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RESEARCH ARTICLE

(E,E)-α-Farnesene as a host-induced plant volatile that attracts *Apanteles taragamae* (Hymenoptera: Braconidae) to host-infested cucumber plants

Ihsan Nurkomar[a,c], Pudjianto[b], Syafrida Manuwoto[b], Damayanti Buchori[b], Shigeru Matsuyama[d], DeMar Taylor[d] and Yooichi Kainoh[d]

[a]Biological Control Laboratory, Department of Plant Protection, Faculty of Agriculture, Bogor Agricultural University, Bogor, Indonesia; [b]Department of Plant Protection, Faculty of Agriculture, Bogor Agricultural University, Bogor, Indonesia; [c]Laboratory of Applied Entomology and Zoology, Graduate School of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Japan; [d]Faculty of Life and Environmental Sciences, University of Tsukuba, Tsukuba, Japan

ABSTRACT

In tritrophic interactions between cucumber plants, the cucumber moth *Diaphania indica* Saunders (Lepidoptera: Crambidae) and a larval parasitoid *Apanteles taragamae* Viereck (Hymenoptera: Braconidae), female *A. taragamae* may use herbivore-induced plant volatiles (HIPVs) to locate their host. However, the specific compound or blend of chemicals attracting *A. taragamae* remains unknown. In this study, differences in volatiles released from uninfested, mechanically damaged and host-infested cucumber plants were examined by the headspace volatile collection method. Responses of the larval parasitoid *A. taragamae* to the volatile extracts were examined in a four-arm olfactometer. We also investigated the attraction of female *A. taragamae* to a single compound identified as an HIPV from host-infested cucumber plants. Parasitoids discriminated between the volatiles from uninfested, host-infested and mechanically damaged plants. Chemical analysis of headspace volatiles from host-infested cucumber plants showed that (E,E)-α-farnesene was released as a major component (73.1%). When (E,E)-α-farnesene was tested alone in the range of 1.7–170 ng, female parasitoids responded to 17 ng only. Therefore, tritrophic interactions between *A. taragamae* and *D. indica* appear to be partly mediated by (E,E)-α-farnesene.

1. Introduction

Plants emit a complex of volatile compounds (Paré & Tumlinson, 1999), and responses to herbivory with the induction of volatiles that play a role in tritrophic interactions (Dicke, Van Loon, & Soler, 2009), called herbivore-induced plant volatiles (HIPVs). These volatiles are the result of induced plant defence in response to herbivory and are reliable indicators of host presence, becoming critical cues for parasitoids to locate their hosts. The

emissions of plant volatiles are affected by several factors including neighbouring plants (Mauchline, Osborne, Martin, Poppy, & Powell, 2005), non-host-insects (De Rijk, Yang, Engel, Dicke, & Poelman, 2016), micro-organisms within the plants (Junker & Tholl, 2013), and abiotic factors (Becker et al., 2015).

Apanteles taragamae Viereck (Hymenoptera: Braconidae) is a koinobiont gregarious larval endoparasitoid that attacks lepidopteran species such as the cucumber moth *Diaphania indica* (Lepidoptera: Crambidae) (Peter & David, 1992). In our preliminary tests using a four-arm olfactometer, *A. taragamae* females showed a strong preference to odours from the host (*D. indica*)-infested over uninfested cucumber plants (Nurkomar, Buchori, Taylor, & Kainoh, 2017). As a koinobiont parasitoid, females of *A. taragamae* need to evaluate the host plant quality from a distance by olfactory cues during habitat location, because they are more dependent on the host plant quality than idiobiont parasitoids. The parasitised host will subsequently feed further on the host plant and take up nutrients that are then allocated to the developing parasitoids (Wäschke, Meiners, & Rostás, 2013).

Dannon, Tamò, Van Huis, and Dicke (2010) showed that females of *A. taragamae* were attracted to volatiles emanating from uninfested cowpea plants (*Vigna unguiculata*), and even more attracted to the volatiles emanating from cowpea infested with the host pod borer *Maruca vitrata* in bioassays using a Y-tube olfactometer. There are several other examples of attraction in larval parasitoids to HIPVs, e.g. Steinberg, Dicke, and Vet (1993) showed that the larval parasitoid *Cotesia glomerata* had a stronger preference for mechanically damaged over undamaged cabbage leaves, and host (*Pieris brassicae*)-infested plants were more attractive than mechanically damaged cabbage leaves. Avila, Withers, and Holwell (2016) also showed that the larval parasitoid *Cotesia urabae* was attracted more by the odours from plants (*Eucalyptus fastigata*) infested with the host *Uraba lugens* (Lepidoptera: Nolidae) than uninfested plants.

Female parasitoids are attracted by a single component or blends of chemicals emitted from damaged plants, but they do not use all the compounds as cues to locate a habitat or a host (Hilker & Meiners, 2006). For example, a blend of 5 of 7 HIPV components from *Pinus sylvestris* is sufficient for the egg parasitoid *Closterocerus rofurum* to locate their host, the pine sawfly *Diprion pini* (Beyaert et al., 2010). *Telenomus podisi* is attracted to one of four HIPV components from soybean, but attracted more to a blend of two compounds to locate their host, the stink bug *Euschistus heros* (Michereff, Borges, Laumann, Diniz, & Blassioli-Moraes, 2013).

