Hexanal, a major volatile found in fresh peanut seed, elicits foraging behavior in the laboratory-reared brown marmorated stink bug, *Halyomorpha halys* (Heteroptera: Pentatomidae)

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(Received October 1, 2018; Accepted November 13, 2018)

Phytophagous insects utilize visual, olfactory and gustatory cues to find food. The brown marmorated stink bug, *Halyomorpha halys* (Stål), quickly approaches fresh peanut seeds newly introduced into the rearing cage in the laboratory but shows less interest in stale peanut seed previously infested by conspecifics. This observation suggests that *H. halys* can perceive the quality of food by detecting the volatile(s) from fresh peanut seeds. A bioassay revealed that *H. halys* adults could more quickly find fresh peanut seeds than three-day-infested peanut seeds, which is consistent with laboratory observations. Hexanal was found to be the major volatile component of fresh peanut seeds but not of previously infested ones. In the two-choice assays, the adult bugs that did respond were significantly attracted to fresh peanut volatiles and hexanal. Hexanal also induced proboscis-protruding behavior in adult *H. halys*, which suggested that this compound is a key stimulant of foraging behavior of laboratory-reared *H. halys* adults.

*Keywords:* *Halyomorpha halys*, *Arachis hypogaea*, hexanal, attractant, proboscis extension, food selection.

**Electronic supplementary materials:** The online version of this article contains supplementary material (Supplemental Figs. S1–S4), which is available at http://www.jstage.jst.go.jp/browse/jpestics/

**Introduction**

Insects are known to perceive food sources through the detection of chemical and/or physical signals; chemical signals are well known to play important roles in food selection as attractants, feeding stimulants, and deterrents.1–5 In studies of this type, researchers observe insect behaviors in the field and then build bioassay systems in the laboratory to test sensory responses in olfactory and gustatory systems. In order to investigate insect behavior and physiology in the laboratory, insects are reared in the laboratory where, in some cases, they are fed on artificial diets or unnatural but suitable food sources. Even though observations under these unnatural conditions may not be reliable indicators of insect behaviors, they can still contribute to our understanding.

The brown marmorated stink bug, *Halyomorpha halys* (Stål) (Heteroptera: Pentatomidae), is a nuisance pest known to invade houses, hotels, and school buildings6,7 and infest soybeans, a wide range of orchard crops such as oranges, persimmons, apples, pears, peaches, and cherries as well as economically important trees such as *Paulownia tomentosa*.8,9 When disturbed, it can discharge a foul-smelling mixture of (E)-2-decenal, 4-oxo-(E)-2-hexenal, and tridecane.10–13 It is native to Japan, China, and Korea, and its distribution has been expanding recently in North America and Europe as an invasive species.14–16 *Halyomorpha halys* is easily reared in the laboratory and can be fed on peanut seeds. Upon the introduction of fresh peanut seeds into their cage, *H. halys* adults were observed to move their antenna frequently, seek out the peanut seeds; and then approach them. After reaching the peanut seeds, the adult bugs start sucking them (Supplemental Fig. S1). However, *H. halys* adults were observed to be less interested in previously infested peanut seeds, often simply ignoring them. These observations suggested that *H. halys* adults discriminate between fresh and previously infested peanut seeds based on olfactory cues. Although *H. halys* adults rarely encounter peanut seeds (which develop in a shell underground) in the wild, the identification of foraging signal(s) used by *H. halys* adults in assessing the peanut seeds’ quality should inform our understanding of the molecular basis underlying their food selection, which may result in a novel method of controlling this noxious and invasive insect pest. Although *H. halys* is known to be attracted to its own aggregation pheromone as well as those of other bugs, little is known about the roles of plant-derived chemical signals that regulate *H. halys* behavior, as pointed out in a recent review by Weber et al. (2017).17

Here, I report a chemical stimulant found in fresh peanut seeds that elicits foraging and probing behaviors of laboratory-rearing *H. halys* adults. The results are expected to contribute to
our understanding of how this polyphagous heteropteran insect selects its food sources.

