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Chemical Ecology

Exposure to Guava Affects Citrus Olfactory Cues and Attractiveness to *Diaphorina citri* (Hemiptera: Psyllidae)

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Abstract

Intercropping can reduce agricultural pest incidence, and represents an important sustainable alternative to conventional pest control methods. Understanding the ecological mechanisms for intercropping could help optimize its use, particularly in tropical systems which present a large number of intercropping possibilities. Citrus is threatened worldwide by greening disease (huanglongbing, HLB) vectored by the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae). Control of HLB and citrus psyllid can be partially achieved through intercropping with guava, *Psidium guajava* L., but the mechanisms remain unclear. We tested the hypothesis that guava olfactory cues affect psyllid behavior by altering the attractiveness of citrus through plant–plant interactions. In choice and no-choice cage experiments, psyllid settlement was reduced on citrus shoots that had been exposed to guava shoot odors for at least 2 h. In Y-tube olfactometer experiments, psyllids oriented to odors of unexposed, compared with guava-exposed, citrus shoots. These behavioral results indicate that a mechanism for the success of guava intercropping for sustainable, ecological disease management may be the indirect effect of guava on citrus attractiveness.

Key words: plant–plant interaction, olfactory cue, *Diaphorina citri*, plant–insect interaction, *Psidium guajava*

Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Psyllidae), is currently the most important host-specific insect pest of citrus-growing regions in the world due to their direct and indirect damage. Adults and nymphs feed on the phloem of immature leaves and twigs, causing withering, distortion, and irregular canopy shape at high densities (Aubert 1987). In addition, continuous honeydew secretion by the insects leads to the growth of moulds on plant parts that may reduce photosynthesis. Asian citrus psyllid, among the insect pests of citrus, is recognized as the most significant pest globally because it carries a phloem-restricted, gram-negative bacterium, *Liberibacter asiaticus*, that causes the devastating citrus greening or huanglongbing (HLB) disease (Halbert and Manjunath 2004). This disease causes yellowing of the veins and adjacent tissues, followed by leaf chlorosis, premature defoliation, dieback, morbidity, and ultimately death. Affected trees have stunted growth, bear multiple off-season flowers, and produce small, irregularly shaped fruit with thick rind and bitter flesh. Once the pathogen infects some trees, the disease spreads quickly to other plants in orchards and the infected trees decline within several years (Yang et al. 2006). The psyllid is now widely distributed in several citrus-producing countries (Da Graca et al. 2008) and causes a great loss to farmers. No effective management approaches to control HLB have yet been established (Halbert and Manjunath 2004), and conventional control of *D. citri* in citrus orchards relies on insecticides that limit, but do not prevent, disease spread (Zaka et al. 2010).

Intercropping, the practice of coplanting multiple crops together, is a commonly used tactic for indirect pest management, particularly in diverse agroecosystems typical of the tropics, and has been used in citrus orchards for several years. Lower psyllid infestation levels and low incidence of HLB have been observed in citrus orchards (cv. King Mandarin) where guava, *Psidium guajava* L. (Myrtaceae), was grown as an intercrop, compared with citrus orchards lacking guava (Beattie et al. 2006). These results suggest that guava could contribute to an effective integrated pest management program for HLB and citrus psyllid. However, a lack of basic ecological knowledge about the mechanisms for the effects of guava on HLB and citrus psyllids has limited the development of this approach.

In numerous systems, it has been hypothesized that plant volatiles may play a role in the success of intercropping (Coll and Bottrell 1994, Manadhar et al. 2009, Erickson et al. 2012). Guava fruits and leaves produce a wide range of volatile compounds, such as sesquiterpenes, aldehydes, and alcohols. Some of these aldehydes and alcohols are the so-called “green leaf volatiles” that can have repellent (Jang and Light 1991) but also attractive (Han et al. 2012) effects on insect herbivores. Major volatiles include β-caryophyllene, (E)-nerolidol, and limonene (Pino et al. 2001, Ogunwande et al. 2003). In interplanting guava and citrus, the protective effect against psyllids appears to function year-round (Rouseff et al. 2008), suggesting it may be mediated by leaf volatiles, rather than by the volatiles of seasonal fruit.