Identification of key compounds that mediate the plant/herbivore/parasitoid interactions is important, because these semiochemicals may be used for manipulation of behaviours in biological control programmes (Peñaflor & Bento, 2013). Tritrophic interactions on cucumber plants have been well documented in the spider mite-predatory mite system including behavioural and chemical evidence that are affected by cucumber plant age (Takabayashi, Dicke, Takahashi, Posthumus, & Van Beek, 1994), cucumber varieties (Agrawal, Janssen, Bruin, Posthumus, & Sabelis, 2002; Kappers, Hoogerbrugge, Bouwmeester, & Dicke, 2011), cucumber accession (Kappers, Verstappen, Luckerhoff, Bouwmeester, & Dicke, 2010), and genes involved in spider mite induced volatile formation (Mercke et al., 2004). However, studies including cucumber leaves, lepidopteran herbivores, and parasitic wasps are limited. In order to analyse cucumber–*D. indica*–and *A. taragamae* system, we hypothesised that volatile compound(s) from *D. indica*-infested

cucumber can attract *A. taragamae*. To test this hypothesis, headspace volatiles were analysed to reveal differences in plant volatiles among the treatments. Finally, we assessed the attraction of female *A. taragamae* to a single major compound identified from host-infested plants.

2. Materials and methods

2.1. Insects

The parasitoid colony of *A. taragamae* was collected from cucumber fields of Bogor, Indonesia, in the pupal stage. Parasitoids were imported from the Biological Control Laboratory, Department Plant Protection, Bogor Agricultural University, Indonesia, to the Laboratory of Applied Entomology and Zoology, University of Tsukuba, Japan. To synchronise the emergence of adults, clusters of cocoon masses were kept in an incubator at 10°C, 50 ± 20% RH for 5–7 days before importation. For importation, 20–30 clusters of parasitoid cocoon masses were packaged and sent to Japan. After transfer to Japan, the clusters of parasitoid cocoon masses were placed in Petri dishes (86 mm in diameter, 13 mm in height) and kept until emergence in plastic cages (16 × 28 × 17 cm). After emergence of adult parasitoids, honey droplets and 12% sugar solution were provided as food. Males and females were confined in the same cage to allow mating. The parasitoids were kept under laboratory conditions at 25 ± 1°C, 60 ± 20% RH, and L16:D8 photoperiod. We used the field collected colonies of parasitoids for experiments, due to difficulties with successive artificial rearing.

D. indica was obtained from Chiba Prefectural Agriculture Research Center, Japan. The moths were placed in transparent plastic cages (16 × 28 × 17 cm). A polyethylene net (15 × 10 cm) (Watts Co., Ltd., Japan) was hung from the ceiling of the cage as an oviposition substrate with adhesive tape. Egg masses on the net were collected daily and transferred into Petri dishes (86 mm in diameter, 13 mm in height) with an artificial diet (Silkmate® 2 M; Nosan Corporation, Yokohama, Japan), then covered with plastic wrap. The late instar larvae were taken out of the Petri dishes after 14 days, and transferred to plastic containers (20 × 15 × 7 cm) containing a paper pad for pupation. Pupae were put into Petri dishes (86 mm in diameter, 13 mm in height) and placed in the rearing cages until emergence.

2.2. Plants and treatments

Plant volatiles can be influenced by both biotic and abiotic factors in the field, so plant cultivation and sampling conditions were standardised using the details outlined below. A local cucumber variety (*Cucumis sativus* L., var Tokiwa, Atariya Noen Co. Ltd, Japan) was used. The seeds were placed in a Petri dish (86 mm in diameter, 13 mm in height) containing wet cotton as seedling substrate. After germination, seedlings were transferred to the potted soil (12.5 cm diameter, 10 cm high) and kept in an incubator at 25 ± 1°C, 60 ± 20% RH., under a L16:D8 photoperiod. Plants were carefully checked to eliminate any plants infested with pests or diseases, and watered every day for three weeks before treatments.

Host-infested plants were prepared by placing 50 first instar larvae (3 days old) of *D. indica* onto a cucumber plant in the afternoon (13:00–15:00) and allowing them to

feed for 48 h. Before the treatment, the soil was covered with aluminium foil to prevent larval faeces and other substances from dropping onto the soil surface. One hour prior to volatile collection, the larvae and faecal pellets were removed from the plant, and then the plants were washed gently with tap water and allowed to dry. For mechanically damaged plants, the lower surfaces of the leaves were scratched in lines, the edges of leaves cut with sterilised scissors, and 3–4 holes (6 mm in diameter) per leaf were made with a paper punch. Damages were made 1 h prior to volatile collections.

2.3. Collection of cucumber plant volatiles

Volatiles from cucumber plants were collected using the headspace volatile collection method (Kobayashi et al., 2012) (Figure 1). The volatiles from an empty chamber (clean air) were also collected as a control. Collections were conducted during the daytime from 08:00 to 16:00.

