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ORIGINAL PAPER

Plant volatiles and density-dependent conspecific female odors are used by Asian citrus psyllid to evaluate host suitability on a spatial scale

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Abstract We investigated how chemical cues derived from female Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae) and their host plants affect host acceptance choices by conspecifics. In four-choice cage and two-choice olfactometer assays, female psyllids avoided conspecific female cues in a density-dependent manner. However, odors from citrus plants actively damaged by psyllid feeding were attractive to conspecific females. When odors from feeding-damaged plants were presented simultaneously with odors from female *D. citri*, attraction of female conspecifics was no longer observed as compared with a clean air control in olfactometer assays. In subsequent experiments, *D. citri* females were released within arenas that contained actively feeding-damaged or non-damaged (control) citrus plants, each with previously psyllid-infested and uninfested young leaves. *D. citri* development is linked to the presence of these newly emerging leaves which is the only site of nymphal development. Female *D. citri* were initially attracted by the actively damaged plants as compared with non-damaged controls. After acceptance of plants that were actively damaged by feeding, *D. citri* females preferentially chose and settled on uninfested young leaves as compared with previously infested young leaves. A herbivore-induced plant volatile attractant and a female-specific odor repellent appear to be complementary foraging cues providing psyllids with information at two spatial scales: (1) the whole plant level for choosing a plant potentially harboring male conspecifics for mating, and (2) the within plant level to reduce intra-conspecific competition by identifying previously exploited resources.

Keywords Intraspecific competition · Herbivore-induced volatiles · Host preference · Oviposition marking

Introduction

Chemical cues used by insect herbivores to find suitable hosts for reproduction and/or feeding can originate from the host plant or from other insects, including conspecifics (Dicke 2000). Plant volatiles have received significant attention because they mediate host plant selection by herbivores and may be exploited for practical insect management (Kos et al. 2013). Volatile release from plants changes quantitatively and qualitatively with biotic stressors that include damage caused by herbivores (Turlings and Wäckers 2004) or pathogens (Davis et al. 2012; Mann et al. 2012). These volatiles are often attractants for natural enemies (Mann et al. 2010; Turlings and Wäckers 2004), but may also attract subsequent herbivores (Carroll et al. 2006; Halitschke et al. 2008; Mann et al. 2012), particularly host specialists (Poelman et al. 2010). On the other hand, once many conspecific herbivores infest a host plant that was attractive, there may be competition for limited resources (i.e., oviposition sites) within a particular host plant. In these cases, several examples of marking pheromones have been illustrated, which allow recognition of previously exploited and therefore unsuitable oviposition sites among conspecific females (Hoffmeister and Roitberg 2002). This phenomenon is particularly common when insects exploit time and/or space limited resources (Prokopy 1981; Nufio and Papaj 2001).

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Herbivores have evolved and function in multitrophic food webs and therefore studies of host selection should also consider the importance of avoiding competition (Dicke 2000). Nevertheless, few studies present a comprehensive design that includes these two ecological components when examining host selection behavior. For many insects, host selection behavior depends on host-specific odor cues, and insects have evolved in an environment that can be surrounded by hundreds of different compounds from different odor sources (Dicke 2000). A foraging herbivore likely integrates both attractant and repellent odors when selecting an appropriate oviposition site and this behavioral response is likely molded by multiple selection pressures, including the need for: (1) finding an appropriate resource for larval development, (2) finding conspecifics of the opposite sex for mating, and (3) avoiding intraspecific competition.

We explored host selection behavior by the Asian citrus psyllid, *Diaphorina citri* Kuwayama (Hemiptera: Liviidae). *D. citri* transmits several bacterial pathogens including *Candidatus* Liberibacter asiaticus (Las) that cause huanglongbing (HLB), a tree killing disease of citrus (Grafton-Cardwell et al. 2013; Hall et al. 2013). HLB is considered the most destructive disease of commercially cultivated citrus crops worldwide. All known citrus cultivars are susceptible to HLB (Folimonova et al. 2009) and prevention of disease transmission has proven difficult (Grafton-Cardwell et al. 2013). First discovered in Florida in 1998 (Halbert 1998), *D. citri* quickly became established throughout the state, making its eradication impossible.

