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Research

First Insights into the Chemical Ecology of an Invasive Pest: Olfactory Preferences of the Viburnum Leaf Beetle (Coleoptera: Chrysomelidae)

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Abstract

The viburnum leaf beetle (VLB), *Pyrrhalta viburni* (Paykull), is an invasive chrysomelid in North America where it infests native *Viburnu*m shrubs in woody areas and managed landscapes. Despite its invasive and destructive nature, little is known about the chemical ecology of this beetle, and efficient chemical lures for monitoring and trapping this insect have yet to be developed. Using two of the main host plants of VLB in its native range, *Viburnum opulus* L. (Caprifoliaceae) and *V. lantana* L., we examined the olfactory preferences of adult females of VLB under laboratory conditions and measured volatile emissions of *Viburnum* twigs with and without VLB damage. VLB females had a clear preference for *V. opulus* and *V. lantana* twigs compared to blank odor sources. In addition, twigs with foliar damage and fresh egg masses were found to be more attractive than noninfested twigs in *V. opulus* when VLB infestation was recent, but not when twigs had been infested for several weeks. Chemical analyses revealed consistent treatment-specific blends of compounds, which may be used for the elaboration of attractive lures. Future research should focus on the identification of these compounds and on exploring the olfactory preferences of VLB with *Viburnum* species present in North America.

Key words: olfactometer tests, VOCs, herbivory, invasion ecology, baiting traps

The viburnum leaf beetle (VLB) *Pyrrhalta viburni* (Paykull) (Coleoptera: Chrsyomelidae) is a specialist leaf-feeder native to Eurasia that attacks plants belonging to the genus *Viburnum* (Caprifoliaceae), which contains ca. 160 species of shrubs and small trees (Winkworth and Donoghue 2005). The first specimens of VLB discovered in North America were collected in Nova Scotia, Canada, in 1924, but there were no reports of breeding populations and damage on local viburnums in Canada until the late 1970s (Majka and LeSage 2007). VLB was first reported in the United States in Maine in 1994 and has since extended its spread to all New England states, New York, New Jersey, Pennsylvania, Ohio, Michigan, Delaware, and Maryland (Giesmann 2017). A second invasion front has also been reported on the west coast in Washington state (Weston et al. 2007). This insect has been shown to spread as fast as 25 miles per year (Weston and Hoebeke 2003). Both larvae and adults can extensively defoliate plants, and 2–4 yr of repeated complete defoliations often result in the death of attacked shrubs (Weston et al. 2007, Desurmont and Agrawal 2014). In its invaded range, VLB has an economic impact for nurseries and landscape managers as well as an ecological impact on wild *Viburnum* populations and the fauna that relies on *Viburnum* shrubs for food or shelter (Sargent 1990, Witmer 2001). A recent 6-yr study in Pennsylvania showed that the local avian community was negatively affected by the invasion of the viburnum leaf beetle and the disappearance of local *Viburnum* shrubs in terms of overall diversity and mass gain for several bird species (Smith and Hatch 2017).

VLB is a univoltine species overwintering as eggs. In its invasive range, larvae typically hatch in April–May, complete their development within a few weeks, then pupate in the ground under a thin layer of soil. Adults typically emerge in June and feed and lay eggs through the summer months. Eggs are laid in round cavities excavated by females in the young twigs of their host plants. These cavities are filled with an average of eight eggs and covered with a frass-like secretion (i.e., 'egg cap') that protects eggs from desiccation during winter months (Weston et al. 2008). Females prefer to lay their eggs on twigs already infested by conspecific females, adjacent to existing egg masses, creating clusters of egg masses typically aligned along the underside of twigs (Desurmont and Weston 2011). This intriguing behavior was shown to benefit the insects by allowing them to overcome plant defenses. Indeed, infested *Viburnum* twigs can produce wounding tissue in response to VLB oviposition, and this wound response can crush the eggs or expel them out of their cavity. High densities of egg masses often kill infested twigs, preventing further wound tissue production and thus enhancing egg survivorship (Desurmont et al. 2009, Desurmont and Weston 2011). The feeding and oviposition preferences of VLB have been explored to a certain extent (Weston and Desurmont 2002, Desurmont and Agrawal 2014, Giesmann 2017) but their olfactory preferences have never been investigated.