**Materials and Methods**

1. **Insects, plants, and chemicals**

Nymphs of *H. halys* were purchased from Sumika Technoservice Corporation (Takarazuka, Japan). The nymphs were kept at room temperature and fed on fresh peanut seeds and water until they became adults. After eclosion, adults were separated by sex and fed on fresh peanut seeds and water during the experimental period. Food but not water was withheld from all of the bugs for one day prior to the bioassays. Peanut seeds (*Arachis hypogaea*) were purchased from the Utane Seed Co., Ltd. (Utsunomiya, Japan). Peanut seeds uninfested by *H. halys* are termed fresh peanut seeds in this study.

Hexanal, (E)-2-decenal, and 1-methylpyrrole were purchased from the Tokyo Chemical Industry Co., Ltd. (Tokyo, Japan). 1-Dodecene, tridecane, and tetradecane were purchased from Wako Pure Chemical Industries, Ltd. (Osaka, Japan). 4-Oxo-(E)-2-hexenal was synthesized according to the method of Moreira and Millar (2005).

2. **Volatile collection and chemical analysis**

Two fresh peanut seeds were put in a 16 mL glass vial capped with a Mininert® Valve (Supelco, Bellefonte, PA, USA) and left at room temperature for 24 hr. Then, the volatiles in the vial were collected using solid phase micro extraction (SPME) fiber (65 μm StableFlex PDMS/DVB, Supelco) for 30 min. The SPME fiber was directly injected into a gas chromatograph-mass spectrometer (GC-MS), Clarus 600 GC/MS (PerkinElmer Inc., Santa Clara, CA, USA) with helium carrier gas at 1.0 mL/min. The oven temperature was programmed to remain at 50°C for 3 min, increase to 290°C at a rate of 10°C/min, and then remain at 290°C for 5 min. The temperature of both the injector and detector were maintained at 250°C. The separated volatile components were ionized at 70 eV. Volatile components were identified by comparing their GC retention times and mass spectra with those of authentic standards. Four fresh peanut seeds were put in a rearing cage (9.1 cm × 14.9 cm i.d.) where eight adults of *H. halys* were located and then kept for 3 days to prepare the *H. halys*-infested peanut seeds. The *H. halys*-infested peanut seeds were prepared as required. Volatiles from the peanut seeds infested by *H. halys* adults for 3 days were also analyzed by the same procedure. Volatile analyses were repeated three times for both fresh and infested peanut seeds.

To quantify the hexanal emitted from the fresh peanut seeds, 1 μL of *n*-hexane containing 10 ng of 1-dodecane as an internal standard was added to the vial through the valve by a Hamilton microsyringe before volatile collection as described above. Hexanal was quantified with selected ion monitoring using the ions m/z 56 for hexanal and m/z 55 for the internal standard (1-dodecane). The ratio of the peak area in the sample (hexanal/internal standard) was calculated, and the quantity of hexanal was determined by comparing with those in the calibration standard (100–500 ng of hexanal). Quantification analyses were repeated seven times for fresh peanut seeds and five times for infested peanut seeds.

To examine the volatile components in the metathoracic scent gland (MTG) complex of *H. halys* adults, the MTG was removed by dissection, and the extracted MTG was immersed in 1 mL of hexane for 5 min. An aliquot of the extract (1 μL) was analyzed by GC-MS under the same conditions as described above.

3. **Behavioral assays of adult *H. halys* toward fresh and infested peanut seeds**

The times required for *H. halys* adults to reach either a fresh or three-day-infested peanut seed were evaluated. A fresh or previously infested peanut seed was gently introduced into a plastic petri dish (1.9 cm × 9.0 cm i.d.) on the side diametrically opposite to where an adult *H. halys* was located. The adult bug moved around freely inside the petri dish, and the time taken for the adult bug to reach the peanut seed was measured for 300 sec (5 min). When the adult bug reached the peanut seed, it started sucking the seed. Each bug was tested twice with both fresh and previously infested peanut seeds in a random order. The interval between trials was more than 1 hr. Twenty-four bugs (12 females and 12 males) were used in this assay. If a stink bug did not reach the peanut seed within 300 sec, the time was recorded to be 300 sec. The data was analyzed with the Wilcoxon signed rank test using JMP 13.0.0 (SAS Institute, Cary, NC, USA).