The chemical ecology of the Psylloidea is a relative new subject of interest (Guedot et al. 2009a), but has expanded given that economically damaging species have been targeted. Many chemical ecology studies of Psylloidea focus on species of economic importance, including *D. citri*. To date, a possible sex pheromone has been demonstrated in only four species of psyllids: *Cacopsylla chinensis* Yang and Li (Wan et al. 2013), *Cacopsylla pyricola* Förster (Guedot et al. 2009a; Guedot et al. 2009b), *Bactericera cockerelli* Sulc (Guedot et al. 2010), and *D. citri* (Wenninger et al. 2008). Research on *D. citri* chemical ecology has largely focused on plant volatiles used for host selection (Patt et al. 2011; Patt and Setamou 2010; Robbins et al. 2012; Wenninger et al. 2009). Mann et al. (2012) demonstrated that HLB-infected citrus trees were more attractive to *D. citri* because of increased release of methyl salicylate (MeSA) as compared with uninfected plants. In addition, Mann et al. (2013) demonstrated the importance of female cuticular hydrocarbons as female produced attractants of males in *D. citri*, which may be the source of a potential short-range sex-attractant pheromone. Even less is known regarding intraspecific competition between female psyllids and how this may affect host site selection. Repellency between conspecific males has been demonstrated in winterform pear psylla (Guedot et al. 2009a), but repellency between females has not been tested in this or other psyllid species previously.

Female overcrowding is likely to be detrimental to offspring fitness, especially in the case of psyllid species, such as *D. citri*, which only lay eggs on newly emerging leaves referred to as ‘flush’ (Hall et al. 2013). This oviposition site is both time and space limited and in an herbivore species such limitations may drive evolution of mechanisms to decrease competition for egg-laying resources (Prokopy 1981; Nufio and Papaj 2001). The ability to mark, recognize, and avoid an exploited resource by egg-laying females benefits the fitness of the subsequent generation for herbivores that are limited by a particular stage of the host for development (Nufio and Papaj 2001; Hoffmeister and Roitberg 2002).

Our objective was to investigate how volatile cues may affect host plant settling behavior of *D. citri* females. We hypothesized that female *D. citri* may deposit odorant cues associated with oviposition that may reduce intraspecific competition. We also hypothesized that feeding-damage-induced odors from citrus plants may be attractive to female *D. citri*, acting as cues to identify plants that harbor conspecific males for mating. Our goal was to further describe host selection behavior of *D. citri* in the context of possible herbivore-induced plant volatiles and ovipositon marking pheromones.

Materials and methods

Insect culture

Adult *D. citri* used in behavioral bioassays were obtained from a laboratory culture maintained at the University of Florida, Citrus Research and Education Center (Lake Alfred, USA). The culture was established in 2000 from field populations in Polk Co., FL, USA (28.0′N, 81.9′W) prior to the discovery of HLB in Florida. The culture was maintained without exposure to insecticides on Valencia sour orange (*Citrus aurantium* L.) in an air-conditioned greenhouse at 27–28 °C, 60–65 % r.h., and L14:D10 photoperiod. Bi-monthly testing of randomly sampled nymphs, adults, and plants by quantitative PCR assays was conducted to confirm that psyllids and plants in this culture were uninfected by Las.

Experiment 1: Response of *D. citri* females to pre-infested plants

The objective of this experiment was to determine whether previous infestation with a range of densities of conspecific female *D. citri* may influence subsequent host selection behavior by conspecific female *D. citri*. Laboratory conditions during the experiment were maintained at 26 ± 1 °C, 49 % r.h. and a L14:D10 photoperiod. We used 15- to 21-month-old curry leaf (*Bergera koenigii* L.) seedlings approximately 12–18 cm in height. Plants used were pruned 1 week prior to the bioassays in order to induce growth of new leaf flush. Four curry leaf seedlings were placed into fine mesh cages (37 × 56 × 35 cm) and randomly arranged 15 cm apart. Each plant was completely enveloped within fine mesh fabric within which we released 0, 1, 5, or 10 adult psyllid males or 0, 1, 5, or 10 adult psyllid females. Adult psyllids were allowed 64 h to settle and subsequently the bags and the psyllids were removed. Within 30 min of psyllid removal from plants, 30 new conspecific females were released centrally within each screen cage arena. The number of *D. citri* and their location on each plant was recorded 3 and 24 h after release. The number of *D. citri* per plant was log-transformed and analyzed with a linear mixed model with the number psyllids used to pre-infest plants as the explanatory variable, and the number of replicates as the random variable. When a significant difference was found, post hoc contrast tests were performed to determine differences between treatments. Statistical analyses were performed with the statistical software R v3.0.1 (http://www.r-project.org).

