Citation for the published paper:
Dahlin, Iris., Vucetic, Anja., Ninkovic, Velemir. (2015) Changed host plant volatile emissions induced by chemical interaction between unattacked plants reduce aphid plant acceptance with intermorph variation. *Journal of Pest Science*. Volume: 88, Number: 2, pp 249-257.
http://dx.doi.org/10.1007/s10340-014-0625-z.

Changed host plant volatile emissions induced by chemical interaction between unattacked plants reduce aphid plant acceptance with intermorph variation

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Abstract

Olfactory orientation by aphids is guided by specific volatile blends released from their hosts. Host plants that co-exist with other plants may be less attractive for aphids due to volatile interactions between neighboring plants which can lead to changes in their volatile emissions. These changes in host plant volatile profiles induced by interactions between undamaged plants could be used to manage aphid populations in crops. When potato plants are exposed to volatiles from onion plants, the volatile profile of potato changes in relation to that of unexposed plants with consistently greater quantities of two terpenoids released. We examined the host plant searching behavior of aphids and showed that induced changes in plant volatile emissions affect aphid behavior. We assessed olfactory responses of winged and wingless aphids, *Myzus persicae* Sulzer (Hemiptera: Aphididae) to the changed volatile emissions. Both morphs were significantly less attracted to odors of potato plants that had been exposed to volatiles from onion than to odors of unexposed potato plants. Further, both morphs were significantly less attracted to synthetic blends mimicking volatiles emitted by onion-exposed potato plants than to blends mimicking non-exposed controls, and to single compounds emitted in greater quantities by exposed potato. Aphid morphs were repelled differently depending on the concentration of odor sources; winged aphids responded to higher doses than did wingless aphids. The aphid responses to changes in plant volatile profiles induced by neighboring plants may facilitate refinement of habitat manipulation strategies (e.g. intercropping) for integrated pest management to reduce aphid occurrence in crops.

Keywords

Alatae, apterae, *Myzus persicae*, olfactory response, plant interaction, volatile chemicals

Key Message

- Polyphagous aphids use plant odors in their host plant detection.
- Co-existence with other plant species may change volatile emission of aphid host plants.
- Green peach aphids are less attracted to hosts with changed volatile profiles.
- Winged and wingless aphids respond differently to those changes.
- Winged aphid responded to higher concentration of odour sources than wingless morphs.
- Habitat manipulation strategies within crop field (e.g. intercropping) can be developed to disrupt aphid orientation and prevent their establishment as a pest.

Author Contribution Statement

VN conceived and designed the experiments. ID and AV performed the experiments. VN analyzed the data. ID, VN and AV wrote the manuscript. All authors read and approved the manuscript.

Introduction

The green peach aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae), is a polyphagous aphid pest with high ecological and agronomical importance worldwide, mainly because it is a vector of viruses of many crops including potato (Solanaceae: *Solanum tuberosum* L.). *Myzus persicae* has developed resistance to at least 70 synthetic compounds and various insecticide resistance mechanisms have been reported worldwide (Silva et al. 2012). So far, there is no alternative to insecticides to control populations of these insects, thus alternative strategies are highly sought after. By understanding how aphids locate their host plants, it may become possible to develop alternatives of controlling populations by taking advantage of functional cues in their host location behavior. As an extremely polyphagous aphid it was previously considered that *M. persicae* does not use olfactory cues from plants in its searching behavior (Hori 1999; Vargas et al. 2005). However, in the last decade it has been shown that *M. persicae* may respond to plant volatiles released from healthy and damaged plants (Eigenbrode 2002; Ngumbi et al. 2007; Alvares et al. 2007; Boquel et al. 2011; Verheggen et al. 2013; Rajabaskar et al. 2013a; Ninkovic et al. 2013). Thus, its olfactory responses to volatile signals may be an important target for disrupting its host searching behavior.

Plants release a variety of different volatile compounds providing herbivore insects with information that allows them to discriminate between host and non-host plants. As well as using volatiles to determine taxonomic identity, aphids can also use plant volatiles to discriminate between the suitability of different plants within the same species (Webster 2012). The emission of volatiles from plants is significantly changed in plants under stress caused by abiotic factors (Gouinguene and Turlings 2002), mechanical damage (Piesik et al. 2010), pathogens (Rajabaskar et al. 2013b), herbivory (Arimura et al. 2009) or co-existence with other con- and heterospecific plants (Ninkovic et al. 2002; Ninkovic 2003; Le Guigo et al. 2010; Glinwood et al. 2011) than in unstressed plants. These changes in their volatile profiles can play important roles in aphid behavior and host plant search. Recently, Ninkovic et al. (2013) found that winged *M. persicae* prefer the odor of unexposed potato plants to the odor of potato plants previously exposed to onion plants. The exposure resulted in greater production of two terpenoids, (*E*)-nerolidol and (3*E*, 7E) - 4, 8, 12-trimethyl-1, 3, 7, 11-tridecatetraene (TMTT), both of which are involved in indirect defenses of plants against herbivorous insects (Degenhardt and Gershenzon 2000; Pophof et al. 2005; Arimura et al. 2009). The changes in volatile emissions of host plants induced by the exposure to volatiles from neighboring plants reduced plant acceptance of winged aphids. Further this can be one of explanations for the reduced abundance of winged *M. persicae* observed in the field where potatoes were intercropped with onion (Ninkovic et al. 2013).

