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RESEARCH ARTICLE

Citrus volatiles induced by herbivory of *Aleurothrixus floccosus* (Hemiptera: Aleyrodidae) elicit attraction to the exotic ladybird *Clitostethus arcuatus* (Coleoptera: Coccinellidae)

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ABSTRACT

Plants undergoing insect infestation release herbivore-induced plant volatiles (HIPVs) into their environment, which are then used by natural enemies for their benefit. The pest *Aleurothrixus floccosus*, which affects citrus orchards in northern Chile, specifically at Pica Oasis, poses a year-round threat. Recently, the introduction of the exotic ladybird *Clitostethus arcuatus* has been noted as a predator of *A. floccosus*. This study delved into how HIPVs emitted from tangelo (*Citrus reticulata* × *C.* ×*paradisi* Macfad.) and lime (*C.* ×*aurantifolia* (Christm.) Swingle) infested-shoots impact the behavioral responses of *C. arcuatus*. The volatile compounds were collected using the headspace technique, revealing notable qualitative changes after herbivory. In two-choice bioassays, the HIPVs elicited an attractive response in *C. arcuatus* compared to *A. floccosus*. At concentrations of 10 and 100 µg mL^{-1}, the predators displayed a distinct preference for methyl salicylate (MeSA). These findings underscore that *C. arcuatus* exploits the HIPVs emitted from citrus infested-shoots, fostering tritrophic interactions. Exploring the impact of whitefly attacks on other fruit trees, emerges as a significant avenue for future investigation.

Key words: Arid agroecosystems and tritrophic interactions, citrus, *C.* ×*aurantifolia*, *Citrus reticulata* × *C.* ×*paradisi*, herbivore-induced plant volatiles, lime, tangelo, volatile organic compounds, woolly whitefly.

INTRODUCTION

The whitefly predator specialist, *Clitostethus arcuatus* (Rossi) (Coleoptera: Coccinellidae), exhibits an extensive distribution that encompasses diverse regions. It is commonly found in the Palearctic area, spanning from various parts of Europe and the Mediterranean to the Northwestern Caucasus. Additionally, this species has been observed in North America specifically in California, as well as in South America, including Argentina, Bolivia, Chile, and Peru (Iqbal et al., 2018; Akhatov and Korotyaev, 2019). This Aleyrodids predator has been observed feeding on all stages of *Aleurothrixus floccosus*, *Siphoninus phillyreae* (Haliday), *Bemisia tabaci* (Gennadius), *Trialeurodes vaporariorum* (Westwood), *Dialeurodes citri* (Ashmead), *Aleurodes proletella* (Linnaeus), *Trialeurodes lauri* (Signoret) and *Aleurocanthus spiniferus* (Quaintance) (Cioffi et al., 2013; Rioja and Ceballos, 2023), even preying on eggs of *Tetranychus urticae* Koch (Acari: Tetranychidae) and aphids (Akhatov and Korotyaev, 2019). In 1995, the exotic ladybird *C. arcuatus* was introduced in Chile for regular biological control to manage the ash whitefly *S. phillyreae*. The releases took place in Santiago city (33°27' S, 70°39' W; 572 m a.s.l.) and Azapa Valley in 2008 (18°30' S, 70°11' W; 369 m a.s.l.) The ladybirds established populations in these areas and eventually expanded to invade and colonize Pica Oasis (19°58' S, 69°46' W; 1117 m a.s.l.) located in the Atacama Desert (Rioja and Ceballos, 2023).

The citrus woolly whitefly *A. floccosus*, on the other hand, is a serious foliar pest worldwide, observed in Africa, Asia, Mediterranean countries and Neotropical region, including USA (Rioja and Ceballos, 2023). Although this pest has been identified in 30 plant families, it has a strong preference for citrus species as lemon (*Citrus* ×*limon* (L.) Burm. f.), lime (*Citrus* ×*aurantifolia* (Christm.) Swingle), mandarin (*Citrus reticulata* Blanco), orange (*Citrus* ×*sinensis* (L.) Osbeck), tangelo (*Citrus reticulata* × *Citrus* ×*paradisi*), and grapefruit (*Citrus* ×*paradisi* Macfad.) (Evans, 2007; Rioja et al., 2021). In northern regions of Chile, *A. floccosus* has several generations per year, infesting commercial citrus orchards at Pica Oasis persistently (Rioja and Ceballos, 2023; we henceforth). In relation to woolly whitefly natural enemies, we found mainly the micro hymenopterans *Cales noacki* Howard (Aphelinidae) and *Amitus spiniferus* Brèthes (Platygasteridae) parasitizing *A. floccosus* nymphs at Pica Oasis. Furthermore, it has been reported that the hyperparasitoid *Signiphora* sp. (Chalcidoidea: Signiphoridae) affects micro wasps (Ripa and Larral, 2008), whereas *C. arcuatus* has been observed preying on all stages of the woolly whitefly on citrus trees (Rioja and Ceballos, 2023).