The volatile-mediated benefits of intercropping could result from two hypothetical mechanisms. First, guava volatiles could be directly repellent to psyllids, and thereby limit pathogen spread (direct repellence hypothesis). In support of this hypothesis, guava leaf volatiles inhibited attraction of psyllids to normally attractive host citrus volatiles (Onagbola et al. 2011) in Y-tube olfactometer tests. Moreover, psyllid settlement on citrus was significantly reduced in the presence of guava leaves in laboratory cage trials (Zaka et al. 2010). Mechanically wounded guava produces toxic and repellent dimethyl disulphides, while citrus does not, suggesting these, or other guava compounds, may be responsible for the observed deterrence (Rouseff 2008). These results are consistent with other studies showing that specific volatiles of nonhost plants can disrupt host selection by insects (Huber and Borden 2001, Hassanali et al. 2008).

Second, guava volatiles could be detected by citrus plants, leading to changes in the characteristics of citrus that mediate host selection. This indirect, or plant–plant communication, hypothesis was proposed by Baldwin and Schultz (1983), in their experiments with poplar (*Populus* × *euroamericana*) and sugar maple (*Acer saccharum* Marsh), which showed that aerial cues released by mechanical damage to the plant leaves could cause biochemical changes in conspecific undamaged neighbors, and which reduced herbivore performance. These results have since been supported in other systems by several studies demonstrating that volatile based, plant–plant communication can cause associational resistance (Karban 2001, Barbosa et al. 2009, Jactel et al. 2011). For example, exposure to the volatiles emitted from thistle, *Cirsium vulgare*, reduced aphid acceptance of barley, *Hordeum vulgare* cv. Kara (Glinwood et al. 2004). Conversely, few studies have tested the effects of exposure to volatiles of undamaged neighbors, a critical context from a practical perspective (Ninkovic et al. 2013). Interplanting in Kenyan cropping systems has been successful in controlling insect herbivores implicating push–pull mechanism (Cook et al. 2007, Khan et al. 2009), and the success of the approach is attributed to the release of volatiles from companion plants (Poveda and Kessler 2012). An understanding of plant–plant interactions and associational resistance in intercropping systems would greatly facilitate the practical implementation of this approach, and yet few studies have examined this mechanism.

To gain a better understanding of the ecological mechanisms of guava–citrus intercropping, we tested the plant–plant interaction hypothesis in laboratory studies, investigating how exposure to putative guava volatiles altered Asian citrus psyllid attraction to citrus olfactory cues and subsequent host acceptance.

Materials and Methods

Insect and Plant Material

Adult *D. citri* were collected from 4-yr-old sweet orange (*Citrus* × *aurantium* L.) trees in the botanical garden (23° 15′ N, 113° 35′ E, 20 m altitude) of South China Agricultural University, Guangzhou, Guangdong, P. R. China, using a mechanical aspirator each morning and held in small plastic cups for use later in the day. Insects were sexed by an abdominal dimorphism, in which the tip of the male abdomen is bent upward and the female abdomen is straight. No specific permissions were required for these activities and the study did not involve any protected species.

All experiments used 4-yr-old guava (*P. guajava* cv. Pearl) and sweet orange plants grown in 20-liter plastic pots with loamy soil mixed with leaf compost (1:1 by volume). These plants were irrigated ad libitum, fertilized fortnightly with N-dominated mixed fertilizer, pruned approximately every 6 wk, and were visually free from any disease or pest. In all behavioral experiments, we used randomly selected, freshly clipped shoots of guava and citrus, which were 40–45 and 25–30 d old, respectively, from different individual trees. Shoots were placed in separate 50-ml flasks filled with water and used within 10 min of excision.

Effect of Guava Exposure on Citrus Attractiveness

Single 15-cm-long freshly cut citrus shoots were exposed to single 15-cm freshly cut guava shoots in a sealed 1.5-liter glass jar for five exposure periods (treatments): 30, 60, 120, and 180 min. Control shoots were not enclosed, and thus were unexposed (0 min). Approximately 30 min after the completion of the exposure, treatment and control citrus shoots were then tested for their attractiveness to psyllids in both "no-choice" and "choice" experiments. In the "no-choice" experiment, four shoots from a single treatment were placed inside a single cage (single chamber), 60 by 30 by 60 cm (l by w by h), which was placed inside the laboratory. The cage was made of celluloid, with a front door of size 60 aluminium mesh screening for air circulation. Two replicate cages (eight shoots) were used for each treatment. Male and female psyllids (25 each) were released into each cage, and the number of psyllids on each shoot was counted 3, 6, 12, and 24 h after their release. In the choice experiment, each replicate cage ($n = 8$) contained one shoot from each treatment with the five shoots placed at randomized equidistant positions within the cages (40 shoots). Male and female Asian citrus psyllids (25 each) were released per cage, and the number of psyllids on each shoot was recorded. All other conditions were identical to the no-choice experiment.