Many aphid species have several distinct morphs during their life cycle, which may specialize on different ranges of host plants and have differing behavioral responses to these plants (Powell and Hardie 2001). Numerous studies have confirmed that volatiles strongly influence the searching behavior of aphids (Beyaert et al. 2010; Webster 2012), but most have focused on only one morph, thus there is little information on between-morph differences in responses to volatiles. The behavior and ecological functions of winged and wingless aphids differ because of their morphological divergence. Aphids perceive plant odors with olfactory sensilla (rhinaria) on their antennae. Secondary rhinaria are much more abundant in winged aphids than in wingless insects, suggesting that these structures might be involved in host location and mate selection (Blackman and Eastop 2000; Sun et al. 2012). Given that winged virginoparae are mostly responsible for finding and colonizing new secondary hosts (Klingauf

1987; Blackman 1990), we hypothesize that winged morphs will show different behavioral responses to plant volatiles than wingless morphs.

The aim of the study presented here was to investigate whether winged and wingless *M. persicae* respond differently to changes in volatile emissions of their hosts. Through their higher mobility, winged aphids have the ability for the establishment of new colonies, while wingless aphids have greater impact in their population development due to their higher reproduction rate (Dixon 1985). If both respond negatively, changes in volatile emissions of plants would be an effective target in pest control. We studied aphid olfactory responses to volatile interactions of onion and potato plants in laboratory experiments using living plants, synthetic blends of plant volatiles and single volatile compounds. The synthetic blends were designed to emulate natural odors from host plants with and without modification by exposure to volatiles from neighboring onion plants.

Materials and Methods

Plants and insects

We obtained potato tubers (Solanaceae: *Solanum tuberosum*, L.cv. Sava) from Lantmännen, Sweden, and onion bulbs (Amaryllidaceae: *Allium cepa*, L.cv. Stuttgarter Riesen) from Weibulls Horto, Sweden. We placed them individually in potting soil (Special Hasselfors garden, Hasselfors, Sweden) in plastic pots (8 x 8 x 8 cm) and grew plants in a greenhouse maintained at 18-22°C with 16 h:8 h light:dark cycles, using HQIE lamps to extend the natural photoperiod as required. To prevent interaction among plants during the pre-experimental period, onion and potato plants were grown in separate greenhouse chambers, and to avoid emissions of mechanically damage-related volatiles, only visibly undamaged plants (aged three weeks) were used in the experiments.

Adult winged and wingless individuals of *M. persicae* derived from a stock culture were grown on potted rapeseed plants (Brassicaceae: *Brassica napus* L.) under similar conditions to the test plants, but in different climate chambers. Production of winged aphids was induced by crowding under long-day conditions. Winged aphids after first take-off were used for behavioral experiments.

Potato plants were exposed to volatiles from onion plants in a series of ‘two-chamber cage’ experiments (Ninkovic et al. 2002), as follows. We placed a series of clear perspex cages in a greenhouse maintained at 18-22°C with 16 h:8 h dark cycles (as above). The cages were divided into two 10 x 10 x 40 cm chambers (inducing and responding) connected by a 7 cm diameter opening in the dividing wall. Air was introduced into the system through the inducing chamber with an onion plant, passed through the hole in the dividing wall into the responding chamber with a potato plant. From the responding chambers air was extracted through a tube attached to a vacuum tank and then vented outside the room by an electric fan preventing that the plants volatiles contaminate the greenhouse. The inducing chamber was left empty for the control treatment. Airflow through the system was adjusted to 1.3 l min^{-1}. Individual pots were watered using an automated drop system (DGT Volmatic) and placed in separate Petri dishes in the chambers to prevent root exudates affecting other plants. Exposure time was set to five days, based on previous studies of volatile interactions between plants (Ninkovic et al. 2013). The plants were used for olfactometer studies immediately after exposure.

Olfactory bioassays with plants

Olfactory responses of aphids were measured using a two-way airflow olfactometer consisting of two stimulus zones, arms (length 4cm) directly opposite each other connected by a neutral central zone (2.5 x 2.5 cm) separating them (Ninkovic et al. 2013). Airflow in the olfactometer was set to 180 ml/min, which established discrete air currents in the side zones. Test aphids were randomly collected from the cultures using a fine paintbrush and placed in Petri dishes with moistened filter paper to prevent dehydration. The aphids were then left in the bioassay room for at least 2 h to acclimatize prior to the experiments. A single aphid was then introduced into the central zone of the olfactometer through a hole in the top and after an adaptation period of 10 min, the position of the aphid in the arms, defined as a visit, was recorded at three minute intervals over a 30 min period. The accumulated number of visits of a single aphid in a single arm after ten recordings was regarded as one replicate. Observations of individual aphids in the central zone cannot conclusively be related to one of the arm zones and are therefore excluded from the analysis. Data were expressed as mean of individual aphid visits per olfactometer arm during observation period. To avoid pseudoreplication, each aphid was only tested once and a clean olfactometer was used for each aphid. The test was terminated if an aphid did not move for longer than 10 minutes and these individuals were not included in the analysis. The olfactometers were washed with 10% Teepol L (TEEPOL, Kent, UK) and rinsed with 80% ethanol solution and distilled water and left to air dry. If an aphid did not move for more than 10 min the test was terminated and data for these individuals were not included in the analysis. Before introducing each test insect the olfactometer was rotated 180° to avoid positional bias. The number of replicates, individual aphids tested, varied between 15 and 21 per experiment.

In tests with plants we compared the aphids' preferences for odors from: (a) a potato plant previously exposed to an onion plant versus an unexposed potato plant, (b) a combination of an unexposed potato and an onion plant versus two unexposed potato plants, (c) an unexposed potato plant versus an onion plant, (d) an unexposed potato plant versus soil with no plants, and (e) an onion plant versus soil with no plants. The two-chamber cages containing plants used as odor sources were connected directly to the arms of the olfactometer (Markovic et al. 2014). For (b), the two plants on each side of the olfactometer were in separate cages and connected to the inlet of the olfactometer by y-connectors to prevent interaction. The airflow in all olfactometer tests was set to 180 ml/min driven by a sucking pump. The pots with soil but no plants were used to account for variations in moisture levels between the chambers with and without plants.