Previous research has established that plants emit constitutively volatile organic compounds (VOCs) into the environment (Conchou et al., 2019; Zhou and Jander, 2022). These volatiles not only reflect the metabolic complexity of plants but also constitute a part of the defense arsenal against biotic (herbivory and pathogen attack) as well as abiotic factors (i.e., temperature, nutrients, and radiation) (He et al., 2018; Ceballos et al., 2023). In contrast, herbivorous insects use these plant volatiles as chemical cues to find suitable hosts and shelters for their offspring (Peterson et al., 2020). However, the process of insect feeding and egg laying trigger cascades of reactions at molecular and physiological levels, enhancing both direct and indirect defense mechanisms (Pashalidou et al., 2020; Ninkovic et al., 2021). The volatiles emitted from infested plants, which undergo qualitative and quantitative changes compared to those from undamaged plants, are referred to as herbivore-induced plant volatiles (HIPVs). These HIPVs are composed of terpenoids, green leaf volatiles (GLVs), jasmonates and aromatic compounds, playing a role in chemically triggering tritrophic interactions (Aartsma et al., 2017; Takabayashi and Shiojiri, 2019; Matsui and Engelberth, 2022; Zhou and Jander, 2022). Therefore, through this altered chemical profile, plants are capable of recruiting predators and parasitoids as ‘bodyguards’ to protect themselves against the herbivory damage. Natural enemies associate these HIPVs with prey availability, stimulating eggs laying and development, and settling on the infested plants (Hilker and Fatouros, 2015). Some studies have reported that the coleopterans *Harmonia axyridis* (Pallas) (Coccinellidae), *Coccinella septempunctata* L. (Coccinellidae), *Parastethorus histrio* (Coccinellidae) and *Oligota pygmaea* (Solier) (Staphylinidae) have shown attraction toward HIPVs emitted from infested plants (Rioja et al., 2018; Xiu et al., 2019). Currently, there is a lack of research on *A. floccosus* predators, which creates a significant research gap. It is crucial to understand how these exotic predators utilize chemical cues to locate their prey in isolated agroecosystems such as Pica oasis. Addressing this gap would contribute to a better comprehension of predator-prey dynamics in these environments.

While HIPVs can be specific for each natural enemy species associated with a plant-herbivore model, the presence of both native and exotic insects engaging in herbivory weakens the tritrophic interactions, avoiding the recruitment of native parasitoids (Thompson et al., 2022). In contrast to native predators, some exotic invasive species such as *Harmonia axyridis* (Coleoptera: Coccinellidae) improve their performance in the presence of chemical signals from infested plants (Rondoni et al., 2017). Hence, research conducted at a third trophic level is necessary to develop effective integrated pest management programs (IPM) and to attain an integration of natural enemies to an efficient habitat management. Based on this context, we hypothesized that *C. arcuatus* is guided to their prey by HIPVs emitted from lime and tangelo shoots infested by *A. floccosus*; consequently, our aim was to determine attraction of *C. arcuatus* by the HIPVs emitted from citrus infested shoots with the woolly whitefly.

MATERIALS AND METHODS

Citrus plants and growth conditions

We used 2-yr-old tangelo plants (*Citrus reticulata* × *C.* ×*paradisi* Macfad.) 'Minneola', and lime (*C.* ×*aurantifolia* (Christm.) Swingle) ecotype 'Limón de Pica'. The citrus plants were grafted on *C. macrophylla* Wester rootstock growing in 20 L pots filled with sand and organic soil; plants were fertilized and irrigated suitably, and kept in anti-aphid screen greenhouses at Huayquique (20°16' S; 70°07' W), Iquique, Tarapacá Region, Chile.

Whiteflies and predators used in bioassays

The wooly citrus whitefly *Aleurothrixus floccosus* (Maskell) (Hemiptera: Aleyrodidae) and the exotic predator *Clitostethus arcuatus* (Rossi) (Coleoptera: Coccinellidae) were collected in citrus orchards at Pica Oasis (19°58' S; 69°46' W), Tarapacá Region, Chile, during the summer of 2021. We cut off orange (*C.* ×*sinensis* (L.) Osbeck) twigs infested with third or fourth nymph stages of *A. floccosus*, which were placed into Flanders cages (50 × 30 × 40 cm) under laboratory conditions. The cages had a glass top and two muslin sleeves on the side and the laboratory conditions were set at 25 ± 2 °C, 60 ± 10% (RH) and 16:8 h photoperiod. We monitored cages daily until the whiteflies emerged. Once the insects had emerged, we transferred them to another Flanders cage containing orange twigs to provide them with a feeding source.

To collect colonizing ladybirds of *C. arcuatus* from young sucker branches infested by adults of wooly citrus whitefly, we used a manual entomological aspirator. The predators were then placed in plastic containers filled with strip paper, which were kept inside a cooler to avoid stress between them. The collected ladybirds were carried to an isolated anti-aphid screen greenhouse (4 × 4 × 2 m) at Huayquique, and were released on broadleaf plantain (*Plantago major* L.) and eggplant (*Solanum melongena* L. 'Early long purple') plants, both of which were infested by the silverleaf whitefly *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae). These plants were cultivated in pots filled with a mixture of peat moss and perlite (3:1). Prior to releasing the predators, we examined the undersides of the leaves on all plants using a 10X handheld magnifying glass to confirm the presence of whitefly eggs. This ensured that there were sufficient eggs available for ladybirds' sustenance.

Herbivory treatment

All plants were cultivated in greenhouses under semi-field conditions. Following 1 mo acclimation, the plants were labeled and randomly allocated to two treatments: Control (uninfested) or herbivory (infested by *A. floccosus*). The labeled plants were distributed across three separate greenhouses: One for tangelo, another for limes and a third for control plants. In addition, a shoot from the middle zone of each citrus plant with 10 to 14 fully expanded yellowish green leaves was selected and considered as a replicate to collect volatile organic compounds (VOCs) (Rioja et al., 2021). To induce herbivory, the following procedure was as follows: Groups of 15 *A. floccosus* females per leaf were placed on a selected citrus shoot. This shoot was then enclosed in a muslin sleeve to prevent the escape of whiteflies. Consequently, the females remained confined for a period of 3 d before the collection of volatiles. Throughout the VOCs collection process, all plants were correctly watered and received fertilization.