Response of Psyllids to Odor of Guava-Exposed Citrus

Response of adult Asian citrus psyllid to the odor of citrus shoots was assessed using a Y-tube olfactometer, in which we paired control citrus shoots with citrus shoots that had been exposed to guava foliage for 3 hr (based on the alightment results), following Horton and Landolt (2007). The Y-tube was 2.5 cm internal diameter with 21.0-cm arms attached to a 19.0-cm neck. Arms were connected to 1.5-liter jars containing single shoots of either guava-exposed or unexposed (control) citrus using silicone tubing, and charcoal-filtered and distilled water-moistened air was pushed through the system at 50 ml/min using a two-way output air pump (JAD air pump, model S-2000, made in United Kingdom). Individual psyllids were released at the Y-tube opening and were recorded as having chosen either control or guava-exposed citrus if, within 5 min, they moved a minimum of 10 cm down an arm from the junction and stayed there for at least 1 min. Pooled responses of 10 individual psyllids comprised a single replicate, and 15 replicates were conducted in the laboratory over three days at 27 ± 2°C and light intensity of a 282 mW/cm^2. Between replicates, positions of the odor sources were exchanged to avoid directional bias, and the Y-tube was washed and dried.

Statistical Analysis

In the no-choice experiment, we used repeated-measures analysis of variance (ANOVA) to test the hypothesis that settlement of psyllids differed among the five exposure treatments, with treatment as a fixed effect, and time as the repeated measure. Number of psyllids was averaged (pooled) across plants within a cage (the experimental unit) for this statistical analysis; however, data are graphically presented as the plant-wise means and standard errors due to the low cage replication at each time point (Fig. 1A). Treatment was modeled as a categorical variable; modeling as a continuous variable gave similar results. Data were log transformed to improve normality of the residuals and homoscedasticity. In the choice experiment, proportions of psyllids on each plant were arcsin-square root transformed and analyzed by repeated-measures ANOVA as for the no-choice experiment (Sokal and Rohlf 1995), followed by a Tukey's test comparing the five treatments (averaged across the four assessment times). Repeated-measures analyses were run in the multivariate modeling platform of JMP v. 11.0, in a restricted maximum likelihood framework. For the Y-tube experiment, proportions of responders were arcsin-square root transformed and analyzed by ANOVA (general linear model) with treatment as a fixed effect (Sokal and Rohlf 1995). We note that for experiments involving proportions of responders, use of linear models (ANOVA) was preferred over χ^2 tests, as ANOVA on transformed proportions considers variation among replicates, where available (as here). However, χ^2 tests yielded qualitatively identical results. All analyses used JMP v11.0 (SAS Institute, 2012).

Results

Effect of Guava Exposure on Citrus Attractiveness

In the no-choice experiment, guava exposure significantly reduced the number of psyllids settling on citrus shoots (Treatment: $F_{4,5} = 5.510$, $P = 0.044$; Fig. 1A). This effect was also significant when considering the linear relationship of settlement with exposure time, i.e., considering exposure as a continuous variable ($F_{1,8} = 22.67$, $P = 0.0014$). While this pattern of settlement appeared to attenuate at the later assessment times (e.g., 24 h after introducing psyllids to the cage, Fig. 1), the effects of assessment time were not statistically significant (Time: $F_{3,3} = 2.274$, $P = 0.2586$; Treatment × Time: $^{\text{approx}}F_{12,8.2} = 1.387$, $P = 0.3256$). Relative to the unexposed control shoots, guava exposure for 30, 60, 120, and 180 min reduced settlement of psyllids by 14, 7, 47, and 46%, respectively (average of four exposure times).

In the choice experiment, psyllid settlement was proportionately greater on control shoots, and declined with increasing guava-exposure time (Fig. 1B; Treatment: $F_{4,35} = 23.459$, $P < 0.0001$). This effect appeared to be independent of the time of assessment (Time: $F_{3,33} = 0.2207$, $P = 0.8813$; Treatment × Time: $^{\text{approx}}F_{12,87.6} = 0.4986$, $P = 0.9103$). A Tukey's multiple comparison procedure on the transformed data (averaged across assessment times) indicated

