Oviposition preferences of the oriental fruit moth *Grapholita molesta* (Lepidoptera: Tortricidae) to pear HIPVs

Chia-Ming Liu1 · Supannee Phukhahad3 · Wanida Auamcharoen3 · Shigeru Matsuyama2 · Yooichi Kainoh2

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Abstract
Herbivore-induced plant volatiles (HIPVs) are regarded as an indirect plant defense against herbivores, since they attract natural enemies to infested plants. On the other hand, HIPVs also affect behavioral responses of herbivores. In a previous study, *Lytopylus rufipes*, a parasitoid of the oriental fruit moth (*Grapholita molesta*), showed positive responses to pear HIPVs, but the influence of pear HIPVs on *G. molesta* is still unclear. To better understand these responses, we first tested oviposition preferences of *G. molesta* to uninfested and infested pear shoots (US and IS, respectively) and uninfested mature leaves (ML) in dual-choice bioassays using a cylindrical tube. Then, preferences to volatile components were also assessed. *G. molesta* females preferred US- and IS- and ML-treated areas compared to the control area (no leaves), respectively. Subsequently, *G. molesta* females preferred IS over US, and US more than ML in bioassays. Furthermore, *G. molesta* females did not show any significant preference for individual volatile components, but more eggs were laid in an area treated with a synthetic pear HIPV blend, compared to the hexane-treated area (control). These results indicate that *G. molesta* females do not avoid infested pear shoots nor HIPVs. Moreover, HIPVs may recruit not only natural enemies, but also *G. molesta* females to the release point of HIPVs. Thus, it is important to examine responses of *G. molesta* females to HIPVs in the field before employing them for pest management.

Keywords *Grapholita molesta* · Oviposition preference · Pear shoots · Individual components · HIPVs

Introduction
Insects have sensitive olfactory systems that enable them to detect volatile chemicals carrying various types of information, and appropriate responses to that information help them to survive in complex environments. For instance, herbivorous insects use host plant volatiles to locate suitable habitats for feeding or oviposition (Schoonhoven et al. 2005). Subsequent herbivory may alter plant metabolic pathways, inducing modifications to foliar volatile composition (Dicke and Hilker 2003; Schoonhoven et al. 2005). Herbivore-induced plant volatiles (HIPVs) are regarded as an indirect defense strategy of plants. They mediate multiple-trophic interactions, such as repelling herbivores or attracting their natural enemies (Dicke et al. 1990; Mumm and Dicke 2010).

For herbivores, release of HIPVs not only indicates the presence of conspecific competitors, which may reduce the quantity and/or quality of the host plant, but also implies a higher risk of encountering natural enemies. Thus, avoiding HIPVs can benefit herbivores with adequate food and/or safer habitats, increasing their fitness. de Moraes et al. (2001) found that the tobacco budworm, *Heliothis virescens* (Lepidoptera: Noctuidae), tends to oviposit on uninfested tobacco plants (*Nicotiana tabacum*) compared to tobacco plants infested by conspecific larvae. This is strong evidence that female moths recognize HIPVs, enabling them to oviposit in uninfested areas where their progeny may have greater fitness. Nevertheless, some herbivores show positive responses to HIPVs, which conflicts with previous observations and may be related to the infestation level and the concentration of HIPVs (Yoneya and Miki 2015; Giacomuzzi et al., 2016, 2017; El-Sayed et al. 2016, 2018). El-Sayed et al. (2016) found that the light brown apple moth, *Epiphyas*
postvittana (Lepidoptera: Tortricidae), prefers apple seedlings infested by conspecific larvae. In a subsequent study, both male and female E. postvittana were attracted by a synthetic blend (phenylacetonitrile: acetic acid = 100:3) suggesting the potential to employ HIPVs for trapping E. postvittana females in orchards (El-Sayed et al. 2019). These results suggest that HIPVs may affect behavioral responses of herbivores in different ways, which would be important for pest management.