Volatile organic compounds collection under semi-field conditions

Collections were performed in vivo using the dynamic headspace technique. We enclosed a selected citrus shoot with 10-14 leaves (4-mo-old) per plant in a polyethylene terephthalate (PET) bottle (1.5 L), cut vertically into halves and wrapped with para-film tape. Purified air (Charcoal filter, 8-20 mesh, Sigma-Aldrich, St. Louis, Missouri, USA) was pumped into the PET bottle at 1000 mL min^{-1}; simultaneously, the inner air from inside the bottle was extracted at 900 mL min^{-1} using a vacuum pump (BOECO, Hamburg, Germany). Plant volatiles were collected in a chemical trap which consisted of a 13 cm × 5 mm glass tube filled with 100 mg Porapak Q 80-100 mesh. This trap was positioned in a custom-made opening at the bottom of the bottle. Immediately after collection, the volatiles were eluted from the trap by passing 1 mL of re-distilled hexane (chromatographic grade, Optima Scientific, Green Bay, Wisconsin, USA). The eluted extracts were stored (-20 °C) and used in behavioral tests with *C. arcuatus* and *A. floccosus* in the week following their collection.

Before use, the Porapak traps underwent meticulous cleaning by passing 1 mL ether and were conditioned at 220 °C for 2 h under a consistent flow of nitrogen. All collections were conducted over a 24 h period in January 2021, during the summer season. Temperatures and relative humidity levels were monitored using a digital thermo-hygrometer (RC-4HC, Elitech, San Jose, California, USA) inside the greenhouses. Additionally, meteorological information was obtained from a local weather station (https://agrometeorologia.cl).

Volatile organic compounds analysis

One microliter of each extract was injected into a gas chromatograph coupled to a mass spectrometer (GCMS-QP2010 Plus; Shimadzu, Tokyo, Japan). The GC was equipped with an RTx5 capillary column (30 m, 0.25 mm internal diameter, 0.25 µm film thickness, Restek Corporation, Bellefonte, Pennsylvania, USA). The oven temperature was initially set at 40 °C and held for 1 min, after which it was raised to 280 °C at a rate of 5 °C min^{-1}. We injected the samples in splitless mode using helium as carrier gas at a constant flow of 1.0 mL min^{-1}. The mass acquisition spanned from 50 to 500 m/z, and ionization was achieved through electron impact at 70 eV using an ion source maintained at 230 °C. Identification of volatiles involved matching their retention times and mass spectra with entries in the NIST database v2.0 (National Institute of Standards and Technology, Gaithersburg, Maryland, USA), along with commercial standards whenever they were available.

Behavioral response to VOCs

To assess the attraction of *C. arcuatus* toward odors emitted by citrus infested plants with *A. floccosus*, we employed a glass Y-tube as a behavioral arena (Li et al., 2014; Rioja et al., 2021), incorporating the collected extracts as stimuli. We designated each arm of the Y-tube (60° angle, 15 cm length and 2.5 cm internal diameter) as stimulus and control zones, and the base as the decision zone. We applied 50 µL citrus extracts onto a paper strip (7 cm × 5 mm, Whatman nr 1 filter paper) and placed it into a glass tube (10 cm high and 2.5 cm outer diameter) connected to the ends of opposite arms within the olfactometer. To maintain an airflow, we drew a stream of air through charcoal filters (8-20 mesh, Sigma-Aldrich, St. Louis, Missouri, USA) from the base of the Y-tube at 300 mL min^{-1} utilizing a vacuum pump (BOECO, Germany). A group of thirty gravid females of *C. arcuatus* were released at the decision zone (Rioja and Ceballos, 2023), after allowing them to 2 min for acclimation were tested for 10 min. We registered the number of insects choosing each zone of the olfactometer. Each *C. arcuatus* group (N = 20 replicates) was tested once using a different and clean olfactometer. Following a 24 h period during which the insects were exclusively fed with honey and under the same conditions described previously, we evaluated the response of *C. arcuatus* to the methyl salicylate (MeSA) commercial standard at four concentrations (1, 10, 100, and 1000 µg mL^{-1}). This compound has been identified in the infested extracts from lime and tangelo. In addition, we examined the volatiles emitted by woolly citrus whitefly; we enclosed 100 live individuals of *A. floccosus* within a glass tube (100 mm long and 10 mm diameter) for 2 h. Subsequently, this tube was connected to the stimulus arm of the olfactometer, while a stream of hexane was directed through the control arm.

The Y-tube was placed on a white surface and was rotated horizontally at an angle of 90° after each test. All bioassays were conducted between 10:00 and 15:00 h, at 25 ± 2 °C and 65 ± 5% RH. We also assessed the attraction of *A. floccosus* (groups of 30 females) as previously described, yet with the olfactometers placed on a black surface to facilitate the visualization of the whiteflies.

Statistical analyses

In addition to characterizing the profile of volatile compounds emitted by tangelo and lime, our objective was to assess the impact of *A. floccosus* herbivory on the presence (or absence) and relative abundance of VOCs on the chemical profiles of each citrus species. We pursued this objective by using Bayesian hypothesis testing (a two-sided t-test for independent samples) through the utilization of the Bayes factor.

This factor quantifies the relative predictive performance of two competing hypotheses -H_1: the abundance of a particular volatile compound is affected by herbivory, and H_0: there is no difference between uninfested and infested plants. We provided the 95% central credible intervals ($CI_{95\%}$) to estimate the means of the identified compounds.

The behavioral experiments were conducted in two stages. First, we assessed the attraction of *A. floccosus* and *C. arcuatus* to volatile extracts from plants with and without damage, of both citrus species. This was achieved using the Bayesian A/B test. Our focus was on determining whether plant volatiles elicited higher attraction than hexane (H_1; prior probability = 0.25), lower attraction than hexane (H-; prior probability = 0.25), or exhibited no difference in attraction compared to hexane (H_0; prior probability = 0.5). Second, in a separate series of experiments, we evaluated the preference of *A. floccosus* and *C. arcuatus* when concurrently exposed to volatiles from plants with and without from both citrus species. These data were analyzed using a Bayesian multinomial test, employing flat priors and assuming an initial hypothesized population frequency of 0.33 for each zone of the olfactometer. All statistical analyses were conducted in JASP version 0.17.1 software (JASP Team, University of Amsterdam, Amsterdam, The Netherlands).