During experiments, each pot was covered with aluminium foil to exclude volatiles from the soil. One potted plant of either treatment (uninfested, host-infested and mechanically damaged) was placed in a 3-L glass separable flask (AS ONE Corporation,
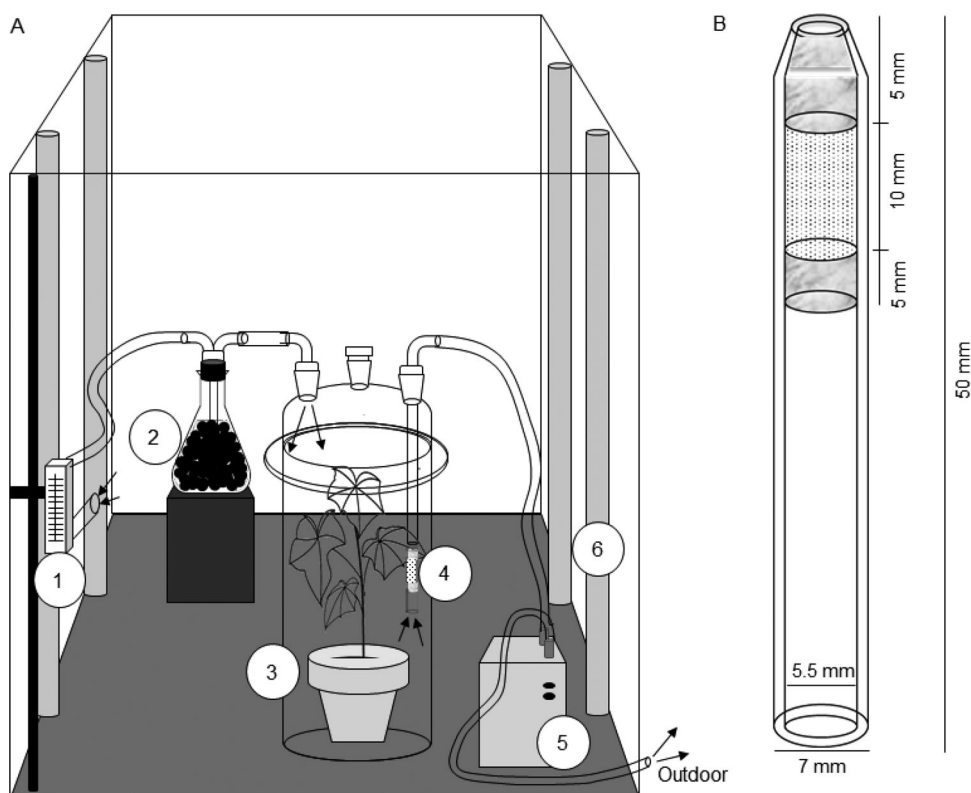

Figure 1. A set-up for collecting headspace plant volatiles (A), and detailed view of the adsorbent column sealed with quartz wool (B). 1, Flow meter; 2, activated charcoal; 3, glass aeration chamber (3-L) containing the cucumber plant (odour source); 4, volatile trap (HayeSep-Q column); 5, electric vacuum pump and 6, light source. Arrow(s) indicate the air flow.

Japan). Charcoal-filtered air was pulled into the chamber through a lateral inlet with Tygon® tubing (AS ONE Corporation, Japan) by a diaphragm pump (KNF, Neuberger, Germany). The air and any headspace volatiles from the plants were passed through an adsorbent cartridge (50 mm in length, OD: 7 mm, ID: 5.5 mm; HayeSep-Q, 60–80 mesh, 0.03 g; Restek Corporation, U.S.A.) for 2 h at 1 L/min at room temperature (20–25°C). Trapped volatiles were eluted from the adsorbent with 1 mL of distilled hexane and stored in glass vials at −25°C until use. The experiments were repeated four times on different days.

2.4. Analyses of the volatiles

The volatiles eluted from the HayeSep-Q adsorbent were analysed by gas chromatography-mass spectrometry (GC-MS) using a DB-5MS column (25 mm × 0.25 mm, 0.25 μm film thickness, Agilent Technologies, Santa Clara, CA, U.S.A.) on an HP 6890N gas chromatograph (Hewlett-Packard, Palo Alto, CA, U.S.A.). Helium was used as the carrier gas at 1 mL/min in the constant flow mode. One microlitre of samples was injected in the splitless mode (sampling time; 0.75 min) at 280°C. Oven temperature was held for 1 min at 45°C, increased to 280°C at 10°C/min, and held at 280°C for 0.5 min. The interface temperature was maintained at 280°C. Electron ionisation mass spectra were obtained at an ionisation voltage of 70 eV, with an ion source temperature of 210°C on an MS-600H mass spectrometer (JEOL Ltd., Tokyo, Japan). Identification of the components in the plant volatiles was attempted with the aid of NIST mass spectra search software (Ver. 1.6), followed by confirmation with commercially available or synthetic compounds of the candidate chemicals. After GC-MS analyses, the remaining sample solutions were subjected to bioassays in Experiment 1.

