



Behavioral responses of adult lacewings, *Chrysoperla externa*, to a rose–aphid–coriander complex



J. Salamanca^{a,*}, M. Pareja^b, C. Rodriguez-Saona^c, A.L.S. Resende^d, B. Souza^a

^a Departamento de Entomologia, Universidade Federal de Lavras, Caixa Postal 3037, CEP 37200-000 Lavras, Minas Gerais, Brazil

^b Departamento de Biologia Animal, Universidade Estadual de Campinas, Caixa Postal 6109, CEP 13083-862 Campinas, São Paulo, Brazil

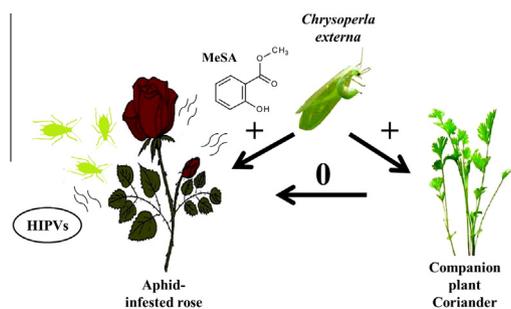
^c Department of Entomology, Philip E. Marucci Center, Rutgers University, Chatsworth, NJ 08019, United States

^d Departamento de Entomologia e Fitopatologia, Universidade Federal Rural do Rio de Janeiro, Caixa Postal 74538, CEP 23890-000 Seropédica, Rio de Janeiro, Brazil

HIGHLIGHTS

- The hypothesis that coriander enhances predator attraction to herbivore-induced plant volatiles was tested.
- Volatiles from aphid-infested rose and coriander attract *Chrysoperla externa* adults.
- *C. externa* oviposition increased on aphid-infested rose plants.
- *C. externa* attraction and oviposition on aphid-infested rose are not influenced by coriander.
- Methyl salicylate is a major volatile compound emitted from aphid-infested rose plants.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:

Received 28 July 2014

Accepted 13 October 2014

Available online 18 October 2014

Keywords:

Natural enemies

Tri-trophic interaction

Companion plants

Herbivore-induced plant volatiles

Methyl salicylate

ABSTRACT

Natural enemy behavior is mediated by cues associated with the host-plant complex, such as volatiles emitted by damaged plants and the surrounding vegetation. We conducted studies to investigate whether: (a) adult attraction of green lacewing, *Chrysoperla externa* Hagen, to and oviposition on rose, *Rosa × hybrida* L., infested by the potato aphid, *Macrosiphum euphorbiae* Thomas, is affected by the presence of coriander, *Coriandrum sativum* L. (a potential companion plant); (b) the role of volatiles on female *C. externa* attraction to uninfested and aphid-infested rose, coriander, and from the rose–coriander complex; and, (c) whether *M. euphorbiae* feeding induces volatile emissions from rose plants. In the greenhouse, numbers of *C. externa* adults were higher on aphid-infested rose and on roses near coriander plants; however, there was no aphid × coriander interaction, indicating that attraction to aphid-infested rose was not influenced by the presence of coriander. Aphids increased the number of eggs laid by *C. externa* on rose but this was also not affected by the presence of coriander. In Y-tube studies, *C. externa* females showed attraction to volatiles from aphid-infested rose, coriander only, and the rose–coriander complex and were not attracted to rose volatiles; however, there was no difference in *C. externa* attraction between aphid-infested rose versus aphid-infested rose plus coriander. Headspace analysis revealed that aphid-infested rose emits greater quantities of methyl salicylate compared with uninfested rose. In conclusion, although *C. externa* adults were attracted to coriander, coriander did not increase attraction or oviposition of this predator to aphid-infested rose.

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* Corresponding author. Fax: +55 35 38291288.

E-mail addresses: jordanosalamanca@gmail.com (J. Salamanca), martinpareja@gmail.com (M. Pareja), crodriguez@aesop.rutgers.edu (C. Rodriguez-Saona), andresresende@gmail.com (A.L.S. Resende), brgsouza@den.ufra.br (B. Souza).

1. Introduction

Plants respond to herbivore feeding by inducing unique blends of volatile organic compounds, commonly referred to as herbivore-induced plant volatiles (HIPVs) (Vet and Dicke, 1992; Dicke and van Loon, 2000). Emission of these volatile blends varies according to the herbivore species feeding on plants (Ozawa et al., 2000; Rodriguez-Saona et al., 2003; Dicke and Baldwin, 2010). Indeed, aphids induce a volatile response in plants that often differs from caterpillar feeding (Turlings et al., 1998; Zhu and Park, 2005). For example, many aphids induce the emission of methyl salicylate (MeSA) in plants, a volatile derivative of the phytohormone salicylic acid that is associated with pathogen defense (Ozawa et al., 2000). These HIPVs are important cues used by the natural enemies, i.e., predators and parasitoids, of herbivores in host/prey location (Hare, 2011). In fact, aphid predators utilize volatiles emitted from aphid-damaged plants to find their prey. For example, Verheggen et al. (2008) found that gravid female hoverflies *Episyrphus balteatus* DeGeer lay more eggs on *Vicia faba* L. plants infested with the pea aphid, *Acyrtosiphon pisum* (Harris), than on non-infested plants. Moreover, Zhu and Park, 2005 showed that the seven-spot ladybeetle *Coccinella septempunctata* (Linnaeus) antennae respond to MeSA.

Companion planting is an agricultural practice where two plant species are grown in close proximity to improve their productivity (Parker et al., 2013). Companion plants can enhance the foraging efficacy of natural enemies in agricultural crops by providing them with a food source such as nectar and pollen, shelter, and/or prey (Harmon et al., 2000; Barbosa et al., 2009). Coriander (*Coriandrum sativum* L.) is one of the most widely studied companion plants in the world (Bugg and Wilson, 1989; Patt et al., 1997; Kasina et al., 2006), and natural enemies are attracted to many of its particular traits such as high pollen and nectar production; thus, potentially increasing their efficiency as biological control agents in agricultural systems (Patt et al., 1997; Colley and Luna, 2000; Morris and Li, 2000; Smith et al., 2000). For example, Patt et al. (1997) showed higher abundance of ladybeetles (Coleoptera: Coccinellidae) in eggplant (*Solanum melongena* L.) when intercropped with coriander than in an eggplant monoculture, which increased egg and larval predation of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say). Similarly, Smith et al. (2000) found greater numbers of generalist predators in tomatoes intermixed with coriander than in tomato monocultures; and, Togni et al. (2009) showed reductions in whitefly nymphal densities when tomatoes were intermixed with coriander than when tomato were planted alone, which was attributed to greater natural enemy abundance. However, to our knowledge, no previous study has investigated the effect of companion plants (e.g., coriander) on the attraction of natural enemies to HIPVs.

