attractant, followed by 2-hydroxy-3-methylbenzaldehyde and linalool (Figure 6).

## 4 Discussion

Our findings demonstrate that the olfactory responses of the chickpea leafminer, *Liriomyza cicerina*, are influenced by multiple factors, including the chemical nature of the volatile compound, the type of variety, and its resistance level, as well as the plant's health status (healthy or infested).

In the present study, Y-tube olfactometer assays revealed that adult *L. cicerina* were more strongly attracted to volatile organic compounds (VOCs) emitted by healthy chickpea plants than to those released from plants infested by *L. cicerina* eggs and larvae. This pattern aligns with previous reports in other plant–insect systems, where herbivore attack often suppresses or alters the emission of attractant VOCs or induces the release of defensive or repellent compounds. For example, Morrell and Kessler et al. (2016) showed that leaf beetle larvae preferred undamaged goldenrod (*Solidago altissima*) over plants previously damaged or exposed to herbivore-induced volatiles. Similarly, Wei et al. (2006) demonstrated that infestation of *Phaseolus vulgaris* by agromyzid flies (*Liriomyza sativae* and *L. huidobrensis*) altered the volatile profile of the plant and reduced host attractiveness. However, contrasting results have also been reported, as herbivore-induced volatiles (HIPVs) may attract both herbivores and natural enemies. For instance, green peach aphids (*Myzus persicae*) and their parasitoids (*Aphidius colemani* and *Aphelinus abdominalis*) were significantly attracted to VOCs from infested cabbage plants (Ahmed et al., 2022). In addition, Carroll et al. (2006) found that *Spodoptera frugiperda* larvae were more strongly attracted to caterpillar-damaged maize seedlings than to undamaged ones, and parasitoids such as *Cotesia marginiventris* consistently preferred HIPVs from host-infested maize compared to healthy plants (Turlings et al., 1990). Likewise, Liu et al. (2024) showed that damaged tea plants emitted elevated levels of S-linalool and  $\beta$ -ocimene, which enhanced parasitoid wasps' attraction for suppressing *Ectropis obliqua* infestations.

When comparing the VOC blend of different chickpea genotypes, our bioassays indicated that *L. cicerina* adults tended to prefer VOC blends emitted by the susceptible variety, although this difference was not statistically significant. This suggests that intraspecific variation in volatile emissions may influence host selection by the insect. Similar patterns have been reported in other plant–insect interactions, where susceptible plants emitted more attractive volatile blends. For example, Wu et al. (2024) showed that the mirid bug *Apolygus lucorum* preferred VOCs from a susceptible cotton cultivar, which emitted a broader range and higher amounts of volatiles overall, over a resistant one, with specific compounds unique to the susceptible genotype eliciting

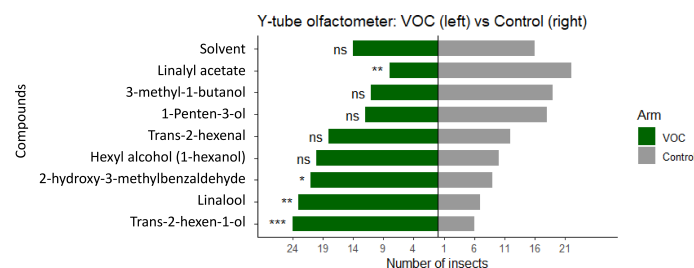


FIGURE 5

Behavioral responses of *Liriomyza cicerina* adults to chickpea volatiles and solvent (dichloromethane) in the Y Tube olfactometer. The asterisks indicate the significance levels (\* = significant at 0.05, \*\* = significant at 0.01, and \*\*\* = significant at 0.001). (N = 30 adults tested).

attraction in Y-tube assays. Such observations support the idea that susceptible plants may offer stronger or more visible olfactory cues that facilitate host location by herbivorous insects. Likewise, [Paterska et al. \(2025\)](#) demonstrated that horse chestnut tree susceptible to the leafminer *Cameraria ohridella* (Lepidoptera: Gracillariidae) released more diverse and abundant VOC blends than resistant trees, especially during peak leafminer activity. Comparable findings were reported by [Poelman et al. \(2009\)](#), who observed that herbivore-susceptible *Brassica oleracea* cultivars emitted higher levels of specific terpenoids that were more attractive to *Cotesia* parasitoids, resulting in higher parasitism rates both in laboratory assays and field conditions. It is important to note that genetic variation in VOC emission observed under controlled laboratory conditions does not always translate to significant ecological effects in the field. For instance,