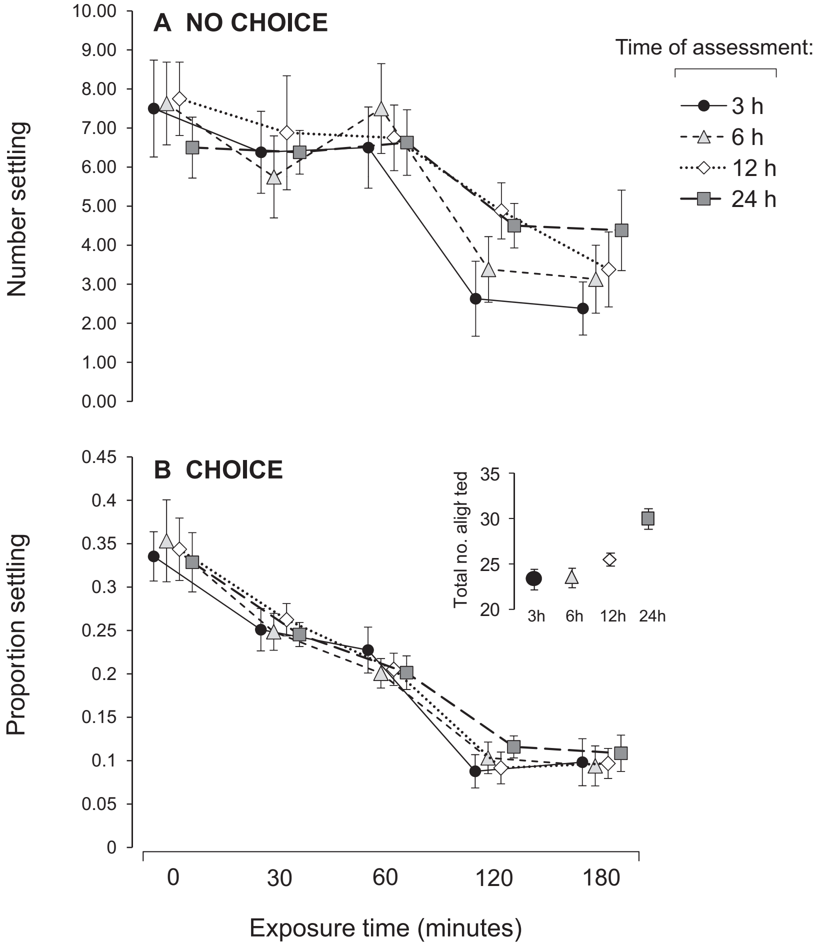

Fig. 1. Settlement of 50 psyllids on citrus shoots that had been exposed to guava shoots for 0 (control), 30, 60, 120, and 180 min in no-choice (**A**) and choice (**B**) experiments. Data are means (± SE) of all shoots in a cage (no-choice) and of the proportions across replicate cages (choice). Data points from the four assessment time points are offset for clarity. Inset (**B**) shows the total number of psyllids (cage averages ± SE), alighting on all shoots in each assessment time in the choice experiment.

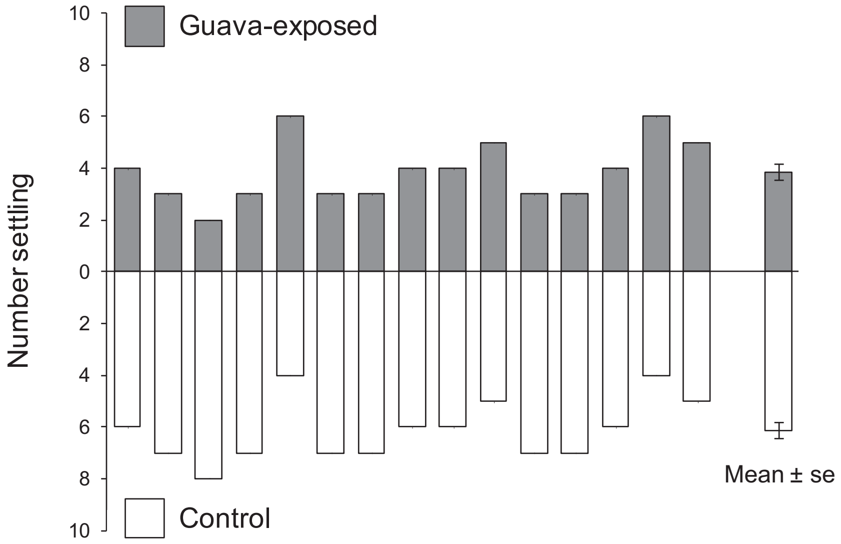

Fig. 2. Response of psyllids in 15 replicate Y-tube olfactometer trials to citrus shoots that had either been exposed to guava volatiles (dark bars) or left untreated (open bars). Data from each trial are shown to illustrate variation among trials; overall mean shown at right. Each trial comprised responses of 10 individuals.

that, relative to controls, there was no effect of 30-min guava exposure, but significant reductions in the average proportion alighting on citrus that had been exposed to guava for 60, 120, and 180 min. Overall alightment rates per cage were higher in the choice experiment (Fig. 1B Inset) than in the no-choice experiment (Fig. 1A).