The oriental fruit moth, Grapholita molesta (Lepidoptera: Tortricidae), is a widely distributed invasive pest that is assumed to be native to Asia (Rothschild and Vickers 1991; Kirk et al. 2013). This obligatory herbivore attacks fruit trees belonging to the family Rosaceae such as pear, peach, and apple trees, and causes economical losses in invaded areas (Rings 1970). The eggs of G. molesta are usually found on the under-surface of leaves near new shoots, and newly hatched neonates excavate tunnels and feed inside the host plant (CABI 2022). This feeding habit protects G. molesta larvae from natural enemies and pesticides. For practical treatments, farmers apply insecticides and sex pheromones to suppress field populations of G. molesta (Trimble et al. 2001; Pastori et al. 2012). Unfortunately, the efficacy of insecticides may be lower than expected because of the feeding habits of G. molesta larvae and the rapid development of insecticide resistance (de Lame et al. 2001; Kang et al. 2003; Navarro-Roldán et al. 2017). On the other hand, a high density of G. molesta may lower the efficacy of mating disruption using sex pheromone against G. molesta, suggesting that other approaches are necessary (Allen and Yetter 1949; Allen 1962). For example, HIPVs are potential attractants to keep natural enemies in the field and to enhance efficacy of biological control (Mills and Heimpel 2018).

In a previous study, G. molesta larvae induced the release of HIPVs from pear trees, and its parasitoid, Lytoptylus rufipes Nees (Hymenoptera: Braconidae), responded positively to these HIPVs (as a volatile bouquet) (Liu et al. 2019). However, responses of G. molesta females to pear HIPVs (attractive, neutral, or deterrent) could affect dynamics of colonies in the field, so it is necessary to clarify behavioral responses of G. molesta females to pear HIPVs. In this study, we conducted dual-choice bioassays with different pear tissues to evaluate oviposition preferences of gravid G. molesta, and documented effects of pear HIPVs on G. molesta.

Materials and methods

Insect colonies and rearing procedures

A G. molesta colony was obtained from the Nagano Fruit Tree Experiment Station in 2015. The rearing procedure was described by Liu et al. (2019). A transparent plastic container (I.D. 15 cm, height 8 cm, a container hereafter) with a lid was used for rearing G. molesta. An egg sheet (ca. 200 eggs) was put in a container with a block of artificial diet (100 g, Silkmate 2 M, Nosan, Yokohama, Japan). In addition, a corrugated cardboard strip (ca. 3 cm x 47 cm) was attached to the wall in the same container as a shelter for pupation at the same time. Pupae were sexed and kept in separate containers, and newly emerged adults (male: female = 60:30) were transferred to another container with a water dispenser. The inner wall of a container was lined with wax paper for egg collection. Rearing conditions were maintained at 25 ± 1 °C and 60 ± 10% RH, with a photoperiod of 16L:8D.

Plant materials

Potted pear trees (Pyrus pyrifolia variety Kosui, 8 years old) were obtained from the Laboratory of Pomology and Post-harvest Physiology of Fruit (University of Tsukuba). To prevent accidental infestation, pear shoots (including the tip and 2 immature leaves) and mature leaves were covered with fine mesh bags until the experiment. Newly hatched (within 24 h) neonates of G. molesta were placed near axils (5 neonates/shoot) for infestation 24 h before experiments. Uninfested shoots (US), infested shoots (IS), and mature leaves (ML) were kept on the pear tree and harvested 15 min prior to experiments.

Daily fecundity and oviposition time of G. molesta

To determine conditions for oviposition preference in G. molesta females, we observed oviposition time and daily fecundity. Newly emerged adults (male: female = 20:10) were placed in a container (size and conditions are described above) and allowed to mate. Successful mating was checked in the evening, and mated females were then placed in separate containers and provided with wet cotton. When we estimated daily fecundity, each moth was transferred to a new container and the number of eggs in the old container was recorded (n = 17). The number of eggs laid on the wall and cover of the container were recorded every hour from 17:00 until 06:00 the next day (n = 53). During the scotophase, red light bulbs (40 W, 10–20 lx) were used for observations. Individual differences in egg production (number and pre-oviposition period) were observed in preliminary experiments.