Management of VLB in North America currently relies on mechanical control (i.e., pruning of twigs infested with egg masses before springtime) for small, localized infestations, and chemical control in managed landscapes. However, no effective management method exists to reduce VLB populations in natural areas (forests, wetlands). Biological control research efforts have shown that the spined soldier bug *Podisus maculiventris* (Say) (Hemiptera: Pentatomidae) can be an effective predator for augmentative biological control (Desurmont and Weston 2008a,b), and efforts to identify natural enemies of VLB in its native range that may have potential as classical biological control agents are currently underway.

Identification and formulation of attractive chemical lures has proven essential for monitoring the spread of invasive pests, and the use of baited traps is considered as an essential method of biosurveillance of nonnative insects (Poland and Rassati 2019). The semiochemicals used to develop attractive lures are typically based on insect pheromones, host plant kairomones, or a combination of both (Baroffio et al. 2018, Fan et al. 2019). In addition to their usefulness to monitor the spread of invasive species, semiochemicals may also be used for lure-and-kill management (El-Sayed et al. 2009), mating disruption (Mazid et al. 2011), conservation biological control (i.e., attraction of natural enemies in infested fields) (Kaplan 2012, Xiu et al. 2019), and biological control of weeds (Coss et al. 2005, Cossé et al. 2006).

Currently, nothing is known about the chemical ecology of the viburnum leaf beetle, and the present study had two main objectives: 1) investigate the olfactory preferences of VLB females to determine whether these insects use olfactory cues to locate its host plants from a distance, and 2) analyze the emissions of volatile organic compounds (VOCs) of intact and infested *Viburnum* plants. For our study, we used two of the three main host plants of VLB in its native range, *V. opulus* L. and *V. lantana* L., and VLB specimens collected in Switzerland where the insect and the two host plants coexist.

Materials and Methods

Insect and Plant Material

The VLB specimens used for the study were reared under laboratory conditions from egg masses initially collected in the Neuchâtel area (Switzerland). Larvae and adults were maintained in meshed rearing cages (30 × 30 × 30 cm, Mega View Science Education Services Co. Ltd, Taiwan) with freshly cut *V. opulus* twigs as food under ambient laboratory temperature conditions (ca. 22–25°C) and under artificial lights providing a16:8 (L:D) h light regime until needed for experimental purposes. Ambient humidity was not measured nor controlled in the rearing room. Mated females that were 1–2 wk old were used for the tests. The plant material used in the behavioral bioassays were *V. opulus* and *V. lantana* twigs cut from shrubs present in the Neuchâtel area (Switzerland) 24 or 48 h before the tests and kept in floral tubes under ambient laboratory conditions until needed for experimental purposes.

Behavioral Bioassays

The preferences of mated VLB females toward the odors of their host plants were investigated using 4-arm and 6-arm olfactometer settings (Turlings et al. 2004, D'alessandro and Turlings 2005). The tests were conducted in a room with no natural light, kept under ambient temperature (ca. 22–25°C) and humidity conditions. In the olfactometers, beetles were given the choice between 4 and 6 odor sources (= treatments). An air flow that was set at 0.6 liter per minute went through each odor source, and all air flows converged to a central glass piece where the beetles were released. Thirty minutes after release, insects were recollected and the treatment they chose at the end of this period was recorded. The olfactometers are built in such a fashion that each insect choosing an arm ends up in a glass bulb from which it is unlikely to come out (Turlings et al. 2004). No additional behavioral observations were conducted during each trial. Beetles that did not make a choice after 30 min were recorded as 'no choice' in the analysis of the results. An olfactometer test (=1 replicate) consisted in four consecutive releases of three beetles. Each beetle was used only once for experimental purposes (i.e., beetles were changed between releases and between replicates). Plants were replaced and glassware was cleaned between replicates. The cleaning process of the glassware consisted in rinsing the glassware sequentially with three solvents: water, acetone, and pentane, and putting the glassware in an oven at 250°C for 3 h. Two series of behavioral bioassays were run with different set of treatments. In the first series, we compared the attractiveness of intact *V. opulus* twigs with no signs of VLB infestation, *V. opulus* twigs showing signs of infestation (foliar damage + VLB egg masses), and two blank odor sources in a 4-arm olfactometer. In the second series, we compared the attractiveness of intact and infested *V. opulus* twigs, intact and infested *V. lantana* twigs, and two blank odor sources in a 6-arm olfactometer. For the first series, both intact and infested twigs were collected directly from the field on *V. opulus* shrubs. Because tests were conducted late August, at a time when VLB adults had already disappeared from the field in the Neuchâtel area for several weeks (G. A. Desurmont, personal observation), we know that the egg masses present on the twigs collected had not been freshly laid. In the second series, we prepared freshly infested *V. opulus* and *V. lantana* twigs in the laboratory by exposing intact twigs to two VLB females and one male 24 h prior to the experiments. Freshly infested twigs contained at least one VLB egg mass. Each beetle was only used once for behavioral tests. We conducted a total of six replicates for the first series (6 × 4 × 3 = 72 beetles tested) and six replicates for the second series (6 × 4 × 4 = 96 beetles tested).

