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Host-Associated Olfactory Cues**

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Attraction of *Paratelenomus saccharalis* (Hymenoptera: Platygasteridae), an Egg Parasitoid of *Megacopta cribraria* (Hemiptera: Plataspidae), to Host-Associated Olfactory Cues¹

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Abstract *Paratelenomus saccharalis* (Dodd) (Hymenoptera: Platygasteridae) is an egg parasitoid of *Megacopta cribraria* (F.) (Hemiptera: Plataspidae). Although the parasitoid has been previously reported in parts of Africa, Europe, Asia, and Australia, it was first reported in North America in 2013 on *M. cribraria* that was introduced from Asia into North America in 2009. Field observations showed that *P. saccharalis* females readily parasitize eggs of *M. cribraria*. However, the cues used by the parasitoid for host location have not been investigated. It was hypothesized that *P. saccharalis* uses olfactory cues to locate *M. cribraria*. The objective of this study was to test the attraction of *P. saccharalis* to host-associated cues in Y-tube olfactometer bioassays. Compared to the control of no host plant or eggs, female *P. saccharalis* showed significantly greater attraction to *M. cribraria*-damaged soybean, *M. cribraria* eggs only, and damaged soybean plus *M. cribraria* eggs, in separate bioassays. However, the parasitoid did not show significant attraction to undamaged soybean. The results suggest that host location by *P. saccharalis* is mediated by olfactory cues from the soybean host and *M. cribraria* eggs. This is the first behavioral study to demonstrate the response of *P. saccharalis* to induced soybean volatiles.

Key Words Y-tube olfactometer, host location, plant volatiles, olfactory response, soybean

Egg deposition and feeding damage by herbivores induce emission of volatile organic compounds from plants (Moraes et al. 2008). Egg parasitoids exploit these volatiles as olfactory cues to locate their host. Herbivore-induced plant volatiles provide reliable host location cues to natural enemies such as parasitoids and predators (Ngumbi et al. 2009, Price et al. 1980). Such olfactory-mediated tritrophic interactions have been investigated and reported in several previous studies (Birkett et al. 2003, Colazza et al. 2004, Moraes et al. 2005, Morawo and Fadamiro 2014, Ngumbi et al. 2009, Takabayashi and Dicke 1996, Tumlinson et al. 1993, Turlings et al. 1993).

Paratelenomus saccharalis (Dodd) (Hymenoptera: Platygasteridae) is a solitary and relatively specialized egg parasitoid of three species of insects in the family Plataspidae, including *Megacopta cribraria* (F.) (Hemiptera: Plataspidae) (Johnson 1996, Wall 1928). The distribution of *P. saccharalis* was limited to the Eastern

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Hemisphere (Johnson 1996) until its recent discovery in North America where it was initially recovered from eggs of *M. cribraria* in Georgia in 2013 (Gardner et al. 2013b). The preferred host of *M. cribraria* is kudzu, *Pueraria montana* var. *lobata* (Willdenow) Ohwi, but it is also a pest of soybean, *Glycine max* (L.) Merrill, in its expanded range in the United States (Eger et al. 2010, Gardner et al. 2013a). Furthermore, overwintering adults of *M. cribraria* can bypass kudzu to feed and reproduce on early planted soybean (Del Pozo-Valdivia and Reisig 2013; Golec et al. 2015). Nymphs and adults of *M. cribraria* aggregate in large numbers on tender stems and leaves of soybean where they suck sap, resulting in significant yield loss (Seiter et al. 2013). In Georgia, field activity of *M. cribraria* peaks around April–May, July–August, and October before adults overwinter around November (Zhang et al. 2012). Gardner et al. (2013b) suggested that *P. saccharalis* was likely introduced into the United States with parasitized eggs of *M. cribraria* from Asia.

In Asia, studies on *P. saccharalis* have focused mainly on parasitism rate and field dispersal (Hirose et al. 1996) as well as the effect of temperature on its development (Takagi and Murakami 1997). Similarly, studies on *P. saccharalis* in the United States have focused on its discovery and parasitism rate on *M. cribraria* eggs in the field (Gardner et al. 2013b, Medal et al. 2015, Tillman et al. 2016). Parasitism rate of *P. saccharalis* is typically high (47–95%) in field-collected eggs (Gardner et al. 2013b), with the population building in late summer.