[Degen et al. \(2012\)](#) found no consistent differences in natural enemy attraction among genotypes, suggesting that environmental factors may mask plant-genotypic effects in real conditions. Furthermore, the increased attractiveness of susceptible genotypes may not be explained by overall VOC abundance, but rather by differences in the blend composition and relative ratios of specific compounds. This agrees with reports show that insect responses to plant odors are often non-linear and depend on blend context rather than the presence of individual compounds alone ([Gols et al., 2011](#); [Wason and Hunter, 2014](#); [De Lange et al., 2019](#)). Although no statistically significant preference was observed, subtle behavioral trends may reflect underlying biochemical differences among genotypes. Plant resistance is often associated with variation in secondary metabolites, such as phenolics and other defensives compounds, which can influence insect host selection ([Brahmi et al., 2021](#)).

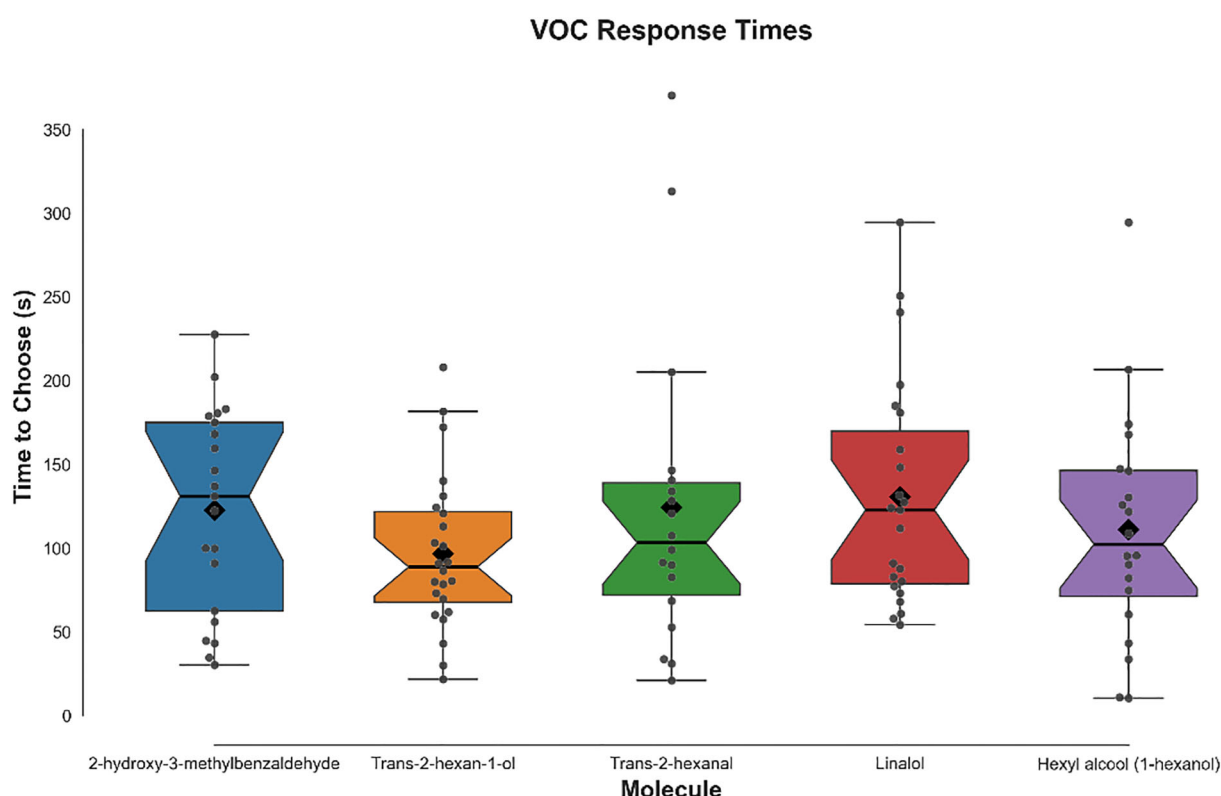


FIGURE 6

Leafminer adults' response time to attractive volatiles in a Y-tube olfactometer. Boxplots represent median, interquartile range, and minimum-maximum values. Black diamonds indicate the mean response time. Individual dots represent single insect observations.

These compounds may mediate resistance through antibiosis, by negatively affecting insect survival, growth, or reproduction, and through antixenosis, by deterring host preference and feeding. Further biochemical characterization would be required to clarify these relationships and determine the mechanisms underlying genotype-specific responses.