RESULTS

VOCs emitted by tangelo and lime

In addition to the identification accomplished through the GC-MS, we estimated the relative abundance of the compounds in the volatile profile of tangelo and lime by comparing plants infested with *A. floccosus* to uninfested ones (Tables 1 and 2). Uninfested tangelo plants exhibited the presence of the terpenoids β-phellandrene (12.07%), (*Z*)-ocimene (2.67%), caryophyllene (13.93%), citronellol (10.40%) and *cis*-*p*-mentha-2,8-dien-ol (15.38%).

Table 1. Percentage of relative abundance (mean ± 95% central credible intervals) of chemicals identified in the volatile profile of tangelo (*Citrus reticulata* × *Citrus* ×*paradisi*) 'Minneola' uninfested and infested with *Aleurothrixus floccosus* in semi-field conditions. [1]Volatile compounds were analyzed in triplicate, and the 95% central credible intervals ($CI_{95\%}$) corresponds to the Bayesian credible interval; BF_{10}: indicates the Bayes factor in favor of H_1 over H_0, larger values of BF_{10} indicate more support for H_1; Bayes factors range from 0 to ∞, and a Bayes factor of 1 indicates that both hypotheses predicted the data equally well; [nd]: compound not detected.

Compounds	Relative abundance (%) Uninfested	Infested	BF_{10}
Alkanes			
3,7-Dimethyl-decane	5.64 ± (1.41-9.87)[1]	4.74 ± (3.10-6.39)	0.69
Alcohols			
2-Ethyl-1-hexanol	4.42 ± (0.93-7.91)	33.99 ± (26.50-41.47)	113.3
Aldehydes			
Octanal	2.56 ± (2.31-2.81)	2.48 ± (0.89-4.06)	0.57
Nonanal	14.21 ± (12.21-16.21)	13.12 ± (10.45-15.79)	0.90
Decanal	13.73 ± (10.89-16.58)	9.00 ± (7.42-10.57)	10.25
Aromatic aldehydes			
3,5-Dimethyl-benzaldehyde	nd	6.02 ± (3.56-8.48)	
Ester			
Methyl salicylate	nd	12.66 ± (6.53-18.78)	
Terpenoids			
β-Phellandrene	12.07 ± (9.11-15.03)	nd	
D-Limonene	5.00 ± (4.09-5.90)	3.82± (0.98-6.67)	1.06
(*Z*)-Ocimene	2.67 ± (1.85-3.48)	nd	
Caryophyllene	13.93 ± (8.66-19.21)	nd	
Azulene	nd	14.23 ± (11.56-16.90)	
Citronellol	10.40 ± (9.43-11.36)	nd	
cis-*p*-Mentha-2,8-dien-1-ol	15.38 ± (13.21-17.55)	nd	

Infested plants exhibited the presence of aromatic aldehyde 3,5-dimethyl-benzaldehyde (6.02), ester methyl salicylate (12.66%) and terpenoid azulene (14.23%) (Table 1). Furthermore, we found a similar abundance (BF_{10} = 0.69) of 3,7-dimethyl-decane (5.64%, uninfested; 4.74%, infested), octanal (BF_{10} = 0.57) (2.56%, uninfested; 2.48%, infested), nonanal (BF_{10} = 0.90) (14.21%, uninfested; 13.12%, infested) and D-limonene (BF_{10} = 1.06) (5.00%, uninfested; 3.82%, infested). However, infested plants showed higher abundance (BF_{10} = 113.3) of 2-ethyl-1-hexanol (33.99%) compared to uninfested plants (4.42%). We found lower abundance (BF_{10} = 10.25) of decanal (9.00%) on infested plants compared to uninfested ones (13.73%) (Table 1).

Similarly, uninfested lime plants exhibited the presence of 2-ethyl-1-hexanol (14.34%); citral (2.71%); 3-ethyl-benzaldehyde (4.31%); (*Z*)-ocimene (1.99%); and bisabolene (7.95%). In contrast, infested plants exhibited the emission of cumene (2.01%); 3-hexen-1-ol acetate (24.52%); methyl salicylate (10.43%); α-thujene (2.12%); α-farnesene (20.81%). Both uninfested and infested plants showed similar abundance levels of octanal (2.83% uninfested; 2.22% infested; BF_{10} = 0.92); nonanal (16.52 uninfested; 1.16% infested; BF_{10} = 0.96).

Decanal exhibited higher abundance levels in uninfested plants (12.46%) over infested ones (4.72%; BF_{10} = 0.92). Similarly, D-limonene was more abundant (BF_{10} = 591.83) in uninfested plants (30.75% compared to the infested ones (4.09%). Conversely, 3,7-dimethyl-decane exhibited higher abundance (BF_{10} = 31.57) in the profile of infested plants (14.92%) (Table 2).

Table 2. Percentage of relative abundance (mean ± 95% central credible intervals) of chemicals identified in the volatile profile of lime (*Citrus ×aurantifolia*) 'Limón de Pica' uninfested and infested with *Aleurothrixus floccosus* (Maskell) in semi-field conditions. [1]Volatile compounds were analyzed in triplicate, and the 95% central credible intervals ($CI_{95\%}$) corresponds to the Bayesian credible interval; BF_{10}: indicates the Bayes factor in favor of H_1 over H_0, larger values of BF_{10} indicate more support for H_1; Bayes factors range from 0 to ∞, and a Bayes factor of 1 indicates that both hypotheses predicted the data equally well; [nd]: compound not detected.