Olfactory bioassays with chemicals

We also investigated whether winged and wingless aphids respond differently to the odors of plants and to synthetic blends mimicking volatile profiles of onion-exposed and unexposed potato plants. For the latter, we used serial dilutions of synthetic blends based on previous chemical analyses of the volatile profiles of potato plants (Ninkovic et al. 2013). The blend mimicking volatiles of onion-exposed potato plants consisted of 0.05 ng/µl (*E*)-2-hexenal; 0.04 ng/µl (*Z*)-3-hexen-1-ol; 0.48 ng/µl myrcene; 0.03 ng/µl limonene; 0.225 ng/µl linalool; 0.25 ng/µl (*Z*)- 4,8-dimethyl-1,3,7-nonatriene; 1.24 ng/µl (*E*)- 4,8-dimethyl-1,3,7-nonatriene; 0.95

ng/µl α-copaene; 0.03 ng/µl α-cedrene; 0.2 ng/µl (*E*)-caryophyllene; 0.09 ng/µl (*E*)-β-farnesene; 0.2 ng/µl (*E*)-nerolidol; 0.5 ng/µl (3*E,7E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. The blend mimicking unexposed plants consisted of 0.056 ng/µl (*E*)-2-hexenal; 0.05 ng/µl (*Z*)-3-hexen-1-ol; 0.54 ng/µl myrcene; 0.03 ng/µl limonene; 0.085 ng/µl linalool; 0.3 ng/µl (*Z*)- 4,8-dimethyl-1,3,7-nonatriene; 0.67 ng/µl (*E*)- 4,8-dimethyl-1,3,7-nonatriene; 0.7 ng/µl α-copaene; 0.03 ng/µl α-cedrene; 0.155 ng/µl (*E*)-caryophyllene; 0.1 ng/µl (*E*)-β-farnesene; 0.03 ng/µl (*E*)-nerolidol; 0.125 ng/µl (3*E,7E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene. We compared aphid olfactory responses to these synthetic blends by adding them in 10 µl micro caps to small pieces of filter paper, allowing them to evaporate for 30 s, and placing the pieces into 2.5 mm diameter glass tubes connected to holes in the sides of the olfactometer arms. Test concentrations in the olfactometer were 1/100, 1/10, 1, 10 and 100 times the reported amount of volatiles emitted from the plants during a period of 24 hours.

Since onion-exposed potatoes emit significantly more (*E*)-nerolidol and TMTT than unexposed potatoes, according to Ninkovic et al. (2013), we also investigated responses of winged and wingless aphids to these compounds, individually, at five concentrations (0.01, 0.1, 1, 10, and 100 ng μl^{-1}) in a series of dose-response olfactometer experiments with redistilled n-hexane as a control.

Statistical analyses

Wilcoxon matched pairs tests were used to compare the number of aphid visits to each olfactometer arm in the olfactory bioassays using Statistica version 10 software (StatSoft Inc., 2011), setting a significance level of $p = 0.05$.

Results

The main achievements of the study are summarized graphically in Figure 1.

Olfactory responses of the aphids to odors from plants

According to numbers of recorded visits to the olfactometer arms both winged and wingless *M. persicae* aphids significantly preferred the odor of unexposed potato plants to the odor of onion-exposed potato plants (Z = 3.57, *p* = 0.0004, n = 18 and Z = 2,012, *p* = 0.04, n = 17, respectively) (Fig. 2). The *p*-values indicate that winged *M. persicae* were more sensitive to the difference in volatile emissions from their host plant than the wingless morphs. In addition, neither winged nor wingless *M. persicae* preferred the odor of unexposed potato plants to those of associated potato and onion plants (Z = 1.85, *p* = 0.06, n = 18 and Z = 1.136, *p* = 0.3, n = 15, respectively). However, while winged *M. persicae* preferred the odor of unexposed potato plants to the odor of onion plants (Z = 3.42, *p* = 0.0006, n = 19), wingless morphs showed no preference for these options (Z = 1.704, *p* = 0.09, n = 17). Both winged and wingless morphs significantly preferred the odor of unexposed potato plants, their secondary host, to the odor of soil with no plants (Z = 3.51, *p* = 0.0005, n = 20; and Z = 2.09, *p* = 0.036, n = 20, respectively). The odor of onion plants did not repel the aphids; neither winged nor wingless *M. persicae* showed a preference between onion plants and soil with no plants (Z = 0.852, *p* = 0.4, n = 21; and Z = 0.327, *p* = 0.7, n = 18, respectively).

Olfactory responses of the aphids to plant volatiles

Winged *M. persicae* only showed statistically significant responses to the mixture of synthetic volatiles at high doses: 10 ng µl^{-1} (Z = 2.97, *p* = 0.003, n = 19) and 100 ng µl^{-1} (Z = 2.43, *p* = 0.015, n = 21) (Fig. 3a), while wingless morphs reacted only to the lowest test doses: 0.01 ng µl^{-1} (Z = 2.68, *p* = 0.007, n = 21) and 1 ng µl^{-1} (Z = 2.52, *p* = 0.01, n = 21) (Fig. 3b). However, both winged and wingless *M. persicae* showed a clear ability to discriminate between the synthetic blends of onion-exposed and unexposed potato plants.

