

Innate olfactory responses of female and male parasitoid *Apanteles taragamae* Viereck (Hymenoptera: Braconidae) toward host plant infested by the cucumber moth *Diaphania indica* Saunders (Lepidoptera: Crambidae)

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RESEARCH ARTICLE



Innate olfactory responses of female and male parasitoid *Apanteles taragamae* Viereck (Hymenoptera: Braconidae) toward host plant infested by the cucumber moth *Diaphania indica* Saunders (Lepidoptera: Crambidae)

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ABSTRACT

The behavioural responses of *Apanteles taragamae*, a larval parasitoid of the cucumber moth *Diaphania indica*, to the volatiles of cucumber plants was investigated in a four-arm olfactometer. Females and males were given a choice between several odour sources that included (1) clean air, (2) uninfested, (3) host-infested, and (4) mechanically damaged cucumber plants. Females and males showed different preferences for volatiles emanating from these plants. Females responded significantly longer to the volatiles from uninfested plants than clean air, and to host-infested plants than uninfested plants. There were no significant differences in female responses to the volatiles from mechanically damaged and uninfested plants. Males responded significantly longer to clean air rather than uninfested plants. The volatiles from both uninfested and host-infested cucumber plants may play important roles in host habitat location of *A. taragamae* females.

ARTICLE HISTORY


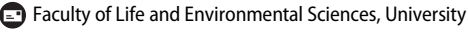
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KEYWORDS

Habitat location; plant volatiles; HIPVs; tritrophic interaction

1. Introduction

The cucumber moth *Diaphania indica* Saunders (Lepidoptera: Crambidae) is occasionally a serious pest of some cucurbit plants (Pandey, 1975) and widespread in Japan, Korea, China, Taiwan, Tropical Asia, Africa, the Netherlands, some Pacific Islands, and the United States (Peter & David, 1992). Schreiner (1991) showed that the infestation of a cucumber leaf by one *D. indica* larva is sufficient to cause a 10% decrease in yield. *Apanteles taragamae* Viereck (Hymenoptera: Braconidae) was recorded as a parasitic Hymenopteran for the first time from the community of cucumber fields in Indonesia (Lizmah, 2015). It is a gregarious larval parasitoid of *D. indica* (Fitriyana, 2015; Lizmah, 2015; Peter & David, 1991, 1992) with a 96% parasitism rate in cucumber plants (Puspaningtyas, 2015). This parasitoid is a promising candidate for biological control of *D. indica*. However, the information about this parasitoid is still limited to

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life history (Dannon, Tamò, Agboton, van Huis, & Dicke, 2012; Dannon, Tamò, van Huis, & Dicke, 2010b; Peter & David, 1992), toxicity of insecticides (Peter & David, 1988), hyperparasitism (Peter & David, 1993), and effects of non-host target (Dannon, Tamo, van Huis, & Dicke, 2012) and host diet (Wetro et al., 2014) on the parasitism rate of *A. taragamae*.

Host-searching behaviour is one important aspect of parasitoid biology. The success of biological control programmes has been attributed particularly to high host-searching efficiency (De Moraes, Cortesero, Stapel, & Lewis, 1999; Neuenschwander, 2001) that results in successful parasitism by parasitoids (Vinson, 1976). Host searching occurs through several stages that lead parasitoids to the proper host (Godfray, 1994). This process appears to be directed through a series of both physical and chemical stimuli (Silva, Moraes, Laumann, & Borges, 2006). At first, parasitoids use volatile chemical cues at a distance from the plant to locate their host habitat, and next parasitoids use herbivore-induced plant volatiles (HIPVs) to locate their host (Vet & Dicke, 1992). However, the parasitoid habitat is surrounded by a complex agroecosystem environment with high chemical complexity from various volatiles released from the plants (Randlkofer, Obermaier, Hilker, & Meiners, 2010). The presence of HIPVs is a solution for parasitoids to cope with this complexity (Dicke, 2015).