Experiment 2: Response *D. citri* to odors of conspecific females

A two-port divided T-maze olfactometer (Analytical Research System, Gainesville, FL, USA) was used to evaluate the behavioral response of *D. citri*. The olfactometer consisted of a 30 cm long glass tube with 3.5 cm internal diameter that was bifurcated into two equal halves with a polytetrafluoroethylene (PTFE) strip forming a T-maze (Mann et al. 2011). Each half served as an arm of the olfactometer enabling the *D. citri* to make a choice between two potential odor fields. To ensure chemical free ambient air supply, both arms of the olfactometer received charcoal purified and humidified air from a custom made air delivery system (ARS, Gainesville, FL, USA). A constant airflow of 0.1 L min^{-1} was maintained through both arms of the olfactometer. The olfactometer was positioned vertically under a fluorescent 23 W light source (FLE23HT3/3/SW, GE Lighting, Cleveland, OH, USA) mounted within a 1.0 × 0.6 × 0.6 m fiberboard box for uniform light diffusion. The measured light intensity was approximately 600 lux above the T-maze. Female *D. citri* adults were released individually at the base of the olfactometer and allowed 300 s to exhibit a behavioral response. A positive response was recorded when a psyllid moved from the base and entered 1 cm into either arm of the olfactometer. Those psyllids that did not leave the base of the olfactometer were designated as non-responders. Odor sources were randomly assigned to one arm of the olfactometer at the beginning of each bioassay, and the T-maze was rotated every five insects to eliminate positional bias. In addition, prior to the odor testing, *D. citri* adult females were exposed to clean air versus clean air in the olfactometer to verify the absence of positional bias. The olfactometer arms were connected to upstream odor sources consisting of glass tubes containing one, five or 10 male or female *D. citri* (Table 1). All assays were conducted between 900 and 1400 hours. Binomial tests were used to compare the number of *D. citri* entering the treatment or control arm of the olfactometer.

Table 1 Response of male or female *D. citri* to varying densities of conspecifics in a two-choice olfactometer

Test subject gender	Treatment odor source	*n*[1]	Treated[2]	*P* value[3]
Male	1 female	25 (22)	0.55	0.832
Male	5 females	31 (20)	0.75	0.041
Male	10 females	32 (22)	0.77	0.017
Female	1 female	24 (18)	0.50	1.000
Female	5 females	41 (33)	0.33	0.080
Female	10 females	32 (25)	0.20	0.004
Male	10 males	33 (25)	0.52	1.000
Female	10 males	40 (22)	0.61	0.523

[1] Total sample size (*n* = number of individuals that made a choice in parentheses)

[2] Proportion of individuals (of those making a choice) choosing the treated air arm as compared with the control

[3] *P* values were obtained with the use of a binomial test

Experiment 3: Response of female *D. citri* to odors of host plants infested with conspecific females

The objective of this experiment was to investigate the effect of citrus volatiles induced by *D. citri* feeding on behavior of conspecific females. *Swinglea glutinosa* Blanco 'Swingle' was used as the host plant for this experiment. The plants were 30–35 cm in height, and pruned 10 days prior to the initiation of experiments in order to induce growth of new leaf flush. The olfactometer and conditions were identical to those described in Experiment 2; however, in this case, the olfactometer arms were connected to citrus plants enclosed inside two-port glass domes (38 cm height, 14.4 cm ID) (Fig. 1). The upper and lower portions of each plant were separated by a PTFE guillotine (2.5 cm width), so that only eight leaves were inside each glass dome. Clean air was pushed into the bell jar to maintain airflow out of the glass dome and into