4. **Two-choice assays for the preference of adult *H. halys* for fresh peanut volatiles and hexanal**

Two-choice assays were designed using a handmade, T-shaped assay chamber (Supplemental Fig. S2). Adult bugs respond to fresh peanut seeds in a cage, proving hexanal’s ability to be dispersed by diffusion; thus, the assay was conducted without any airflow. Two glass vials (100 mL each) were connected by a hollow plastic tube (9.0 cm × 2.5 cm i.d.). One end of a second, smaller plastic tube (4.7 cm × 1.2 cm i.d.) was inserted halfway between the two ends of the first plastic tube to make a three-way branch (a T shape). Two fresh peanut seeds were put into a third glass vial that was immediately substituted for one of the two empty glass vials connected to the first plastic tube. An adult bug to reach the peanut seed was measured for 300 sec. The cap and maintained at room temperature for 24 hr. This vial was uncovered and immediately substituted for one of the two empty glass vials connected to the first plastic tube to serve as an odor source. An empty glass vial set on the other side of the chamber was used as a control. An adult *H. halys* was introduced into the chamber from the end of the smaller tube. The bugs were observed to walk to the intersection of the plastic tubes, whereupon they could choose which vial to access. The number of *H. halys* adults that entered into either vial within 10 min was counted. Bugs that remained in the plastic tube after 10 min without choosing a vial were counted as nonresponsive.

Each pair of glass vials was used only once. The responses of 20 females and 20 males were observed individually. Hexanal,
a major component of fresh peanut seed volatiles, was also tested as an odor source. Hexanal was dissolved in hexane to prepare 0.5, 1.0, and 2.5 mg/mL solutions. Two microliters of each hexanal solution (1, 2, and 5 µg) was loaded onto a piece of qualitative filter paper (Advantec, Grade No. 1, Tokyo, Japan), which was deposited into a glass vial. Two-choice assays were performed between hexanal and hexane (a control), as described above. Fifteen females and fifteen males were tested in this assay. All data, including that of bugs that did not choose either vial, were analyzed with a theoretical ratio (1:1) by Fisher’s exact test using JMP 13.0.0.

5. Assays for the proboscis-protruding behavior of adult H. halys in response to hexanal exposure

The frequency and duration of proboscis-protruding behavior of adult H. halys after exposure to hexanal were measured. An adult H. halys was introduced to a petri dish (1.9 cm × 9.0 cm i.d.), followed by a piece of filter paper infused with 5 µg of hexanal. Care was taken to ensure that the filter paper did not touch the stink bug. The frequency of proboscis-protruding behavior was monitored for 10 min. Two microliters of hexane were used as a control treatment. Each adult bug was tested twice with two different treatments (hexanal and hexane) in a random order. Six replicates were done using three females and three males. All data were analyzed with paired t-test using JMP 13.0.0.

**Results**

1. Volatiles of peanut seeds

GC analyses revealed that hexanal was the major volatile component emitted by fresh peanut seeds (peak 1 in Fig. 1A). On the other hand, hexanal was not detected in peanut seeds previously infested by H. halys (Fig. 1B and 1C), suggesting that this compound is specific to fresh peanut seeds. The amount of hexanal collected from the two fresh peanut seeds in the vial was 310.9 ± 15.1 ng/vial (mean ± S.E.; N = 7). Two minor components, tetradecane and an unidentified sesquiterpene, were detected from both fresh and previously infested peanut seeds (peaks 2 and 3 in Fig. 1A–C). 1-Methylpyrrole was detected only in infested peanuts (peak 4 in Fig. 1B and 1C). Tridecane, a major secretory component of adult H. halys (Supplemental Fig. S3), was sometimes detected in the infested peanut seeds (peak 6 in Fig. 1C; two of three samples in the qualitative analysis and three of five samples in the quantitative analysis).