As shown in Fig. 4, winged morphs visited the olfactometer arm containing the highest doses of (*E*)-nerolidol significantly less than the control: 100 ng µl^{-1} (Z = 2.56, *p* = 0.01, n = 17) and 10 ng µl-1 (Z = 2.46, *p* = 0.01, n = 18), while wingless morphs showed this preferential response to four of five used concentrations: 100 ng µl^{-1} (Z = 2.72, *p* = 0.007, n = 18), 10 ng µl-1 (Z = 3.18, *p* = 0.002, n = 18), 1 ng µl^{-1}, (Z = 2.11, *p* = 0.04, n = 18) and 0.1 ng µl-1 (Z = 2.11, *p* = 0.04, n = 19).

When TMTT was used as the test volatile, winged morphs visited the arm offering it at the highest tested concentration, 100 ng µl^{-1} (Z = 2.63, *p* = 0.009, n = 17), significantly less often than the control, while wingless morphs significantly responded in this manner to 10, 0.1, and 0.01 ng µl^{-1} doses of TMTT (Z = 1.99, *p* = 0.046, n = 19; Z = 2.46, *p* = 0.01, n = 20; and Z = 2.64, *p* = 0.008, n = 18, respectively) (Fig. 5).

Discussion

The importance of plant volatiles in searching behavior of extremely polyphagous aphids such as *M. persicae* for a host plant is still unclear. Some studies have shown the unimportance of olfactory cues for this aphid (e.g. 1959; Hori, 1999; Vargas et al., 2005). However our results and some others have clearly shown that *M. persicae* responds to olfactory cues released from one of its secondary hosts (Eigenbrode et al. 2002; Ngumbi et al. 2007; Amarawardana et al. 2007; Ninkovic et al. 2013). The presented results also show that both winged and wingless *M. persicae* morphs can detect slight changes in concentrations and profiles of host plant’s volatiles, including changes induced by exposure to volatiles from another plant. These findings demonstrate that volatile signals may be stimulants in the process of plant acceptance even for polyphagous aphids, confirming that aphids are heavily dependent on olfactory cues when searching for a suitable host in complex habitats (Pettersson et al. 2007; Webster 2012).

Olfactory responses of aphids to odors from plants

Host plants that co-exist with other plants may be less attractive and suitable for aphids due to induced resistance from their association with neighboring plants (Dahlin and Ninkovic 2013). Ninkovic et al. (2013) found that the migration of *M. persicae* into a potato field was significantly reduced when potato plants were sown together with onion plants due to the change in volatile emissions from potato plants making them less attractive for winged aphids. Our results confirm this interactive effect of volatiles from different plants for both winged and wingless *M. persicae*. Similar effects have been observed for the response of the wingless oligophagous aphid *Rhopalosiphum padi* L. (Hemiptera: Aphididae) to barley plants exposed to volatiles from weeds (Glinwood et al. 2004; Ninkovic et al. 2009; Dahlin and Ninkovic 2013) or other barley cultivars (Ninkovic et al. 2002; Kellner et al. 2010). These volatile interactions can reduce the attraction of potential host plants for wingless aphids as well as for flying, host-seeking aphids, which may have profound consequences for the establishment of new colonies by wingless aphids and hence aphid numbers (Wiktelius 1989; Ninkovic and Åhman 2009).

In other studies it has been speculated that intercropped plants may mask olfactory cues used by herbivores to find their hosts (Randlkofer et al. 2010; Finch and Collier 2012). However, we found that onion plants did not mask the odor of potato plants for *M. persicae*; a mixture of odors from onion and potato plants was as attractive as the odor of only potato plants. This suggests a mechanism based on volatile exchange between plants rather than odor masking. The ability to locate and recognize host plants is essential for the survival of aphids; they can detect slight changes in volatile emissions of their secondary hosts, even changes induced by interaction with neighboring plants. The changes in volatile emission have informative value for the aphids in terms of the host plant quality (Pickett and Glinwood 2007). The ability of onion to induce changes in potato volatile emission, reducing their attraction for *M. persicae,* can have a great potential as aphid control agent. Thus, intercropping with onion plants or plants that emit similar volatiles may substantially improve integrated pest management in potato fields. Volatile compounds released from living plants could also be used in integrated pest management strategies against other pests such as thrips (Egger and Koschier 2014).

Olfactory responses of aphids to odors from synthetic blends and single volatile compounds

Aphids perceive plant odors through highly specialized olfactory receptor neurons. The similarity of the responses of both winged and wingless *M. persicae* to the synthetic blends of volatiles and living plants we observed suggests that blends of chemicals can adequately represent the fragrances of onion-exposed and unexposed potato plants. For both aphid morphs the synthetic blend of exposed plants was significantly less attractive than the blend from unexposed potato plants, but winged and wingless morphs were sensitive to different doses of the blends. Flying aphids should be able to discriminate different plant odors from greater distance than wingless morphs that tend to migrate locally within a reduced range of host (Wiktelius 1989). Alate aphids possess more olfactory sensilla than apterous forms, thus alate aphid forms of *Sitobion avenae* have higher sensitivities and selectivity to leaf odor components than apterous (Yan and Visser 1982).

Aphids recognize and locate their hosts by detecting emissions of characteristic blends of volatile compounds, and respond more strongly to blends than to individual components (as reviewed in Bruce and Pickett 2011). However, concentrations of single compounds in blends can play a critical role in aphids' acceptance of host plants. We found that winged and wingless aphids responded negatively to both the single compounds (*E*)-nerolidol and TMTT, which are released in higher amounts by potato plants that have been exposed to onion plants (Ninkovic et al. 2013), and to synthetic blends made of these compounds together with other compounds released by potatoes. Thus, TMTT and (*E*)-nerolidol might act as signals for the location of aphid host plants, but as repellents if the emission of these chemicals is increased in fields by diverse plant associations (Hedge et al. 2011; Kos et al. 2013; Markovic et al. 2014).

Our finding that winged aphids responded to relatively high concentrations of single volatile compounds released by plants, is in accordance with previous reports (Webster et al.