2.5. Four-arm olfactometer bioassays

Responses of the parasitoids were observed in a four-arm olfactometer (24 × 24 cm, 2 cm in height) used in a two-choice configuration (Fujinuma, Kainoh, & Nemoto, 2010; Vet, van Lenteren, Heymans, & Meelis, 1983) by connecting two pairs of diagonal inlets to glass Y-tubes carrying sample holders (glass tube, ɸ7.5 mm, L: 100 mm) with charcoal filters (Figure 2(A,B). The olfactometer was illuminated with a ceiling light (ca. 11 800 lx) and two additional lights (ca. 2 950 lx). The air was sucked from a hole in the centre of the olfactometer with an electric vacuum pump (KNF, Neuberger, Germany) so the air flow from outside passed through the charcoal, the sample holder and then into the olfactometer. The flow rate of the pump was set at 1 L/min.

The sample solution was applied on a filter paper (0.5 × 4 cm) and the solvent was allowed to evaporate. Then, the filter paper was inserted into the sample holder. One female parasitoid was released at the centre of the olfactometer and its behaviour was observed for 5 min with a camera (Elmo SUV-CAM II, Elmo USA Corp.) connected to a TV monitor (EIZO, Eizo Nanao Corp., Japan). For recording the behavioural data, a laptop computer (Panasonic CF-N10) was used with the event recording software The Observer XT, ver. 9.0 (Noldus Information Technology, The Netherlands). Data were analysed in terms of behavioural parameters, i.e. residence time in each triangular arena of the olfactometer (C1, C2, T1, and T2; Figure 2(C). Bioassays were repeated 8–15 times
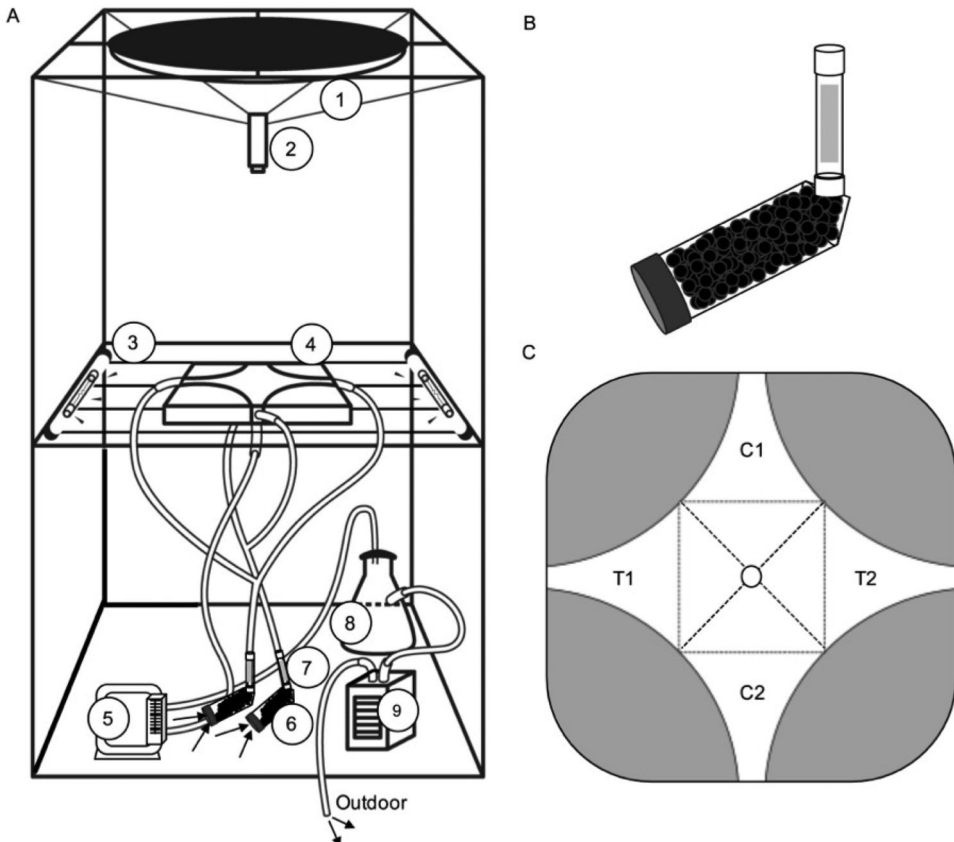
Figure 2. The dynamic four-arm olfactometer set-up (A), detailed view of the glass tube for the application of a chemical on the filter paper equipped with an activated charcoal filter (B), and top view of the four-arm olfactometer arena (C), indicating the control arena (C1, C2) and the treatment arena (T1, T2). 1, Light source (ca. 11 800 lx); 2, camera recorder; 3, light source (ca. 2 950 lx); 4, four-arm olfactometer; 5, flow meter; 6, activated charcoal filter; 7, odour source (filter paper); 8, a glass bottle (a bumper for pulsating flow from pump) and 9, electric vacuum pump. Arrow(s) indicate the air flow.

depending on the experiments. Each filter paper was tested once with a single female parasitoid. The arena of the olfactometer was cleaned with tissue paper soaked in 70% ethanol after every two replications. In all cases, 3–7-day-old mated females without previous oviposition experience were used dependent on availability. To calm down the wasps, a female parasitoid was placed in 5 mL test tubes with a droplet of honey and a piece of moistened cotton for 1 h prior to an experiment. Behavior of the parasitoids in the central square (no response) was excluded based on the method of Fujinuma et al. (2010).