(E)-2-Decenal, 4-oxo-(E)-2-hexenal, and tridecane were detected as major components in the MTG of H. halys adults (Supplemental Fig. S3). Hexanal was not detected in the MTGs of H. halys adults, and the volatile profile of adult H. halys was completely different from that of fresh peanut seeds.

2. Preference of H. halys adults for fresh peanut seeds and hexanal

Halyomorpha halys adults were able to reach fresh peanut seeds more quickly than infested ones (p < 0.0001; Fig. 2), a result consistent with the observations of H. halys being reared under laboratory conditions (see Introduction). All 24 of the adult bugs tested were able to reach the fresh peanut seeds within the experimental period (300 sec), whereas only thirteen reached the infested peanut seeds. The average time required for bugs to reach fresh peanut seeds (mean ± S.E. = 105.8 ± 17.9 sec) was almost half that for infested peanut seeds (225.9 ± 20.8 sec; Fig. 2). There was no significant difference in the abilities of male and female bugs to find fresh peanut seeds (female, 85.7 ± 24.7 sec; male, 125.9 ± 25.8 sec; p = 0.2985). The times taken by the bugs to reach the fresh peanut seeds were not significantly affected by whether they had been previously tested with infested peanut seeds (fresh peanut seed was tested first, 112.3 ± 29.1 sec, N = 7 females and N = 7 males; fresh peanut seed was tested second, 99.3 ± 22.2 sec, N = 7 females and N = 5 males; p = 0.9080).

Two-choice assays revealed that H. halys adults positively

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\begin{align*}
\text{Retention time (min)} & \quad 5 \quad 10 \quad 15 \\
1 \quad 2 \quad 3 \\
5 & \quad 6 \\
4 \quad 2 \quad 3
\end{align*}
\]

Fig. 1. Typical gas chromatograms of volatiles from fresh peanut seeds (A) and three-day-infested peanut seeds (B and C). 1, Hexanal; 2, tetradecane; 3, unidentified sesquiterpene; 4, 1-methylpyrrole; 5, unidentified compound; 6, tridecane

\[
\begin{align*}
\text{Time required to reach peanut seed (sec)} & \quad 0 \quad 20 \quad 40 \\
\text{Fresh peanut seed} & \quad 105.8 \pm 17.9 \\
\text{3 day-infested peanut seed} & \quad 225.9 \pm 20.8 \\
\end{align*}
\]

Fig. 2. Responses of adult H. halys to peanut seeds. Time required to reach fresh and three-day-infested peanut seed (means ± S.E. sec.; each N = 24). An asterisk indicates a significant difference between treatments (Wilcoxon signed rank test, ** p < 0.01).
chose fresh peanut volatiles over air \((p=0.0397; \text{Fig. 3A})\). Adult \(H.\) halys showed a significant preference for 1 \(\mu\)g of hexanal over hexane \((p=0.0411; \text{Fig. 3B})\), whereas the adult bugs did not significantly respond to higher doses of hexanal \((2 \text{ and } 5 \mu\text{g})\) infused into the filter paper \((\text{Fig. 3B})\). About one third of the bugs tested did not respond to either hexanal or hexane. During the two-choice assays, 45% of the stink bugs attracted to the fresh peanut seeds stretched their proboscises near the peanut seeds. Proboscis-protruding behavior was also observed in 56%, 64%, and 71% of the bugs attracted to 1, 2, and 5 \(\mu\)g of hexanal, respectively. These stink bugs walked around the hexanal-infused filter paper with their proboscises protruding \((\text{Supplemental Fig. S4})\) but did not walk on top of it or attempt to feed on it.