The potato aphid, *Macrosiphum euphorbiae* (Thomas), is an important pest of roses, damaging new shoots directly by sucking phloem sap and injecting toxic substances, which results in leaf deformation and delay in growth, and indirectly by acting as an important vector of viral diseases (Carvalho et al., 2009). Worldwide, chemical control is used widely to reduce aphid populations through the application of high insecticide concentrations, which leaves toxic residues in crops and can lead to pest resistance (Dik et al., 2002). Biological control can be used as an alternative control method. For instance, lacewings (Neuroptera: Chrysopidae) are important aphid predators (Principi and Canard, 1984). A commonly used and well-studied biological control agent against aphids in the Neotropical region is the green lacewing, *Chrysoperla externa* (Hagen), due to its high adaptability to different weather conditions, high reproductive potential, efficient search capacity, high abundance in various agriculture crops, and ease of mass

rearing under laboratory conditions (Duelli, 2001; Souza and Carvalho, 2002; Carvalho and Souza, 2009; Salamanca et al., 2010). In addition to aphids, this predator is an effective natural enemy of whiteflies, thrips, mites and some Lepidoptera (Principi and Canard, 1984; Carvalho and Souza, 2009). These features make *C. externa* a good candidate for augmentative and conservation biological control.

Adult lacewings use volatiles emitted from plants in response to herbivore attack (i.e., HIPVs) to locate prey, feeding sites (e.g., nectar, honeydew), as well as sites suitable for mating and oviposition (McEwen et al., 1993; Kunkel and Cottrell, 2007). For example, the lacewing *Chrysoperla carnea* (Stephens) *sensu lato* is attracted to traps baited with 2-phenylethanol, a volatile emitted from alfalfa and corn, two host plants of its prey (Zhu et al., 2005). They also utilize volatiles produced by attractive companion plants (Ballal and Singh, 1999), such as coriander. In a recent study, Resende (2012) showed in a four-arm olfactometer that virgin *C. externa* adults are more attracted to volatiles from coriander than to those from other companion plants such as dill, *Anethum graveolens* L., and anise, *Pimpinella anisum* L.

In the present study, we tested the hypothesis that coriander as a companion plant enhances attraction and oviposition of the green lacewing *C. externa* on rose, *Rosa × hybrida* L., plants infested with the potato aphid, *M. euphorbiae*. Specifically, we conducted greenhouse and laboratory studies to determine: (1) adult *C. externa* attraction and oviposition on rose plants damaged by *M. euphorbiae* and on undamaged plants, (2) whether these behaviors are affected by the presence of coriander; (3) the role of volatiles on female *C. externa* attraction to uninfested and aphid-infested rose, coriander, and from the rose–coriander complex; and, (4) the HIPVs from rose plants induced by *M. euphorbiae* feeding.

2. Materials and methods

2.1. Study sites

Behavioral experiments were conducted from January to December, 2012, in a greenhouse at 26 ± 3 °C, 40 ± 5% r.h., and 12L:12D photoperiod, and in the laboratory of Chemical Ecology at 25 ± 2 °C, 70 ± 10% r.h., and 12L:12D photoperiod, both located in the Department of Entomology, Universidade Federal de Lavras (Lavras, Minas Gerais, Brazil). Headspace volatile collections were conducted in a greenhouse (23 ± 2 °C, 50 ± 10% r.h., 14L:10D photoperiod) at the P.E. Marucci Center, Rutgers University (Chatsworth, NJ, USA).

2.2. Plants

Rose, *R. × hybrida* cv. “Vegas,” plants were purchased from a local vendor (Floricultura Canto Verde, Lavras, Minas Gerais, Brazil) and planted individually in soil with garden compost composed of cow manure and 4-14-8 N-P-K in 10 L pots. For greenhouse experiments, plants were used during the growing stage and were approximately 60 cm in height. For laboratory experiments, plants were 20 cm in height. Prior to experiments, the pot and soil were completely covered with aluminum foil to minimize possible effects of volatiles emitted by the compost (Pinto-Zevallos et al., 2013). All pots received irrigation as needed, as well as 20-0-25 N-P-K fertilizer and granular simple super phosphate every 30 days.

Coriander seeds (*C. sativum* cv. “Verdão”) were obtained from ISLA Sementes Ltda. (Porto Alegre, Rio Grande do Sul, Brazil) and grown in Plantmax® substrate in 5 L pots, with 10 plants per pot. For greenhouse experiments, plants were grown in the greenhouse

for 40 to 50 days after planting, and used when they were 30 cm in height. For laboratory experiments, the plants were grown in the greenhouse in 2 L pots for 20–30 days after planting, and used when they were ~15 cm tall. As with rose plants, all pots and soil were completely covered with aluminum foil. Pots received irrigation daily and were fertilized only once during the study.

2.3. Insects

C. externa was reared in the Department of Entomology, Universidade Federal de Lavras at 25 ± 2 °C, $70 \pm 10\%$ r.h., and L12:D12 photoperiod. Adults were reared with 1:1 yeast:honey. Larvae were fed Mediterranean flour moth eggs, *Anagasta kuehniella* (Zeller) (Insecta Agentes Biológicos, Lavras, Minas Gerais, Brazil). *C. externa* adults (80 females and 80 males) were placed in cages (20 cm high \times 20 cm \varnothing) for 10–12 days to allow mating. For greenhouse studies, mated males and females were used. For experiments in the laboratory, only mated females were used.

Potato aphids, *M. euphorbiae*, were transferred from rose plants grown in a greenhouse at the Agricultural and Livestock Research Enterprise of Minas Gerais (São João Del Rei, Minas Gerais, Brazil) to Petri dishes (15 cm \varnothing) containing lettuce (*Lactuca sativa* L.) leaves on a thin layer of 1% agar. Aphids were maintained in an air-conditioned room at 22 ± 1 °C, $70 \pm 10\%$ r.h., and L12:D12 photoperiod. A *M. euphorbiae* colony was also maintained on potato and tomato plants in a greenhouse at the P.E. Marucci Center (Chatsworth, NJ, USA) under conditions described above. The age of aphids used in greenhouse and laboratory experiments was standardized by placing 30 adults from the rearing colony in Petri dishes (9 cm \varnothing) containing lettuce leaf discs (~9 cm \varnothing); these adults remained in the dishes for 48 h to obtain 2nd and 3rd instar nymphs.

2.4. Greenhouse study

We conducted greenhouse studies to determine the attraction and oviposition preference of adult *C. externa* for rose plants damaged by aphids over uninfested plants, and whether these behaviors are influenced by the presence of coriander. Fourteen potted rose plants were placed in two rows on metal benches (3 m long \times 1 m wide \times 1 m high) for a total of 4 metal benches (total

of 56 rose plants), with a spacing of 30 cm between plants and 40 cm between rows (Fig. 1). The metal benches were arranged one meter from each other. Four experimental treatments were tested in a 2×2 factorial design: (1) aphid-infested rose plants plus coriander as a companion plant; (2) aphid-infested rose plants without coriander; (3) uninfested rose plants plus coriander; and, (4) rose plants without coriander or aphids (control). Each bench received one of the treatments (Fig. 1). In treatments where the rose plants were infested with aphids, fifty 2nd–3rd instar *M. euphorbiae* nymphs were placed on each plant 48 h before releasing *C. externa* adults to allow time for the aphids to establish on the rose plants. In treatments that had coriander as a companion plant, seven pots with coriander were placed on each bench, arranged in between rows of rose plants (see Fig. 1).