Chemical Analyses

Plants that were used for the 6-arm olfactometer bioassays were immediately used for volatile collections afterward. Plants were placed in a VOC collection setup for 6 h (Ton et al. 2007), and the VLB adults that were used to infest the plants from the 'freshly infested' treatments were left on the plant during the VOC collections. VOCs were collected using trapping filters containing 25 mg of 80–100 mesh SuperQ adsorbent. Before use, trapping filters were cleaned with 300 µl of methylene chloride (HPLC grade). After each collection, VOCs were extracted from the filters with 150 µl of methylene chloride, two internal standards (IS) (*n*-octane and nonyl acetate in 10 µl of methylene chloride) were added to each sample, and the samples were then stored at −80°C until analysis. VOCs were analyzed with an Agilent 6890 gas chromatograph, which was coupled to a 5973 Network mass selective detector (transfer line 230°C, source 230°C, ionization potential 70 eV). A 2-µl aliquot of each sample was injected in pulsed splitless mode onto a nonpolar column (HP-1 ms, 30 m, 0.25 mm ID, 0.25 µm film thickness, Agilent J&W Scientific, USA). Helium at constant flow (1.9 ml/min) was used as carrier gas. After injection, temperature was maintained at 40°C for

3 min, then increased to 100°C at 8°C/min, and then to 220°C at 5°C/min. The quantities of the major components of the blends were estimated based on the peak areas of the compounds compared to the peak areas of the internal standards. Compounds were identified by comparing the spectra obtained from the samples with those from a reference database (NIST mass spectral library). However, these identifications could not be confirmed by comparing the spectra of the samples to pure reference compounds. Thus, individual compounds were only labeled by their retention times in the analyses.

Statistical Analyses

Preferences of VLB females were analyzed for each test using a generalized linear model (GLM) with a poisson distribution fitted by maximum quasi-likelihood estimation, using treatment as a fixed effect and replicate as a random effect. Means were then compared using individual contrasts ($\alpha = 0.05$). Results of the VOCs collections with were analyzed in several ways. Firstly, in order to test the hypothesis that VLB infestation induces the production of VOCs in *Viburnum* twigs, the total amounts of VOCs (= sum of the relative quantities of individual compounds found in each sample, compared to internal standards) produced by plants from the different treatments were compared using a nonparametric Kruskal–Wallis test ($\alpha = 0.05$). Quantities of VOCs emitted were not standardized by mass of plant tissue. Secondly, the complete blends of volatiles produced by plants belonging to the different treatments (62 compounds total) were compared using a nondiscriminant principal component analysis (PCA). For each sample, each compound received a score of 0 (absent) or 1 (present), and this dataset was used to run the PCA model. We used the two first principal components, accounting for 40.6% and 14.1% of the total variation in the data. All statistical procedures were performed using the JMP12 statistical software (SAS Institute, Inc., Cary, NC).

Results

Behavioral Bioassays

In the first series of tests in a 4-arm olfactometer, VLB significantly preferred *V. opulus* twigs compared to the blank odor sources, but did not discriminate between infested and noninfested *V. opulus* twigs (GLM: $\chi^2 = 38.8$; $P < 0.0001$; Fig. 1A). In the second series, VLB females showed a strong attraction toward freshly infested *V. opulus* twigs. Intact and infested *V. lantana* twigs showed intermediate attractiveness, and the blank odor sources and intact *V. opulus* twigs were the least attractive treatments (GLM: $\chi^2 = 44.5$; $P < 0.0001$; Fig. 1B). The overall participation of the beetles was 66.7% for the first series of tests (48 beetles made a choice out of 72 beetles tested) and 48.6% in the second series of tests (35 beetles made a choice out of 72 beetles tested).