Oviposition preference of G. molesta on pear tissues

To examine whether volatiles released from different host plant parts affect oviposition preferences of female oriental fruit moths, dual-choice bioassays among control, US, IS,
and ML were conducted. This bioassay was modified from the method described by Piyasaengthong et al. (2016). According to preliminary observations of oviposition behaviors, mated female moths showed stable egg production (in number) on the 3rd day after mating, if they laid 1–10 eggs on the first day after mating. Therefore, mated females were prepared as described above and moths that laid 1–10 eggs on the first day after mating were used in bioassays on the 3rd day. An acrylic cylinder (I.D. 9.6 cm, length 32 cm, a cylindrical container hereafter) was used as an area for oviposition bioassays (Fig. 1). Wax paper was attached to the inner surface of the cylindrical container before an experiment. Quarter lines and centerlines were labeled to identify locations of samples (on quarter lines) and the release point (on the centerline). Plant samples were harvested and weighed, and then soaked in water with wet cotton for ca. 15 min immediately prior to experiments. Pear shoots were harvested from the tip of a branch, and ML were harvested at least 30 cm from the tip. The cut surface was covered with wet cotton to prevent desiccation during the experiment and then wrapped with aluminum foil. Samples were covered with a white mesh (double layer) to prevent possible effects of visual or tactile stimulation and then hung at the 1st and 3rd quarter positions in the cylindrical container to give a 16-cm distance to each sample. Wet cotton covered with aluminum foil was used as a blank (control). Ten mated females were anesthetized with CO\textsubscript{2} and placed at the center of the cylindrical container. Wet cotton as a water source was placed in a plastic cup (I.D. 2.5 cm, height 1.2 cm) at the center of the cylindrical container. Each opening of the cylindrical container was covered with a piece of mesh to prevent the escape of moths during experiments. Experiments were set up at 18:00 and finished at 06:00 on the next day. After every experiment, the wax paper was collected and the number of eggs on the wax paper was counted. Bioassays were conducted in an air-controlled room at $25 \pm 1$ °C and 60 ± 10% RH.

**Collection of headspace volatiles from mature leaves of pear**

Headspace volatiles were collected following the method described in Liu et al. (2019). Twelve mature leaves were harvested, and the cut edge was soaked in water in a beaker for ca. 15 min immediately prior to volatile collection. The beaker was covered with aluminum foil and placed in a 2-L cylindrical separable flask (i.d. 120 mm, o.d. 130 mm, height 230 mm; AS ONE Corporation, Osaka, Japan) with a cover having two necks. Air aspirated by a pump was filtered with activated charcoal into the chamber, and headspace volatiles were adsorbed with a column of HayeSep Q adsorbent (ca. 100 mg, 60–80 mesh, Restek Corporation, USA). Headspace volatiles were collected for 2 h from 1300 to 1500 at $25 \pm 1$ °C and 60 ± 10% RH under fluorescent lights (ca. 2950 lx) and the airflow was maintained at 1 L·min\textsuperscript{-1} by adjusting the valve of the flowmeter. Collected volatiles were eluted with 1 mL hexane, and extracts were kept at −20 °C in a freezer until chemical analysis.

![Fig. 1](image-url) A bioassay setup with a cylindrical container for *Grapholita molesta* oviposition; B plant samples used in the assays
Oviposition response to pear HIPVs

To investigate the effects of pear HIPVs on oviposition preferences of *G. molesta*, volatile components of pear HIPVs were applied as odor sources instead of plant tissues in bioassays. Pear HIPVs, including (Z)-3-hexenyl acetate (H), (E)-β-ocimene (O), linalool (L), (E,4,8-dimethyl-1,3,7-nonatriene (DMNT, D), and (E,E)-α-farnesene (F), were identified by Liu et al. (2019). Authentic chemicals H and L were obtained from Tokyo Chemical Industry Co., Ltd., O (purity > 97%, (E)-isomer > 98%) was synthesized following the method described in Yildizhan and Schulz (2011), D (purity > 99%, (E)-isomer > 98%) was synthesized followed the method described in Leopold (1986) with a slight modification, and F (purity > 98%) was extracted from apple peels and purified. The volatile mixture (VM, Table S1) of pear HIPVs was formulated based on the HLODF mixture in Liu et al. (2019) with a 6-h quantity (72-times higher dose). A Teflon disk was separated from a Teflon/silicon septum (diameter 1.2 cm, TS-12712, GL Sciences Inc., Tokyo, Japan) and used as a volatile carrier. Chemicals (as hexane solutions, 10 μL) and solvent controls (hexane, 10 μL) were loaded onto Teflon disks and allowed to evaporate prior to experiments.