The olfactometer assays assessed in this study show distinct effects of individual volatiles on leafminer adult behavior. Specifically, the green leaf alcohol trans-2-hexen-1-ol, the monoterpene linalool, and the benzenoid derivative 2-hydroxy-3-methylbenzaldehyde elicited strong attraction in *L. cicerina*. Hexyl alcohol (1-hexanol) and trans-2-hexenal also tended to attract adults, although their effects were not statistically significant. In contrast, linalyl acetate, 3-methyl-1-butanol, and 1-penten-3-ol consistently produced repellent responses.

These results advance our understanding of host-location mechanisms in this species, and both corroborate and contrast with previous reports on the ecological roles of plant VOCs in mediating insect preference. For instance, our findings regarding linalool align with earlier studies identifying this compound as a strong attractant in diverse insect–plant systems. Reisenman et al. (2010) reported linalool as an oviposition attractant for female *Manduca sexta* moths (Lepidoptera: Sphingidae), while Niogret and Epsky (2018) showed that it was highly attractive to sterile males of *Ceratitis capitata* (Diptera: Tephritidae), with its effectiveness comparable to that of multi-component volatile blends from essential oils, particularly ginger root oil, typically employed in trap baits. Yuan et al. (2008) demonstrated that linalool emitted by rice plants upon the fall armyworm, *Spodoptera frugiperda*, (J.E. Smith, 1797) (Lepidoptera: Noctuidae) attack as an indirect defense strategy attracts parasitoid wasps *Cotesia marginiventris* (Hymenoptera: Braconidae), as confirmed by GC-EAD and behavioral assays. Nevertheless, opposite effects have also been documented. Papanastasiou et al. (2020) demonstrated that linalool acts as an oviposition deterrent to female *Ceratitis capitata* (Diptera: Tephritidae). Field trials also showed decreased female captures on linalool-treated trees, further supporting its role as a repellent or deterrent. Likewise, Wu et al. (2024) found that linalool emitted by cotton plants significantly repelled *Apolygus lucorum* (Hemiptera: Miridae), suggesting that its effects on insect behavior depend on its concentration, enantiomeric form, and ecological context.

Regarding the effect of trans-2-hexen-1-ol, our results indicate that this compound exerts a strong attractive effect on *L. cicerina* adults. Consistent with this, Yan et al. (2023) identified trans-2-hexen-1-ol, a green leaf volatile (GLV) commonly released by mechanically damaged or herbivore-attacked leaves, as one of the most potent attractants for the diamondback moth *Plutella xylostella* (Lepidoptera: Plutellidae). Electrophysiological and behavioral assays confirmed strong antennal responses and attraction under laboratory conditions, and field-trapping experiments further validated its effectiveness in attracting adult moths. Similarly, Song et al. (2025) demonstrated antennal responses of *Athetis dissimilis* (Lepidoptera: Noctuidae) to this compound, supporting its role as a key GLV cue in mediating insect orientation behavior.

Our assays also showed that 2-hydroxy-3-methylbenzaldehyde was attractive to *L. cicerina*. While this compound has been reported in the headspace of several plant species and identified in plant extracts with larvicidal activity against mosquitoes (Remia and Logaswamy, 2010), its role as an olfactory cue remains largely unexplored. Moreover, our olfactometer results showed only weak, non-significant attraction of 1-hexanol and trans-2-hexenal. Nevertheless, other studies have reported significant behavioral responses to these volatiles. For example, Bueno et al. (2023) found that *Lutzomyia longipalpis* (Diptera: Psychodidae) females were strongly attracted to 1-hexanol, particularly at higher release rates. Similarly, Rharrabe et al. (2014) observed that 1-hexanol induced attraction in *Spodoptera littoralis* larvae (Lepidoptera: Noctuidae) in a dose-dependent manner, while Jian et al. (2025) showed that in both Y-tube assays and field experiments, 1-hexanol from *Acacia confusa* (an intercropping plant in tea plantations) enhanced the attraction of tea leafhoppers and acts as a host-location or feeding attractant.