2010; Hori 1998), while wingless individuals responded to low concentrations of the synthetic blend of volatiles, and TMTT. A possible explanation for this is that small changes in odor emissions of host plants are more important for wingless aphids than huge deviations. Wingless aphids are usually in closer contact with plants and their odors. Huge concentrations of odors from exposed plants are overwhelming and unrecognizable for them, and thus these odors are meaningless and without benefit for wingless aphids that usually have low intention to leave a host plant. However, (*E*)-nerolidol was effective at a wide range of doses, repelling wingless aphids across the range of test concentrations. Morphs of other aphid species such as *Sitobion avenae* (F.) and *R. padi* also reportedly have differing capacities to detect volatile semiochemicals (Yan and Visser 1982; Quiroz and Niemeyer 1998). An important difference between winged and wingless aphids is the greater abundance of secondary rhinaria on the antennae of winged morphs (Pickett et al. 1992), but the function of these organs is still unknown. Pickett and colleagues (1992) suggested that they might play a role in host searching behavior and mate selection, but they have no proven role in the detection of plant odors (Hardie et al. 1994; Park et al. 2000; Park and Hardie 2004).

Integrated pest management based on plant-insect relationships is a promising method as alternative strategy to decrease the excessive reliance on insecticides. By understanding how different aphid morphs locate their host plants, it is possible to control populations by taking advantage of functional cues in their host location behavior. Through manipulation of botanical composition in crop fields (e.g. by intercropping), aphid orientation may be disrupted reducing their abundance and prevent their establishment as a pest. Based on our findings about the volatile interactions between plants and between plants and insects, functional biodiversity in agro-ecosystems can be exploited as a component of integrated pest management. Application of volatile chemicals in the field might be difficult; the effects depend on correct concentration and emission rate and applications might have to be repeated. We recommend rather using living plants that emit permanently the “right dose”.

Acknowledgements

We gratefully acknowledge Jan Pettersson for useful discussions and valuable comments on the manuscript. We thank Elham Ahmed and Erika Qvarfordt (Swedish University of Agricultural Sciences, Department of Ecology) for their help in the laboratory and Dimitrije Markovic for making the illustration figure. We thank two anonymous reviewers for their comments and encouragements. This work was supported by the Swedish Foundation for Strategic Environmental Research (MISTRA) through the PlantComMistra program, the Ministry of Education, Science and Technological Development of the Republic of Serbia (Project No. III 46008), and the Carl Trygger Foundation for Scientific Research.

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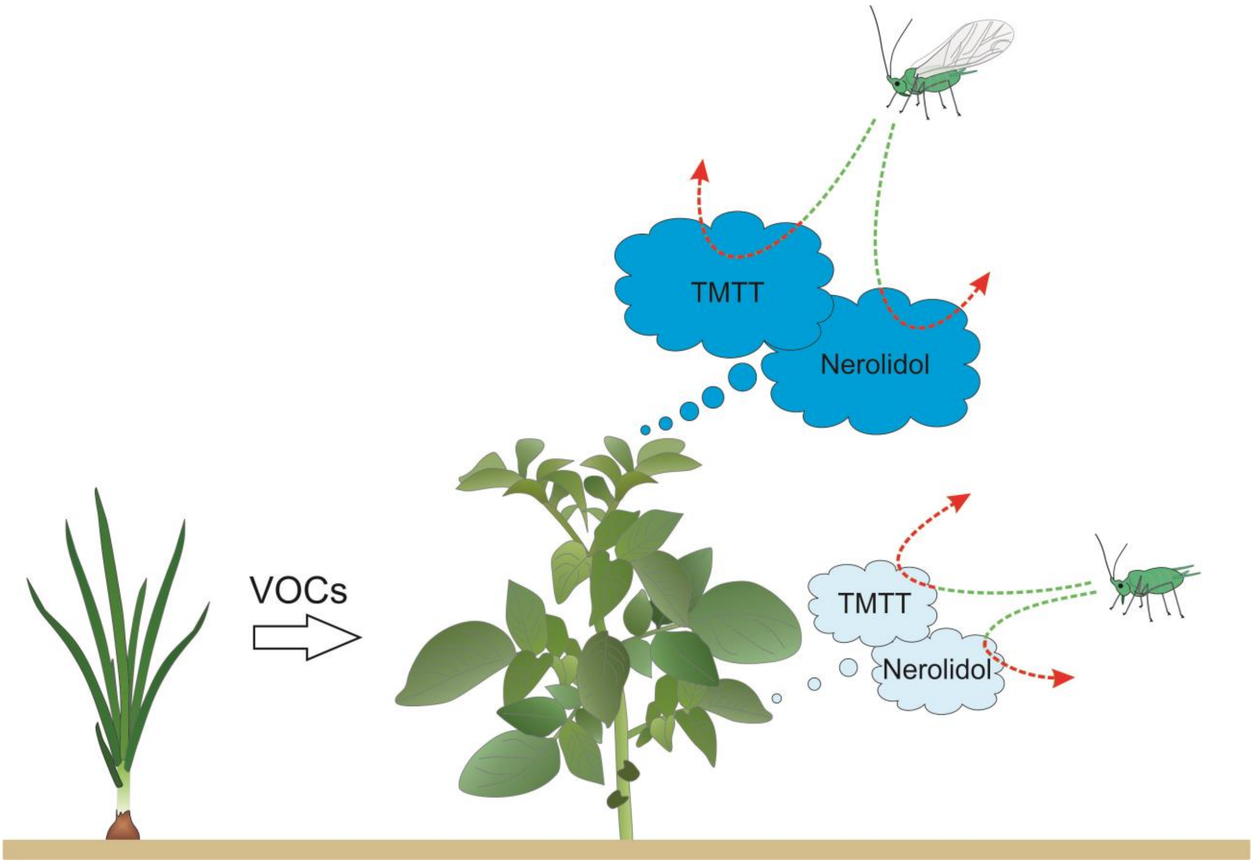

Fig. 1 Volatile organic compounds (VOCs) from onion plants induce changes in the volatile emission of neighboring potato plants with a higher release of the terpenoids TMTT and nerolidol. High doses of these compounds repelled winged aphids, while wingless aphids were repelled by low doses.

