

EXPOSURE OF LIMA BEAN LEAVES TO VOLATILES FROM HERBIVORE-INDUCED CONSPECIFIC PLANTS RESULTS IN EMISSION OF CARNIVORE ATTRACTANTS: ACTIVE OR PASSIVE PROCESS?

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Abstract—There is increasing evidence that volatiles emitted by herbivore-damaged plants can cause responses in downwind undamaged neighboring plants, such as the attraction of carnivorous enemies of herbivores. One of the open questions is whether this involves an active (production of volatiles) or passive (adsorption of volatiles) response of the uninfested downwind plant. This issue is addressed in the present study. Uninfested lima bean leaves that were exposed to volatiles from conspecific leaves infested with the spider mite *Tetranychus urticae*, emitted very similar blends of volatiles to those emitted from infested leaves themselves. Treating leaves with a protein-synthesis inhibitor prior to infesting them with spider mites completely suppressed the production of herbivore-induced volatiles in the infested leaves. Conversely, inhibitor treatment to uninfested leaves prior to exposure to volatiles from infested leaves did not affect the emission of volatiles from the exposed, uninfested leaves. This evidence supports the hypothesis that response of the exposed downwind plant is passive. *T. urticae*-infested leaves that had been previously exposed to

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volatiles from infested leaves emitted more herbivore-induced volatiles than *T. urticae*-infested leaves previously exposed to volatiles from uninfested leaves. The former leaves were also more attractive to the predatory mite, *Phytoseiulus persimilis*, than the latter. This shows that previous exposure of plants to volatiles from herbivore-infested neighbors results in a stronger response of plants in terms of predator attraction when herbivores damage the plant. This supports the hypothesis that the downwind uninfested plant is actively involved. Both adsorption and production of volatiles can mediate the attraction of carnivorous mites to plants that have been exposed to volatiles from infested neighbors.

Key Words—*Phytoseiulus persimilis*, *Tetranychus urticae*, lima bean, herbivore-induced plant volatiles, plant–plant interactions.

INTRODUCTION

Ecosystems are composed of complex food webs consisting of trophic interactions between plants and animals and among animals (Polis and Strong, 1996). In addition to direct trophic interactions, there are many indirect interactions (Abrams et al., 1996). For example, plants may interact with carnivorous animals through plant volatiles whose production is induced by herbivory; these volatiles are called herbivore-induced plant volatiles (hereafter called HIPV) (Vet and Dicke, 1992; Turlings et al., 1995; Takabayashi and Dicke, 1996; Dicke et al., 2003). When these volatiles attract carnivorous enemies of herbivores, and consequently reduce the herbivores' damage, the release of volatiles by plants is considered to be an induced, indirect defense (Price et al., 1980; Dicke and Sabelis, 1988; Turlings et al., 1993; Takabayashi and Dicke, 1996; Dicke, 1999; Sabelis et al., 1999). The attraction of carnivorous arthropods can enhance the fitness of plants that are infested with herbivorous arthropods (Van Loon et al., 2000; Hoballah-Fritzsche and Turlings, 2001).

A well documented system with induced, indirect plant defense consists of lima bean plants, two-spotted spider mites (*Tetranychus urticae*), and natural enemies of the spider mites. When spider mites infest lima bean leaves, the leaves emit feeding-induced volatiles that attract carnivores, such as the predatory mites *Phytoseiulus persimilis* (Dicke et al., 1999) and *Amblyseius womersleyi* (Maeda et al., 1999), and the predatory insects *Scolothrips takahashii* (Shimoda et al., 1997, 2002) and *Oligota kashmirika benefica* (Shimoda and Takabayashi, 2001; Shimoda et al., 2002). Once the infested plants emit HIPV, the volatiles can also be exploited by other organisms, such as conspecific and heterospecific herbivores (e.g., Dicke, 1986; Bernasconi et al., 1998; Landolt et al., 1999; Dicke and Van Loon, 2000; Horiuchi et al., 2002), and neighboring plants (see review in Dicke and Bruin, 2001).