Over the years, numerous studies have demonstrated the attraction of parasitoids by HIPVs (Avila, Withers, & Holwell, 2016; Mumm & Dicke, 2010; Salehi & Keller, 2010; Steinberg, Dicke, & Vet, 1993). However, no study reports the attraction of *A. taragamae* by HIPVs in the cucumber–*D. indica* system. In the current study, we assessed the value of cucumber plants in the host-searching process of *A. taragamae* and investigated the role of uninfested, host-infested, and mechanically damaged cucumber plant volatiles in a series of bioassays using a four-arm olfactometer.

2. Materials and methods

2.1. Plant

Seeds of a local cucumber (*Cucumis sativus* L.) variety Tokiwa (Atariya Noen Co. Ltd, Japan) were sown in Petri dishes (86 mm in diameter, 13 mm in height) containing wet cotton as the planting substrate. After the seeds germinated, plants were transferred to potted soil (12.5 cm diameter, 10 cm in height) for the experiments. Plants were kept in an incubator at $25 \pm 1^\circ\text{C}$, $60 \pm 20\%$ RH, L16:D8 photoperiod. Plants were watered every day and those infested with pests or diseases were eliminated. Three-week-old cucumber plants were used in all experiments.

2.2. Insects

Parasitoids and hosts were imported from the Laboratory of Biological Control, Department of Plant Protection, Bogor Agricultural University, Indonesia, to the Laboratory of Applied Entomology and Zoology, University of Tsukuba, Japan (Importation Number: 2016.2.12.00.K10.E.005971). Both insects were imported in the pupal stage. Insects were collected from the cucumber field in Bogor, Indonesia, either in the larval or pupal stages. After pupation, the insects were kept in an incubator at 10°C for 5–7

days before importation to Japan. One day after arrival, the insects were moved to an insect rearing cabinet and kept in the laboratory at $25 \pm 1^\circ\text{C}$, $60 \pm 20\%$ RH, and an L16:D8 photoperiod.

Diaphania indica pupae and moths were reared in transparent plastic cages ($16 \times 28 \times 17$ cm) with 12% sugar solution provided as a food source and a plastic mesh netting (15×10 cm) as an oviposition substrate. Egg masses on the plastic net were collected daily and transferred to Petri dishes (86 mm in diameter, 13 mm in height) containing an artificial diet (Silkmate® 2M; Nosan Corporation, Yokohama, Japan), then covered with plastic wrap until pupation. Pupae were transferred to new Petri dishes (86 mm in diameter, 13 mm in height) and placed in the rearing cage until emergence.

A cluster of *A. taragamae* cocoon masses was placed in a transparent plastic cage ($16 \times 28 \times 17$ cm) until emergence. Honey droplets and 12% sugar solution were provided as food. Due to difficulties in successive parasitoid rearing, all parasitoid adults collected from the field were directly used in the experiments.

2.3. Olfactometer set-up

The behavioural responses of *A. taragamae* were investigated in a four-arm olfactometer (24×24 cm, 2 cm in height) using two-choice tests by connecting pairs of diagonal inlets to glass Y-tubes carrying the odour source from one plant confined inside 3 l glass flasks (AS ONE Corporation, Japan) with charcoal filters. The design of the four-arm olfactometer was similar to that of Vet, Lenteren, Heymans, and Meelis (1983) and Fujinuma, Kainoh, and Nemoto (2010) (Figure 1(a,b)). Air was supplied to the arena with an electric vacuum pump (KNF, Neuberger, Germany) adjusted by a valve and flowmeter to a constant flow rate of 1000 ml/min. Light sources (ca. 2950 lx) were placed on two sides of the flasks. A third light (ca. 11,800 lx) was coupled to a video camera (Elmo SUV-CAM II, Elmo USA Corp.) and placed above the arena of the olfactometer for observations. Each parasitoid was released at the central arena of the olfactometer and its behaviour was recorded for 5 min with The Observer XT (ver. 9.0) (Noldus Information Technology, Netherlands) software. Behaviour of the parasitoids in the olfactometer arena was analysed from the following behavioural parameters: residence times and number of visits to each triangular arena of the olfactometer (C1, C2, T1, and T2; Figure 1(b)). We excluded data from the central arena following the method of Fujinuma et al. (2010), since the preference of parasitoids for the odour source is clearly discriminated in the triangular arena.