Prior to release, 80 adults (40 males and 40 females) of *C. externa* were placed in each of two cylindrical PVC cages (20 cm high \times 20 cm \varnothing) and covered with a nylon mesh ($N = 160$ adults per replicate). Each of the cages was placed in the greenhouse between two metal benches, as shown in Fig. 1 (under “Release Zone”). *C. externa* releases were done in the afternoon (14:00 h); at the time of release, the cover (i.e., mesh) was removed from the cage, allowing the lacewings to exit the cage. Attraction of *C. externa* to each treatment was measured by counting the number of adults on rose and coriander plants daily for a total of 7 days; both males and females were released in the greenhouse to ensure oviposition for the entire duration of the study. *C. externa* oviposition was measured by counting the number of eggs on each rose and coriander plant daily for a total of 7 days. After each count, all eggs were removed from the plants using forceps. The entire experiment was replicated 4 times (i.e., trials), each done in a different month from May to August.

2.5. Laboratory/olfactometer study

The olfactory response of mated *C. externa* to various combinations of rose–coriander odors was assessed in a dual-choice Y-tube glass olfactometer (15 cm in length and 2 cm in internal \varnothing , with a 120° angle between arms), modified from Han and Chen (2002). The above-ground portion of plants (odor sources) was placed inside a transparent 40 cm \times 50 cm polyester bag (Conserv Indústria de Embalagens Ltda., Porto Alegre, Rio Grande do Sul,

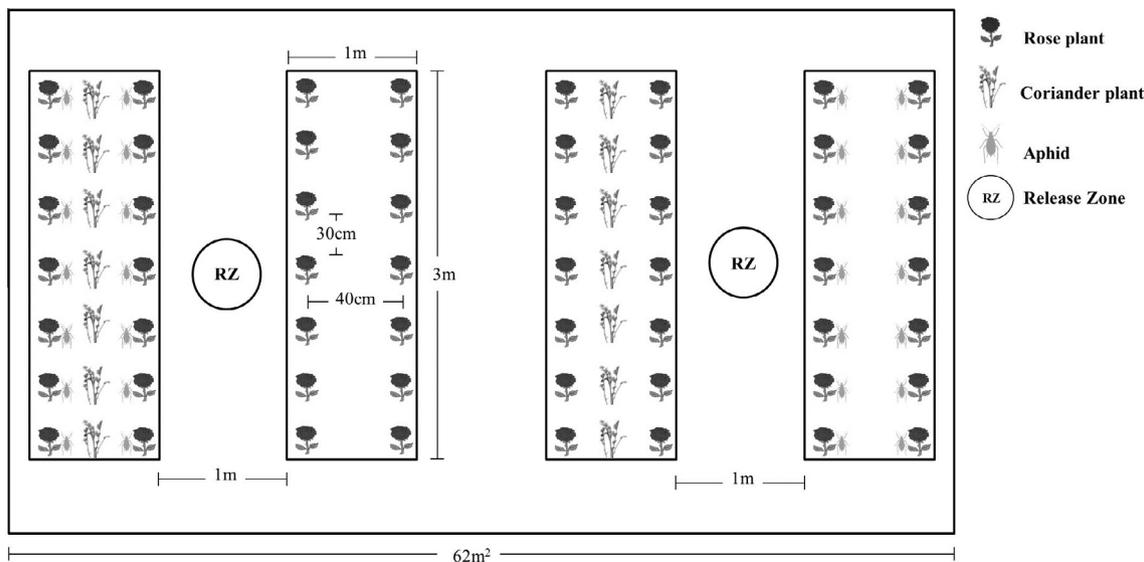


Fig. 1. Schematic representation of the greenhouse experiment. The experimental design was a factorial 2×2 : (1) aphid-infested rose plants plus coriander as a companion plant; (2) aphid-infested rose plants without coriander; (3) uninfested rose plants plus coriander; and, (4) rose plants without coriander or aphids (control). Treatments were randomly assigned to each of 4 metal benches.

Brazil) (as described by Stewart-Jones and Poppy, 2006). Charcoal-filtered air at a rate of 3.5 L/min entered the bags via silicone tubes. Air exited the bags and entered each arm of the olfactometer via Teflon tubes at a flow rate of 1.5 L/min. A vacuum pump (High Output Pump; EMD Millipore Corporation, Billerica, MA, USA) was used to push and pull air through the system.

Olfactometer experiments were conducted at 25 ± 2 °C, $70 \pm 10\%$ r.h., and L12:D12 photoperiod. A single *C. externa* female was released at the base of the olfactometer and its behavior observed for up to 10 min. A female was considered to have made a choice if it entered either arm, crossed a line drawn 2 cm from the intersection of the olfactometer, and remained there for at least 30 s. For each odor combination 100 mated females were tested ($n = 100$ female lacewings for each treatment; total of 600 females tested). Only gravid females were used in olfactometer experiments; a female was considered gravid if its abdomen was swelled with eggs (Fréchette et al., 2006). Each insect was used only once and then discarded. After each test, the olfactometer was washed with soapy water and then with 70% ethanol; and dried in an oven at 120 °C to eliminate any possible contamination. After every ten insects tested, both the polyester bags and plants were replaced with new ones, and the position of the two arms of the olfactometer was switched every five insects.

The following six odor combinations were tested: (1) rose plant vs. clean air; (2) coriander vs. clean air; (3) rose plant vs. rose plant + coriander; (4) rose plant vs. aphid-infested rose plant; (5) aphid-infested rose plant vs. aphid-infested rose plant + coriander; and, (6) rose plant + coriander vs. aphid-infested rose plant + coriander. For the treatments containing rose plants infested with aphids, fifty 2nd-3rd instar nymphs were placed on each plant, and were allowed to feed for 48 h prior to the start of the experiment. Odors from a single rose plant were tested in the olfactometer. For experiments with coriander, the pot containing coriander plants was placed on top of the soil of the pot with the rose plant such that the coriander and rose plants were next to each other. A polyester bag (described above) was then placed over the two plants.

2.6. Volatile collection and analysis

Because *C. externa* was attracted to volatiles from aphid (*M. euphorbiae*)-infested roses regardless of the presence of coriander in both greenhouse and laboratory experiments (see Section 3), we collected volatiles from aphid-infested rose to understand the mechanisms underlying this behavior. Uncut terminals (~15 cm long) from different rose plants of similar size as those used in behavioral assays were either infested with aphids (mean \pm SE aphids per terminal = 169 ± 18) or kept uninfested ($N = 4$ replicates per treatment). All terminals were bagged with a spun polyester sleeve (Rockingham Opportunities Corp., Reidsville, NC, USA). Aphids were placed on terminals inside the bags and allowed to feed for 5 days prior to volatile collection, and remained on the plants during volatile collections.