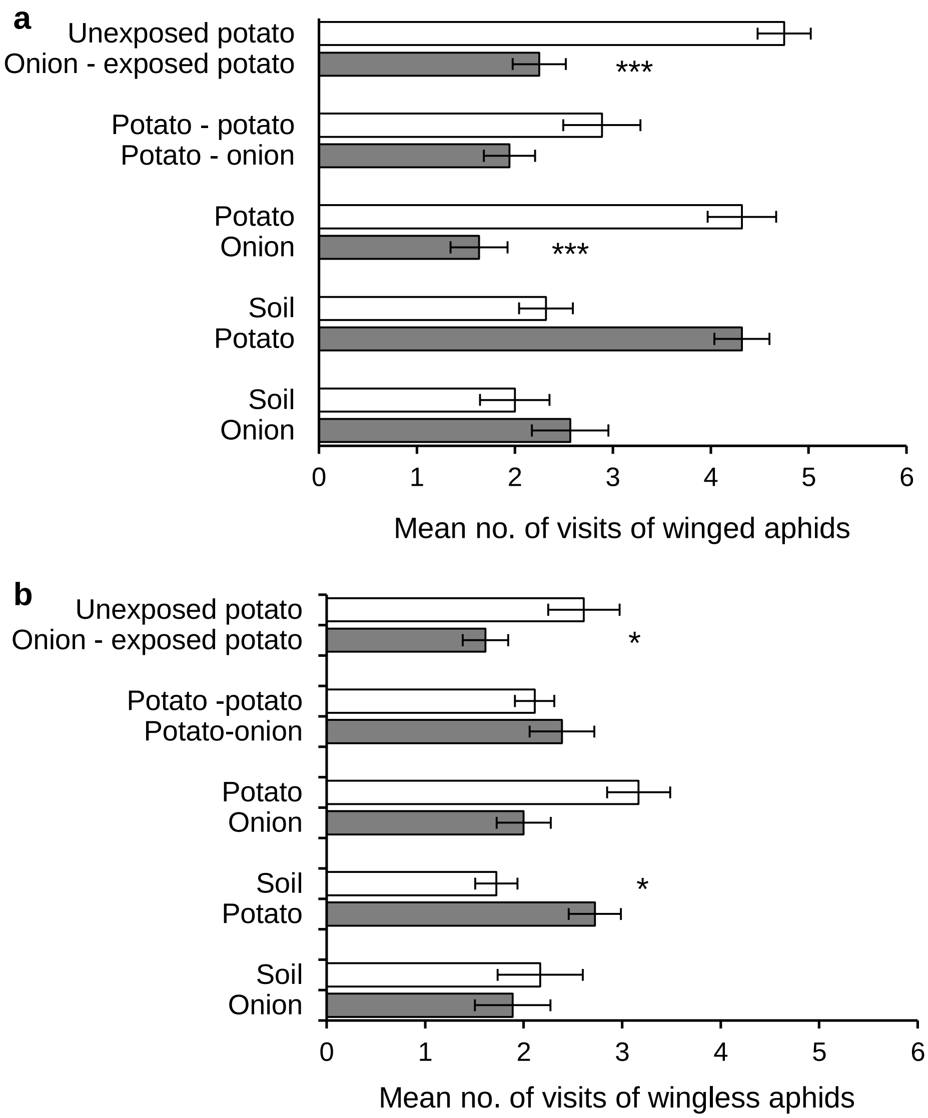

Fig. 2 Behavioral responses of winged (a) and wingless (b) *Myzus persicae* to indicated choices of volatiles from plants. Error bars indicate ± SE. Asterisks indicate preferences at significance levels of * $p \leq 0.05$, and *** $p \leq 0.001$ (Wilcoxon matched pairs test).