Statistical analysis

All data were analyzed using the software package R v.3.4.0 (R Core Team, 2017) for statistical analyses. The number of eggs laid in each area was compared using Wilcoxon matched-pairs signed-ranks test. The total number of eggs laid in each treatment in plant- or chemical-treated bioassays was compared using the Kruskal–Wallis test followed by pairwise comparisons using the Wilcoxon rank sum test with Bonferroni correction.

Results

The oviposition peak and the period of *G. molesta*

Female *G. molesta* were isolated after mating and the number of eggs was recorded every day. Most mated females started to oviposit 1 day after mating, and the number of eggs was 7.5 ± 2.0 eggs/day (mean ± SE). The largest number of eggs/day was 11.4 ± 3.0, 3 days after mating, and then steadily decreased thereafter (Fig. S1). A decline in oviposition behavior could have caused a bias in the bioassays, so female moths were used in bioassays within 3 days after mating. *G. molesta* females started laying eggs from 17:00, but the number was relatively low. Female moths tended to lay eggs from 1 h before scotophase, and the highest number was observed from 22:00 to 23:00 (Fig. S2). After 00:00, moths stopped moving until the end of observations.

Oviposition preference of *G. molesta* for pear leaves under different conditions

Pear leaves in different conditions (US, IS, and ML) were prepared as odor sources for dual-choice bioassays to determine when gravid *G. molesta* showed any preference among pear volatiles. Female moths preferred to lay eggs on any type of pear leaf (treatment) area compared to control areas (blank). They laid 53.3 ± 3.7 (mean ± SE) eggs in US areas vs. 24.8 ± 2.2 eggs in control areas (Z = −2.80, P = 0.002, Fig. 2, I), 51.8 ± 2.6 eggs in IS areas vs. 18.6 ± 2.8 eggs in control areas (Z = −2.80, P = 0.002, Fig. 2, II), and 16.2 ± 4.4 eggs in ML areas vs. 17.0 ± 3.1 eggs in control areas (Z = −0.77, P = 0.484, Fig. 2, III). Furthermore, when evaluating oviposition preference between areas containing different types of pear leaves, female moths laid 78.2 ± 7.7 eggs in US areas vs. 39.4 ± 5.2 eggs in ML areas (Z = −2.80, P = 0.002, Fig. 2, IV), and 36.9 ± 4.4 eggs were laid in IS areas vs. 22.0 ± 3.0 eggs at US areas (Z = −2.64, P = 0.006, Fig. 2, V). Female moths laid the most eggs in bioassay IV (mean ± SE = 117.6 ± 10.9), followed by bioassays I, II, and V (mean ± SE = 78.1 ± 4.0, 70.4 ± 4.0, and 58.9 ± 6.0, respectively), and the least number of eggs was observed in bioassay III (mean ± SE = 27.3 ± 5.1) (χ² = 33.97, df = 4, P < 0.001).

![Fig. 2 Oviposition preferences of *Grapholita molesta* to pear leaves in dual-choice bioassays (n=10 in I, II, III, and IV; n=16 in V). Bars represent the number of eggs laid in each treated area (open square—blank, gray shaded square—US: uninfested shoots, IS: infested shoots, IS: mature leaves). Error bars represent ± SEM and asterisks indicate significance in Wilcoxon matched-pairs signed-ranks test (P<0.05) and “ns” means not significantly different (P≥0.05)](image-url)
Oviposition response to HIPVs released from pear shoots