Volatile emissions were sampled in the greenhouse under conditions described above using a pull system (Tholl and Röse, 2006). The aboveground portion of each terminal was enclosed inside a 20×20 cm volatile collection bag made of non-absorbent Vac-Pak material (Richmond Products, Norwalk, CA, USA). Binder clips were used to close the bag opening around the stem. Volatiles from inside the bag were collected in 30 mg Super-Q adsorbent traps (Alltech, Deerfield, IL, USA) by pulling air at a rate of 600 mL min^{-1} with the aid of a 12 V vacuum pump (Sensidyne, Clearwater, FL, USA). Volatiles were collected for 3 h (11:00–14:00 h). Volatiles were collected from bags containing aphid-infested and uninfested rose terminals ($N = 4$), as well as from bags containing aphids only (~200 per bag) to test for prey-associated volatiles, and empty

bags to test for contamination ($N = 3$ replicates per treatment). After collection, bags were cleaned with tap water and 70% ethanol and reused.

Volatiles were analyzed as described in Rodriguez-Saona et al. (2009) and Rodriguez-Saona et al. (2011a). The collected volatiles from Super-Q traps were eluted with dichloromethane (150 μ l) containing 400 ng of *n*-octane (Sigma–Aldrich Corp., St. Louis, MO, USA) as internal standard (IS). A Hewlett Packard 6890 Series Gas Chromatograph (GC) equipped with a flame ionization detector and a HP-1 column (10 m \times 0.53 mm \times 2.65 μ m; Agilent Technology, Santa Clara, CA, USA) under a helium flow of 5 mL/min (carrier gas, velocity = 39 cm/s) was used for volatile analysis. The GC oven was programmed at an initial temperature of 40 °C held for 1 min, and then raised at 14 °C/min to 180 °C where it was held for 2 min, and then increased at 40 °C/min to a final temperature of 200 °C, and held at this temperature for 2 min. Compounds (ng/hr) were quantified based on comparison of peak areas with that of the IS.

Identification of compounds was performed on a Varian 3400 GC coupled to a Finnigan MAT 8230 mass spectrometer (MS) equipped with a C-1701 column (60 m \times 0.32 mm \times 1.00 μ m; Supelco, USA) at the Rutgers Mass Spectrometry and Chromatography Support Facility (New Brunswick, NJ). The GC oven was programmed at an initial oven temperature of 50 °C held for 3 min, then increased at 10 °C/min to a final temperature of 260 °C. The MS data were acquired and processed in a Finnigan MAT SS300 data system, and compounds were identified by GC retention index, and comparison of their retention times to those of commercially available pure standards and their spectral data to those from NIST library.

2.7. Statistical analyses

The number of adults and eggs on plants (rose and coriander) were counted daily. A two-way ANOVA was used to determine the effects of aphids and coriander, and their interaction, on *C. externa* attraction (i.e., number of adults) and oviposition (i.e., number of eggs) behavior in a completely randomized block design; blocked by trial. Total numbers were the sum of all 7 days. Data were natural log-transformed (ln) before analysis to satisfy the homogeneity of variance assumption for ANOVA. Means and standard errors (SE) of the non-transformed data are presented in Tables and Figures. The olfactory response was analyzed with a Chi-square (χ^2) test, with an expected response of 50% of *C. externa* for either olfactometer arm. Insects that did not respond to either arm were not considered in the analyses. Behavioral analyses were conducted in R 3.0.2 (R Development Core Team, 2013).

The effect of aphids on volatile emissions from rose plants was analyzed using principal component analyses (PCA) (Minitab v. 16; Minitab Inc., State College, Pennsylvania, USA). PCA was performed on the data because individual volatile compounds within blends are not independent (Hare, 2011). The score and loading plots were used to visualize the results. The score plot was used to determine the relationships among treatments and the loading plot to determine the relationships among volatiles. We also used non-parametric Kruskal–Wallis rank sum tests (R Development Core Team) to examine the effects of treatment (aphid-infested rose plants, uninfested rose plants, and aphids only) on volatile emissions.

3. Results

3.1. Greenhouse study

Numbers of *C. externa* adults were 1.5 times greater on plants with aphids than on plants without aphids (Fig. 2A and Table 1).

There were also 1.7 times more adults on plants next to coriander than on plants without coriander (Fig. 2A and Table 1). However, there was no aphid \times coriander interaction (Table 1), indicating that the attraction of lacewing adults to aphid-infested plants was not influenced by the presence of coriander.

Aphids, but not coriander, also increased the number of eggs laid by *C. externa* on plants (Fig. 2B,C and Table 1). These results did not differ whether we counted the total number of eggs laid on both the rose plant and the neighboring coriander (Fig. 2C and Table 1), or those eggs that were laid only on the rose plant (Fig. 2C and Table 1). There was, however, no aphid \times coriander interaction (Table 1), indicating that *C. externa* oviposition on aphid-infested plants was also not influenced by the presence of coriander.

3.2. Laboratory/olfactometer study

In the absence of aphids, *C. externa* preferred clean air over rose plant volatiles ($\chi^2 = 4.263$, $df = 1$, $P = 0.038$) (Fig. 3A). In contrast, when coriander was tested, *C. externa* females preferred volatiles from coriander over clean air ($\chi^2 = 10.922$, $df = 1$, $P < 0.001$) (Fig. 3A). *C. externa* also preferred volatiles from coriander and rose, when together, over those from rose alone ($\chi^2 = 9.561$, $df = 1$, $P = 0.002$) (Fig. 3A), showing a strong attraction of *C. externa* to

volatiles from coriander regardless of the presence of rose plant volatiles.

In the presence of aphids, *C. externa* preferred volatiles from rose plants infested with *M. euphorbiae* over uninfested plants ($\chi^2 = 17.779$, $df = 1$, $P < 0.001$) (Fig. 3B). Yet, this attraction was not affected by the presence of coriander such that *C. externa* was equally attracted to volatiles from aphid-infested rose compared with volatiles from aphid-infested rose and coriander ($\chi^2 = 0.052$, $df = 1$, $P = 0.818$) (Fig. 3B). *C. externa* was also equally attracted to volatiles from rose plants and coriander compared with volatiles from aphid-infested rose and coriander ($\chi^2 = 0.316$, $df = 1$, $P = 0.573$) (Fig. 3B), again indicating that the presence of coriander did not enhance *C. externa* attraction to aphid-infested plants.