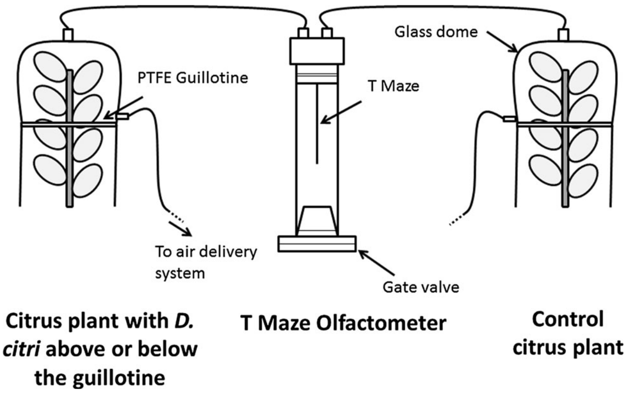

Fig. 1 Schematic diagram of the olfactometer apparatus used to test the effect of *D. citri* feeding on behavioral response of *D. citri*

the olfactometer at 0.1 L min^{-1}. The plants were positioned under a 150 W high-pressure sodium grow light (Hydrofarm, Petaluma, CA, USA). Twenty *D. citri* females were used to damage the plants. Those psyllids were placed either on the upper or on the lower portion of the canopy (above or below the guillotine). When positioned on the upper portion of the canopy, the psyllids were inside the glass dome and consequently the odor blend consisted of damaged citrus volatiles and *D. citri* female headspace volatiles. When the psyllids were placed on the lower portion of the canopy, they were outside the glass dome and consequently the headspace volatiles from those psyllids were excluded from the odor treatment, which only consisted of damaged citrus volatiles. All assays were conducted between 900 and 1400 hours.

Diaphorina citri females were challenged in the T-maze against the following two treatments: (1) headspace volatiles from herbivore-damaged plant and *D. citri* females (psyllids on the upper portion of the canopy) versus headspace volatiles from an uninfested plant and (2) headspace volatiles from systemically herbivore-damaged plant without headspace volatiles from female psyllids (psyllids on the lower portion of the canopy) versus headspace volatiles from an uninfested plant. For each treatment, T-maze choice tests were performed at 30 min or 24 h after initiation of psyllid feeding. For each treatment combination and for each time period, the choice test consisted of four replicates with 20–40 *D. citri* females tested per replicate. In total, we tested approximately 130 *D. citri* for each treatment in the olfactometer. We carried out heterogeneity Chi squared tests to ensure that data from each replicate were homogenous (Zar 2009) and then performed Chi squared tests on the pooled value of each treatment. Response data of *D. citri* obtained in the two treatments were found to be homogenous because the sum of the individual Chi squares for each replicate was not significantly different from the overall Chi squared of the pooled data (Zar 2009). In this case, pooling the data to perform an overall Chi squared was justified (Zar 2009).

Experiment 4: Response of *D. citri* females to both damaged citrus volatiles and female-derived odorants

Based on the results of the previous experiments (see the "Results" section), we hypothesized that (1) psyllid-damaged plants should attract conspecific females as compared with undamaged counterparts, but that (2) female *D. citri* should avoid previously infested leaf flush on these plants as compared with uninfested (clean) flush. Two-year-old *Citrus sinensis* (L.) Osbeck 'Valencia' citrus plants, approximately 50–60 cm in height, were pruned 2 weeks prior to the assays in order to induce growth of new leaf flush. Plants used in the experiment had 2–4 new leaf flush between 0.5 and 5 cm in length. Two plants were placed within a fine mesh cage (65 × 120 × 65 cm) 16 cm apart per replicate. Within each replicate cage, the lower half of the canopy of each plant was enveloped with a fine mesh bag. One plant received 20 *D. citri* females (hereafter referred as 'damaged' plant) and the other was left uninfested (referred to as 'control' plant). On the upper portion of the canopy of both treatments ('damaged' and 'control'), each leaf flush was completely enveloped within fine mesh fabric. Half of these enveloped leaf flush received an additional 10 adult *D. citri* females and the other half were left uninfested. After 64 h, the bags surrounding the flush and the psyllids were removed. Consequently, there were four flush odor treatments within a single mesh cage arena per replicate: (1) flush pre-infested by female psyllids on a plant damaged by psyllid herbivory, (2) uninfested flush on a plant damaged by psyllid herbivory, (3) flush pre-infested by female psyllids on undamaged control plant and (4) uninfested flush on undamaged control plant.