Concerning trans-2-hexenal, our findings agree with Onnink et al. (2017), who demonstrated the attractiveness of this molecule to female *Megacopta cribraria* (Hemiptera: Plataspidae). Similarly, Huang et al. (2022) have reported that trans-2-hexenal was attractive to the aphid *Acyrtosiphon pisum* (Harris, 1776) (Hemiptera: Aphididae). Contrasting evidence has also been reported. For instance, Bian et al. (2025) showed that trans-2-hexenal exerted a highly significant repellent effect on *Aphis gossypii* (Hemiptera: Aphididae) in Y-tube assays. Similarly, Chen et al. (2015) demonstrated that trans-2-hexenal produced extremely high deterrence rates (96–98%) in *Bradysia odoriphaga* adults (Diptera: Sciaridae), in addition to pronounced fumigant toxicity and strong antennal responses, underscoring its potential as both a repellent and toxicant. Additionally, Cui et al. (2021) reported that while trans-2-hexenal exhibited weak repellency to *Tribolium castaneum* (Coleoptera: Tenebrionidae), it exhibited potent fumigant and insecticidal effects against several developmental stages of *T. castaneum*.

Our results indicate that linalyl acetate, 1-penten-3-ol, and 3-methyl-1-butanol act as repellents to *Liriomyza cicerina*, suggesting that these compounds may play a defensive role in chickpea plant by limiting leafminer infestation. Our findings regarding linalyl acetate are consistent with those of Wang et al. (2024), who reported its repellent effect on *Drosophila suzukii* (Diptera: Drosophilidae). However, they differ from the results of Hamamura and Naito (1961), who identified linalyl acetate as attractants for silkworm, *Bombyx mori* (Lepidoptera: Bombycidae), larvae suggesting its role as a chemical cue in host plant recognition.

In contrast, 1-penten-3-ol is frequently described as a green leaf volatile attractive to herbivores such as *Plutella xylostella* (L.) (Lepidoptera: Plutellidae) (Yan et al., 2023) and tea pests (Han et al., 2012), influencing host location and feeding behavior, and it has also been shown to function as a kairomone cue that enhances parasitoid activity when incorporated into synthetic volatile blends in tea systems (Wu et al., 2022). Collectively, these contrasting outcomes emphasize that the behavioral responses to VOCs are strongly influenced by insect sensory ecology, compound

concentration, and the blend composition. The present study focused on behavioral responses to selected volatile compounds previously identified in chickpea. However, quantitative GC-MS analysis was not conducted to characterize VOC emission profile from the specific genotypes or infested plants. Therefore, although the observed behavioral responses suggest that these compounds may contribute to host selection, further chemical characterization is necessary to confirm their emission patterns and relative abundance in healthy versus infested plants. Integrating detailed VOC profiling with behavioral and field validations experiments would strengthen our understanding of genotype and infestation related differences and support the development of sustainable IPM strategies.

In addition, males and females' adults of leafminer were pooled to evaluate general orientation responses. Sex- specific behavioral differences may occur, particularly if oviposition cues primarily drive female attraction. Future studies should therefore evaluate male and female responses separately and test binary or multi-component blends to determine potential synergistic or antagonistic interactions among VOCs. Because insect responses often depend on blend composition and relative ratios rather than individual compounds alone, such approaches would improve the ecological relevance and practical application of these semiochemicals.

## 5 Conclusion

This study enhances our understanding of the ecological role of volatile organic compounds (VOCs) in mediating chickpea–leafminer interactions, demonstrating that plant genotype, health status, and specific volatile identity strongly influence insect behavior.

We demonstrated that *Liriomyza cicerina* adults respond differentially to individual volatiles: linalyl acetate elicited the strongest repellent effect, whereas compounds such as trans-2-hexen-1-ol, linalool, and 2-hydroxy-3-methylbenzaldehyde significantly attracted adults. Moreover, leafminers were more attracted to healthy than infested plants, suggesting that herbivory suppresses attractive volatile emissions or induces repellent molecules. Intraspecific variation among chickpea genotypes also shaped insect preference, with susceptible varieties possibly emitting more attractive blends, supporting the hypothesis that host susceptibility may be linked to qualitative and quantitative differences in VOC emissions, although this was not quantified by GC analysis.

Overall, these findings clarify host-location mechanisms in *L. cicerina* and identify key VOCs with potential applications for pest management. Breeding or selecting chickpea lines with less attractive VOC profiles could reduce pest pressure, while attractive compounds may serve as lures in monitoring or push–pull systems. Conversely, repellent VOCs could be incorporated into intercropping or behavioral disruption strategies. Future research should validate these approaches under semi or field conditions, quantify VOCs emission using GC analysis, evaluate synthetic blends across genotypes and infestation stages, and confirm antennal sensitivity to candidate compounds. Together,

these steps will support the development of VOC-based, sustainable management strategies for chickpea leafminer.

## Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author.