3.3. Volatile analysis

Since *C. externa* was attracted to volatiles from aphid-infested rose plants regardless of the presence of coriander, we analyzed volatile emissions from aphid-infested roses (prey-plant complex), uninfested roses (plant alone), and aphids (prey alone) to investigate the mechanism of this attraction. To understand how the volatile profiles differ among treatments, we first performed PCA and present the results in Fig. 4 – Fig. 4A shows the score plot and Fig. 4B shows the loading plot. The first 2 PCs explained 86.4% of the variation. PCA analysis clearly separated the volatile blends of uninfested rose plants, aphid-infested rose plants, and aphids alone treatments (Fig. 4A). The first PC component explained 72.5% of the variation and separated the aphid-infested rose treatment from the uninfested and aphid alone treatments; while the second PC component explained 13.9% of the variation and separated the uninfested plants and aphid alone treatments (Fig. 4A).

Aphid-infested roses emitted ~40-times higher amounts of volatiles compared with uninfested (control) plants (Table 2). Five volatiles were emitted in higher quantities in aphid-infested rose than in uninfested plants (Figs. 4B and 5A,B); however, amounts for only four of them were significantly different between treatments (Table 2). Aphids alone emitted high amounts of β -farnesene [34.8 ± 4.9 ng/h (mean \pm SE)] (Table 2; Figs. 4B and 5C). No β -farnesene was detected from aphid-infested and uninfested rose plants (Table 2).

4. Discussion

In greenhouse and laboratory studies, we demonstrated that: (1) the green lacewing, *C. externa*, is attracted to aphid-infested rose plants; (2) *C. externa* is also attracted to coriander, a potential companion plant; (3) aphid-infested rose plants, but not coriander, induce oviposition in *C. externa*; (4) the attraction of *C. externa* to aphid-damaged rose plants is not influenced by the presence of coriander; and, (5) aphid-infested plants emit higher quantities of four volatiles than uninfested plants, in particular MeSA, that are derived from the plant and not from the prey.

C. externa adults were attracted to and preferred to oviposit on aphid-infested rose. These results are consistent with previous studies showing attraction and oviposition preference of lacewings to aphid-infested plants. For example, *Chrysoperla comanche* (Banks), *Chrysopa nigricornis* (Burmeister), and *Chrysoperla rufilabris* (Burmeister) preferred pecan trees, *Carya illinoensis* K., infested by the black-margined aphid, *Monellia caryella* (Fitch), and the black pecan aphid, *Melanocallis caryaefoliae* (Davis), for oviposition; still, they showed no preference for uninfested trees (Petersen and Hunter, 2002; Kunkel and Cottrell, 2007). Ours is, however, the first study to show attraction and oviposition preference of *C. externa* to rose plants infested by *M. euphorbiae*.

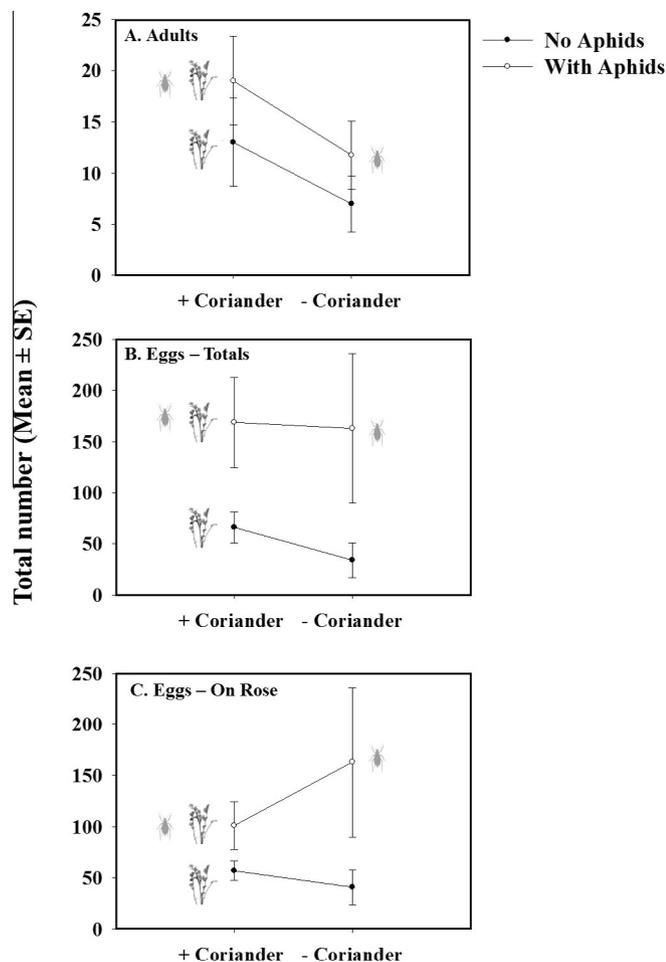


Fig. 2. Effect of coriander (*Coriandrum sativum*) and potato aphids (*Macrosiphum euphorbiae*) infestation on the number of *Chrysoperla externa* adults on rose plants and/or coriander (A) and number of eggs oviposited on rose plants and/or coriander (B), and eggs oviposited on rose plants only (C) in a greenhouse factorial experiment. See Table 1 for statistics. Data are means \pm SE.

Table 1
Results of analysis of variance (ANOVA, $\alpha = 0.05$) comparing the effects of aphids, coriander, and their interaction on the number of *Chrysoperla externa* adults and eggs on plants. The experiment was a factorial design with rose plants either with aphids, coriander, both, or neither.

Stage	Variable	df ^d	F	P
Adults ^a	Aphids	1, 9	10.499	0.010
	Coriander	1, 9	15.95	0.003
	Aphids × Coriander	1, 9	0.142	0.715
	Block (trial)	3, 9	17.373	<0.001
Eggs (total) ^b	Aphids	1, 9	10.099	0.011
	Coriander	1, 9	2.433	0.153
	Aphids × Coriander	1, 9	0.107	0.750
	Block (trial)	3, 9	3.467	0.064
Eggs (on rose plant) ^c	Aphids	1, 9	6.584	0.030
	Coriander	1, 9	0.386	0.549
	Aphids × Coriander	1, 9	0.816	0.389
	Block (trial)	3, 9	3.047	0.085

^a Number of *C. externa* adults on rose plants or rose plants with coriander.

^b Total number of *C. externa* eggs laid on rose plants or rose plants with coriander (i.e., sum of eggs laid on rose and eggs laid on coriander).

^c Total number of *C. externa* eggs laid only on rose plants when rose plants were alone or with coriander.

^d Numerator, denominator (error).