After removing the bags and the psyllids used for pre-infestation, we introduced 30 new and sexually mature female *D. citri* into each cage. The number of psyllids per plant and per flush was counted after 24 h, and the flush were removed and measured for length. There were nine replicates, and for each replicate, there were one to two leaves flush per treatment. To account for the different number of flush per treatment per replicate, we averaged the number of psyllids counted per treatment. We compared the number of psyllids found per centimeter of leaf flush between treatments. Data were Poisson distributed, so we analyzed the number of females per centimeter of flush with a generalized linear model (GLM) with Poisson distribution and a log link function. The plant treatment

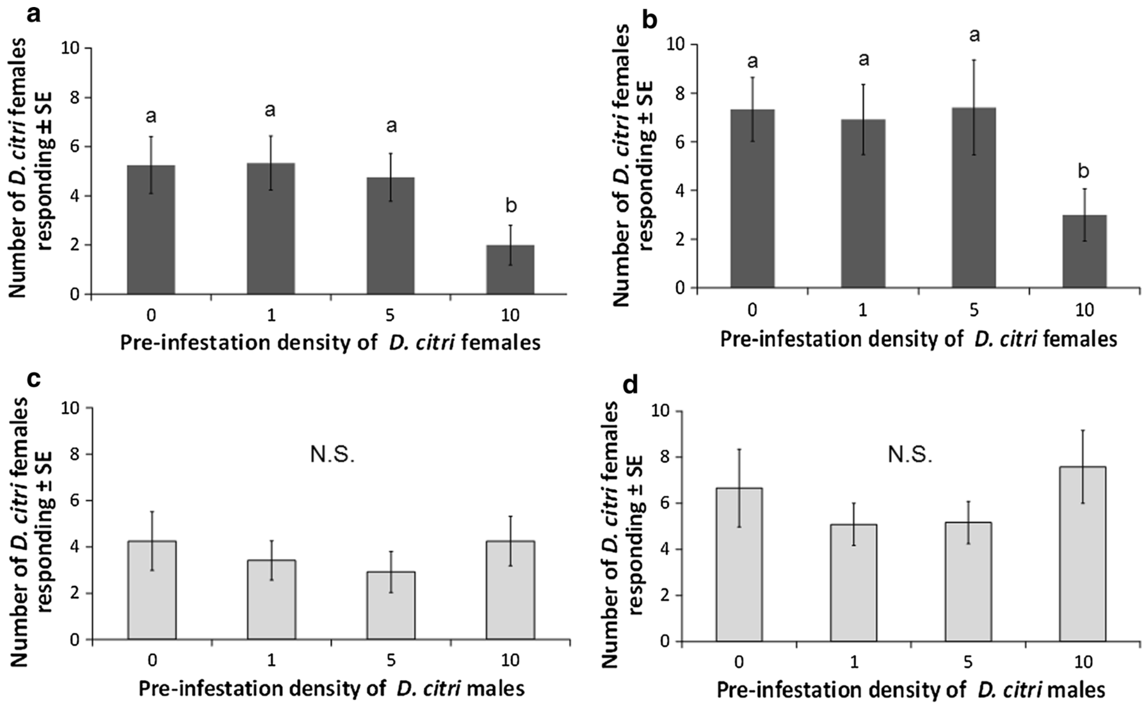

Fig. 2 Mean number (±SE) of *D. citri* females counted when given a choice between *Bergera koenigii* plants pre-infested for 64 h with varying densities of female (**a**, **b**) or male (**c**, **d**) conspecifics at 3 (**a**, **c**) or 24 (**b**, **d**) hour intervals after initial infestation, respectively. *Bars* labeled by *different letters* are significantly different at $\alpha < 0.05$ level

(damaged or control), flush treatment (pre-infested or uninfested), and cage number were used as explanatory variables. We started with a full model including these three variables and their interaction, and subsequently removed nonsignificant interactions ($\alpha > 0.10$) to obtain the minimal adequate model (Crawley 2009). Finally, we compared the number of psyllids on the damaged plants to that on the control plants with paired *t* tests, after log transformation of the data to correct heterogeneity.