Chemical Analyses

There were significant differences in total emissions of VOCs among the different treatments tested ($\chi^2 = 24.6$; $P < 0.0001$): infested *V. opulus* twigs as well as infested and intact *V. lantana* twigs were found to emit more VOCs than intact *V. opulus* twigs and blanks (Fig. 2). In other words, VLB infestation induced higher emissions of VOCs in *V. opulus*, but not in *V. lantana*. In total, 62 compounds, excluding contaminants, were found in the VOCs emissions of the different treatments and were used to run the PCA analysis (Supp Table 1 [online only]). The first principal component explained 40.6% of the total variation in the data, and the second main component 14.1%. The PCA analysis revealed a clear structure in emissions of VOCs, with the blends emitted by infested *V. opulus* twigs diverging from all the other treatments. Emissions of infested and intact *V. lantana* significantly overlapped, and the emissions of intact *V. opulus* twigs, which were very low quantitatively, still separated from the blanks and the other treatments (Fig. 3).

Discussion

The use of baiting traps is an essential component of biosurveillance and management programs against a variety of invasive and outbreaking insect pests such as the gypsy moth (Tobin and Blackburn 2007), the brown marmorated stink bug (Leskey and Nielsen 2018), and bark and ambrosia beetles (Rabaglia et al. 2008). The current study was conducted to explore for the first time the chemical ecology of VLB, a destructive invader in North America. Much is already known about the feeding and oviposition preferences of VLB females (Weston and Desurmont 2002, Desurmont and Agrawal 2014), which can be highly selective when choosing oviposition sites (Desurmont and Weston 2010, Desurmont et al. 2014), but their olfactory preferences had never been investigated.

The results of this study are highly promising. VLB females had no trouble making choices in olfactometer settings, although the overall 57.6% of participation of the insects during the tests indicates that there may be room for improving the setup and testing protocol in order to enhance insect motivation. Females showed clear patterns of preferences: the most attractive treatments were intact and infested *V. opulus* twigs in the 4-arm olfactometer (Fig. 1A) and infested *V. opulus* twigs and both intact and infested *V. lantana* twigs in the 6-arm olfactometer (Fig. 1B). Interestingly, the *V. opulus* twigs with 'old' signs of infestation (foliar damage and egg masses laid in the field during the weeks prior to the test) used in the 4-arm olfactometer tests were not more attractive than intact *V. opulus* twigs, in contrast to the freshly infested *V. opulus* twigs (foliar damage and egg masses laid within 24 h prior to the test) used in the 6-arm olfactometer tests, which were more attractive than intact *V. opulus* twigs. This suggests that cues associated with insect infestation lose their attractiveness over time (Maja et al. 2014, Desurmont et al. 2015). In our experiments, insects used to infest twigs for the 'infested *V. opulus*' and 'infested *V. lantana*' treatments were left on the plants during the olfactometer tests as well as during the VOCs collections, which means that the blends associated with these treatments may have contained not only plant volatiles but also compounds associated with VLB adults and their egg masses. Further research should aim at dissecting the part played by plant-associated and insect-associated cues in the attraction of VLB adults.

We saw a trend toward higher attractiveness of freshly infested *V. opulus* twigs compared to the other treatments in the 6-arm olfactometer. This trend is consistent with the oviposition preferences of VLB females, which have been shown to prefer twigs already infested by conspecifics for oviposition (Desurmont and Weston 2011, Desurmont et al. 2012). However, oviposition preference for infested twigs does not depend on the 'freshness' of infestation, as the remains of 1-yr old egg masses have been shown to retain their attractiveness as oviposition cues to VLB females (Desurmont et al. 2009). Volatile cues associated with VLB infestation may gradually vanish postinfestation while nonvolatile cues (e.g., remains of 'egg caps') remain on twigs in the long term.