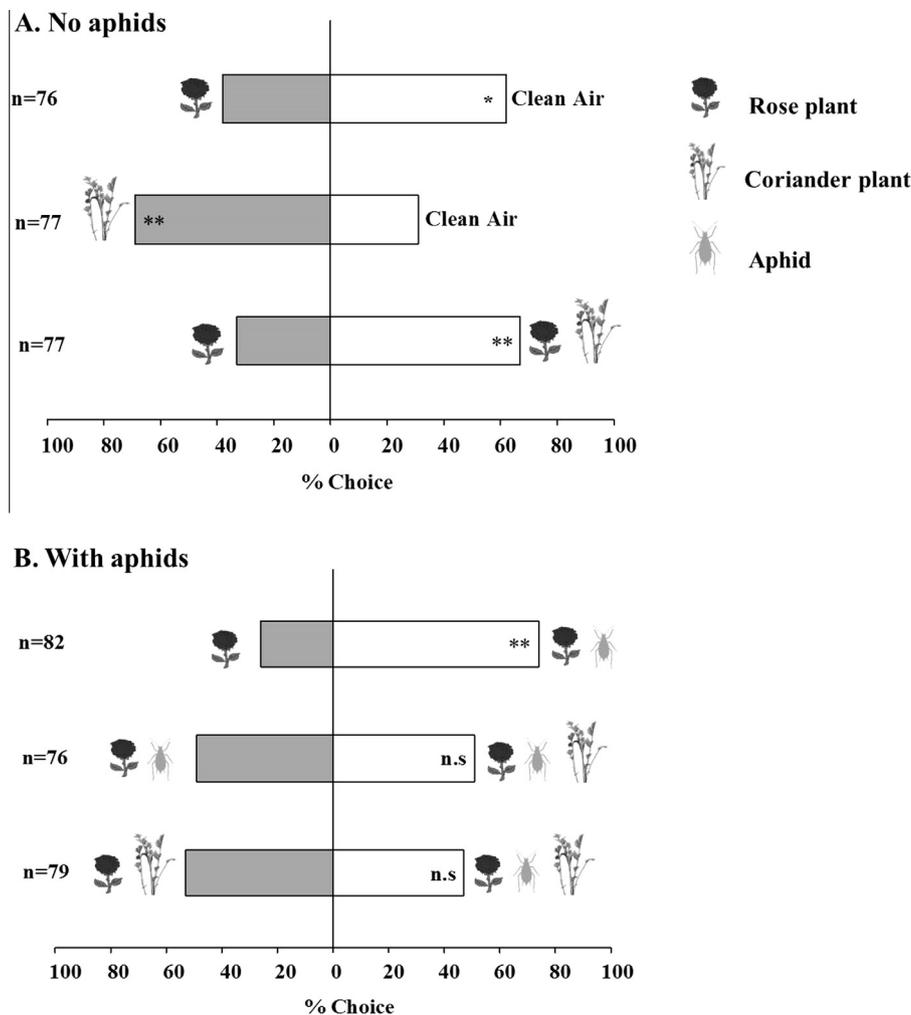


Fig. 3. Olfactory responses of mated *Chrysoperla externa* females in a Y-tube olfactometer to: (A) odor sources without the potato aphid, *Macrosiphum euphorbiae*, and (B) odor sources with the potato aphid *M. euphorbiae*. *n* = number of insects responding to one of the two odors (out of 100 individuals). χ^2 test: ** = $P \leq 0.01$; * = $0.01 < P \leq 0.05$; n.s. = no significant difference ($P > 0.05$).

Our data support the optimal foraging theory for invertebrate predators (Kindlmann and Dixon, 1993), which indicates that mated females should lay their eggs preferentially on host plants of high quality for their offspring. According to this theory, females,

which aim to maximize their offspring performance, should not lay their eggs in places where there is scarcity of prey. Female *C. externa* oviposition choice for aphid-infested plants would provide food and assure the development and survival of their

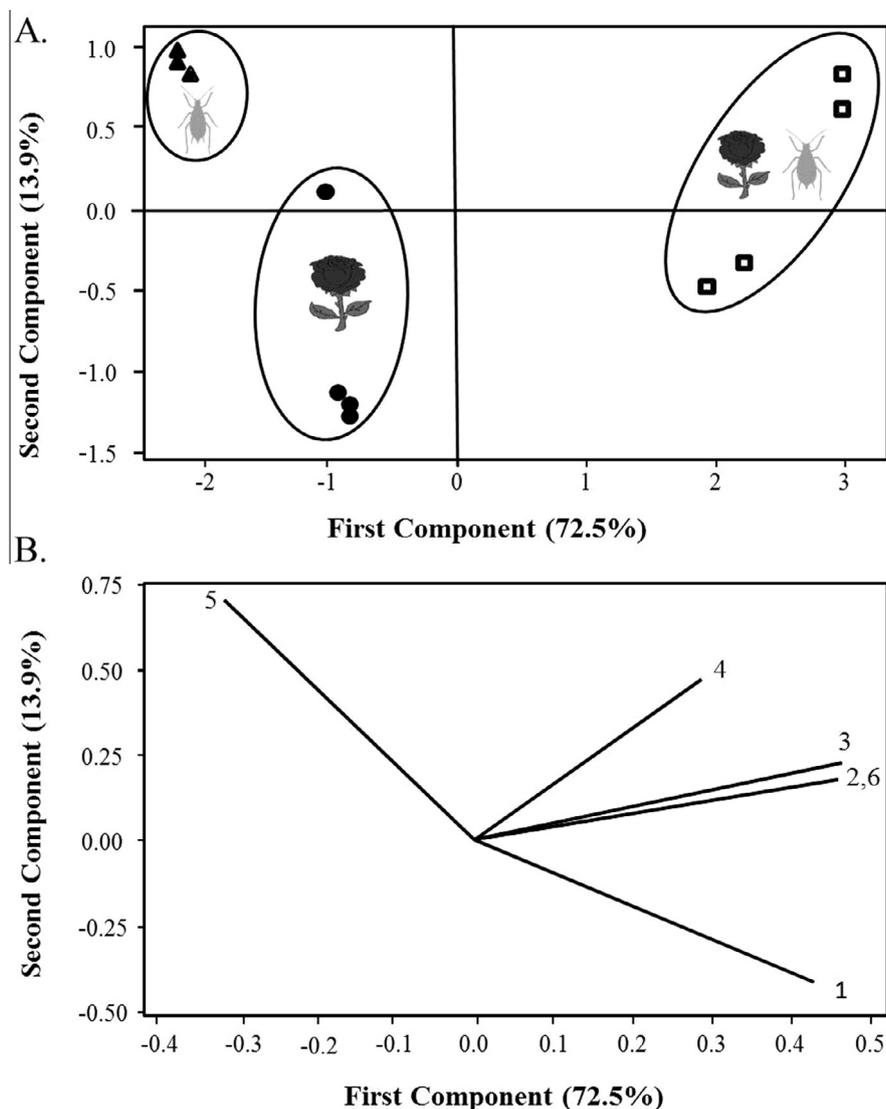


Fig. 4. Principal component analysis (PCA) of volatile compounds emitted from rose plants infested by potato aphid *Macrosiphum euphorbiae* (squares), uninfested rose plants (circles), and *M. euphorbiae* alone (triangles). The score plot (A) visualizes the relationship among treatments according to the first 2 PCs (with the explained variances in brackets). The loading plot (B) visualizes contribution of each of the volatile compounds to the first 2 PCs. See Table 2 for identity of compounds 1–6.