2.4. Behavioural responses of *A. taragamae* to cucumber plant volatiles

To determine the effect of cucumber plant volatiles on the behavioural responses of *A. taragamae*, two-choice tests were performed between odour source combinations of (1) uninfested plant vs. clean air, (2) host-infested plants vs. uninfested plants, (3) mechanically damaged plants vs. clean air, and (4) mechanically damaged plants vs. uninfested plant. The combinations of plants tested are hereafter referred to as 'plant sets'. Each test was replicated five times and each replication was tested using five parasitoids for one plant set. In total, 25 females and 25 males were used for the five plant sets. Cucumber plants were prepared as follows.

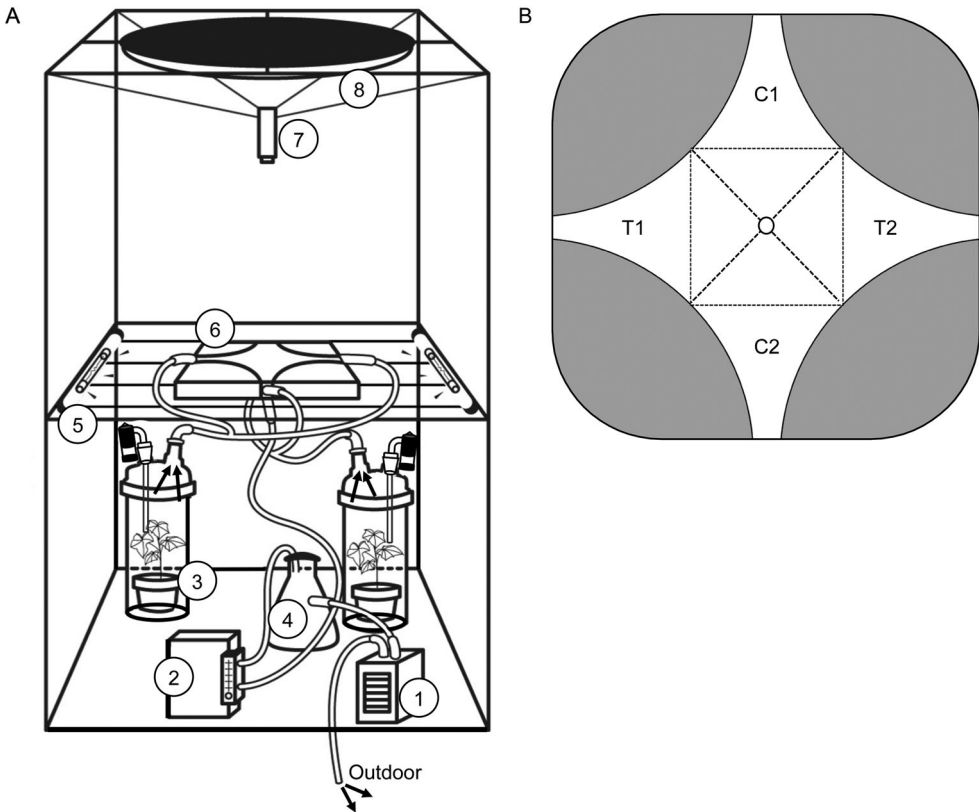


Figure 1. Four-arm olfactometer set-up (a), and top view of the four-arm olfactometer arena, indicating the control arena (C1, C2) and the treatment arena (T1, T2) (b). (1) Electric vacuum pump, (2) Flow-meter, (3) Glass flask with charcoal filter containing one plant (odour source), (4) Glass bottle (bumper for pulsating flow from pump), (5) Light source (ca. 2950 lx), (6) Four-arm olfactometer, (7) Video camera, (8) Light source (ca. 11800 lx).

