



Deterrent effects of intact plants on host-searching behavior of parasitoid wasps

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Abstract

Female parasitoids distinguish between host-infested and intact plants using chemical cues; however, the contribution of intact plants to host searching of parasitoids has not been investigated so far. Here, we tested how host-searching behavior of the parasitoid wasp, *Cotesia kariyai* (Watanabe) (Hymenoptera: Braconidae), was affected by intact maize plants in a wind tunnel. To determine the best color for material to create a plant model, we observed flight responses of female wasps to paper plant models of four different colors. Wasps tended to land more frequently on green models than other models. Therefore, a green paper model was used for subsequent experiments. In a no-choice test, female wasps showed higher landing rates on a paper plant model treated with herbivore-induced plant volatiles (HIPVs) than on an intact plant. Moreover, in two-choice tests, wasps preferred the plant model with HIPVs over an intact plant with HIPVs. Intact plants seem to deter *C. kariyai* females. Our findings suggest that information from intact plants also contributes to the host-searching behavior of females in the natural environment.

Keywords *Cotesia kariyai* · Braconidae · Color preference · HIPVs · Tri-trophic interactions

Introduction

To achieve reproductive success, parasitoid insects need to be able to locate suitable hosts in complex environments (Godfray 1994; Wäschke et al. 2013). Parasitoids of herbivorous insects employ a variety of visual (Henneman et al. 2002; Vinson 1976; Yamawaki and Kainoh 2005) and chemical cues (Afsheen et al. 2008; Horikoshi et al. 1997; Vet and Dicke 1992; Wäschke et al. 2013) from host insects, host byproducts, and host-infested plants to find suitable hosts.

Numerous hymenopteran and dipteran parasitoids use herbivore-induced plant volatiles (HIPVs) to locate host habitats. Females of these parasitoid species are attracted

more by volatiles from host-infested plants than by volatiles from intact (i.e., uninfested) plants (e.g., McCormick et al. 2012; Turlings and Erb 2018; Wäschke et al. 2013). Several studies have focused on deterrent effects of plant volatiles on parasitoids searching for hosts (Wäschke et al. 2013). For instance, the pupal parasitoid, *Dentichasmias busseolae* Heinrich (Hymenoptera: Ichneumonidae), is deterred by volatiles from a non-host plant (*Melinis minutiflora* Beauv.; Poaceae) of its host caterpillar, *Chilo partellus* (Swinhoe) (Lepidoptera: Crambidae) (Gohole et al. 2003). Females of *Trichogramma chilonis* Ishii (Hymenoptera: Trichogrammatidae), an egg parasitoid of *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae), are also deterred by odors from the non-host pigeon pea (*Cajanus cajan* L.; Fabaceae) (Romeis et al. 1997). Those studies demonstrated that parasitoids avoid odors from plants that are not eaten by their host insects, to increase host-searching efficiency. Negative effects of plant volatiles were emphasized by studies focusing on parasitoid discrimination between host and non-host plants of host insects (Wäschke et al. 2013). However, a few studies have investigated whether volatiles from intact plants of the herbivore's host plant species have negative effects on parasitoid behavior.

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In this study, we evaluated effects of intact plants on the host-searching behavior of parasitoids to clarify how parasitoids discriminate between host-infested plants and intact plants in a complex habitat. We demonstrated the effects of volatiles from intact maize plants (*Zea mays* L.; Poaceae) on the host-searching behavior of *Cotesia kariyai* (Watanabe) (Hymenoptera: Braconidae), a larval endoparasitoid of *Mythimna separata* (Walker) (Lepidoptera: Noctuidae), in wind tunnel experiments. *Cotesia kariyai* makes use of HIPVs from host-infested maize plants to locate its host's habitat (Fujiwara et al. 2000; Hou et al. 2005; Kuramitsu et al. 2019; Takabayashi et al. 1991, 1995). Experiments using a Y-tube olfactometer (Takabayashi et al. 1991) and a four-arm olfactometer (Thanikkul et al. 2017) have demonstrated that female *C. kariyai* preferred volatiles of host-infested maize plants to volatiles of intact plants. Those studies compared the responses of *C. kariyai* to volatiles from infested and intact plants, but effects of volatiles from intact plants on host-searching behavior of female *C. kariyai* have not been explored. In this study, we examined flight responses of female *C. kariyai* to infested/intact maize plants or to visually similar paper plant models in the presence of an infested plant (emitting HIPVs) in wind tunnel experiments to evaluate the influence of intact plants on parasitoid host-searching behavior. Prior to these experiments, we also observed flight responses of female wasps to paper plant models of four different colors (green, yellow, blue, and red) in a wind tunnel to determine the optimal color for paper plant models.