## Author contributions

LM: Methodology, Investigation, Writing – original draft, Data curation, Visualization. KE: Conceptualization, Writing – review & editing, Methodology, Supervision. RB: Investigation, Writing – review & editing. MO: Writing – review & editing, Formal analysis, Visualization. IM: Funding acquisition, Validation, Writing – review & editing. S-AK: Conceptualization, Writing – review & editing. ME: Writing – review & editing, Conceptualization.

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## Conflict of interest

The authors declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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## Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2026.1806412/full#supplementary-material>

## References

- Ahmed, Q., Agarwal, M., Alobaidi, R., Zhang, H., and Ren, Y. (2022). Response of aphid parasitoids to volatile organic compounds from undamaged and infested Brassica oleracea with *Myzus persicae*. *Molecules* 27, 1522. doi: 10.3390/molecules27051522
- Bian, Z., Zhang, Y., Liu, B., Zhang, T., Yuan, H., and Lu, Y. (2025). Exploring repellency of odors from non-host plants native to Xinjiang, China to *Aphis gossypii*. *Front. Plant Sci.* 16. doi: 10.3389/fpls.2025.1563752
- Brahmi, H., Lazraq, A., Boulamtat, R., El Fakhouri, K., Bassi, F. M., and El Bouhssini, M. (2021). Effect of temperature on the expression of resistance to Hessian fly (Diptera: Cecidomyiidae) in durum wheat cultivars. *Phytoparasitica* 49, 357–362. doi: 10.1007/s12600-020-00877-6
- Bueno, A. C., Machado, V. E., and da Rocha Silva, F. B. (2023). Semiochemical delivery systems based on natural polymers to attract sand flies (Diptera: Psychodidae). *Parasites Vectors* 16, 303. doi: 10.1186/s13071-023-05931-w
- Carroll, M. J., Schmelz, E. A., Meagher, R. L., and Teal, P. E. A. (2006). Attraction of *Spodoptera frugiperda* larvae to volatiles from herbivore-damaged maize seedlings. *J. Chem. Ecol.* 32, 1911–1924. doi: 10.1007/s10886-006-9117-9
- Ceylan, F. Ö., Sari, H., Sari, D., Adak, A., Erler, F., and Toker, C. (2018). Revealing of resistant sources in Cicer species to chickpea leaf miner, *Liriomyza cicerina* (Rondani). *Phytoparasitica* 46, 635–643. doi: 10.1007/s12600-018-0699-x
- Chen, C., Mu, W., Zhao, Y., Li, H., Zhang, P., Wang, Q., et al. (2015). Biological activity of trans-2-hexenal against *Bradysia odoriphaga* (Diptera: Sciaridae) at different developmental stages. *J. Insect Sci.* 15, iev075. doi: 10.1093/jisesa/iev075
- Chrigui, N., Sari, D., Sari, H., Eker, T., Cengiz, M. F., Ikten, C., et al. (2021). Introgression of resistance to leafminer (*Liriomyza cicerina* Rondani) from *Cicer reticulatum* Ladiz. to *C. arietinum* L. and relationships between potential biochemical selection criteria. *Agronomy* 11, 57. doi: 10.3390/agronomy11010057
- Cruz, A. F., Hamel, C., Yang, C., Matsubara, T., Gan, Y., Singh, A. K., et al. (2012). Phytochemicals to suppress Fusarium head blight in wheat–chickpea rotation. *Phytochemistry* 78, 72–80. doi: 10.1016/j.phytochem.2012.03.003
- Cui, K., He, L., Cui, G., Zhang, T., Chen, Y., Zhang, T., et al. (2021). Biological activity of trans-2-hexenal against the storage insect pest *Tribolium castaneum* (Coleoptera: Tenebrionidae) and mycotoxigenic storage fungi. *J. Econ. Entomol.* 114, 979–987. doi: 10.1093/jee/toab001
- De Lange, E. S., Salamanca, J., Polashock, J., and Rodriguez-Saona, C. (2019). Genotypic variation and phenotypic plasticity in gene expression and emissions of herbivore-induced volatiles, and their potential tritrophic implications, in cranberries. *J. Chem. Ecol.* 45, 298–312. doi: 10.1007/s10886-018-1043-0
- Degen, T., Bakalovic, N., Bergvinson, D., and Turlings, T. C. (2012). Differential performance and parasitism of caterpillars on maize inbred lines with distinctly different herbivore-induced volatile emissions. *PLoS One* 7, e47589. doi: 10.1371/journal.pone.0047589
- El Bouhssini, M., Mardini, K., Malhotra, R. S., Joubi, A., and Kagka, N. (2008). Effects of planting date, varieties and insecticides on chickpea leaf miner (*Liriomyza cicerina* R.) infestation and the parasitoid *Opius monilicornis* F. *Crop Prot.* 27, 915–919. doi: 10.1016/j.cropro.2007.11.006