To investigate the effect of HIPVs released from larva-infested pear shoots on oviposition of female moths, comparisons were conducted between pear HIPVs (5 volatile components and a quinary blend) versus a solvent control. When comparing volatile components with the solvent control, mated females did not show a significant preference in bioassays ($P > 0.4637$, Fig. 3, H, O, L, F, and D). In contrast, female moths preferred to lay eggs in the HIPV-treated area (mean $\pm$ SE = 99.6 $\pm$ 8.3) compared to the control area (41.8 $\pm$ 6.1) ($Z = -3.41$, $P < 0.001$, Fig. 3, VM). Considering the quantitative effects on oviposition preference, $10 \times$-diluted VM (VM $10 \times$ dil.) was also tested. Female moths laid more eggs in the HIPV-treated area (41.6 $\pm$ 4.0) compared to the control area (28.2 $\pm$ 3.7) ($Z = -2.56$, $P < 0.008$, Fig. 3, VM10d). Moreover, the total number of eggs laid in the bioassay between HIPVs and solvent (141.4 $\pm$ 12.1) was significantly higher than in the other bioassays ($\chi^2 = 33.91$, df = 6, $P < 0.001$, Fig. 3).

Discussion

We hypothesized that plant volatile profiles could affect the oviposition preference of *G. molesta* females when they find a suitable habitat for their offspring. To investigate this hypothesis, we conducted dual-choice bioassays in cylindrical tubes with pear leaves, and the results show a clear preference for pear shoots, but not for mature leaves (ML).

Moreover, *G. molesta* females laid more eggs in the infested shoot (IS)-treated area than in the uninfested shoot (US)-treated area. Subsequently, the effect of a synthetic volatile mixture from pear shoot volatiles and of each component of the VM on *G. molesta* oviposition preference was evaluated. Females showed a significant preference for the VM and $10 \times$-diluted VM, but not for individual components. These results indicate that the volatile bouquet may be important in host selection by *G. molesta*. Furthermore, *G. molesta* females laid more eggs when exposed to the volatile mixture than to individual components and to diluted VM, implying that the concentration of pear HIPVs may affect the egg deposition.

(Z)-3-Hexenyl acetate is a constitutive volatile component of plants in the family Rosaceae, which may be recognized by herbivores as an indicator of suitable habitat (Il’ichev et al. 2009; Najar-Rodriquez et al. 2013; Lu and Qiao 2020). Recently, Chen et al. (2019) found a general odorant receptor, GmolOR9, of *G. molesta*, which may be related to detection of host plant volatiles. Injection of double-stranded RNA for GmolOR9 decreased electroantennogram responses to (Z)-3-hexenyl acetate of *G. molesta* females, but this phenomenon was not observed in males. These results imply that perception of (Z)-3-hexenyl acetate is more important for females than males of *G. molesta*. Nevertheless, our results do not support direct causality between perception of (Z)-3-hexenyl acetate and oviposition preference. The entire volatile bouquet of host plant may be necessary for *G. molesta* females when searching for suitable habitat for their progeny.

Volatile emissions of plants may relate to their susceptibility to detection by herbivores, which was defined as “apparency” by Feeny (1976), and a higher apparency usually indicates a habitat with abundant available food for herbivores. Some herbivores use HIPVs as a “lighthouse” to discover the right habitat, because uninfested plants usually have lower volatile emission rates (Liu et al. 2019). Yoneya and Miki (2015) developed a model to predict evolutionarily stable strategies of natural enemies and herbivores, which are driven by resistance levels induced by herbivory. Briefly, when a plant has a low direct resistance to herbivory, herbivores tend to accept HIPVs released from lightly infested plants, as well as natural enemies, because of the higher apparency. Nevertheless, successful colonization by herbivores upgrades the infestation level, which further decreases the plant quality and increases the predation risk, so herbivores might ultimately avoid HIPVs released from highly infested plants (Landolt 1993; Halitschke et al. 2008). In the first experiment, female moths laid the fewest eggs in the ML-blank bioassay, and the number of eggs laid in the IS-treated area was more than the US-treated area, which in turn was more than the ML-treated area. These behavioral responses to pear leaves are highly related to the quantity of
pear leaf volatiles, as the quantity of volatiles released from IS was higher than US, followed by ML (Table S2). In addition, results in subsequent bioassays with VM and diluted VM provide strong evidence for quantity effects and support the apparency hypothesis of Yoneya and Miki (2015).