2.5.1. Experiment 1: Behavioural responses of A. taragamae to the cucumber plant volatiles extracts

Four different combinations of two-choice tests were carried out with (1) uninfested plants and clean air, (2) host-infested plants and clean air, (3) host-infested and uninfested plants, and (4) mechanically damaged plants and clean air. Forty-two microlitres of each sample, containing volatiles collected for 5 min during the 2 h collection period,

was separately applied to the filter paper. Tests were replicated 8–15 times depending on the availability of samples.

2.5.2. Experiment 2: Behavioural responses of A. taragamae to (E,E)-α-farnesene

Behavioural responses of *A. taragamae* to (E,E)-α-farnesene were tested, because this compound was detected as a major volatile specifically emanating from the host-infested plants. The identification and quantification of (E,E)-α-farnesene were performed by GC-MS analysis of the pure material (>99%) obtained from an apple peel extract by successive chromatography on silica gel and silver-nitrate-impregnated silica gel. Using this material, three 10-fold doses ranging from 1.7 to 170 ng per filter paper were tested in the two-choice configuration of the olfactometer against hexane controls with 15 replications each. According to the quantitative analyses, 170 ng of (E,E)-α-farnesene was calculated as the dose collected from one host-infested cucumber plant for 5 min during a 2 h collection period.

2.6. Statistical analysis

To compare the preferences of parasitoids between the treatments and the controls, the sum of residence time a wasp spent in the areas of the treatments and controls was calculated. Data were subjected to paired *t*-test analyses. Data of parasitoids that did not respond were recorded, but excluded from the statistical analysis. The R Statistic version 3.1.3 (RCoreTeam, 2015) was used to perform these analyses.

3. Results

3.1. Volatile analyses of cucumber plants

Analyses of headspace volatiles from cucumber plants showed qualitative and quantitative differences in profiles among uninfested, host-infested and mechanically damaged plants (Figure 3). In total, 11 compounds were tentatively identified or confirmed by authentic compounds, and 3 compounds remain unidentified. Host-infested plants released larger quantities of volatiles than either uninfested or mechanically damaged plants. The most important compound that was associated with the host-infested plants was (E,E)-α-farnesene, released in the highest proportion (73.1%). (E,E)-α-Farnesene was also detected in volatiles from mechanically damaged plants, but in a much lower proportion (13.3%). We categorised the other compounds in the volatile extract of the host-infested plants, namely 3-methylbutylaldoxime, (Z)-3-hexenyl acetate, and indole, as minor compounds, because they were released in small proportions, 3.8%, 2%, and 5.2%, respectively. (E)-β-Ocimene and linalool were identified by comparisons with authentic samples. Perillene was tentatively identified by a mass spectral search.