Table 2

Amounts of volatiles emitted from aphid-infested rose plants, uninfested rose plants (control), and aphids alone and results of Kruskal–Wallis rank sum test. Data are means \pm SE.

Volatile No.	Retention time	Volatile identity	Uninfested rose plant ^a	Aphid-infested rose plants ^a	Aphids alone ^b	Chi-square ^c	P			
1	8.09	6-Methyl-5-hepten-2-one	8.40 \pm 2.98	b	63.47 \pm 1.76	a	n.d.	c	8.46	0.015
2	8.81	Limonene	n.d.	b	71.65 \pm 12.25	a	n.d.	b	9.39	0.009
3	9.54	Methyl salicylate	n.d.	b	209.75 \pm 66.99	a	n.d.	b	9.39	0.009
4	10.46	Unknown ^d	1.75 \pm 1.75	a	18.53 \pm 12.69	a	n.d.	a	2.39	0.301
5	12.19	β -Farnesene	n.d.	b	n.d.	b	34.74 \pm 4.95	a	9.71	0.008
6	12.88	α -Farnesene	n.d.	b	39.17 \pm 11.34	a	n.d.	b	9.45	0.009
		All	10.15 \pm 1.48	c	402.59 \pm 81.58	a	34.75 \pm 4.96	b	8.91	0.011

^{a,b}Means ng/h \pm SE; n.d. = not detected (zero values were assigned to non-detectable values for statistical analysis). Means with different letters within the same row are significantly different ($P \leq 0.05$).

^a N = 4.

^b N = 3.

^c df = 2.

^d Concentration was too low for positive peak identification.

offspring, and this explains our results in the greenhouse where *C. externa* females laid more eggs on aphid-infested rose plants and fewer eggs on uninfested plants, as well as those obtained in the laboratory where the predator showed preference for the odors

of aphid-infested over uninfested rose plants, and for clean air over uninfested rose plants. Previous studies had shown that *M. euphorbiae* is a prey suitable to the larvae of this chrysopid, the predatory stage (Espinoza, 2013).

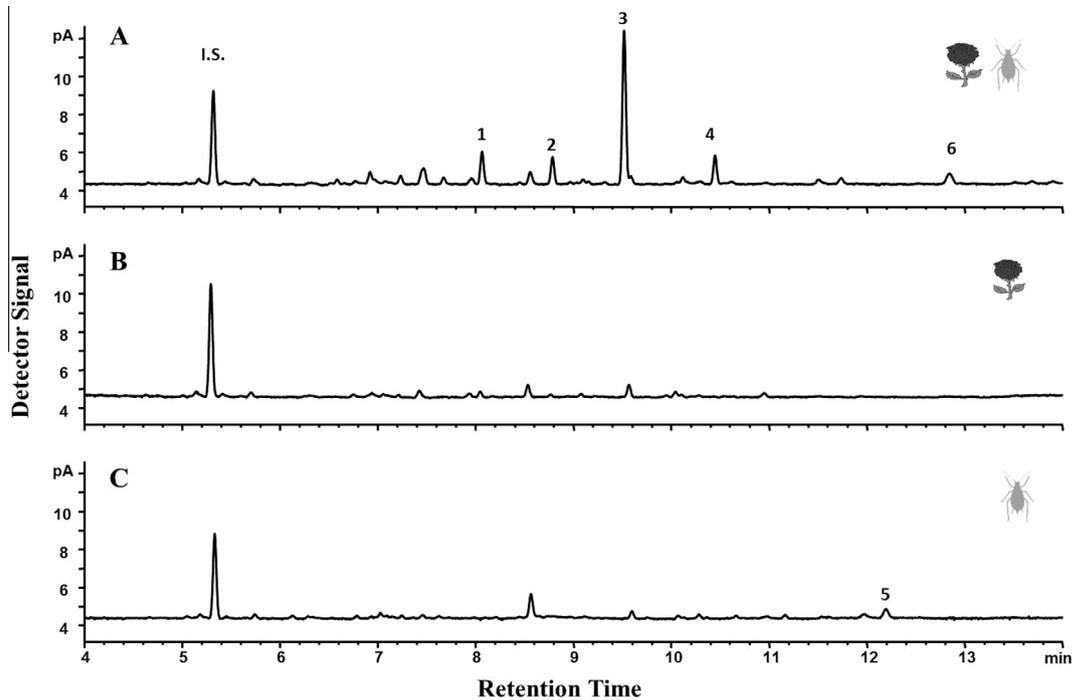


Fig. 5. Representative GC-FID profiles of headspace volatiles collected from rose plants infested by potato aphid *Macrosiphum euphorbiae* (A), uninfested rose plants (B), and *M. euphorbiae* alone (C). See Table 2 for identity of compounds 1–6. I.S. = internal standard (*n*-octane). All other GC peaks were detected also in empty bags and thus considered contaminants.

In order to oviposit in suitable environments, female lacewings need to assess the environment. One way this is achieved is through the use of chemical cues, which can have different informative value (Hilker and McNeil, 2008), often indicating the presence of prey. Chemical cues used by *C. externa* in locating these prey-rich environments could come from three possible sources: (1) HIPVs emitted by aphid-infested rose plants, which often act as medium- to long-range synomones during predator prey-searching behavior (Vet and Dicke, 1992; Rodriguez-Saona et al., 2012); (2) volatiles emitted from its prey; in our case the aphid *M. euphorbiae*; and (3) by-products of its prey (i.e., honeydew) – the latter two often acting as short-range kairomones during predator prey-searching behavior (Pickett et al., 1992; Goldansaz et al., 2004). Our laboratory results showed that volatiles from rose plants infested with aphids were attractive to *C. externa* females, providing evidence that HIPVs are likely involved in this attraction. Although there are no other studies on the response of *C. externa* to HIPVs, other species of green lacewings, such as *C. carnea sensu lato*, showed higher attractiveness to the odors of eggplant (*S. melongena* L.), okra (*Abelmoschus esculentus* L.) and pepper (*Capsicum annum* L.) infested with *Tetranychus ludeni* (Zacher) compared to uninfested plants (Reddy, 2002). Han and Chen (2002) also showed that volatiles from shoots of tea plants (*Camellia sinensis* L.) damaged by *Toxoptera aurantii* (Boyer) are more attractive to *Chrysoperla sinica* (Tjeder) than those released by undamaged plants. Therefore, lacewings appear to use HIPVs for locating aphid-rich habitats.