3. Proboscis-protruding behavior of \(H.\) halys adults

In the above two-choice assay, some \(H.\) halys adults that entered the glass vial containing filter paper infused with hexanal showed proboscis-protruding behavior when near the filter paper. This observation suggested that hexanal could induce proboscis-protruding behavior. The frequency of proboscis-protruding behavior induced by hexanal \((5 \mu\text{g})\) was significantly higher than that induced by the control treatment, hexane \(\text{mean}\pm\text{S.E.}=4.3\pm1.1\text{ times for hexanal, }1.0\pm0.5\text{ times for hexane; }p=0.0483; \text{Fig. 4A})\). When exposed to hexanal, the duration of proboscis-protruding behavior was significantly increased as compared to that of the group given the control treatment \((112.8\pm31.4\text{ sec vs. }7.3\pm4.2\text{ sec}; p=0.0174; \text{Fig. 4B})\).

![Fig. 3. Preference of adult \(H.\) halys for fresh peanut volatiles (A) and hexanal (B). Numbers in parentheses in each bar represent the numbers of adult \(H.\) halys that reached each source. Numbers in parentheses outside the bar indicate the bugs that did not choose any source. Asterisks indicate significant differences between adult \(H.\) halys choices against expectations of random choice \((1:1)\) (Fisher’s exact test, * \(p<0.05)\).](image)

![Fig. 4. Proboscis-protruding responses of adult \(H.\) halys to hexanal. Frequency (A) and total time (B) of proboscis-protruding behavior within 10 min (means±S.E.; each \(N=6)\). Asterisks indicate that the differences between treatments were significant (paired \(t\)-test, * \(p<0.05)\).](image)

### Discussion

The present results indicate that adult \(H.\) halys discriminate between fresh and previously infested peanut seeds by detecting a general plant odor, hexanal. This is consistent with previous reports that, in general, phytophagous insects utilize host odors to find suitable food sources.\(^{1-2}\) It has also been reported that the plant-feeding mirid bug, \(Lygus\) lincolaris, shows positive EAG responses to general plant odors, such as \((Z)-3\text{-hexen}-1\text{-ol}, (E)\text{-2-hexen}-1\text{-ol, and } (E)\text{-2-hexenal, which are found in one of its host plants, cotton.}^{19}\) In general, a wide variety of heteropteran species use hexanal and \((E)\text{-2-hexenal as alarm pheromones and allomones.}^{20}\) The olfactory detection of hexanal may be conserved across most heteropteran species, although behavioral outputs in response to this compound differ between species.

The preference of adult \(H.\) halys for hexanal could explain their preference for fresh peanut volatiles under laboratory conditions. Because \(H.\) halys is a polyphagous insect, it may possess the ability to detect a multitude of chemical stimuli, although hexanal is a primary attractant. As Clavijo McCormick et al. (2014) pointed out, minor components of plant volatile blends can attract or deter pollinators, herbivores, and their predators;\(^{21}\) and the minor components detected in fresh peanut volatiles, such as the unidentified sesquiterpene, may influence the foraging behavior of adult \(H.\) halys. \(Halyomorpha\) halys adults were not observed to completely ignore the three-day-infested peanut seeds, which did not emit hexanal. Because the adult \(H.\) halys walked around the petri dish during the experimental period, it is possible that at least some of them found the previously infested peanut seeds by chance. Adult \(H.\) halys are likely to use food source contact stimuli as cues, even when the food is olfactorily unattractive and the quality of the food is low.

Adult and nymph \(H.\) halys were previously reported to prefer uninjured blueberry fruits to injured ones of inferior nutritional quality.\(^{22}\) \(Halyomorpha\) halys feeds on sweet persimmon fruit with a low concentration of tannin but not on astringent fruit with a high concentration of tannin.\(^{23}\) The nutritional changes in peanut seeds after infestation by adult \(H.\) halys are still unclear, although the present study did establish that \(H.\) halys feeding alters their volatile profiles. Evidently, the presence of hexanal is
interpreted by *H. halys* as an indicator of high food quality, and a decrease in the emission of hexanal accounts for the lack of interest of *H. halys* in previously infested peanut seeds.