In contrast to *V. opulus*, there was no detectable difference in attractiveness between infested and noninfested *V. lantana* twigs in our tests. Chemical analyses revealed that there was no obvious induction of VOCs caused by VLB infestation in *V. lantana* and that the blends emitted by infested and noninfested *V. lantana* twigs

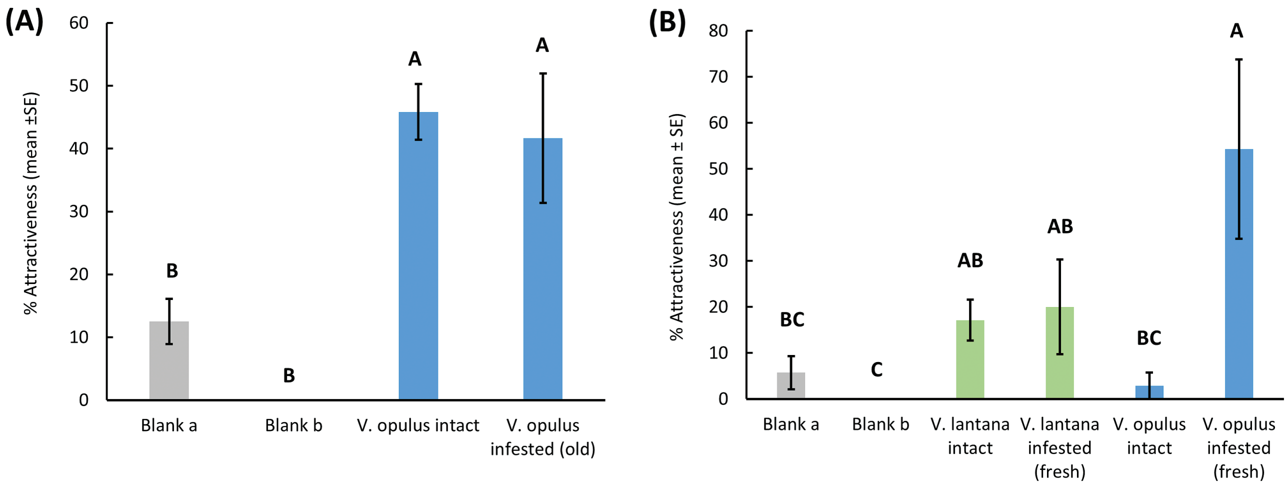

Fig. 1. Preferences of VLB females in (A) a 4-arm olfactometer setting and (B) a 6-arm olfactometer setting (% attractiveness, mean ± SE). In the 4-arm olfactometer, infested *V. opulus* twigs were directly collected in the field at the end of the season (old infestation). In the 6-arm olfactometers, infested *V. opulus* and *V. lantana* twigs were infested in the laboratory 24 h prior to the tests (fresh infestation). Treatments followed by a different letter are statistically different (GLM individual contrasts, $\alpha = 0.05$).