Host-infested plants were prepared by introducing 50 (3-day-old) first instar larvae of *D. indica* onto a 3-week-old cucumber plant in the afternoon (13:00–15:00), and the larvae allowed to feed for 48 h. During the feeding period, the pot was covered with aluminium foil to prevent contamination of the soil surface with larval faeces and other substances. Afterwards, the larvae and faecal pellets were removed from the plants, and the plants were gently washed with tap water and allowed to dry for 1 h prior to the experiments. For mechanically damaged plants, the lower surfaces of the leaves were scratched in lines and the edges of leaves were cut with sterilised scissors; 3–4 holes (6 mm in diameter) per leaf were made with a paper punch 1 h prior to the experiments. During the experiments, the soil of the potted cucumber plants was covered with aluminium foil to prevent effects of volatiles from the soil.

Mated females (3–5 days old) with no previous oviposition experience and mated males (3–5 days old) were introduced separately into 5 ml test tubes containing small droplets of honey and water. Parasitoids were then individually released at the centre arena of the olfactometer. After testing five parasitoids, the position of the odour sources was changed and the arena was cleaned with tissue paper soaked in 70% ethanol.

2.5. Statistical analysis

Preference of a parasitoid was determined by comparing the sum of the residence times spent in each triangular arena, treatment and control. To account for differences in activity among parasitoid individuals in the olfactometer arena, we calculated the sum of the residence times in the triangular arena of the treatments and controls and used this sum for data analysis. We used linear mixed models (LMMs) to compare the effect of plant set as a random factor ('lmer' in the package lme4; Bates, Mächler, Bolker, & Walker, 2014), because we used one plant set for five parasitoids. In the models, the dependent variable was residence time. Fixed factors were treatment and control as (1) uninfested plant vs. clean air, (2) host-infested plant vs. uninfested plant, (3) mechanically damaged plant vs. clean air, and (4) mechanically damaged plant vs. uninfested plant. These analyses were performed with R Statistic version 3.1.3 (R Core Team, 2015).

3. Results

3.1. Behavioural responses of *A. taragamae* to cucumber plant volatiles

Females stayed longer in the triangular arena of the olfactometer with volatiles from uninfested plants than clean air (LMMs, $\chi^2 = 26.967$, $df = 1$, $P = 2.069e-07$), and stayed longer in host-infested than uninfested plants (LMMs, $\chi^2 = 8.868$, $df = 1$, $P = .0032$). Females also stayed longer in the triangular arena of the olfactometer with the volatiles from mechanically damaged plants than clean air (LMMs, $\chi^2 = 24.169$, $df = 1$, $P = 8.825e-07$). However, there was no significant difference between mechanically damaged and uninfested plants (LMMs, $\chi^2 = 0.059$, $df = 1$, $P = .807$) (Figure 2). Taken together, the olfactory responses of female *A. taragamae* rank in the following order: host-infested plant > mechanically damaged plant = uninfested plant > clean air.