1-Methylpyrrole was detected only in infested peanut seeds, but its role in the foraging behavior of adult *H. halys* was not determined. Tridecane was sometimes detected in the *H. halys*-infested peanut seeds. Adult *H. halys* secrete tridecane; therefore, this compound is thought to be transferred from the stink bug to the peanut seeds in a manner similar to that of the *H. halys*-infested pods of the common bean, *Phaseolus vulgaris*.24) Future studies should seek to determine whether 1-methylpyrrole and tridecane function as indicators of previous infestation by conspecifics.

In addition to its attractant activity, hexanal was also found to elicit proboscis-protruding behavior in *H. halys* adults. This suggests that hexanal concentrations above a certain threshold can alter the behavior of *H. halys* during its approach to a food source—a reasonable supposition given that having found a food source, *H. halys* must stop looking for food and start feeding. Floral volatiles are known to evoke proboscis extension in the cabbage butterfly,27) and *(E)-phytol derived from Spodoptera litura* larvae is known to induce proboscis-protruding behavior of an asopine predatory stink bug28); however, little is known about volatiles that evoke proboling behavior. The array of chemical signals that regulate the sequence of foraging and sucking behavior of *H. halys* is intriguing and important, as understanding them could inform the development of baits controlling this noxious pest species.

Insect responses to a certain chemical signal might differ based on physiological and internal conditions. For example, hexanal attracts the second-generation carrot rust fly, *Psila rosae*, but not the first generation.26) Also, insects are known to learn olfactory cues from their food sources.27) The stink bugs used in this study were reared in the laboratory with an unnatural food source, peanut seeds, and thus olfactory learning and/or adaptation under laboratory conditions should be considered. It is not clear whether the preference of adult *H. halys* for hexanal is innate or due to olfactory learning. Future studies should address this question, perhaps by using wild-caught *H. halys* or lines reared on foods that do not emit hexanal. Nevertheless, hexanal is a ubiquitous fruit flavor component present in apples and soybeans, both of which are host plants of *H. halys*.28,29) The preference of adult *H. halys* for this general plant odor may contribute to its polyphagy.

**Acknowledgements**

This work was financially supported by Akita Prefectural University.

**References**

1) J. H. Visser: *Annu. Rev. Entomol.* **31**, 121–144 (1986).

2) K. Honda, H. Ômura and N. Hayashi: *J. Chem. Ecol.* **24**, 2167–2180 (1998).

3) T. J. A. Bruce, L. J. Wadhams and C. M. Woodcock: *Trends Plant Sci.* **10**, 269–274 (2005).

4) T. Murata, N. Mori and R. Nishida: *J. Chem. Ecol.* **37**, 1099–1109 (2011).

5) A. Wada-Katsumata, J. Silverman and C. Schal: *Science* **340**, 972–975 (2011).

6) M. Watanabe, R. Arakawa, Y. Shinagawa and T. Okazawa: *Jpn. J. Sanit. Zool.* **45**, 311–317 (1994), in Japanese with English summary.

7) D. B. Inklely: *J. Entomol. Sci.* **47**, 125–130 (2012).

8) M. Tomokuni, T. Yasunaga, M. Takai, I. Yamashita, M. Kawamura and T. Kawasawa: ’A Field Guide to Japanese Bugs: terrestrial heteropterans,” Zenkoku Nosen Kyouiku Kyokai, Tokyo, 1993 (in Japanese).

9) D.-H. Lee, B. D. Short, S. V. Joseph, J. C. Bergh and T. C. Leskey: *Environ. Entomol.* **42**, 627–641 (2013).

10) C. Kitamura, S. Wakamura and S. Takahashi: *Appl. Entomol. Zool.* **19**, 33–41 (1984).