Compounds	Relative abundance (%)		
	Uninfested	Infested	BF_{10}
Alkanes			
3,7-Dimethyl-decane	6.14 ± (4.08-8.19)[1]	14.92 ± (11.63-18.22)	31.57
Alcohols			
2-Ethyl-1-hexanol	14.34 ± (6.91-21.77)	nd	
Aldehydes			
Octanal	2.83 ± (1.02-4.63)	2.22 ± (2.01-2.35)	0.92
Nonanal	16.52 ± (13.82-19.23)	14.16 ± (8.06-20.26)	0.96
Decanal	12.46 ± (7.10-17.81)	4.72 ± (-4.59-14.02)	2.39
Citral	2.71 ± (1.73-3.69)	nd	
Aromatic aldehydes			
3-Ethyl-benzaldehyde	4.31 ± (2.68-5.94)	nd	
Aromatic hydrocarbons			
Cumene	nd	2.01 ± (1.58-2.43)	
Esters			
3-Hexen-1-ol acetate	nd	24.52 ± (22.89-26.15)	
Benzoate ester			
Methyl salicylate	nd	10.43 ± (8.75-12.10)	
Terpenoids			
D-Limonene	30.75 ± (26.76-34.74)	4.09 ± (2.69-5.49)	591.83
(*Z*)-Ocimene	1.99 ± (1.46-2.52)	nd	
α-Thujene	nd	2.12 ± (1.34-2.90)	
Bisabolene	7.95 ± (2.87-13.05)	nd	
α-Farnesene	nd	20.81 ± (19.06-22.56)	

Behavioral responses of *C. arcuatus* and *A. floccosus* to VOCs and HIPVs

We assessed the attraction of *A. floccosus* and *C. arcuatus* to plant without (VOCs) and with (HIPVs) damage caused by *A. floccosus* using a Bayesian A/B test. First, we conducted a series of experiments using hexane (control) and plant volatiles (stimulus). Second, in a separate set of experiments, involving different individuals, we assessed the preference of the insects when they were simultaneously exposed to VOCs and HIPVs from both citrus species. These data were analyzed using a Bayesian multinomial test. The VOCs emitted by tangelo (BF_{10} = 3.01×10^5) and lime (BF_{10} = 1345.11) were found to be more attractive to the ladybird *C. arcuatus* compared to the hexane. In the olfactometer, 34% ($CI_{95\%}$ 0.306-0.381) of individuals chose hexane when there was no other stimulus was present; this percentage increased to 49% ($CI_{95\%}$ 0.452-0.532) using tangelo as the stimulus and remained at 46% ($CI_{95\%}$ 0.452-0.532) when the lime was used as the stimulus (Figure 1). Nonetheless, we observed a stronger attraction of *A. floccosus* to VOCs from tangelo (BF_{10} = 8.09×10^{27}) and lime (BF_{10} = 5.17×10^{47}) compared to hexane. In the olfactometer, 39% ($CI_{95\%}$ 0.347-0.424) of individuals chose hexane in the absence of stimulus. This preference increased to 80% ($CI_{95\%}$ 0.765-0.828) when tangelo was used as stimulus. When stimulated with lime, the preference was at 46% ($CI_{95\%}$ 0.452-0.532) (Figure 1).

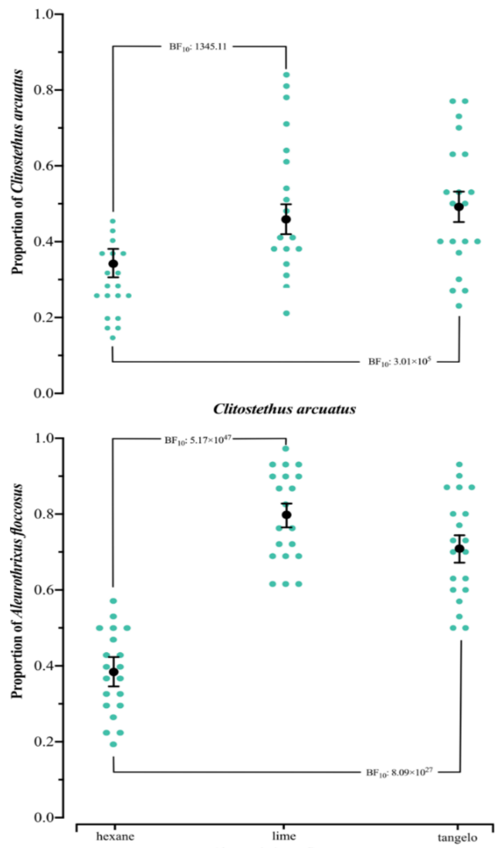

Figure 1. Proportion of insects that chose the stimulus in the olfactometer. Black dots represent the median of the observed proportion and its vertical bar represents the 95% central credible interval based on the Bayesian A/B test. The evidence supporting the difference between groups, connected by a bracket, is given by the Bayes factor (BF_{10}). BF_{10}: Indicates the Bayes factor in favor of H_1 over H_0, larger values of BF_{10} indicate more support for H_1; Bayes factors range from 0 to ∞, and a Bayes factor of 1 indicates that both hypotheses predicted the data equally well.

Aleurothrixus floccosus exhibited greater preference for the volatiles emitted by uninfested lime compared to those emitted by tangelo ($BF_{10} = 2.11 \times 10^{83}$). In contrast, *C. arcuatus* showed a comparable attraction to volatiles from infested lime and infested tangelo plants ($BF_{10} = 1.91 \times 10^{49}$) (Figure 2). However, when exposed to volatiles emitted by *A. floccosus vs*. those from infested plant volatiles, *C. arcuatus* showed a stronger preference for HIPVs from both lime ($BF_{10} = 2.43 \times 10^{78}$) and tangelo ($BF_{10} = 2.00 \times 10^{110}$) (Figure 3). Moreover, *C. arcuatus* adults showed preference for odors from tangelo infested shoots compared to volatiles from confined *A. floccosus* adults (Figure 3). Similarly, the predators displayed a preference for lime-infested shoots odors over those of *A. floccosus* adults.