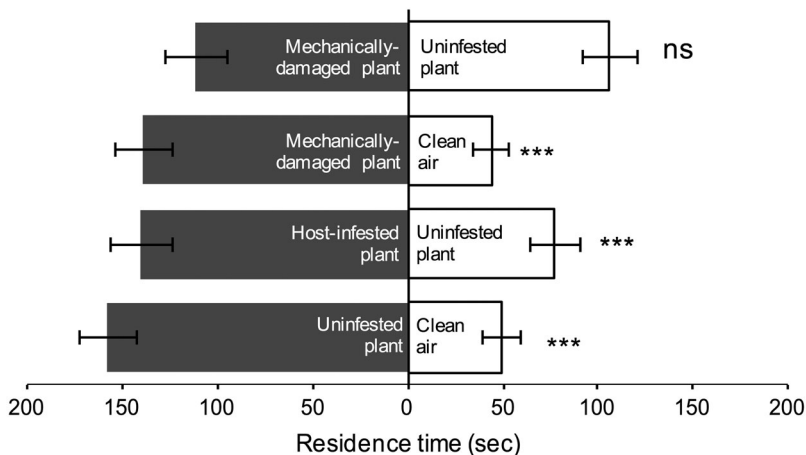


Figure 2. Behavioural responses of female *Apanteles taragamae* offered choices between the volatiles from cucumber plants that were uninfested, host-infested, mechanically damaged, and clean air in a four-arm olfactometer ($N = 25$). Asterisks indicate the significant levels (LMMs: *** $p < .0001$, ** $p < .001$, * $p < .05$, ns, not significant).

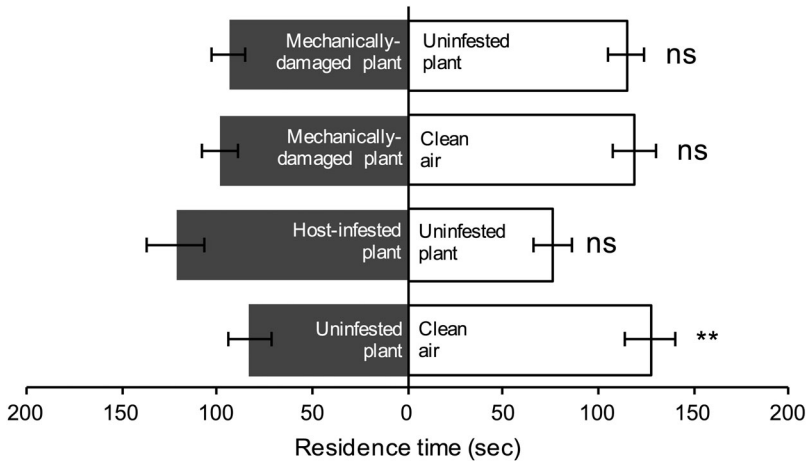


Figure 3. Behavioural responses of male *Apanteles taragamae* offered choices between the volatiles from cucumber plants that were uninfested, host-infested, mechanically damaged, and clean air in a four-arm olfactometer ($N = 25$). Asterisks indicate the significant levels (LMMs: *** $p < .0001$, ** $p < .001$, * $p < .05$, ns, not significant).

Male behaviour differed from females. Males did not show significant differences in residence time spent between triangular arenas with the volatiles from host-infested and uninfested plants (LMMs, $\chi^2 = 2.845$, $df = 1$, $P = .09$), mechanically damaged plants and clean air (LMMs, $\chi^2 = 1.919$, $df = 1$, $P = .165$) and mechanically damaged and uninfested plants (LMMs, $\chi^2 = 2.643$, $df = 1$, $P = .104$). However, the males stayed longer in arenas with clean air than uninfested plants (LMMs, $\chi^2 = 6.803$, $df = 1$, $P = .009$) (Figure 3).

4. Discussion

In the host-searching process, parasitoids use long- and short-range cues to find their host. The long-range cues come either from plant-derived volatiles or HIPVs, while the short-range cues come from chemicals associated with the host and host by-products, e.g. frass, cuticle, regurgitant, and trace of host (Vet & Dicke, 1992). In the current study, we assessed the value of cucumber plants in the host-searching processes of *A. taragamae*.