Like many other egg parasitoids, *P. saccharalis* is challenged with seasonal availability of suitable hosts and the inconspicuous nature of host eggs. Hence, natural selection should favor the development of highly adaptive host location strategies. Consequently, several species of egg parasitoids use olfactory cues to locate their hosts (Colazza et al. 2004, Hilker et al. 2002, Hilker and Fatouros 2015, Michereff et al. 2011, Moraes et al. 2008). However, little is known about the cues used by *P. saccharalis* for host location. To test this hypothesis that *P. saccharalis* uses host-associated olfactory cues for host location, we investigated the attraction of *P. saccharalis* to various host-associated factors including undamaged soybean, damaged soybean, *M. cribraria* eggs only, and damaged soybean plus *M. cribraria* eggs in Y-tube olfactometer bioassays. This study has potential practical application in the development of attractants for *P. saccharalis* to enhance its effectiveness as a biological control agent against *M. cribraria*.

Materials and Methods

Insects. Parasitized eggs of *M. cribraria* were collected in July 2016 from kudzu in Auburn, Alabama, and maintained under laboratory conditions [$25 \pm 1^\circ\text{C}$, $75 \pm 5\%$ relative humidity (RH), and 14:10 h (L:D)] until adult emergence. Newly emerged female *P. saccharalis* were introduced into rearing cages ($75 \times 75 \times 115$ cm) (BugDorm-2, Megaview Science Education Services Co., Ltd., Taichung, Taiwan) containing *M. cribraria* adults, nymphs, and eggs. *Paratelenomus saccharalis* females were allowed to parasitize host eggs under laboratory conditions. Parasitized eggs of *M. cribraria* were transferred from the rearing cage into petri dishes (35 mm diameter \times 10 mm high) and kept under controlled laboratory conditions (i.e., $25 \pm 1^\circ\text{C}$, $75 \pm 5\%$ RH, and 14:10 h [L:D] photoperiod) until parasitoid emergence. Naïve (and presumed mated) female parasitoids

(approximately 3 d old) fed with 10% (w/v) sugar water were used for the bioassays. Sugar solution was provided by filling 0.5-ml microcentrifuge tubes and threading a cotton string through a hole in the cap of the tubes. Sex was determined using antennal morphology. In female *P. saccharalis*, the distal four antennal segments are enlarged, whereas males do not have enlarged antennal segments (Walker A. Jones, pers. comm.).

Plants. Soybean (var. Pioneer P49T97R-SA2P) at the vegetative (V3–V4) growth stage (Fehr et al. 1971) was used for the bioassays. Seedlings were grown from seeds purchased from Taleecon Farmers' Cooperative (Notalsuga, AL) in 30-well seed trays at one seed per well, under controlled greenhouse conditions ($26 \pm 2^\circ\text{C}$ and $55 \pm 5\%$ RH). One-week-old seedlings were transplanted into pots (12.7 cm diameter \times 15 cm high) at 4 seedlings per pot in Sunshine potting mixture #8 (SunGro Horticulture, WA). Plants were irrigated daily and fertilized twice a week with Scotts Peat-Lite Special fertilizer (Scotts-Sierra Horticultural Product Company, Marysville, OH).

Treatments. The olfactory response of *P. saccharalis* was tested with the following treatments: (1) undamaged soybean (i.e., plant with no mechanical or herbivore damage); (2) damaged soybean (i.e., plant infested with *M. cribraria* nymphs and adults); (3) *M. cribraria* eggs only; and (4) damaged soybean plus *M. cribraria* eggs. To infest treatment plants (feeding damage and oviposition), 30 nymphs and 20 pairs of adult *M. cribraria* were introduced to plants for 24 h in cages (60 \times 60 \times 60 cm) (BugDorm-2, Megaview Science Education Services Co., Ltd., Taichung, Taiwan). Eggs of *M. cribraria* were collected from the side of cages for use in bioassays testing attraction of parasitoids to egg mass only.