Recognizing and responding appropriately to plant volatiles is essential for herbivores, especially when exploring suitable habitats for oviposition (Vallat and Dorn 2005; Najar-Rodriguez et al. 2013). Positive responses of herbivores to HIPVs suggest a complex relationship that HIPVs not only indicate predation risk, but also help herbivores to evaluate the quality or quantity of food. The final response, whether positive or negative, is an integrated assessment of predation risk and food supply (Yoneya and Miki 2015; Giacomuzzi et al. 2016, 2017; El-Sayed et al. 2016, 2018). For instance, higher emission of HIPVs may indicate a higher infestation level with higher direct and/or indirect defenses (resistance); therefore, herbivores tend to avoid highly infested plants (Bernasconi et al. 1998; de Moraes et al. 2001; Yoneya and Miki 2015). However, the resistance level may not be upgraded after colonization of G. molest. When a G. molest larva feeds on a primary shoot of a pear branch, lateral shoots develop shortly after the infestation. After frequent infestations, a series of such pear tree responses may result in a bushy morphology, which increases the quantity of food. Consequently, an infestation may create a habitat with extremely high resource density; therefore, the pear tree can support more G. molest larvae. On the other hand, the bushy pear may also disrupt host location by natural enemies, since it provides shelter for G. molest larvae, and the increased population would reduce the individual parasitism risk (Rusch et al. 2015). Thus, laying eggs on pear trees that are infested by conspecific larvae may benefit G. molest with more abundant food and mitigated predatory/parasitism risk.

In summary, this study demonstrates that pear HIPVs not only attract L. rufipes, but also G. molest females for oviposition. This phenomenon makes interactions more complex in apple, pear, peach, and apricot orchards, and raises more questions that are worth answering, such as (1) whether seasonal changes affect the perception of volatile components or mixtures by G. molest females, (2) whether fitness of G. molest differs when breeding in habitats with or without infested shoots, and (3) whether application of supplementary pear HIPVs affects G. molest and L. rufipes. Answering these questions may aid development of novel pest management strategies in orchards to reduce insecticide use.

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Author contributions CML, SM, and YK conceived the study. SM carried out chemical analyses and synthesis. CML designed the bioassay and carried out chemical and statistical analyses. CML and SP carried out bioassays. CML drafted the manuscript with assistance from SM and YK, and WA provided technical suggestions. All authors edited the manuscript and approved the final version.

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References
Allen HW, Yetter WP (1949) Bassus diversus, an oriental fruit moth parasite established in the United States. J Econ Entomol 42:540. https://doi.org/10.1093/jeet/42.3.540
Allen BW (1962) Parasites of the oriental fruit moth in the eastern United States. USDA Tech Bull No. 1265
Bernasconi ML, Turlings TCJ, Ambrosetti L, Bassetti P, Dorn S (1998) Herbivore-induced emissions of maize volatiles repel the corn leaf aphid, Rhopalosiphum maidis. Entomol Exp Appl 87:133–142. https://doi.org/10.1046/j.1570-7458.1998.00315.x
CABI (2022), current year. Grapholita molesta. In: Invasive Species Compendium. Wallingford, UK: CABI International. www.cabi.org/isc/datasheet/29904. Accessed 5 Aug 2022
Chen LH, Tian K, Wang GR, Xu XL, He KH, Liu W, Wu JX (2019) The general odorant receptor GmolOR9 from Grapholita molesta (Lepidoptera: Tortricidae) is mainly tuned to eight host-plant volatiles. Insect Sci 27:1233–1243. https://doi.org/10.1111/1744-7917.12725
Collatz J, Dorn S (2013) Tritrophic consequences arising from a host shift between apple and walnut in an oligophagous herbivore. Bio Control 65:330–337. https://doi.org/10.1016/j.biocontrol.2013.03.011
De Lame FM, Hong J, Shearer PW, Brattsten LB (2001) Sex-related differences in the tolerance of Oriental fruit moth (Grapholita molesta) to organophosphate insecticides. Pest Manag Sci 57:827–832. https://doi.org/10.1002/ps.368
De Moraes CM, Mescher MC, Tumlinson JH (2001) Caterpillar-induced nocturnal plant volatiles repel conspecific females. Nature 410:577–580. https://doi.org/10.1038/35069058
Dicke M, Hilker M (2003) Induced plant defences: from molecular biology to evolutionary ecology. Basic Appl Ecol 4:3–14. https://doi.org/10.1016/S1437-1919-00129
Dicke M, Van Beek TA, Posthumus MA, Ben Don N, Van Bokhoven H, De Groot A (1999) Isolation and identification of volatile kairomone that affects acarine predator–prey interactions involvement of host plant in its production. J Chem Ecol 16:381–396. https://doi.org/10.1017/S002358129900063
El-Sayed AM, Knight AL, Byers JA, Judd GJR, Suckling DM (2016) Caterpillar-induced plant volatiles attract conspecific adults in nature. Sci Rep 6:37555. https://doi.org/10.1038/srep37555
El-Sayed AM, Knight AL, Basoalto E, Suckling DM (2018) Caterpillar-induced plant volatiles attract conspecific herbivores and a generalist predator. J Appl Entomol 142:495–503. https://doi.org/10.1111/jen.12495
Oviposition preferences of the oriental fruit moth *Grapholita molesta* (Lepidoptera:…