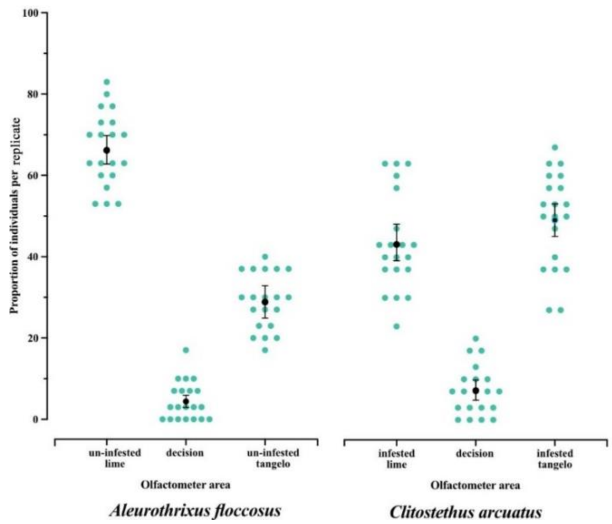

Figure 2. Proportion of individuals selecting each olfactometer area (arm). Each green dot represents an N = 30 insects per replicate; black dots represent the mean observed proportion (N = 20 replicates) and its vertical bars the 95% central credible intervals based on independent binomial distributions with flat priors, and the initial hypothesized population frequency was 0.33 for each zone the olfactometer.

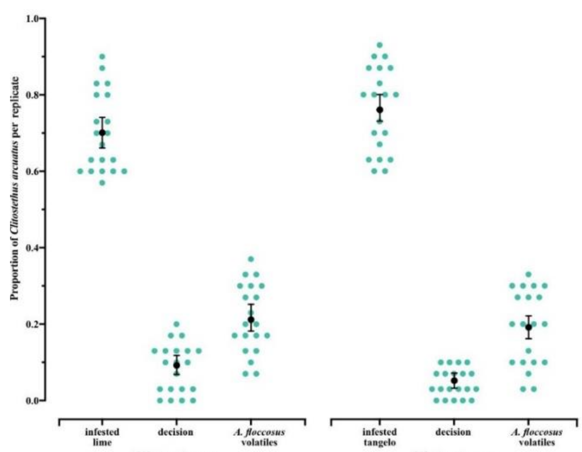

Figure 3. Proportion of individuals selecting each olfactometer area (arm). Each green dot represents an N = 30 insects per replicate; black dots represent the mean observed proportion (N = 20 replicates) and its vertical bars the 95% central credible intervals based on independent binomial distributions with flat priors, and the initial hypothesized population frequency was 0.33 for each zone the olfactometer.

The CG-MS data analysis reveals that both tangelo and lime shoots infested with *A. floccosus* emit MeSA in response to herbivory. As a result, we exposed the exotic ladybird to MeSA at four different concentrations as odor sources. Our observations showed that *C. arcuatus* exhibited a preference for MeSA at 10 µg mL^{-1} ($BF_{10} = 2.42\times10^{25}$) and 100 µg mL^{-1} ($BF_{10} = 9.32\times10^{34}$) (Figure 4).