Results

Experiment 1: Response of *D. citri* females to pre-infested plants

We tested whether density of male or female *D. citri* pre-infesting leaves affected subsequent settling by female psyllids on citrus flush. Fewer *D. citri* females were found on flush that were pre-infested with 10 females than on leaves pre-infested with 0, 1 or 5 females (After 3 h: $F_{3,33} = 4.416$, $P = 0.010$, Fig. 2a; after 24 h: $F_{3,33} = 3.691$, $P = 0.021$, Fig. 2b). In contrast, female colonization of flush was not influenced by the presence of male *D. citri* at any of the pre-infestation densities tested (after 3 h: $F_{3,33} = 0.438$, $P = 0.728$, Fig. 2c; after 24 h: $F_{3,33} = 0.155$, $P = 0.926$, respectively, Fig. 2d).

Experiment 2: Response of *D. citri* to odors of conspecific females

We examined the response of male and female psyllids in T-maze choice tests to odors from female or male psyllids of various densities in the absence of simultaneous host plant odors. Significantly more males entered an arm containing 5 or 10 females than an arm receiving clean air only (Table 1). Conversely, significantly more females entered an arm receiving clean air than an arm containing air from 10 conspecific females. However, there was no difference in behavioral response of females between the blank control versus arms receiving odors from 1 or 5 females (Table 1). Finally, psyllids of neither sex of *D. citri* were attracted to the volatiles from conspecific males versus a blank control (Table 1).

Experiment 3: Response of female *D. citri* to citrus plant odor infested with conspecific females

Diaphorina citri females did not exhibit a behavioral preference when presented simultaneously with odors from conspecific *D. citri* females and feeding-damaged plant volatiles, as compared with undamaged plant volatiles both 30 min ($\chi^2 = 1.222$, $df = 1$, $P = 0.269$, Fig. 3a) and 24 h after damage was initiated ($\chi^2 = 0.032$, $df = 1$, $P = 0.569$, Fig. 3a). Thirty min after initiation of feeding infestation,

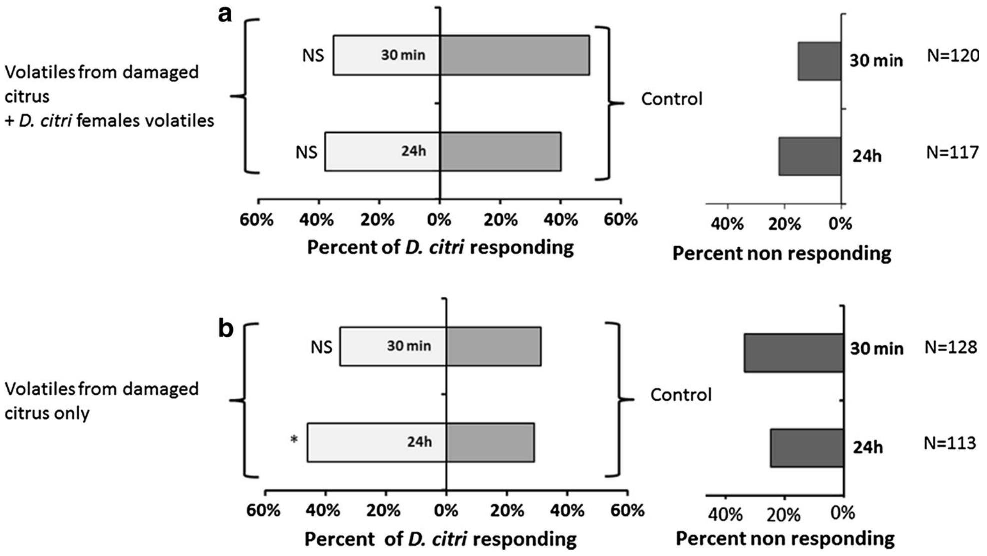

Fig. 3 Response of *D. citri* females to citrus plant odors with (**a**) or without (**b**) simultaneously presented odors from female conspecifics. *NR* non-responding psyllids