El-Sayed AM, Sporle A, Gemenos C, Jósval JK, Simoons GS, Sukling DM (2019) Leafroller-induced phenylacetonitrile and acetic acid attract adult *Lobesia botrana*in European vineyards. J Biosci 74:161–165. https://doi.org/10.1151/jzsc-2018-01163

Feeny P (1976) Plant apparency and chemical defense. In: Wallace JW, Mansell RL (eds) Biochemical interaction between plants and insects. Springer, New York, pp 1–40. https://doi.org/10.1007/978-1-4684-2646-5_1

Giacomuzzi V, Cappellin L, Khomenko I, Biasioli F, Schütz S, Tasin M, Knight AL, Angeli S (2016) Emission of volatile compounds from apple plants infested with *Pandemis heparana* larvae, antenunal response of conspecific adults, and preliminary field trial. J Chem Ecol 42:1265–1280. https://doi.org/10.1007/s10886-016-0794-8

Giacomuzzi V, Matthias J, Basoalto E, Knight AL (2017) Survey of conspecific herbivore-induced volatiles from apple as possible attractants for *Pandemis pyrusana* (Lepidoptera: Tortricidae). Pest Manag Sci 73:1837–1845. https://doi.org/10.1002/ps.4548

Halitschke R, Stenberg JA, Kessler D, Kessler A, Baldwin T (2008) Shared signals ‘alarm calls’ from plant increase apparency to herbivores and their enemies in nature. Ecol Lett 11:24–34. https://doi.org/10.1111/j.1461-0248.2007.01123.x

Il’ichev AL, Kugimiya S, Williams DG, Takabayashi J (2009) Volatile compounds from young peach shoots attract males of oriental fruit moth. J Plant Interact 4:289–294. https://doi.org/10.1080/1472-6785.2009.978-1-4684-2646-5_1

Kanga LHB, Pree DJ, van Lier JL, Walker GM (2003) Management of insecticide resistance in oriental fruit moth (*Grapholita molesta*; Lepidoptera: Tortricidae) populations from Ontario. Pest Manag Sci 59:921–927. https://doi.org/10.1002/ps.702

Kirk H, Dorn S, Mazzi D (2013) Worldwide population genetic structure of the oriental fruit moth (*Grapholita molesta*), a globally invasive pest. BMC Ecol 13:12. https://doi.org/10.1186/1472-6785-13-12

Kurokura T, Mimida N, Battey NH, Hytönen T (2013) The regulation of seasonal flowering in the Rosaceae. J Exp Bot 64:4131–4141. https://doi.org/10.1093/jxb/ert123