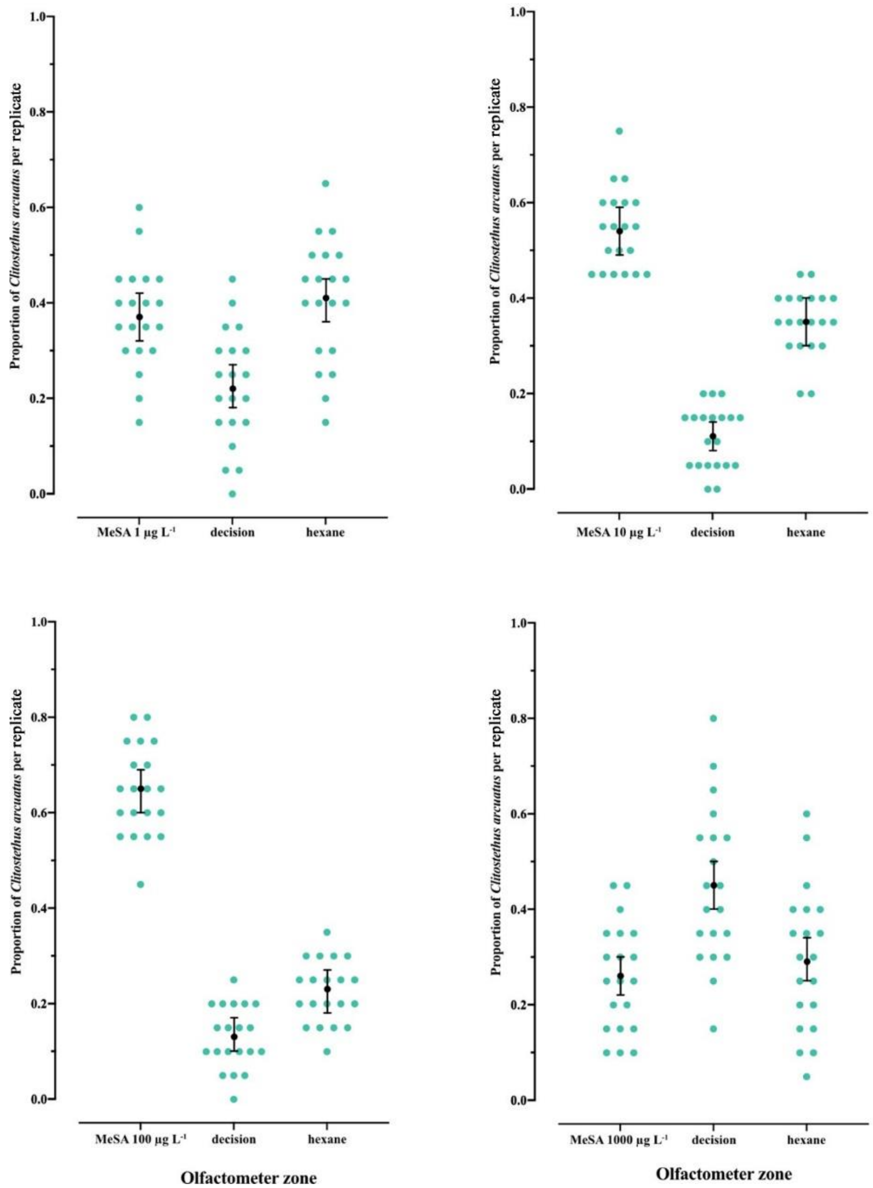

Figure 4. Proportion of individuals selecting each olfactometer area (arm). Each green dot represents an N = 30 insects per replicate; black dots represent the mean observed proportion (N = 20 replicates) and its vertical bars the 95% central credible intervals based on independent binomial distributions with flat priors, and the initial hypothesized population frequency was 0.33 for each zone the olfactometer. MeSA: Methyl salicylate.

DISCUSSION

Effects of infestation by *A. floccosus* on the emission of VOCs by citrus

We used the dynamic headspace technique in vivo to collect volatiles from citrus under semi-field conditions during the summer. This approach allowed us to obtain VOCs blends closely resembling agricultural conditions. This stands in contrast to other collection methodologies where tissue extraction may introduce 'wounding effects' triggering alternative biosynthetic pathways such as green leaf volatiles (GLVs) (Toll et al., 2021). The GC-MS analysis of the VOCs revealed differences in emissions between *A. floccosus*-infested and uninfested shoots of each citrus species. In the case of tangelo infested-shoots, we observed elevated abundances of alcohols, aldehydes, terpenoids, and MeSA compounds. Similarly, in the lime ecotype 'Limón de Pica', we collected greater proportions of terpenoids, acetate ester, aldehydes, alkanes and MeSA compounds in infested shoots. Most of these HIPVs have been previously identified from infested plants by phytophagous arthropods (Rioja et al., 2018; Silva et al., 2021; Alsabte et al., 2022). Nevertheless, the emissions of HIPVs differed in varying proportions across citrus plant species. In line with our findings, after 3 d of infestation by *A. floccosus*, tangelo exhibited increased levels of 2-ethyl-1-hexanol and azulene. Notably, these two compounds were not detected in infested lime shoots. A separate study focused on *Datura stramonium* L. plants infected by the *Tomato yellow leaf curl virus* (TYLCV), which is transmitted by *B. tabaci*, reported higher concentrations of 2-ethyl-1-hexanol alcohol emitted by infected plants compared to healthy plants (Chen et al., 2017). Moreover, the alcohol 2-ethyl-1-hexanol was found to be most abundant in alfalfa (*Medicago sativa* L.) 'Longdong' plants infested by the pea aphid *Acyrthosiphon pisum* (Harris) (Hemiptera: Aphididae) (Wang et al., 2022).

Regarding the azulene terpenoid, studies have revealed variation in its emissions. Eggplant (*Solanum melongena*) 'Kuai Yuan Qie' plants infested by the whitefly *Trialeurodes vaporariorum* Westwood (Hemiptera: Aleyrodidae) were found to emit azulene at higher abundances compared to uninfested plants. Conversely, the same researchers discovered that tomato (*Solanum lycopersicum*) 'Yang Guang 906' plants infested by *T. vaporariorum*, experienced a reduction in the proportions of this terpenoid (Darshanee et al., 2017). We also observed greater abundance of the 3-hexen-1-ol acetate compound (24.52%) lime-infested shoots, whereas it was not detected in tangelo-infested shoots. In research involving lima beans (*Phaseolus lunatus* L. 'Sieva') and cucumber (*Cucumis sativus* L. 'Lange Groene Giganten'), plants infested by *Spodoptera exigua* Hübner (Lepidoptera: Noctuidae), the authors de Boer et al. (2008) reported a larger quantity of (*Z*) 3-hexen-1-ol acetate emitted after herbivory. Thus, the chemical profiles of citrus shoots undergo qualitative change after herbivory as well as citrus species during the summer season. For instance, Jones and Killiny (2021) studied the effect of herbivory by the Asian citrus psyllid *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae) on VOCs emitted by 'Sugar Belle' hybrid mandarin previously known as LB8-9 ['Clementine' mandarin (*C. reticulata*) × 'Minneola' tangelo (*Citrus* × *Tangelo*), 'Duncan' grapefruit (*C. paradisi*) × 'Dancy' tangerine (*C. reticulata*)] grafted on three different rootstocks C35, sour orange and US-897. These authors collected VOCs from excised leaves from uninfested and infested plants, and found that the chemical profiles emitted by 'Sugar Belle' changed after herbivory, where even recorded fewer differences between the different scion/rootstock combinations. Likewise, lemon (*Citrus lemon* L. 'Batem pınarı'), orange (*Citrus sinensis* 'Washington navel') and tangerine (*Citrus reticulata* L. 'Okitsu wase') branches infested with the California red scale (*Aonidiella aurantii*) demonstrated increased emissions of D-limonene, β-ocimene and MeSA in contrast to uninfested branches (Alsabte et al., 2022).

Our results differ from those of Alsabte et al. (2022), in terms of proportions and detected compounds. This discrepancy suggests that insect species associated with citrus, potentially influenced by its mouthparts and elicitors, trigger unique defense responses through released HIPVs. Additionally, it is worth noting that *A. floccosus* and *A. aurantii* adults exhibit a distinct behavior infesting citrus leaves, while the nymphs and females of the California red scale target various parts of citrus plants, including leaves, branches, and fruits. This distinction implies the presence of specific triggering reactions, wherein even biological agents such as predators utilize these distinct scents of HIPVs as cues to locate their prey and host plants. Therefore, further research focusing on the molecular and physiological level of herbivory on citrus plants is crucial for understanding the complexity of tritrophic interactions in field conditions.