11) R. L. Baldwin VI, A. Zhang, S. W. Fultz, S. Abubeker, C. Harris, E. E. Conner and D. L. Van Hekken: *J. Dairy Sci.* **97**, 1877–1884 (2014).

12) C. Harris, S. Abubeker, M. Yu, T. Leskey and A. Zhang: *PLoS One* **10**, e0140876 (2015).

13) Y.-Z. Zhong, J.-P. Zhang, L.-L. Ren, H.-X. Zhan, G.-H. Chen and F. Zhang: *J. Pest Sci.* **90**, 1097–1105 (2017).

14) E. R. Hoebeke and M. E. Carter: *Proc. Entomol. Soc. Wash.* **105**, 225–237 (2003).

15) T. C. Leskey, G. C. Hamilton, A. Nielsen, D. F. Polk, C. Rodriguez-Saona, J. C. Bergh, A. Herbert, T. P. Kuhar, D. Pfeiffer, G. P. Dively, C. R. R. Hooks, M. J. Raupp, P. M. Shrewsbury, G. Krawczyk, P. W. Shearer, J. Whalen, C. Koplinka-Loehr, E. Myers, D. Inklely, K. A. Hoelmer, D.-H. Lee and S. E. Wright: *Outlooks Pest Manag.* **23**, 218–226 (2012).

16) K. B. Rice, C. J. Bergh, E. J. Bergmann, D. J. Biddinger, C. Dieckhoff, G. Dively, H. Fraser, T. Gariepy, G. Hamilton, T. Haye, A. Herbert, K. Hoelmer, C. R. Hooks, A. Jones, G. Krawczyk, T. Kuhar, H. Martinson, W. Mitchell, A. L. Nielsen, D. G. Pfeiffer, M. J. Raupp, C. Rodriguez-Saona, P. Shearer, P. Shrewsbury, P. D. Venugopal, J. Whalen, N. G. Wimn, T. C. Leskey and J. F. Tooker: *J. Integr. Pest Manag.* **5**, 1–13 (2014).

17) D. C. Weber, W. R. Morrison III, A. Khrimian, K. B. Rice, T. C. Leskey, C. Rodriguez-Saona, A. L. Nielsen and B. R. Blaauw: *J. Pest Sci.* **90**, 989–1008 (2017).

18) J. A. Moreira and J. G. Millar: *J. Chem. Ecol.* **31**, 965–968 (2005).

19) S. Chinta, J. C. Dickens and J. R. Aldrich: *J. Chem. Ecol.* **20**, 3251–3267 (1994).

20) K. Noje, T. Kakuda, M. Abe and S. Tamogami: *J. Chem. Ecol.* **41**, 757–765 (2015).

21) A. C. McCormick, J. Gershenzon and S. B. Unsicker: *Plant Cell Environ.* **37**, 1836–1844 (2014).

22) Y. Zhou, M. M. Giusti, J. Parker, J. Salamanca and C. Rodriguez-Saona: *Environ. Entomol.* **45**, 1227–1234 (2016).

23) J. Kim and C. G. Parker: *Plant Biol.* **45**, 71–76 (2015).

24) D. F. Fraga, J. Parker, A. C. Busoli, G. C. Hamilton, A. L. Nielsen and C. Rodriguez-Saona: *J. Pest Sci.* **90**, 1107–1118 (2017).

25) T. Yasuda: *Entomol. Exp. Appl.* **82**, 349–354 (1997).

26) A. B. Stevenson and E. S. Barszcz: *Proc. Entomol. Soc. Ont.* **128**, 85–91 (1997).

27) R. Glinwood, E. Ahmed, E. Qvarfordt and V. Ninkovic: *Oecologia* **166**, 637–647 (2011).

28) S. Arai, M. Noguchi, M. Kaji, H. Kato and M. Fujimaki: *Agric. Biol. Chem.* **34**, 1420–1423 (1970).

29) T. Matoba, H. Hidaka, H. Narita, K. Kitamura, N. Kaizuma and M. Kito: *J. Agric. Food Chem.* **33**, 852–855 (1985).