Bioassays. The olfactory response of *P. saccharalis* to host-associated cues was tested in two sets of Y-tube olfactometer bioassays. In the first bioassay, parasitoids were given a choice between each treatment (i.e., plant, egg mass or combination) versus the control (no plant and no eggs). In the second bioassay, parasitoids were given a choice between a host-damaged plant (feeding damage plus oviposition) and an undamaged plant. The Y-tube olfactometer set-up was similar to that previously described by Chen and Fadamiro (2007) with slight modifications (Fig. 1). Briefly, the Y-tube olfactometer (Analytical Research Systems, Gainesville, FL) consists of a central tube (10 mm diameter \times 13.5 cm long) and two lateral arms (10 mm diameter \times 6.5 cm long). Each arm is connected to an extending glass tube (8 mm diameter \times 14cm long). A sieve inlaid in each extending glass tube prevented escape of insects. Humidified and purified (charcoal filtered) air from an air delivery system (Analytical Research Systems, Gainesville, FL) was passed through Teflon tubes at 200 ml/min into air-tight glass chambers (5 L) containing treatments. Each glass chamber also has an air outlet carrying odorous air into each arm of the olfactometer. Air was removed by suction from the central tube of the olfactometer at 400 ml/min to avoid mixing of odors. Illumination was provided by a white light lamp (20 W, 250 Lux) suspended above the apparatus. To reduce contamination, each plant pot with soil was wrapped in aluminum foil. The control for the first set of bioassays was a pot with soil wrapped in aluminum foil, but without a plant. When attraction of parasitoids to the egg mass only was tested, the eggs were placed on Whatman® No. 1 filter paper (Fisher Scientific, Hampton, NH) inside a small (400 ml) glass chamber (Morawo and

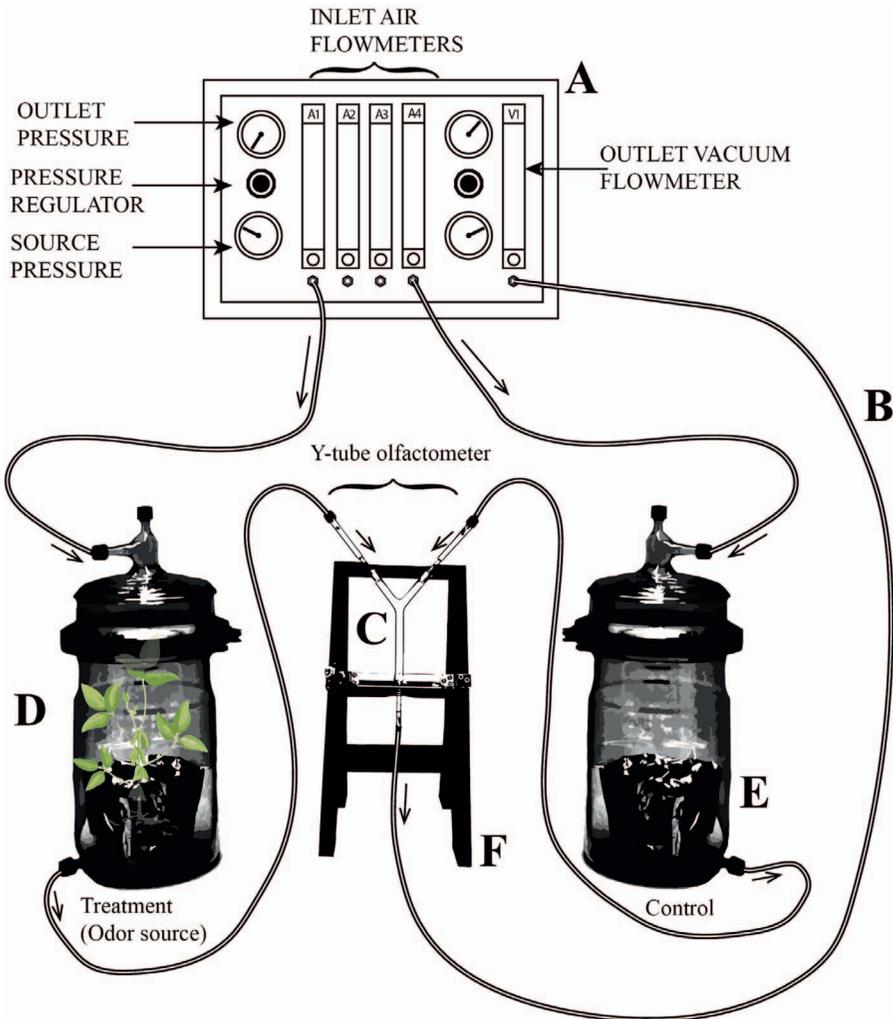


Fig. 1. Y-tube olfactometer set-up for testing olfactory response of female *Paratelenomus saccharalis* to host-associated olfactory cues. Description of main parts: A, air delivery system; B, Teflon tube; C, Y-tube olfactometer (made with glass); D, air-tight glass chamber containing odor stimulus; E, air-tight glass chamber containing control; F, wooden stand for the olfactometer.