Kurokura T, Mimida N, Battey NH, Hytönen T (2013) The regulation of seasonal flowering in the Rosaceae. J Exp Bot 64:4131–4141. https://doi.org/10.1093/jxb/ert123

Landolt PJ (1993) Effects of host plant leaf damage on cabbage looper moth attraction and oviposition. Entomol Exp Appl 67:79–85

Leopold EJ (1986) Selective hydroboration of a 1,3,7-triene: homogeraniol. Org Synth 64:164–164. https://doi.org/10.1002/0471264180.os064.25

Liu CM, Matsuyama S, Kainoh Y (2019) Synergistic effects of volatiles from host-infested plants on host-searching behavior in the parasitoid wasp *Lygus rugulipenis* (Hymenoptera: Braconidae). J Chem Ecol 45:684–692. https://doi.org/10.1007/s10886-019-01088-y

Lu P, Qiao H (2020) Peach volatile emission and attractiveness of different host plant volatiles blends to *Cydia molesta* in adjacent peach and pear orchards. Sci Rep 10:13658. https://doi.org/10.1038/s41598-020-70685-9

Mills NJ, Heimpel GE (2018) Could increased understanding of foraging behavior help to predict the success of biological control? Curr Opin Insect Sci 27:26–31. https://doi.org/10.1016/j.cois.2018.02.013

Mumm R, Dicke M (2010) Variation in natural plant products and the attraction of 360 bodyguards involved in indirect plant defense. Can J Zool 88:628–667

Najar-Rodriguez A, Orschel B, Dorn S (2013) Season-long volatile emissions from peach and pear trees in situ, overlapping profiles, and olfactory attraction of an oligophagous fruit moth in the laboratory. J Chem Ecol 39:418–429

Navarro-Roldán MA, Avilla J, Bosch D, Valls J, Gemenos C (2017) Comparative effect of three neurotoxic insecticides with different modes of action on adult males and females of three tortricid moth pests. J Econ Entomol 110:1740–1749. https://doi.org/10.1093/jee/tox113

Pastori PL, Arioli CJ, Botton M, Monteiro LB, Stoltman L, Mafra-Neto A (2012) Integrated control of two tortricids (Lepidoptera) pests in apple orchards with sex pheromones and insecticides. Rev Colomb Entomol 38:224–230

Piyasaengthong N, Sato Y, Kinosita N, Kainoh Y (2016) Oviposition preference for leaf age in the smaller tea tortrix *Adoxophyes honnai* (Lepidoptera: Tortricidae) as related to performance of neonates. Appl Entomol Zool 51:363–371

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Rings RW (1970) Economic aspects of the biology and control of the Oriental Fruit moth, *Grapholitha molesta* Busck, in the United States. Ohio J Sci 70:58–61

Rothschild GHL, Vickers RA (1991) Biology, ecology and control of the oriental fruit moth. In: van der Geest LPS, Evenhuis HH (eds) Tortricid pests: their biology, natural enemies, and control. Elsevier Science Publishers, Amsterdam, pp 389–412

Rusch A, Delbac L, Muneret L, Thiéry D (2015) Organic farming and host density affect parasitism rates of tortricid moths in vineyards. Agric Ecosyst Environ 214:46–53

Schoonhoven LM, van Loon JJA, Dicke M (2005) Insect-plant biology, 2nd edn. Oxford University Press, Oxford

Trimble RM, Pree DJ, Carter NJ (2001) Integrated control of oriental fruit moth (Lepidoptera: Tortricidae) populations from Ontario. Pest Manag Sci 59:921–927. https://doi.org/10.1002/ps.702

Vallat A, Dorn S (2005) Changes in volatile emissions from apple trees and associated response of adult female codling moths over the fruit-growing season. J Agric Food Chem 53:4083–4090. https://doi.org/10.1021/jf048499u

Yildizhan S, Schulz S (2011) Easy access to (E)-β-ocimene. Synlett 2011:2831–2833. https://doi.org/10.1055/s-0031-12898

Yoneya K, Miki T (2015) Co-evolution of foraging behaviour in her -bivores and their enemies predicts multifunctionality of herbivore-induced plant volatiles. Funct Ecol 29:451–461

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