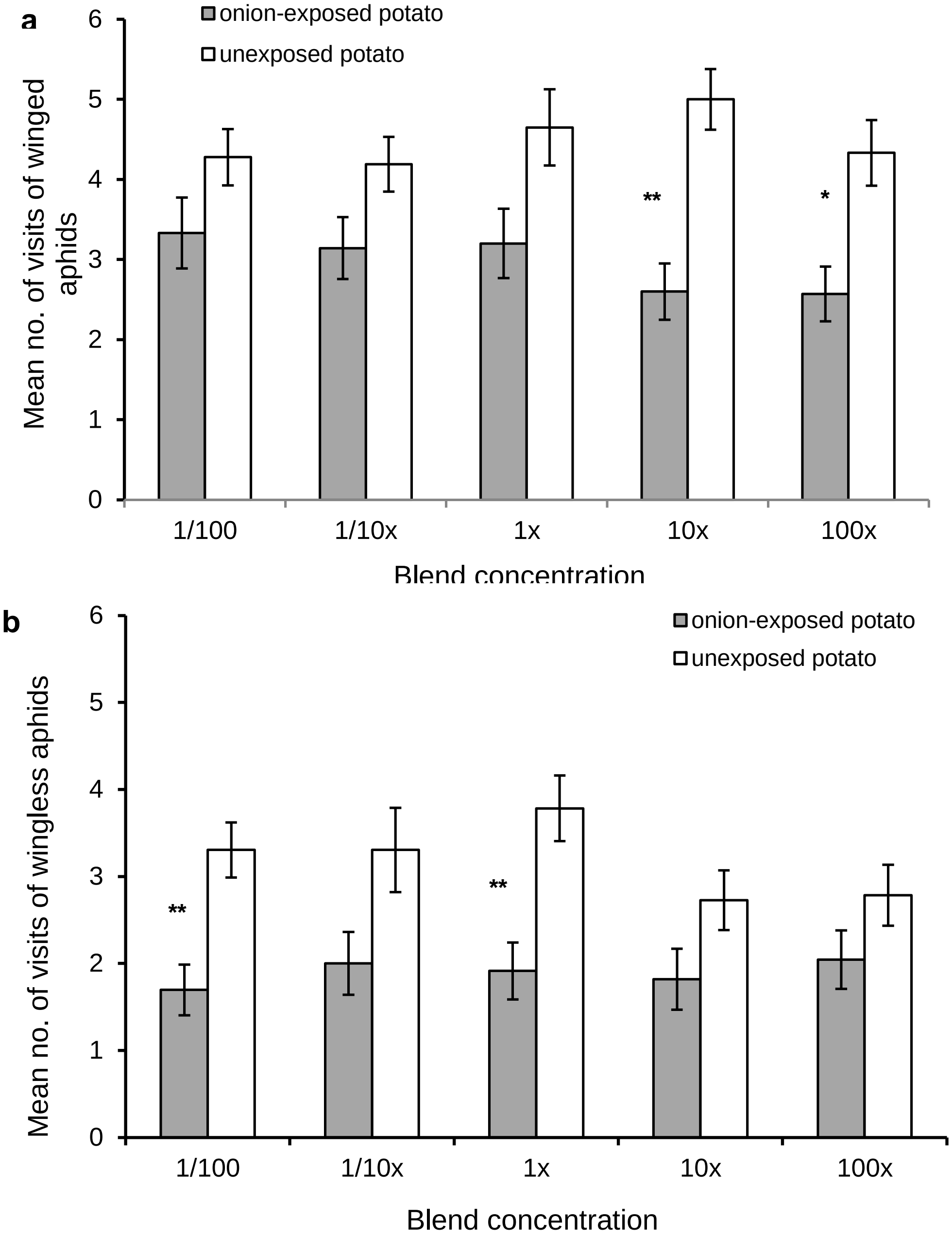

Fig. 3 Preferential responses of winged (a) and wingless (b) *Myzus persicae* to synthetic blends of volatile organic compounds of potato plants that had been exposed (treatment) and unexposed (control) to onion plants. Synthetic blends were at 1/100, 1/10, 1, 10 and 100 times the original concentration of volatiles identified in potato headspace. Error bars indicate ± SE. Asterisks indicate preferences at significance levels of * $p \leq 0.\ 05$, and *** $p \leq 0.\ 001$ (Wilcoxon matched pairs test).