Females of *A. taragamae* showed a preference for uninfested plants over clean air, indicating volatiles released from uninfested plants help *A. taragamae* find the host habitat. Several researchers have reported similar behavioural responses in other parasitoids (Avila et al., 2016; Dannon, Tamò, Van Huis, & Dicke, 2010a; Ngi-Song et al., 1996; Takabayashi et al., 1998). During the parasitoid host-searching process, a plant has an important involvement in the recruitment of a natural enemy of the herbivore. Vet and Dicke (1992) concluded that chemical cues from herbivores can only be detected at a close range. Parasitoids must first search for habitats where hosts are likely to be present. Therefore, we can conclude that volatiles from undamaged plants are used as the first cue for *A. taragamae* to locate the habitat of their host.

Apanteles taragamae females also showed stronger attraction to volatiles released by host-infested plants than uninfested plants. This is consistent with the results of Dannon et al. (2010a) who 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 by the host pod borer *Maruca vitrata* in bioassays using a Y-tube olfactometer. Similarly, Steinberg et al. (1993) showed the larval parasitoid *Cotesia glomerata* had a stronger preference for mechanically damaged over undamaged cabbage leaves, and host-infested plants were more attractive than mechanically damaged cabbage leaves. Avila et al. (2016) also showed the larval parasitoid *Cotesia urabae* was attracted by odours from uninfested plants (*Eucalyptus fastigata*) and even more attracted by plants infested with the host *Uraba lugens*. Dicke, Van Loon, and Soler (2009) concluded the volatiles released by uninfested plants do not clearly indicate the presence of a host and plants provide more reliable cues through interactions with the herbivore as damage to invite parasitoids to find their host. These volatiles are the result of the tritrophic interactions and are reliable to indicate host presence, becoming critical cues for parasitoids to locate their hosts.

In contrast to females, male parasitoids are not attracted to plant odours. Males did not show differences in residence time in the olfactometer arena with volatiles from uninfested, host-infested, and mechanically damaged plants. Males were attracted and stayed longer in clean air and not attracted by the odours of uninfested plants. In other parasitoids, males were only attracted by odours from conspecific virgin females (Avila et al., 2016; Bouchard & Cloutier, 1985). In our current study, we did not test the attraction of males to female *A. taragamae*. However, Peter and David (1992) reported that males became highly agitated when released with freshly emerged females. Therefore, we conclude that *A. taragamae* males may forage for females in response to female sex pheromones rather than respond to plant volatiles.

Our results suggest that *A. taragamae* females effectively respond to volatile compounds from cucumber plants, and also to synomones emitted by cucumbers with feeding damage to orient and locate their host habitat. Having detected the host habitat, female parasitoids may refine their search using kairomones emitted by host or host by-products, e.g. frass, cuticle, regurgitant, and trace of host. In addition, as a part of a natural complex habitat, female parasitoids may also face qualitative differences from host and non-host-infested plants during foraging (Dicke et al., 2009), because the release of HIPVs by non-hosts may also effect parasitoid behaviour. For example, the parasitoid *Diaeretiella rapae* showed greater preference for volatiles from the host *Myzus persicae* than non-host (*Plutella xylostella*) infested cabbage plants; changes in a plant volatile profile induced by non-host damage also did not hinder responses of the parasitoid to host-induced signals (Agbogba & Powell, 2007). In contrast, the attraction of parasitoid *Cotesia marginiventris* to maize-infested plant by its host *Spodoptera littoralis* is altered by simultaneous attack of non-host *Euscelidius variegatus* (Erb et al., 2015). More behavioural analyses are needed to confirm the effects of non-host damage on the responses of *A. taragamae* female foraging behaviour.

In summary, females were only slightly attracted to the volatiles emanating from uninfested plants, but more attracted to the volatiles emanating from host-infested cucumber plants. The volatiles released by host-infested plants must provide useful information for *A. taragamae* to locate its host, since only specific chemical cues are attractive or ecologically relevant to natural enemies. The results of this study can now be used as baseline information to identify the semiochemicals emitted by host-infested plants and assess their effects on parasitoid behaviour, so these semiochemicals can possibly be used in the biological control of this important cucumber pest in the future.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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