Materials and methods

Insects

Mythimna separata and *C. kariyai* were obtained from stock populations at the Laboratory of Applied Entomology and Zoology, University of Tsukuba, Japan. *Mythimna separata* caterpillars were reared on an artificial diet (Silkmate 2M, Nosan Corporation, Kanagawa, Japan) and *C. kariyai* were reared following the method of Fukushima et al. (2001) under laboratory conditions (25 °C ± 1 °C, 60% ± 20% r.h., photoperiod: 16L–8D). Experiments used 1–4-day-old mated, naïve females. For all experiments, 10–15 replicates were performed per day.

Plants

Maize ('Honey-Bantam Peter 610'; Sakata Seed Co., Kanagawa, Japan) was used as a food source for *M. separata* caterpillars. Maize plants were grown individually from seeds in plastic flowerpots (5.5 cm in diam., 7.0 cm in height) in a greenhouse (25 °C ± 1 °C, photoperiod:

16L–8D). In all experiments, 2–3-week-old plants (ca. 30 cm high) were used. All plants were watered daily.

To obtain host-infested maize plants, we introduced 10 third instar *M. separata* caterpillars into a cage with a potted maize plant. Caterpillars were allowed to feed on maize plants for 10 h before the experiments. All caterpillars and their feces were removed from the plant before experiments.

Experiment 1: color preferences of *C. kariyai* when influenced by HIPVs

Parasitoid females show innate color preferences during host searching (Ichiki et al. 2011; Kawamata et al. 2018). To determine the appropriate color for our paper plant model, we observed flight responses of female wasps in relation to four colored paper plant models (green, yellow, blue, and red) in a wind tunnel following experimental methods of Ichiki et al. (2011). Briefly, plant models comprised four paper leaves cut from fine colored paper (Muse Co., Ltd., Tokyo, Japan). They were radially attached to a bamboo stick (4 mm in diam., 10 cm in length) with cellophane tape, and the base of the stick was inserted into a rubber stopper. Reflectance spectra of the colored papers, intact maize plants, and infested maize plants (Online Resource 1) were measured from 400 to 700 nm using a spectrophotometer (CM-700d; Konica Minolta, Inc., Tokyo, Japan).

Wind tunnel tests were implemented following the methods of Fukushima et al. (2001), using a wind tunnel 30 cm in height × 30 cm in width × 150 cm in length at a wind speed of 25–30 cm s⁻¹, 25 °C ± 1 °C, 60% ± 20% r.h., and ~700 lx. A metal platform (15 cm in height, 8 × 8 cm top size) was placed 25 cm downwind from the paper plant model to serve as a release point for the parasitoid female. A host-infested maize plant was placed 10 cm upwind from the model (35 cm upwind from the platform) as a source of HIPVs. A black mesh screen was placed between the model and the infested maize plant to obstruct visual cues from the infested plant.

Female wasps were selected randomly from the rearing cage and individually placed in a covered Petri dish (5.3 cm in diameter, 1.5 cm in height) with a piece of moist cotton wick. The Petri dish was placed on the metal platform, the cover was removed, and the behavior of each wasp was observed for 5 min. Females that did not land on the paper plant model within 5 min were scored as showing no response to the paper model.

Experiment 2: effects of intact plants on *C. kariyai* flight responses

To evaluate effects of intact plants on *C. kariyai*, we compared flight behaviors of wasps in response to an intact plant with or without a plant emitting HIPVs, with flight behaviors

in response to an infested plant or a plant model with or without HIPVs. Experimental setups and methods were the same as in Experiment 1. A green paper model was used for this experiment since female wasps landed most frequently on green paper models in Experiment 1 (see below).

Experiment 3: female wasp preferences between an intact plant with HIPVs and a plant model with HIPVs

To evaluate wasp preferences between an intact plant with HIPVs and a plant model with HIPVs, we conducted a two-choice test. The experimental setup was the same as in Experiment 1. A single intact plant and a single green paper model were placed 10 cm apart, 25 cm upwind of the platform. We observed wasps for ≤ 5 min after their release from the platform and recorded the location where the wasp landed first. If the wasp did not make a choice within 5 min, the trial was recorded as “no choice.”

Statistical analysis

In Experiments 1 and 2, we compared landing rates of female wasps in each treatment using a Chi-squared test and Ryan's multiple range test. All analyses were performed in R v. 3.2.3 software (R Core Team 2015) and Ryan's multiple range test was performed using an open source package (https://aoki2.si.gunma-u.ac.jp/R/src/p_multi_comp.R, “encoding=euc-jp”). In experiment 3, we determined preferences of wasps between the intact plant and the plant model using a binomial test under the null hypothesis that wasps had a 1:1 distribution over the two “plants”, ignoring trials in which wasps did not make a choice.