3.2. Behavioural responses of A. taragamae to the cucumber plant volatile extracts

Females showed different residence times in the arena of the olfactometer with the volatiles from the extracts of uninfested, host-infested, and mechanically damaged plants.
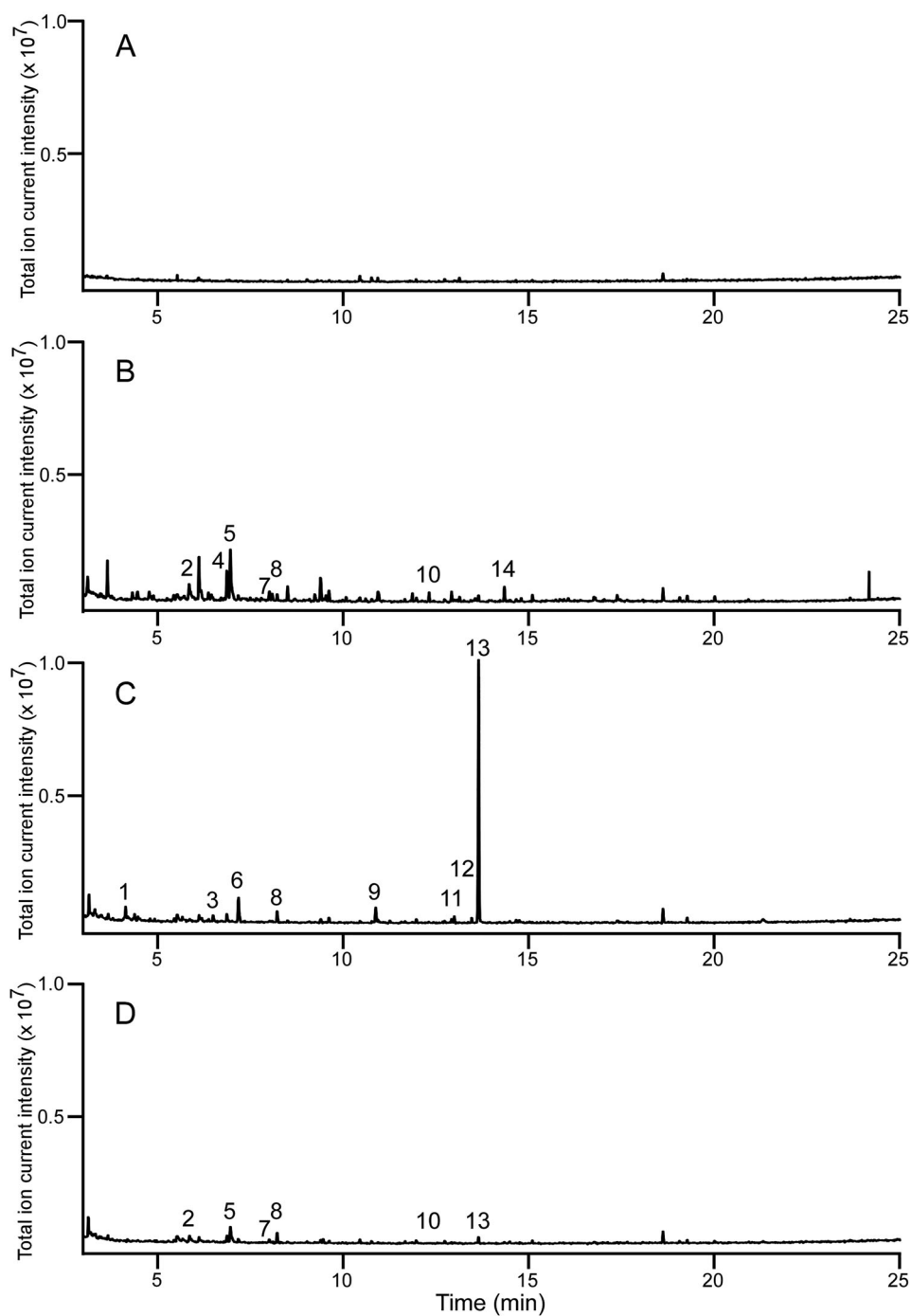
Figure 3. Comparisons of typical total ion chromatograms of headspace volatiles from clean air (A), uninfested (B), host-infested (C), and mechanically damaged (D) cucumber plants. For comparison, the Y-axis was fixed. 1, 3-methylbutylaldoxime; 2, benzaldehyde; 3, (Z)-3-hexenyl acetate; 4, 2-ethyl-1-hexanol; 5, benzyl alcohol; 6, (E)-β-ocimene; 7, linalool; 8, perillene; 9, indole; 10, geranyl acetone; 11, UK1; 12, UK2; 13, (E,E)-α-farnesene and 14, UK3. UK: unknown.
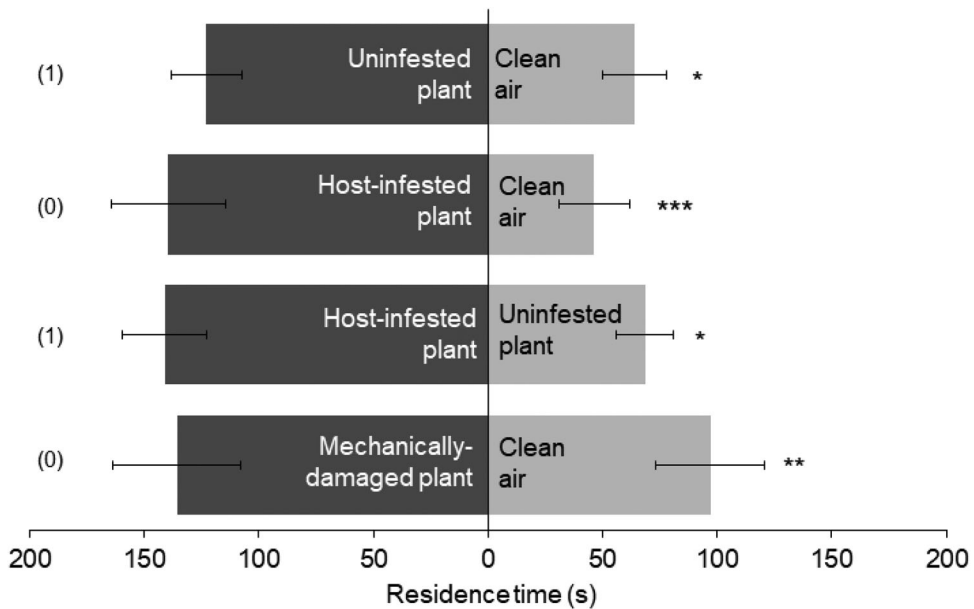
Figure 4. Behavioural responses of females *A. taragamae* offered choices between the volatiles from the extracts of an uninfested plant and clean air ($N = 8$), a host-infested plant and clean air ($N = 8$), a host-infested and uninfested plant ($N = 15$), and a mechanically damaged and clean air ($N = 8$) in a four-arm olfactometer. Each value shows the mean residence time (s) in treated and control (hexane) arenas (mean ± S.E.). Numbers in parentheses indicate the numbers of parasitoids that did not respond to either of the odour sources tested. Asterisks indicate significant differences in the paired *t*-test ***: $P < .001$, **: $P < .01$, *: $P < .05$.