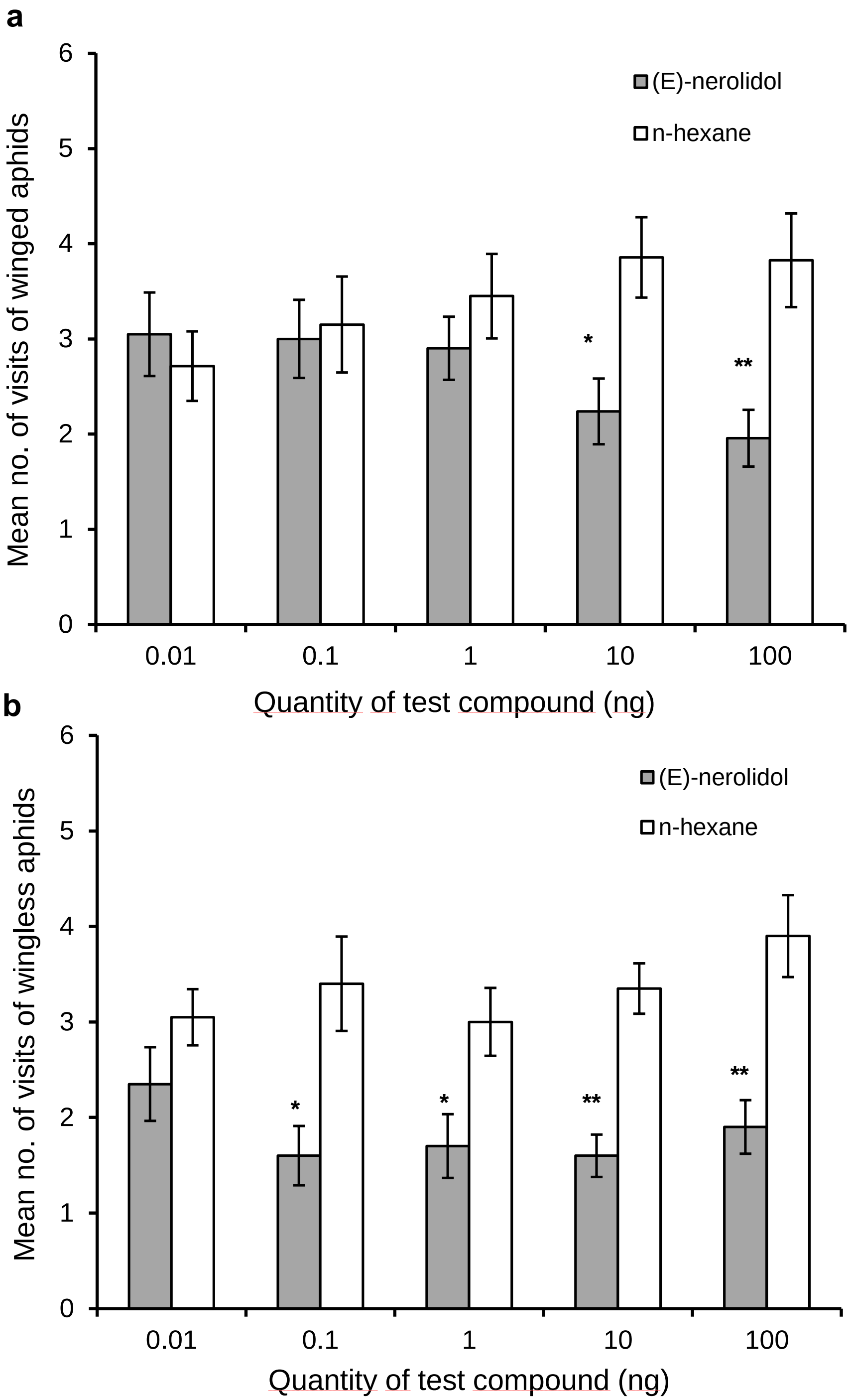

Fig. 4 Preferential responses of winged (a) and wingless (b) *Myzus persicae* to indicated amounts of (*E*)-nerolidol, a terpenoid released more strongly from potato plants when exposed to onion plants, vs. n-hexane controls. Error bars indicate ± SE. Asterisks indicate preferences at significance levels of * $p \leq 0.\ 05$, and *** $p \leq 0.\ 001$ (Wilcoxon matched pairs test).

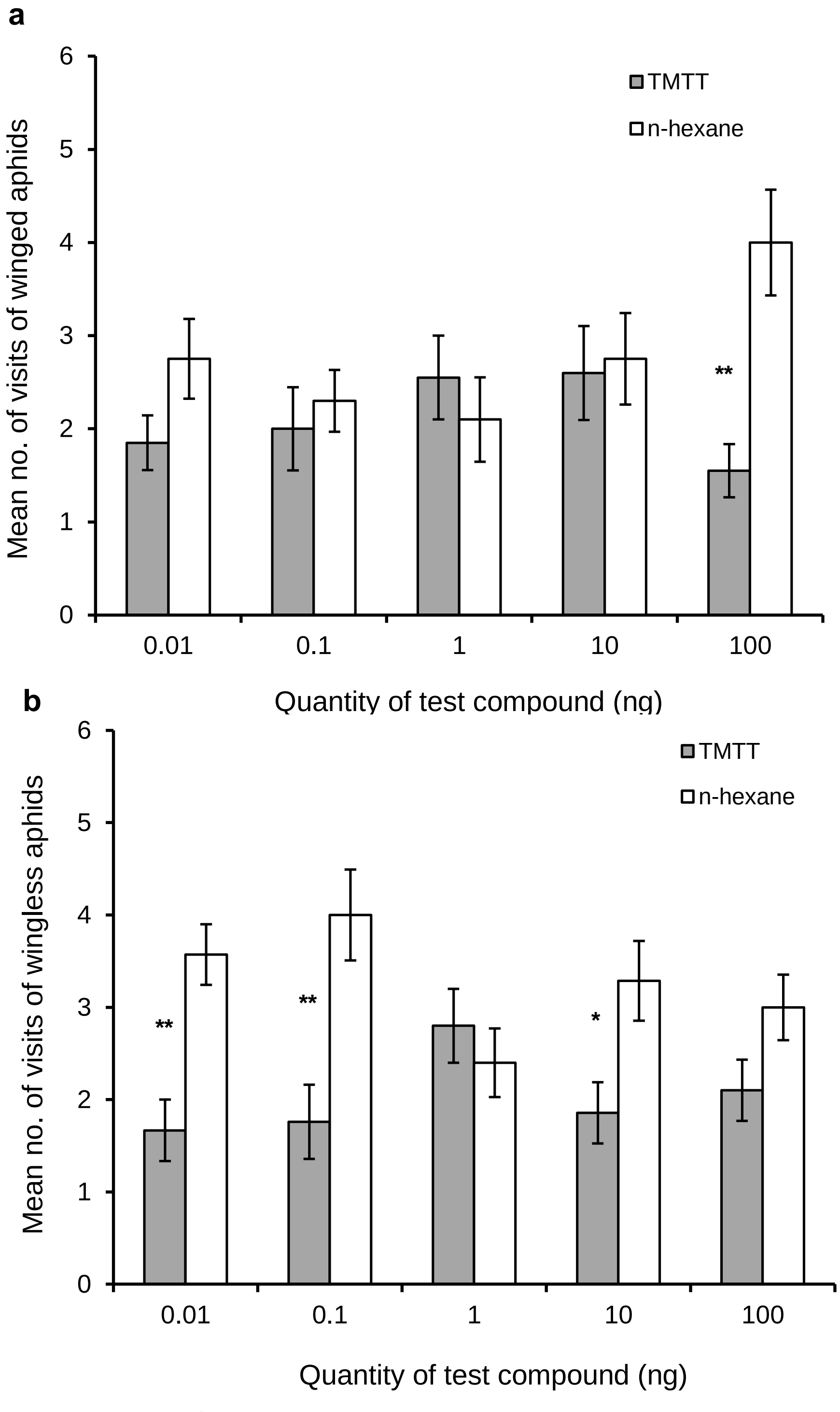

Fig. 5 Preferential responses of winged (a) and wingless (b) *Myzus persicae* to indicated amounts of (3E, 7E) 4, 8, 12-trimethyl-1, 3, 7, 11-tridecatetraene (TMTT), a terpenoid released more strongly from potato plants when exposed to onion plants, vs. n-hexane controls. Error bars

indicate ± SE. Asterisks indicate preferences at significance levels of * $p \leq 0.05$, and *** $p \leq 0.001$ (Wilcoxon matched pairs test).