Behavioral responses of *Clitostethus arcuatus*

In this study, we discovered that the exotic ladybird *C. arcuatus* females were strongly attracted to HIPVs emitted from both tangelo and lime shoots infested by the woolly whitefly *A. floccosus*. Similarly, Alsabte et al. (2022) conducted tests using the predator *Rhyzobius lophanthae* Blaisdell (Coleoptera: Coccinellidae) in a Y-tube olfactometer. They presented the predator with odor sources from both uninfested and infested citrus plants containing California red scales, and observed a preference for HIPVs emitted from lemon, orange and tangerine infested branches (Alsabte et al., 2022). Other studies reveal that ladybirds like *Propylaea japonica* (Thunberg) are attracted toward infested plants (Wang et al., 2015). Furthermore, the invasive success of *Harmonia axyridis* can be attributed to an enhanced use of chemical cues emitted from aphid infested plants (Rondoni et al., 2017). The micro-coleopterans *Parastethorus histrio* and *Oligota pygmaea* prefer odors from avocado shoots infested with *Oligonychus yothersi* (Acari: Tetranychidae) (Rioja et al., 2018). Hence, our finding holds significant importance given that *C. arcuatus* is an invader predator of whiteflies at Pica Oasis as mentioned previously. Additionally, this fact suggests that the exotic ladybird uses HIPVs blends to find its prey. Moreover, *C. arcuatus* is found on olive (*Olea europaea* L.) trees infested with *Siphoninus phillyreae* preying all whiteflies stages (González, 2006; Rioja and Ceballos, 2023). According to these data, the exotic ladybird appears to exploit certain essential chemical compounds emitted from whiteflies infested plants. Further studies are required to shed light on this phenomenon.

Behavioral responses toward MeSA synthetic compound

It is important to note that HIPVs blends can be specific to both plant species and the herbivorous attacker. Insects such as the whitefly, with its stylets, induce changes in the HIPVs through the salicylic acid (SA) pathway (Silva et al., 2021). Interestingly, we observed relative abundances of MeSA (at 10.43% and 12.65%) in both lime and tangelo infested shoots. Previous studies have shown that plants infested with insects and mites experience increased emissions of MeSA such as tomato plants infested with whiteflies as *T. vaporariorum* (Pierre et al., 2011; Rioja et al., 2018).

The effects of synthetic MeSA have been studied under field conditions (Lee et al., 2022), utilizing bottle-type HIPVs dispensers that attract parasitoids (Uefune et al., 2012). Laboratory trials have also shown that the predatory mite *P. histrio* and *O. pygmaea* were attracted toward MeSA (Rioja et al., 2018). According to our findings, both citrus infested shoots emitted MeSA. Therefore, synthetic MeSA was offered at four different concentrations to *C. arcuatus* in a Y-tube olfactometer. This aimed to construct a preference curve, revealing that the exotic ladybird female exhibited a preference for MeSA at 10 and 100 μg mL^{-1} concentrations. In another study, using a Y-tube olfactometer, the ladybird predator of California red scales *Rhyzobius lophantae* was attracted to MeSA at 1 and 10 μL mL^{-1} concentrations (Alsabte et al., 2022). As a result, this compound emitted from infested citrus shoots can be considered a 'key' factor in attracting natural enemies in citrus orchards. Further investigations are required to assess the efficacy of MeSA synthetic standard in semi-field and field conditions as evidenced at Pica Oasis commercial orchards, in the context of the ecological management of *A. floccosus*, and sustainable production.

Behavioral responses of *A. floccosus*

In our study, we observed that *A. floccosus* exhibited a preference for uninfested lime shoots over infested ones. This behavior led us to consider the potential role of com-pounds, namely 3-hexen-1-ol acetate, MeSA, α-farnesene and azulene as repellents against *A. floccosus*. Based on our findings, it was also possible to observe that 2-ethyl-1-hexanol apparently acts as an attractant, its effects varying depending on its concentration. In this sense, Chen et al. (2017) research reports that *B. tabaci* Q was strongly attracted to synthetic 2-ethyl-1-hexanol. To advance our understanding, it is necessary to conduct field evaluations of lures in real-world scenarios, incorporating the compounds addressed in this investigation as they present a potential ecological management of the woolly citrus whitefly.

CONCLUSIONS

Our findings indicate substantial qualitative variations in the chemical profiles of both citrus species before and after a 3 d infestation with *Aleurothrixus floccosus* under semi-field conditions. Notably, aldehydes, terpenoids, alcohols, esters, and methyl salicylate (MeSA) compounds were predominantly emitted from infested-shoots. These results suggest alterations occurring at the molecular and physiological levels, a phenomenon that merits further investigation through future studies.

Findings also demonstrate that herbivore-induced plant volatiles (HIPVs) emitted from infested citrus shoots elicited the attraction of female exotic ladybird *Clitostethus arcuatus*. Furthermore, these ladybirds exhibited a preference for the MeSA standard at concentrations of 10 and 100 μg mL^{-1}, suggesting that this compound can be considered as a 'key' factor in the attraction and foraging of *C. arcuatus* at Pica Oasis. Hence, additional research is required to assess the effectiveness of attractive lures at semi-field and field conditions using compounds such as MeSA, 3-hexen-1-ol acetate, azulene and α-farnesene.

Ultimately, the behavioral responses of *A. floccosus* indicate that alkanes and the presence of 2-ethyl-1-hexanol alcohol could potentially influence the attraction or repellency of the woolly whitefly. Therefore, it becomes crucial to conduct further evaluations of these compounds to develop sustainable and organic ecological management programs of *A. floccosus* in the context of agricultural production.

Author contribution

Conceptualization: T.R., R.C. Methodology: T.R., R.C. Formal analysis: T.R., R.C. Investigation: T.R. Resources: T.R., R.C. Writing-original draft: T.R., R.C. Writing review & editing: T.R., R.C. The authors have read and agree with the manuscript.

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