Females showed a longer residence time in the arena with the volatiles from the extracts of uninfested plants than clean air (paired *t*-test, $P = .02$, $n = 8$), and host-infested plants than clean air (paired *t*-test, $P = .01$, $n = 8$). Furthermore, females spent more time in the sample arenas when offered extracts of host-infested versus uninfested plants (paired *t*-test, $P = .01$, $n = 15$). Females also showed a longer residence time in the arena with the volatiles from the extracts of mechanically damaged plants than clean air (paired *t*-test, $P = .04$, $n = 8$) (Figure 4).

3.3. Behavioural responses of A. taragamae to (E,E)-α-farnesene

When (E,E)-α-farnesene was tested, females showed significantly longer residence times in the sample area at a dose of 17 ng (paired *t*-test, $P = .005$, $n = 15$), and spent shorter residence times at a dose of 170 ng (paired *t*-test, $P = .02$, $n = 15$), when compared with the respective controls (hexane). There was no significant difference in residence times at a dose of 1.7 ng (paired *t*-test, $P = .103$, $n = 15$) (Figure 5).

4. Discussion

The present study showed that the volatiles released from host-infested cucumber plants were more attractive for females of *A. taragamae* than uninfested plant volatiles by using
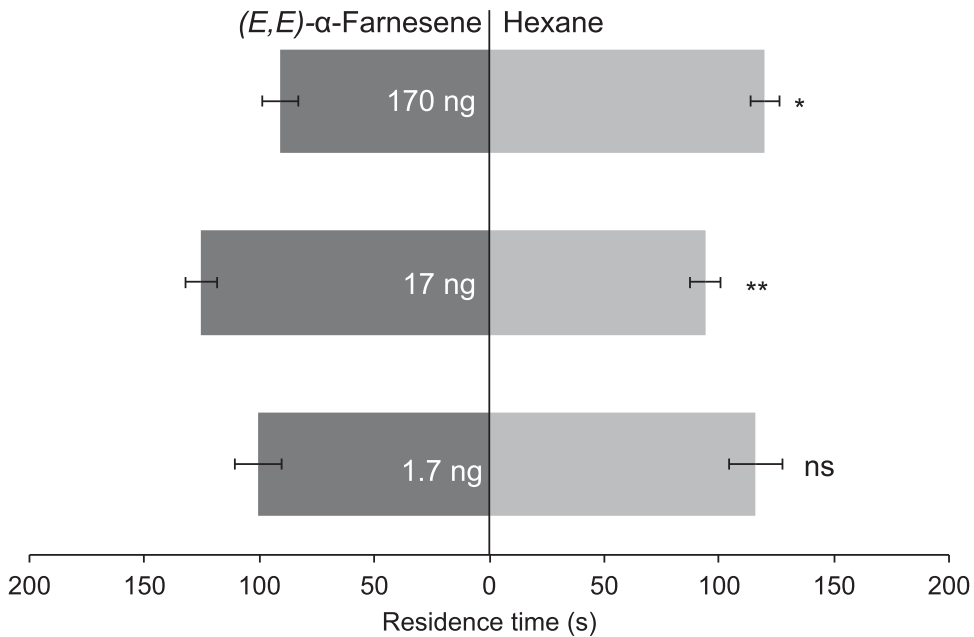
Figure 5. Behavioural responses of females *A. taragamae* offered choices between (*E,E*)-α-farnesene and control (hexane) at different doses tested ($N = 15$). Each value shows the mean residence time (s) in treated and control (hexane) arenas (mean ± S.E.). Asterisks indicate the significant difference by the paired *t*-test **: $P < .01$, *: $P < .05$, ns: $P > .05$.

extracts from the headspace collections. Furthermore, we demonstrated positive behavioural responses of female *A. taragamae* to the major HIPV (*E,E*)-α-farnesene. (*E,E*)-α-Farnesene was released in the highest proportion in the volatiles from host-infested plants of the 14 compounds identified from uninfested, host-infested and mechanically damaged plants. In the mechanically damaged plants, (*E,E*)-α-farnesene was also detected but in far less amounts, which is often the case with HIPVs (Bouwmeester et al., 2003; Suckling et al., 2012; Turlings, Tumlinson, Heath, Proveaux, & Doolittle, 1991). Therefore, (*E,E*)-α-farnesene was judged as a major HIPV in the cucumber – *D. indica* system. However, we were unable to conclusively show it is the most attractive compound.