- Erler, F., Ceylan-Baloglu, F. O., Erdemir, T., and Toker, C. (2009). Preliminary results on evaluation of chickpea, *Cicer arietinum*, genotypes for resistance to the pulse beetle, *Callosobruchus maculatus*. *J. Insect Sci.* 9, 58. doi: 10.1673/031.009.5801
- Food and Agriculture Organization (FAO) (2025). *FAOSTAT Database: Crops and livestock products*. Available online at: <https://www.fao.org/faostat/en/#data/QCL> (Accessed January 15, 2026).
- Gasiński, A., Noguera-Artiaga, L., and Kawa-Rygielska, J. (2025). Influence of malted chickpea on the composition of volatiles in hummus. *Molecules* 30, 1231. doi: 10.3390/molecules30061231
- Gols, R., Bullock, J. M., Dicke, M., Bukovinsky, T., and Harvey, J. A. (2011). Smelling the wood from the trees: non-linear parasitoid responses to volatile attractants produced by wild and cultivated cabbage. *J. Chem. Ecol.* 37, 795–807. doi: 10.1007/s10886-011-9993-5
- Hamamura, Y., and Naito, K. (1961). Food selection by silkworm larvae, *Bombyx mori*: Citral, linalyl acetate, linalol, and terpinyl acetate as attractants of larvae. *Nature* 190, 879–880. doi: 10.1038/190879a0
- Han, B., Zhang, Q. H., and Byers, J. A. (2012). Attraction of the tea aphid, *Toxoptera aurantii*, to combinations of volatiles and colors related to tea plants. *Entomol. Exp. Appl.* 144, 258–269. doi: 10.1111/j.1570-7458.2012.01303.x
- Huang, T. Y., Zhang, R. B., Yang, L. L., Song, C., Francis, F., and Bing, W. (2022). Identification and functional characterization of *ApiOr23* in pea aphid *Acyrtosiphon pisum*. *J. Integr. Agr.* 21, 1414–1423. doi: 10.1016/S2095-3119(20)63577-8
- Jian, G., Li, J., and Wu, Y. (2025). Mechanism mediating the biosynthesis of the anti-insect volatile (Z)-3-hexenyl acetate in *Acacia confusa* Merr. an intercropping plant in tea plantations. *Mol. Hortic.* 5, 47. doi: 10.1186/s43897-025-00165-z
- Karolkowski, A., Guichard, E., Briand, L., and Salles, C. (2021). Volatile compounds in pulses: a review. *Foods* 10, 3140. doi: 10.3390/foods10123140
- Kessler, A., Mueller, M. B., Kalske, A., and Chautá, A. (2023). Volatile-mediated plant–plant communication and higher-level ecological dynamics. *Curr. Biol.* 33, R519–R529. doi: 10.1016/j.cub.2023.03.045
- Khrisanapant, P., Kebede, B., Leong, S. Y., and Oey, I. A. (2019). Comprehensive characterisation of volatile and fatty acid profiles of legume seeds. *Foods* 8, 651. doi: 10.3390/foods8120651
- Liu, G., Wang, Q., Chen, H., Wang, Y., Zhou, X., Bao, D., et al. (2024). Plant-derived monoterpene S-linalool and  $\beta$ -ocimene generated by CsLIS and CsOCS-SCZ are key chemical cues for attracting parasitoid wasps for suppressing *Ectropis obliqua* infestation in *Camellia sinensis* L. *Plant Cell Environ.* 47, 913–927. doi: 10.1111/pce.14803
- Makhlouf, L., El Fakhouri, K., Kemal, S. A., Aasfar, A., Meftah Kadmiri, I., and El Bouhssini, M. (2024a). Advances in analytical techniques for assessing volatile organic compounds in pulse crops: a comprehensive review. *Front. Hortic.* 3. doi: 10.3389/fevo.2024.1394041
- Makhlouf, L., El Fakhouri, K., Kemal, S. A., Maafa, I., Meftah Kadmiri, I., and El Bouhssini, M. (2024b). Potential of volatile organic compounds in the management of insect pests and diseases of food legumes: a comprehensive review. *Front. Plant Sci.* 15. doi: 10.3389/fpls.2024.1430863
- Morrell, K., and Kessler, A. (2016). Plant communication in a widespread goldenrod: keeping herbivores on the move. *Funct. Ecol.* 31, 1049–1061. doi: 10.1111/1365-2435.12793
- Muehlbauer, F. J., and Sarker, A. (2017). “Economic importance of chickpea: Production, value, and world trade,” in *The chickpea genome* (Cham, Switzerland: Springer), 5–12. doi: 10.1007/978-3-319-66117-9\_2
- Niogret, J., and Epsky, N. D. (2018). Attraction of *Ceratitis capitata* (Diptera: Tephritidae) sterile males to essential oils: The importance of linalool. *Environ. Entomol.* 47, 1287–1292. doi: 10.1093/ee/nvy096
- Onnink, C. M., Williams, A. A., and Williams, J. S. (2017). Electrophysiological and behavioral evidence for (E)-2-hexenal as a female-attracting pheromone produced by disturbed *Megacopta cribraria* (Hemiptera: Plataspidae). *J. Entomol. Sci.* 52, 39–51. doi: 10.18474/JES16-18.1
- Oubayoucef, A., Boulamtat, R., El-Fakhouri, K., Lhaloui, S., Dakka, N., and El-Bouhssini, M. (2022). Effect of chickpea genotypes on *Liriomyza cicerina* oviposition preference and insect performance. *J. Entomol. Acarol. Res.* 54, 9532. doi: 10.4081/jear.2022.9532