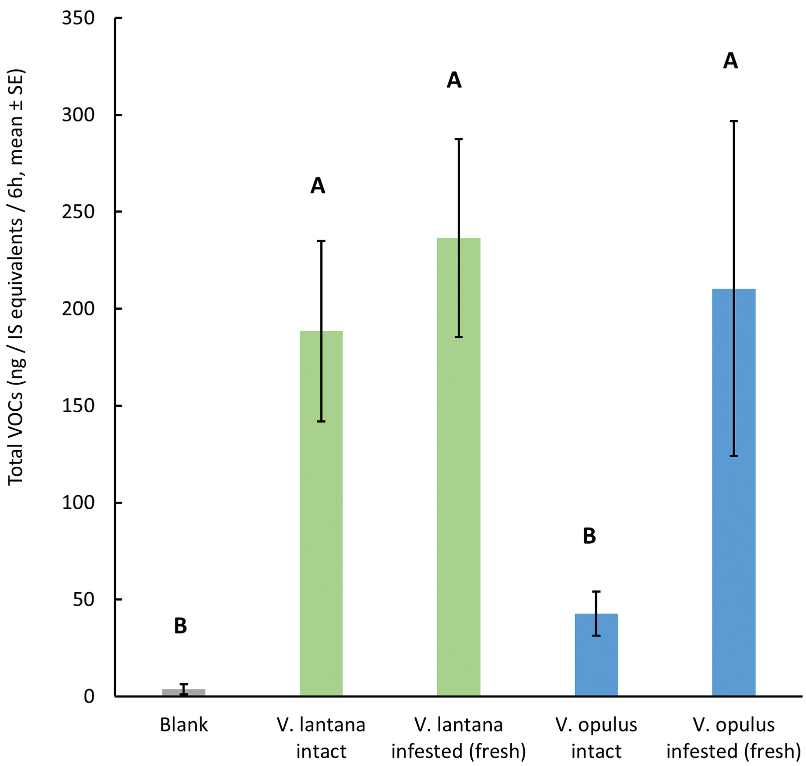

Fig. 2. Quantitative analysis of the VOCs emissions of *Viburnum* plants. Total VOCs emissions (ng/IS equivalents/6 h, mean ± SE). Infested *V. opulus* and *V. lantana* twigs were infested in the laboratory 24 h prior to the tests (fresh infestation). Treatments followed by a different letter are statistically different (Kruskal–Wallis test, $\alpha = 0.05$).

largely overlapped: it is, therefore, possible that VLB females could not distinguish infested from noninfested *V. lantana* twigs. It is also possible that attraction to infested *V. lantana* twigs could not be detected in the 6-arm olfactometer because of the predominant attractiveness of infested *V. opulus* twigs. Additional tests centered on *V. lantana* would be needed to test these hypotheses. Furthermore, it should be noted that our VLB colony was maintained on *V. opulus* twigs prior to the tests, which could have impacted the preferences of adults. Conducting the same tests with VLB populations reared on *V. lantana* or an alternative host plant would be needed to evaluate the ability of VLB adults to associate their foraging preferences to their past feeding experiences.

In total, 62 compounds were found in the VOCs emissions of the different treatments (Supp Table 1 [online only]). Although these compounds could not be identified with certainty during the study, the PCA analysis based on the variation in emissions of all 62 compounds showed treatment-specific structure. In particular, the treatment 'infested *V. opulus*,' which was highly attractive in

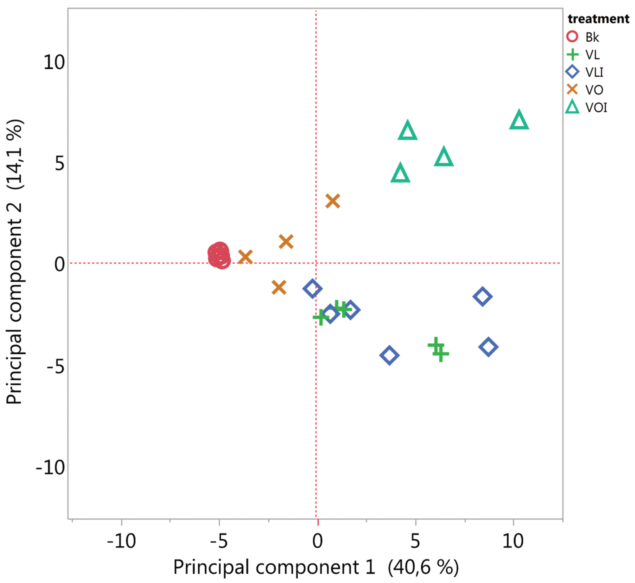

Fig. 3. Qualitative analysis of the VOCs emissions of *Viburnum* plants. Principal component analysis based on the 62 VOCs emitted by *Viburnum* plants. The horizontal and vertical axes show projections on to the first and second principal components, respectively. Each dot represents an individual plant. Bk, blank odor source; VL, *V. lantana* intact; VLI, *V. lantana* infested (fresh infestation); VO, *V. opulus*; VOI, *V. opulus* infested (fresh infestation).

the 6-arm olfactometer, consistently diverged from all other treatments, indicating that some compounds, associations of compounds, or ratios of compounds are specifically emitted by freshly infested *V. opulus* twigs.

The results of this study constitute a first step in understanding the chemical ecology of a destructive invader in North America. Future research should focus in priority in identifying the compounds associated with the attraction of VLB adults, in particular those specific to freshly infested *V. opulus*. Because *V. opulus* and *V. lantana* have coevolved with VLB in its native range, they are adequate targets for the identification of attractive plant volatiles. Conducting similar studies with North American *Viburnum* species, particularly species favored for oviposition and larval feeding (Desurmont et al. 2011), would be beneficial to estimate the likelihood of these species to be readily located in the field and better understand the invasion ecology of this pest.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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