A mixture of HIPVs, or possibly one volatile, may inform parasitoids of the presence of hosts in the vicinity of damaged plants, and the plants subsequently benefit from the messages that are sent (Finidori-Logli, Bagnères, & Clément, 1996). It is still not known what blend characteristics make the volatile blend attractive to natural enemies of herbivorous hosts (presence or concentrations of single compounds, ratios of compounds in a blend, background odour may all play a role in different degrees). Also, single compounds can be attractive when offered alone, but they lose their attractiveness or can even become repellent when offered in a mixture and vice versa (Webster, Bruce, Pickett, & Hardie, 2010). In our study, female *A. taragamae* showed a strong preference to 17 ng of (*E,E*)-α-farnesene but not to the other doses (Figure 5). Research on the other host-parasitoid systems suggests the sensitivity of parasitoids is narrowly tuned to the dose of chemical cues. Büchel et al. (2011) showed that *Oomyzus gallerucae* (Hymenoptera: Eulophidae), an egg parasitoid of the elm leaf beetle *Xanthogaleruca luteola* (Coleoptera: Chrysomelidae),

only responded to (*E,E*)-α-farnesene at 11.5 ng. Similarly, Michereff et al. (2013) reported that *T. podisi* (Hymenoptera: Scelionidae), an egg parasitoid of *E. heros* (Hemiptera: Pentatomidae), showed an attraction to (*E,E*)-α-farnesene at a 10^{-5} M concentration. Further studies on dose-responses of *A. taragamae* to (*E,E*)-α-farnesene may reveal whether a larger dose of this chemical is annoying or a signal to avoid heavily infested plants. Moreover, the presence of minor compounds (indole) may also contribute to the host searching process of *A. taragamae*. Indole has been reported as a plant volatile that attracts parasitoids such as *Cotesia marginiventris*, a larval parasitoid of several lepidopteran species (D'Alessandro, Held, Triponez, & Turlings, 2006; Turlings et al., 1991; Turlings, Tumlinson, & Lewis, 1990). Indole has also been reported in the *Spodoptera litorallis* – maize (D'Alessandro et al., 2006; Erb et al., 2015; Sobhy et al., 2012) and cotton systems (Sobhy, Erb, & Turlings, 2015), and in the *Epiphyas postvittana*–apple system (Suckling et al., 2012). These examples indicate the necessity to evaluate the other HIPVs that were identified in this study for both their individual effects and various combinations on the searching behaviour of *A. taragamae*.

The results of this study provided chemical evidence for these observations and may help manipulate the behaviour of *A. taragamae* with the use of semiochemicals. Generally, the steps for determining the use of semiochemicals in pest management involve identification, production and application of the semiochemicals in the field (Vet & Dicke, 1992). Several studies have shown that the application of semiochemicals in the field can increase both abundance and parasitism rate of a parasitoid. For example, the application of (*E,E*)-α-farnesene in cotton increases parasitism rates of *Lygus* sp. by the egg parasitoid *Anaphes iole* (Williams, Rodrigues-Saona, Castle, & Zhu, 2008). Similarly, the application of jasmonic acid in rice increases the parasitism rate of the brown plant hopper egg parasitoid *Anagrus nilaparvatae* (Lou, Du, Turlings, Cheng, & Shan, 2005). The application of *S. litoralis* larvae regurgitant to the scratched leaves of maize increases the abundance and parasitism rate of Hymenoptera parasitoids (Ockroy et al., 2001). In contrast, the application of borneol in apple plantations increases the abundance of tachinid fly parasitoids, but not the parasitism rate (Roland, Denford, & Jiminez, 1995). Applications of semiochemicals may reduce host searching efficiency of parasitoids when the host is not present (Puente, Kennedy, & Gould, 2008). Vet and Dicke (1992) explain that failures in the application of semiochemicals in the field are due to the incompatibility of the parasitoid behaviour with a blanket spray distribution. Therefore, various aspects should be considered with the use of semiochemicals in pest management, including selection of the compound(s) as single components or mixtures, dosages, time and method for application (Blassioli-Moraes, Borges, & Laumann, 2013).

Other possibilities for the success of semiochemicals in pest management can be utilised through manipulation of the response by natural enemy or manipulation of the source of the semiochemicals (Vet & Dicke, 1992). (*E,E*)-Farnesene has been found as a component of apple peels (Huelin & Murray, 1966), and pheromones of ants (Cavill, Williams, & Whitfield, 1967; Vander Meer, Williams, & Lofgren, 1981) and aphids (Pickett & Griffiths, 1980). As a component of HIPVs, the compound appears to be evolutionarily conserved in the plant kingdom in terms of the distribution among both arboreous and herbaceous plants. For example, (*E,E*)-α-farnesene has been reported from cotton (Loughrin, Manukian, Heath, Turlings, & Tumlinson, 1994), elm (Büchel et al., 2011), apple (Suckling et al., 2012), grapevine (Krugner, Wallis, & Walse, 2014),

soybean (Michereff et al., 2011), and also cucumber (Iris F Kappers et al., 2011). This information is important for *D. indica* management by cultivation methods such as cucumber intercropping to manipulate the sources of the semiochemicals.

In summary, female *A. taragamae* utilises host-infested plant volatiles to locate their hosts. Attraction of females to host-infested plants is partly mediated by (E,E)-α-farnesene, found in very high proportions from host-infested plants. In other parasitoid/host/plant systems, the attraction of parasitoids to (E,E)-α-farnesene increases when combined with other compounds (Michereff et al., 2013) (Krugner et al., 2014). Therefore, female *A. taragamae* may also use other chemical cues to locate their host. Further research is needed to test the attractiveness of minor compounds singly or in combinations with (E,E)-α-farnesene for better understanding of the semiochemicals used by *A. taragamae* during the host searching process.

Disclosure statement

No potential conflict of interest was reported by the authors.

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