Methyl salicylate (MeSA) was the most abundant and consistently-emitted HIPV from *M. euphorbiae*-infested rose plants. Field trials in various agricultural crops have demonstrated attraction of several species of lacewings, such as *C. nigricornis* and *Chrysopa oculata* (Say), to sticky traps baited with MeSA (James, 2003, 2006; James and Price, 2004; Mallinger et al., 2011; Rodriguez-Saona et al., 2011b). Hegde et al. (2011) also showed that MeSA, a volatile released from cotton plants infested with *Aphis gossypii* (Glover), elicits electrophysiological activity from the antennae of

Chrysoperla lucasina (Lacroix) females. MeSA is a commonly induced volatile in aphid-damaged plants and has been shown to attract other aphid natural enemies (Zhu and Park, 2005; Pareja et al., 2009; Kaplan, 2012), and to mediate direct interactions between aphids and their host plants (Glinwood and Petterson, 2000; Ninkovic et al., 2003). This compound therefore appears to be a reliable indicator of aphid presence on plants.

In addition to HIPVs, volatiles emitted by herbivores themselves may be used by predators to select oviposition sites and for localization of prey for their offspring, especially when only the larvae are predatory (Dicke et al., 1990), as with *C. externa*. Among the volatiles released by aphids, the alarm pheromone β -farnesene, which can act as a kairomone, is known to attract aphidophagous insects to the location where their prey can be found (Pickett et al., 1992; Francis et al., 2004, 2005). In the laboratory, *C. carnea sensu lato* adults respond to this alarm pheromone (Zhu et al., 1999). In our headspace analysis, β -farnesene was detected only when volatiles from aphids alone were collected, and not when aphids were feeding on the rose plant. This indicates that β -farnesene was emitted from aphids only when disturbed, i.e., when removed from their host plant, and thus it is unlikely that this compound was responsible for the attraction of *C. externa* in the greenhouse and laboratory.

Honeydew excreted by *M. euphorbiae* present on rose plants may also have influenced the attraction and oviposition behavior of *C. externa* because, besides being a food resource to adults and larvae of chrysopids, it has breakdown products of tryptophan, such as acid hydrolyzed tryptophan, isomers of tryptophan, hydrogen peroxide tryptophan and indole acetaldehyde, that can act as kairomones attracting the predator to prey habitats (Hagen, 1986). In the study conducted by McEwen et al. (1993), adults of *C. carnea sensu lato* showed positive responses to honeydew of *Saissetia oleae* (Olivier), reducing their mobility and increasing turning frequency. This can increase the chance of the predator remaining in the area with a subsequent increase in oviposition. Honeydew of *T. aurantii* was also an important stimulus for the

search behavior of *C. sinica* – in the presence of honeydew the predator actively searched with increased turning rates and reduced walking speeds (Han and Chen, 2002). Future studies need to investigate the role of honeydew on *C. externa* attraction and oviposition behaviors. *C. externa* likely utilizes a combination of chemical cues emitted from both plants and prey to locate suitable oviposition sites; the emission of these cues is expected to be highly variable and may explain the large variation in adult oviposition on aphid-infested rose plants.

We also found that *C. externa* is attracted to the companion plant coriander and its volatiles in greenhouse and laboratory experiments, respectively. Other studies have shown that coriander plants intercropped with different plants are attractive to various natural enemies, including several species of green lacewings (Patt et al., 1997; Smith et al., 2000; Kasina et al., 2006; Medeiros et al., 2009; Satpathy and Mishra, 2011; Resende, 2012). Thus, coriander may be used in association with rose crops, and other crops of agricultural importance, to attract *C. externa*. Previous olfactometer assays also showed attraction by *C. externa* adults to coriander volatiles (Resende, 2012); however, the mechanism of this attraction remains unknown. Coriander emits more than 40 volatiles from their leaves, any one of which could play a role on natural enemy attraction (Potter and Fagerson, 1990; Deng et al., 2003). Resende (2012) identified (*E*)-2-decenal and decanal as two major components of coriander essential oil. Future studies are needed to determine the effects of these volatiles on *C. externa* attraction.

Coriander did not increase the attraction to or oviposition of the predator *C. externa* on aphid-infested rose plants. Intercropping or companion planting can enhance, reduce, or have no effect on the attraction of natural enemies to crops. However, only a few studies have investigated the role of volatiles from non-host plants on the foraging behavior of natural enemies to crops. For example, attraction of the parasitoid *Cotesia rubecula* (Marshall) was higher to volatiles from Brussels sprouts (host plants) when mixed with non-host potato volatiles (Perfecto and Vet, 2003). On the other hand, Gohole et al. (2003) showed that *Dentichasmias busseolae* (Heinrich), a pupal parasitoid of the spotted stemborer *Chilo partellus* (Swinhoe), was repelled by the non-host plant molasses grass and preferred volatiles from infested and uninfested host plants in the absence of molasses grass over those in the presence of the grass. In contrast, the weevil parasitoid *Mesopolobus incultus* (Walker) was attracted to host-plant volatiles irrespectively of the presence of non-host plant volatiles (Wäschke et al., 2014). Confirming the lack of an effect of coriander on the attraction of *C. externa* to HIPVs in the greenhouse, olfactometer experiments showed a near 50% response of *C. externa* females for each arm when offered odors of aphid-infested rose plants + coriander vs. aphid-infested rose plants, and aphid-infested rose plants + coriander vs. rose plants + coriander. Thus, both aphid infestation and coriander independently caused the attraction of *C. externa* females, but there was no synergistic effect when together.

The present study has practical implications for the manipulation of natural enemies in agroecosystems. We tested the hypothesis that companion plants can enhance the attraction of natural enemies to HIPVs. Synthetic versions of HIPVs, in particular MeSA, are currently being tested to attract natural enemies to agricultural crops (Rodríguez-Saona et al., 2011b, 2012). Recently, these HIPVs have been tested in combination with rewarding plants in an 'attract-and-reward' approach (Simpson et al., 2011). For example, Orre Gordon et al. (2013) tested a combination of MeSA with buckwheat, *Fagopyrum esculentum* (Moench), as a floral resource and found that, although no synergistic effect was observed, they attracted different natural enemies. In the present study, an attractive companion plant coriander did not enhance attraction of the lacewing *C. externa* to HIPVs emitted from aphid-infested rose plants. Future studies will evaluate MeSA lures, such as the

commercially-available PredaLure® (AgBio Inc., Westminster, CO, USA), for *C. externa* attraction to crops.

Acknowledgments

We thank to Sergio Gamboa, Robert Holdcraft, and Dr. Elvira de Lange for assistance with colony maintenance, bioassays, and volatile collection and analysis. We also thank Drs. Thomas Hartman (Rutgers U.) and Aijun Zhang (USDA-ARS, Beltsville, MD) for help in volatile identification, and Dr. Daniel Ward (Rutgers U.) for advice on statistical analysis. An early version of this manuscript was kindly reviewed by Dr. Elvira de Lange and three anonymous reviewers. Funding for this work was provided by the Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) through a postgraduate grant to JS and to Programa Primeiros Projetos Research Grant CRA APQ 04256-10 to MP.

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