Fadamiro 2016), whereas the control chamber contained only a filter paper. For the second bioassay, an undamaged plant was used as the control.

Female parasitoids were released individually into the olfactometer from the bottom of the central tube. A parasitoid was recorded to have made a choice for the olfactory cue offered through an arm when it walked to the sieve inlay of that arm of the olfactometer. An insect that did not make a choice after 10 min was recorded as

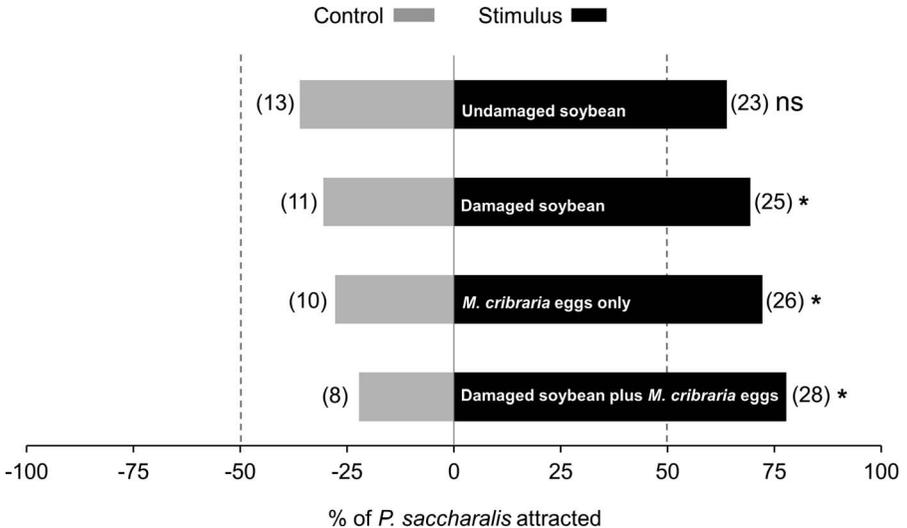


Fig. 2. Attraction of female *Paratelenomus saccharalis* in Y-tube olfactometer when given a choice between control (no host plant or eggs) versus undamaged soybean, damaged soybean, *Megacocta cribraria* eggs only, or damaged soybean plus *M. cribraria* eggs. Soybean was damaged by feeding activities of nymphs and adults of *M. cribraria*. Eggs were placed on filter paper for the “eggs only” treatment. $n = 36$ wasps per test. Numbers in parenthesis indicate actual number of insects that made a choice for either arms of the olfactometer. “ns” indicates no significant difference. Asterisks (*) indicate significant difference between stimulus and control ($P < 0.05$; Binomial test).

a “non-responder” (<8% in all bioassays) and excluded from statistical analysis. To minimize positional bias, the olfactometer arm was rotated 180° after testing four insects. Insects were used once and discarded. There were 36 insect replicates (responders) per treatment. After bioassays with each treatment were completed, the olfactometer was washed with soap, rinsed, and cleaned with acetone. Bioassays were conducted between 0900 and 1700 h at $26 \pm 2^\circ\text{C}$ and $55 \pm 5\%$ RH.

Statistical analysis. Attraction of female parasitoids to the stimulus (treatment) versus the appropriate control in Y-tube olfactometer was statistically compared using a two-sided binomial test at $P < 0.05$ by using SAS v. 9.2 (SAS Institute Inc. 2008).

Results and Discussion

Compared to the controls (i.e., no stimulus), female *P. saccharalis* showed significantly greater attraction to all host-associated olfactory cues tested, with the exception of undamaged soybean (Fig. 2). *Paratelenomus saccharalis* was significantly attracted to damaged soybean (69.44 %; $df = 1$; $P = 0.0288$), *M.*