- Papanastasiou, S. A., Ioannou, C. S., and Papadopoulos, N. T. (2020). Oviposition-deterrent effect of linalool - a compound of citrus essential oils - on female Mediterranean fruit flies, *Ceratitis capitata* (Diptera: Tephritidae). *Pest Manag. Sci.* 76, 3066–3077. doi: 10.1002/ps.5858
- Paterska, M., Bandurska, H., Dziadas, M., Zawieja, B., and Chadzinikolau, T. (2025). Analysis of the profile of volatile compounds during the growing season in leaves of Aesculus trees differing in susceptibility to horse chestnut leaf miner (*Cameraria ohridella* Deschka & Dimić). *Molecules* 30, 518. doi: 10.3390/molecules30030518
- Poelman, E. H., Oduor, A. M. O., Broekgaarden, C., Hordijk, C. A., Jansen, J. J., van, L. J., et al. (2009). Field parasitism rates of caterpillars on Brassica oleracea plants are reliably predicted by differential attraction of *Cotesia* parasitoids. *Funct. Ecol.* 23, 951–962. doi: 10.1111/j.1365-2435.2009.01570.x
- Reisenman, C. E., Riffell, J. A., Bernays, E. A., and Hildebrand, J. G. (2010). Bernays EA and Hildebrand JG, antagonistic effects of floral scent in an insect-plant interaction. *Proc. R. Soc. B. Biol. Sci.* 277, 2371–2379. doi: 10.1098/rspb.2010.0163
- Rembold, H., Wallner, P., Nitz, S., Kollmannsberger, H., and Drawert, F. (1989). Volatile components of chickpea (*Cicer arietinum* L): Seed. *J. Agric. Food. Chem.* 37, 659–662. doi: 10.1021/jf00087a018
- Remia, K. M., and Logaswamy, S. (2010). Larvicidal efficacy of leaf extract of two botanicals against the mosquito vector *Aedes aegypti* (Diptera: Culicidae). *Indian J. Nat. Prod. Res.* 1, 208–212.
- Rharrabe, K., Jacquin-Joly, E., and Marion-Poll, F. (2014). Electrophysiological and behavioral responses of *Spodoptera littoralis* caterpillars to attractive and repellent plant volatiles. *Front. Ecol. Evol.* 2. doi: 10.3389/fevo.2014.00005
- Sabraoui, A., Lhaloui, S., and Bouchelta, A. (2019). El Fakhouri K and El Bouhssini M, grain yield losses due to leaf miner (*Liriomyza cicerina* R.) in winter- and spring-planted chickpea in Morocco. *Crop Prot.* 117, 115–120. doi: 10.1016/j.cropro.2018.04.004
- Soltani, A., Ben Abda, M., Amri, M., Carapelli, A., and Mediouni Ben Jemâa, J. (2020). Seasonal incidence of the leaf miner *Liriomyza cicerina* Rond (Diptera: Agromyzidae) in chickpea fields and effects of climatic parameters, chickpea variety, and planting date on the leaf miner infestation rate. *Euro-Mediterr. J. Environ. Integr.* 5, 58. doi: 10.1007/s41207-020-00198-4
- Soltani, A., Yangu, I., Haouel Hamdi, S., Sahbani, Z., Mesaoud, C., and Mediouni Ben Jemâa, J. (2021). Secondary metabolites fluctuation caused by *Liriomyza cicerina* (Diptera: Agromyzidae) infestation in chickpea, faba bean and lentil crops. *Int. J. Trop. Insect Sci.* 42, 1105–1112. doi: 10.1007/s42690-021-00626-0