Results

Experiment 1: color preference of *C. kariyai* influenced by HIPVs

The landing rate of female wasps on paper plant models differed between colors ($\chi^2 = 15.13$, d.f. = 3, $p < 0.05$; Fig. 1). Wasps landed significantly more often on green (53.8%) and yellow models (45.0%) than on a blue model (5.0%). Although they landed most frequently on the green model, the difference of landing ratios among green, yellow, and red models (20.0%) was not significant.

Experiment 2: effects of intact plants on *C. kariyai* flight responses

The landing rate of wasps on the target differed among treatments ($\chi^2 = 45.931$, d.f. = 4, $p < 0.001$; Fig. 2). Wasps landed

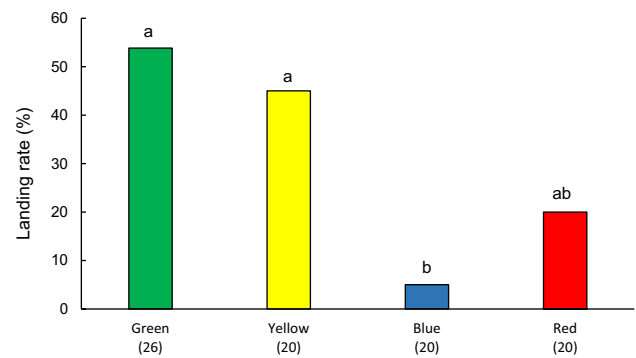


Fig. 1 Flight responses of naïve female *C. kariyai* to four colors (green, yellow, blue, and red) of paper plant models exposed to HIPVs in a wind tunnel. The percentage of female wasps landing on each target plant was recorded. Different letters above bars indicate a significant difference between values (Ryan's multiple range test for proportions after χ^2 test, $p < 0.05$). Numbers in parentheses indicate the number of wasps tested

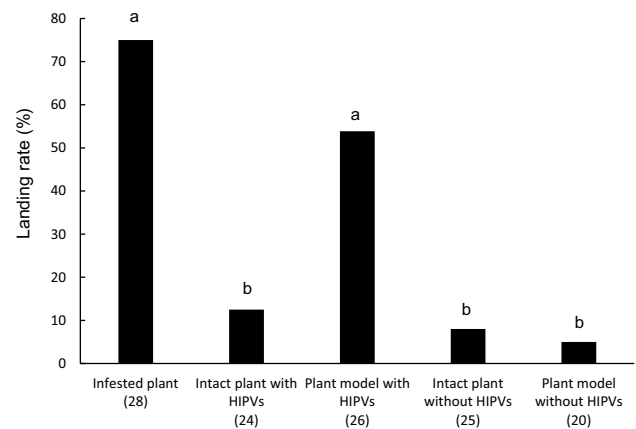


Fig. 2 Flight responses of naïve female *C. kariyai* to a host-infested maize plant, an intact plant with HIPVs, a green paper model with HIPVs, a green paper model without HIPVs, and an intact plant without HIPVs in the wind tunnel. The percentage of female wasps landing on each target was recorded. Different letters above bars indicate a significant difference between values (Ryan's multiple range test for proportions after χ^2 test, $p < 0.05$). Numbers in parentheses indicate the number of wasps tested

significantly more often on an infested plant (75.0%) and on a plant model exposed to HIPVs (53.8%) than on an intact plant with HIPVs (12.5%), a plant model without HIPVs (5.0%), or an intact plant without HIPVs (8.0%).

Experiment 3: female wasp preferences between an intact plant with HIPVs and a plant model with HIPVs

Of 34 females, 19 made a choice between an intact plant and a plant model exposed to HIPVs. Of these, 16 (84.2%) chose the model and 3 (15.8%) chose the intact plant. The

number of landings on the model was significantly higher (binomial test; $p < 0.01$).

Discussion

Cotesia kariyai females preferred green and yellow paper models over blue (Fig. 1). Although there were no significant differences in landing rates among green, yellow, and red models, wasps tended to land more frequently on green and yellow models than on the red one. Between green and yellow, wasps landed on the green model more frequently than on the yellow model, but only slightly. Moreover, compared to the reflectance spectrum of the yellow model, the higher reflectance range of the green model overlapped well with that of intact and infested plants (Online Resource 1). Therefore, we used a green paper model for Experiments 2 and 3.