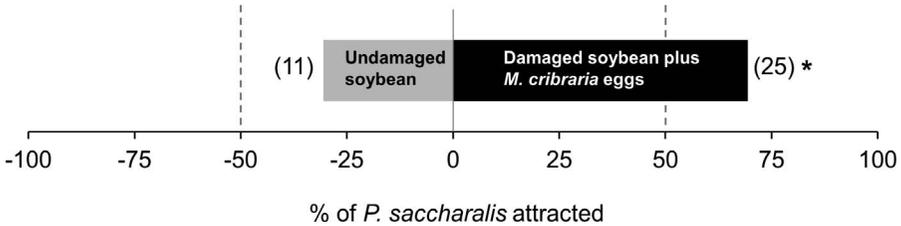


Fig. 3. Attraction of female *Paratelenomus saccharalis* in Y-tube olfactometer when given a choice between undamaged soybean versus damaged soybean plus *Megacopta cribraria* eggs. Soybean was damaged by feeding activities of nymphs and adults of *M. cribraria*. $n = 36$ wasps per test. Numbers in parenthesis indicate actual number of insects that made a choice for either arms of the olfactometer. Asterisks (*) indicate significant difference between the two treatments ($P < 0.05$; Binomial test).

cribraria eggs only (72.22 %; $df = 1$; $P = 0.0113$), and damaged soybean plus *M. cribraria* eggs (77.78 %; $df = 1$; $P = 0.0012$) in separate Y-tube olfactometer bioassays (Fig. 2). Compared to undamaged soybean, *P. saccharalis* also showed significantly greater attraction to damaged soybean plus *M. cribraria* eggs (69.44 %; $df = 1$; $P = 0.0288$) (Fig. 3).

These results suggest that host location by the egg parasitoid is mediated by olfactory cues from the soybean plant host and *M. cribraria* eggs. Furthermore, a combination of damaged soybean and host eggs elicited significant attraction of *P. saccharalis* indicating that plant volatiles induced by both *M. cribraria* feeding damage and egg deposition may act in concert as reliable host location cues for *P. saccharalis*. Feeding and oviposition activities by herbivorous insects have been shown to induce volatiles that attract egg parasitoids (Colazza et al. 2004, 2007, Moraes et al. 2005, Mumm and Hilker 2005, Hilker and Fatuoros 2015). For instance, a study by Colazza et al. (2004) demonstrated that the combination of herbivore damage and oviposition by *Nezara viridula* (L.) on *Vicia faba* L. and *Phaseolus vulgaris* L. elicited attraction in the egg parasitoid, *Trissolcus basalus* (Wollaston), whereas, parasitoids did not show preference for undamaged leaves. Similarly, female *P. saccharalis* were not significantly attracted to undamaged soybean in the present study, suggesting that herbivore-induced volatiles are more reliable cues for host location in this parasitoid species.

Egg parasitoids are also known to make use of chemical cues associated with other developmental stages (i.e., nymphs and adults) of their hosts. This is known as infochemical detour strategy (Vet and Dicke 1992). For instance, soybean and pigeon pea (*Cajanus cajan* [L.] Millsp.) infested with nymphs of *Euschistus heros* (F.) were attractive to females of the egg parasitoid, *Telenomus podisi* (Ashmead) (Moraes et al. 2005). In the present study, the egg parasitoid *P. saccharalis* was attracted to olfactory cues emitted by soybean damaged by feeding activities of nymphs and adults of *M. cribraria* (without host eggs), suggesting that they also employ the infochemical detour strategy. Although eggs of herbivorous insects have small biomass and likely release relatively lower quantities of volatiles, olfactory

cues from eggs can also serve as reliable host location cues for egg parasitoids, especially at short range (Fatouros et al. 2008, Vinson 1998). However, it is more likely that constitutive or herbivore-induced plant volatiles serve as background odors to enhance the detectability of egg volatiles (Beyaert et al. 2010, Hilker and McNeil 2008). Beyaert et al. (2010) reported that the egg parasitoid *Closterocerus ruforum* (Krausse) recognizes the key resource-indicating volatile associated with eggs of its host, the pine sawfly *Diprion pini* (L.), only when it is perceived in the context of pine volatiles (background odors). This agrees with results of the present study in which a combination of damaged soybean and *M. cribraria* eggs was very attractive to *P. saccharalis*.

In conclusion, results of the present study suggest that *P. saccharalis*, an egg parasitoid of *M. cribraria*, uses host-associated olfactory cues to locate their hosts. A combination of volatiles induced by plant damage and oviposition may serve as reliable cues for foraging egg parasitoids. This study has potential practical application in the development of attractants for *P. saccharalis* to enhance its effectiveness as a biological control agent against *M. cribraria*. While soybean is the commercial crop of interest focused on in this study, an alternative strategy aimed at recruiting parasitoids into kudzu may also prevent *M. cribraria* populations from reaching nearby soybean fields. Future studies should identify specific volatile compounds mediating attraction of *P. saccharalis* to plant and herbivore hosts.

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