Response of Psyllids to Odor of Guava-Exposed Citrus

In the Y-tube olfactometer, 61.3% of psyllids oriented to odors of control citrus, over citrus that had been exposed to guava for 3 h (38.7%; $F_{1,\ 28} = 5.21$, $P < 0.0001$; Fig. 2).

Discussion

Our results show that when citrus is exposed to guava, there is reduced settlement of adult Asian citrus psyllid, indicating less acceptability of guava volatile-exposed citrus shoots to the herbivores. These results support the indirect plant–plant interaction hypothesis for the effects of guava intercropping on psyllids. Behavior of herbivores and their natural enemies can be affected by the exposure of plants to volatiles of another plant of same species or different species. For example, in certain undamaged barley cultivars, exposure to volatiles of conspecific (Glinwood et al. 2009, Ninkovic and Ahman 2009) or heterospecific neighbors (Glinwood et al. 2004) reduces host acceptability to aphids and increases attractiveness to predatory ladybirds (Ninkovic and Pettersson 2003). The relation across multitrophic levels influenced by chemical interactions among neighboring plants is allelobiosis (Ninkovic et al. 2006), and our results are consistent with an allelobiosis interpretation of guava–citrus–psyllid interactions.

Our Y-tube experiment confirms that the indirect mechanism observed in the settlement assays is mediated at least in part by olfactory responses of psyllids to altered citrus shoot odor. Response of Asian citrus psyllid to citrus odors was also affected by the volatiles of *Allium* spp. in T-olfactometer tests (Mann et al. 2011). These results complement prior olfactometer experiments showing that *D. citri* were directly repelled by odors from mechanically wounded guava leaves (Onagbola et al. 2011), and that odor of fresh guava leaf volatiles, alone or in combination with citrus leaf volatiles, were repellent to psyllid adults in a dose-dependent manner (Zaka et al. 2010). Thus, both direct repellence and indirect plant–plant interaction mechanisms may operate in this system. However, determining the relative importance of the two mechanisms in a field setting remains an important goal for future research.

Avoidance of guava-exposed citrus by psyllids may reflect an avoidance of plants of reduced quality, consistent with several studies of plant–plant volatile interaction in which herbivory-induced volatiles increased defense activation in neighboring plants (Engelberth et al. 2004, Ton et al. 2007). Our study does not allow us to determine whether responses by psyllids reflect decreased attractiveness of citrus, or changes to repellent compounds. Prior studies have established a role of terpenoid volatiles in mediating host finding and acceptance by many insects, including Asian citrus psyllid (Sanchez 2009, Patt and Setamou 2010). Preliminary analysis of the volatile emissions of citrus shoots indicated that total monoterpenoid emissions show a significant threefold reduction after exposure to guava shoots (J. C. B., unpublished data); however, the role of specific volatile compounds in mediating the psyllid responses we report here remains to be verified.

Understanding plant–plant interactions is of interest from both an ecological perspective but also for the development of novel crop protection strategies that involve either engineering or selecting resistant crop plants or treating crops with allelopathic agents to make them less attractive to insects (Agelopoulos et al. 1999). The success of this approach depends in part on the target crop being sensitive to volatiles from an emitter intercrop that may or may not be attacked, and yet extremely few studies have examined crop responses to volatiles of undamaged neighbors. Consistent with the results of the present study, Ninkovic et al. (2013) reported that potato plants exposed to onion plants showed a fourfold increase in emission of two terpenoids, and a significant decrease in their attractiveness to winged aphids. The similarity of these results with the guava–citrus system strongly suggests that future studies of intercropping systems may identify additional cases of associational resistance based on plant–plant communication from undamaged neighbors.

Finally, interplanting of guava may be an option of protecting against psyllids in citrus groves. There are examples of compounds known to be allelopathic agents in plant–plant interactions that directly repel or deter herbivores, e.g., caffeine (Kim et al. 2006). Our study establishes an aerial allelopathic interaction between guava and citrus plant that can make the host less acceptable to psyllids, potentially by changing its volatile emissions. The present study also suggests that future research should focus on understanding the behavioral activity of volatiles in the naturally mixed vegetation of citrus and guava; such studies could indicate whether it is possible to optimize guava planting to take advantage of behaviorally active volatile compounds in integrated pest management of Asian citrus psyllids.

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