- Song, Y. Q., Zhang, T. S., Yuan, H. Z., Han, S. J., and Li, B. L. (2025). Electroantennographic response and odorant-binding protein expression alterations induced by host plant volatiles in *Aethis dissimilis* (Hampson). *Front. Physiol.* 16. doi: 10.3389/fphys.2025.1619418
- Toker, C., Canci, H., and Yildirim, T. (2007). Evaluation of perennial wild Cicer species for drought resistance. *Genet. Resour. Crop Evol.* 54, 1781–1786. doi: 10.1007/s10722-006-9197-y
- Toker, C., Erler, F., Canci, H., and Ceylan, F. O. (2010). Severity of leaf miner (*Liriomyza cicerina* Rond.) damage in relation to leaf type in chickpea. *Turkish J. Entomol.* 34, 211–226.
- Turlings, T. C. J., Tumlinson, J. H., and Lewis, W. J. (1990). Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250, 1251–1253. doi: 10.1126/science.250.4985.1251
- Wang, Y., Wen, F., Zhou, X., Chen, G., Tian, C., Qian, J., et al. (2024). Deterrent effects of clary sage oil and two major constituents against *Drosophila suzukii* (Diptera: Drosophilidae). *Insects* 15, 733. doi: 10.3390/insects15100733
- Wason, E. L., and Hunter, M. D. (2014). Genetic variation in plant volatile emission does not result in differential attraction of natural enemies in the field. *Oecologia* 174, 479–491. doi: 10.1007/s00442-013-2787-4
- Wei, J. N., Zhu, J., and Kang, L. (2006). Volatiles released from bean plants in response to agromyzid flies. *Planta* 224, 279–287. doi: 10.1007/s00425-005-0212-x
- Wu, J., Cao, Y., Teng, D., Shan, S., Geng, T., Huang, X., et al. (2024). Volatiles of clary sage oil and two major constituents against *Drosophila suzukii* (Diptera: Drosophilidae). *Front. Plant Sci.* 15. doi: 10.3389/fpls.2024.1428234
- Wu, Y., Han, S., Wang, M., Zhang, Q. H., and Han, B. (2022). Control of tea aphids via attracting the parasitic wasp *Aphelinus* sp. with synthetic semiochemicals. *Front. Ecol. Evol.* 10. doi: 10.3389/fevo.2022.958871
- Yan, X. Z., Ma, L., Li, X. F., Chang, L., Liu, Q. Z., Song, C. F., et al. (2023). Identification and evaluation of cruciferous plant volatiles attractive to *Plutella xylostella* L. (Lepidoptera: Plutellidae). *Pest Manag. Sci.* 79, 5270–5282. doi: 10.1002/ps.7735
- Yıldırım, E. M., Ünay, A., and Civelek, H. S. (2010). The effect of *Liriomyza trifolii* (Burgess) (Diptera: Agromyzidae) on some leaf characteristics of bean (*Phaseolus vulgaris* L.). *J. Food Agric. Environ.* 8, 839–841.
- Yuan, J. S., Köllner, T. G., Wiggins, G., Grant, J., Zhao, N., Zhuang, X., et al. (2008). Elucidation of the genomic basis of indirect plant defense against insects. *Plant Signal. Behav.* 3, 720–721. doi: 10.4161/psb.3.9.6468
- Zhang, J., Wang, J., Zhu, C., Singh, R. P., and Chen, W. (2024). Chickpea: Its origin, distribution, nutrition, benefits, breeding, and symbiotic relationship with *Mesorhizobium* species. *Plants* 13, 429. doi: 10.3390/plants13030429
- Zhao, Y. X., and Kang, L. (2002). Role of plant volatiles in host plant location of the leafminer, *Liriomyza sativae* (Diptera: Agromyzidae). *Physiol. Entomol.* 27, 103–111. doi: 10.1046/j.1365-3032.2002.00275.x