The reflectance spectrum of maize plants and the green model was highest between 520 and 580 nm. In addition, the yellow model showed higher reflectance at ≥ 550 nm (Online Resource 1). Female wasps seem to detect host-infested plants using HIPVs and color stimuli with a maximum reflectance at around 550 nm. *Exorista japonica* (Townsend) (Diptera: Tachinidae), a parasitoid fly of many lepidopteran insects, including *M. separata*, also prefers a green paper model when HIPVs are present (Ichiki et al. 2011). Most parasitoids probably use color stimuli as well as olfactory cues to locate host habitats.

In Experiment 2, wasps landed significantly less often on the intact plant without HIPVs and the model without HIPVs than on the infested plant or the model with HIPVs (Fig. 2). This difference confirms that HIPVs influence host-searching behavior, as described previously (Fujiwara et al. 2000; Takabayashi et al. 1991, 1995). Interestingly, wasps landed significantly less often on an intact plant with HIPVs than on the model with HIPVs (Fig. 2). The wasp landing rate on an intact plant with HIPVs was similar to that on the plant model without HIPVs and the intact plant without HIPVs. These results clearly indicate that intact plants deter landing by *C. kariyai*. Results of two-choice tests between an intact plant and a plant model, both exposed to HIPVs, also indicate deterrent effects of the intact plant on host searching of the wasps.

Parasitoids, including *C. kariyai*, use HIPVs from infested plants to locate their host habitats, namely, patches containing host plants where parasitoid host herbivores develop (Meiners and Peri 2013; Takabayashi et al. 1991, 1995). In the host habitat, parasitoids use various host-related infochemicals, including volatiles and contact chemicals (Afsheen et al. 2008; Godfray 1994; Vet and Dicke 1992). To discriminate between host-infested and intact plants, *C. kariyai* females use HIPVs from infested plants (Takabayashi

et al. 1991, 1995; Fujiwara et al. 2000), host feces, exuviae, and feeding traces on infested plants (Takabayashi et al. 1985). In addition, our results suggest that deterrent effects of intact plants also contribute to female wasp discrimination between host-infested and intact plants in the host habitat.

Volatile chemicals of intact plants apparently deter host-searching *C. kariyai*. Takabayashi et al. (1995) analyzed chemical components of both intact and infested plants, and demonstrated that intact plants emit unique compounds or larger amounts of certain compounds than infested plants. Therefore, we hypothesize that one or more of these intact plant-derived volatiles deter host searching in *C. kariyai*. Furthermore, not only volatile chemicals, but also contact (non-volatile) chemicals or visual stimuli of intact plants may deter host-searching parasitoids (Afsheen et al. 2008; Quicke 2015). In addition, effects of HIPVs on parasitoid color preferences may also influence parasitoid host-searching behavior (Uefune et al. 2013). To identify which factors of intact plants have deterrent effects, behavioral bioassays in a wind tunnel or multi-arm olfactometer with these candidate chemicals and visual stimuli must be conducted.

Our results suggest that intact host plants for insect herbivores that serve as hosts for parasitoids also convey information to the parasitoids, as do infested host plants. Parasitoids detect not only the presence of their hosts, but also the absence of those hosts from food plants utilized by the host insects. Although several studies have demonstrated that non-food plants of the host insect have negative effects on host-searching parasitoids (Gohole et al. 2003, 2005; Romeis et al. 1997; Wäschke et al. 2013), as far as we know, this is the first report to show that intact host plants of host insects actually deter parasitoids. In contrast to our results, previous studies conducted with other parasitoid species have indicated that volatiles from intact plants either attract parasitoids (Hatano et al. 2008; Martin et al. 1990; Pareja et al. 2007) or have neutral effects on parasitoid host-searching behavior (Ichiki et al. 2011). Most studies on the effects of host-plant-derived volatiles on host-searching behavior of parasitoids have focused on positive effects of HIPVs (McCormick et al. 2012; Turlings and Erb 2018). Therefore, those studies did not observe behavior of parasitoids in the presence of intact plants exposed to HIPVs. During host searching, parasitoids must first locate host plant habitat (long-range), then an infested plant (close-range), and finally the host (Aartsma et al. 2017, 2019; Gohole et al. 2005). Our results document deterrent effects of intact plants on close-range host searching by parasitoids. However, the role of intact plants on long-range host-searching behavior of parasitoids is unknown.

Recently, Ozawa et al. (2018) demonstrated that greater biomass of intact plants synergistically increased the attractiveness of attractants emitted from host-infested cabbage plants to *Cotesia vestalis* (Haliday) (Hymenoptera:

Braconidae), a larval parasitoid of *Plutella xylostella* (L.) (Lepidoptera: Plutellidae). To generalize the effects of intact plants on parasitoid host-searching behavior, further studies of how intact plants affect the behavior of host-searching parasitoids under the influence of HIPVs need to be carried out with other parasitoid–host plant systems.

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