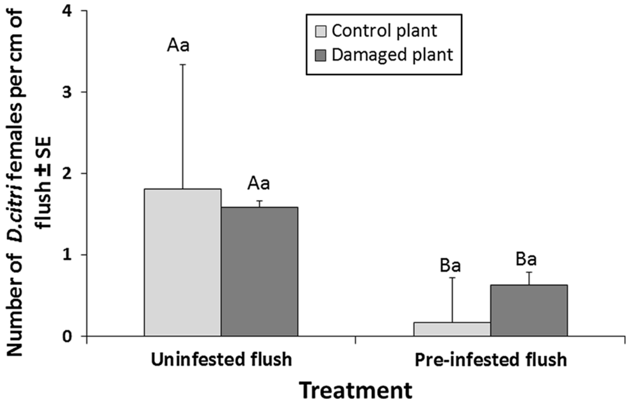

Fig. 4 Mean number of *D. citri* females counted per cm of newly flushing leaves, 24 h after initial infestation on uninfested or pre-infested flush of control or damaged plants. *Bars* labeled by *different capital letters* within plant treatment are significantly different at $\alpha < 0.05$ level. *Bars* labeled by the *same lower case letters* within flush treatment are not significantly different at $\alpha < 0.05$ level

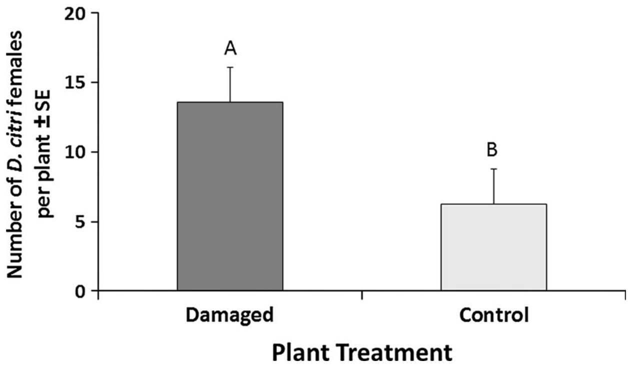

Fig. 5 Mean number of *D. citri* females counted on psyllid-damaged or control plants (including mature and newly flushing leaves). *Bars* labeled by *different letters* are significant different at $\alpha < 0.05$ level

there was no difference in female *D. citri* response to psyllid-damaged plants without odors of conspecific females versus undamaged plants ($\chi^2 = 0.294$, $df = 1$, $P = 0.588$, Fig. 3b). However, female *D. citri* were more attracted to volatiles from psyllid-damaged plants without simultaneous occurrence of odors from female *D. citri* headspace after 24 h of feeding damage than volatiles from undamaged plants ($\chi^2 = 4.247$, $df = 1$ $P = 0.039$, Fig. 3b).

Experiment 4: Response of *D. citri* females to both damaged citrus volatiles and female-derived odorants

We allowed female psyllids to settle on damaged or control plants, each containing leaf flush that was either previously uninfested or infested with other female *D. citri*. At the flush level, fewer *D. citri* females were found per centimeter of flush on those leaves that were pre-infested with conspecific females than on previously uninfested flush ($F_{1,25} = 15.589$, $P < 0.001$, Fig. 4). The number of female *D. citri* per centimeter of flush on damaged versus control plants was not different ($F_{1,25} = 0.131$, $P = 0.717$, Fig. 4). However, more psyllid females were found on damaged plants (including mature and newly flushing leaves) than control plants ($t = 2.328$, $df = 1$, $P = 0.048$, Fig. 5).

Discussion

Host selection by herbivorous insects is a complex process that includes integration of several potentially competing infochemicals that are emitted by the plants or by other insects (Dicke 2000). When insects search for a suitable host, they may directly evaluate both the quality of a potential host as well as the presence of competitors. Conspecific competitors may be particularly avoided on a fleeting host resource that can support only a limited number of offspring (Nufio and Papaj 2001). Our goal was to investigate the effect of female colonization density on the host selection behavior of *D. citri*. We also investigated the possible effect of female-related odors on host plant acceptance of this species. We hypothesized that female *D. citri* may integrate odors from both host plants and conspecifics when selecting newly expanding leaf flush, which is an ephemeral and critical resource for reproduction in this species.

Odors from *D. citri* females were found to repel conspecific females, but not males. Our results indicate that female *D. citri* are not only repelled by conspecific females but are also capable of detecting and avoiding leaf flush that was previously infested by conspecific females. This suggests that females may intentionally or unintentionally deposit a chemical on plants during infestation that is subsequently detected by conspecific females. However, avoidance of this odor is dosage dependent as we observed this repellency to only occur with the odors from 10 *D. citri* females, but not fewer. Also, this repellency occurs in the absence of host plants, as verified by the olfactometer experiments, which tested psyllid odors in the absence of host plants. This odor could be related to the male-attractant pheromone suggested by Wenninger et al. (2008) and/or could be derived from the cuticular hydrocarbon(s) characteristic of female *D. citri* that attract conspecific males (Mann et al. 2013).

Male to female attraction in *D. citri* has been observed previously (Wenninger et al. 2008). However, conspecific avoidance among females has not been observed previously. It is possible that previous investigations did not find female–female avoidance because the densities of females were not varied sufficiently among newly developed ‘flush’ leaves. Repellency between conspecific males has been previously documented in winterform pear psylla (Guedot et al. 2009a), but female–female repellency was not tested in this case. Consequently, the current investigation may be the first to describe density-dependent repellency between females in the Psylloidea.

We also demonstrated that *D. citri* females are attracted by volatiles emitted by plants damaged by conspecific psyllid feeding damage. This attractiveness was not found when both damaged citrus volatiles and female repellent cues were presented simultaneously, probably because these two cues interfered between each other (Pregitzer et al. 2012; Deisig et al. 2012). Feeding by *D. citri* on citrus is known to induce release of MeSA (Mann et al. 2012). MeSA is a known attractant for *D. citri* at the specific dosage released by psyllid-damaged plants (Mann et al. 2012). Therefore, we speculate that this infochemical may have been involved in attracting female *D. citri* to damaged plants. The ecological benefit of female *D. citri* attraction to psyllid-damaged plants may be their requirement of multiple matings to maintain optimal fertility and fecundity (Wenninger and Hall 2008). Thus, consistently finding males for mating is necessary (Wenninger and Hall 2008) and female *D. citri* may take advantage of plants that emit damage-induced volatiles because it facilitates host detection (Halitschke et al. 2008) and mate finding.

Also, release of MeSA by psyllid-infested plants may indicate that the host is more suitable for *D. citri* offspring development. Production of MeSA is associated with the activation of the salicylic acid (SA) pathway that regulates systemic acquired resistance against a wide variety of invading pathogens (Walling 2000; Thaler et al. 2010). Activation of SA resistance can suppress jasmonic acid (JA) signaling, and consequently compromise plant capability to induce defense response to herbivore attack (Bostock 2005; Walters and Heil 2007). For instance, induction of SA-regulated defenses by the whitefly, *Bemisia tabaci* Gennadius in *Arabidopsis thaliana* (L.) Heynh is associated with a reduction of induced JA-regulated defenses that constrains *B. tabaci* nymph development (Zarate et al. 2007). Thus, induction of the SA pathway by *D. citri* may be associated with a reduction in JA-regulated defenses. This reduction of JA-regulated defense might be beneficial for the development of *D. citri* nymphs and could explain why *D. citri* are more attracted by plants that release MeSA as a result of herbivore damage as compared with non-damaged plants, which do not release MeSA at detectible levels (Mann et al. 2012).

With respect to host site selection for maximizing fitness of offspring, density-dependent repellency among female *D. citri* combined with attraction to damage-induced plant volatiles may function in a complementary manner for oviposition site selection. We hypothesize that host selection by *D. citri* females may involve initial whole plant selection and subsequent specific oviposition site selection within plants. During the first step, *D. citri* females may select the host plant based on host-specific volatiles. For example, MeSA may be a cue that facilitates mate finding among *D. citri* conspecifics or indicates suitability of the plant. Once *D. citri* females infest a host plant, they must choose among available flush for oviposition. Selection of previously uninfested newly flushing leaves, based on detection of female-deployed odorants associated with oviposition, may facilitate reduced competition among conspecific *D. citri* for ephemeral resources.

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