In this paper, we focus on the effects of herbivore-induced plant volatiles on neighboring plants. In the tritrophic system of lima bean plants, *T. urticae* and

P. persimilis, Dicke et al. (1990) showed that uninfested lima bean plants that had been exposed to volatiles from *T. urticae*-infested lima bean plants were more attractive to *P. persimilis* than uninfested, unexposed plants. Two hypotheses might explain their results: (1) the emitted HIPV induce the production of carnivore-attracting volatiles in neighboring plants; or (2) HIPV adsorbed onto the neighboring plants, and were subsequently released, which resulted in predator attraction (Dicke et al., 1990; Bruin et al., 1995). The first hypothesis involves an active mechanism, while the second involves a passive mechanism. Recently, Arimura et al. (2000a,b, 2001) reported that defense genes were activated in uninfested lima bean plants in response to exposure to volatiles from *T. urticae*-infested lima bean plants. This shows that the exposed plants actively responded to the volatiles. However, it remains to be investigated whether such exposed, uninfested plants also actively produce predator-attracting volatiles.

In this study we addressed the effects of exposure of undamaged lima bean plants to HIPV on the emission of predator-attracting volatiles. We especially asked whether the exposed undamaged leaves are actively (production of volatiles) or passively (adsorption and re-release of volatiles) involved.

METHODS AND MATERIALS

Plants and Mites. Lima bean (*Phaseolus lunatus* L.) plants were grown in soil in a greenhouse at $25 \pm 2^\circ\text{C}$, 60–70% relative humidity (RH), and a photoperiod of 16 hr. We used plants that were grown for 10–15 days after germination; these plants had two primary leaves, and the first trifoliate leaf had just started to unfold.

Herbivorous spider mites (*Tetranychus urticae* Koch) were reared on kidney bean plants (*Phaseolus vulgaris* L.), grown under similar conditions to the lima bean plants, but in a climate-controlled room ($25 \pm 2^\circ\text{C}$, 60–70% RH, 16L-8D). Adult females were used for all experiments. Predatory mites (*Phytoseiulus persimilis* Athias-Henriot) were reared on detached kidney bean leaves that were heavily infested by spider mites, under the same conditions. New *T. urticae*-infested leaves were added every other day.

Chemical Analysis. Leaf volatiles were collected in 2 l glass containers. Volatile compounds were drawn from the headspace of the container by holding the infested plant in a glass tube packed with Tenax TA adsorbent (100 mg, mesh 20/35) for 3 hr, at a flow rate of 100 ml/min in a climate-controlled room at $25 \pm 2^\circ\text{C}$.

The adsorbed compounds were eluted with 2 ml of diethyl ether, and 0.5 μg of *n*-eicosane (the internal standard) was then immediately added to the eluate. The eluate was concentrated with a stream of gaseous N_2 and injected into the injection port (250°C) of a gas chromatograph-mass spectrometer (GC-MS) [GC: Hewlett Packard 6890 with an HP-5MS capillary column (i.d. = 0.25 mm, length = 30 m,

film thickness = 0.25 μm); MS: Hewlett Packard 5973 mass selective detector, 70 eV]. The GC oven temperature was programmed to rise from 40°C (5-min hold) to 280°C at 15°C/min.

The chemical structure of each compound was elucidated by comparing the mass spectra and retention time with those of authentic chemical samples. (*E*)- β -ocimene, (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), and (*E,E*)-4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) were provided by W. Boland (Max Planck Institute of Chemical Ecology, Germany). Linalool and methyl salicylate (MeSA) were purchased from Wako Chemical Company, Japan. Peak area of each compound in the total ion currency was measured by relative comparison with the internal standard. Emission rates were statistically compared between treatments for each compound by using the Mann-Whitney *U* test.

Primary leaves of lima bean plants were used in all experiments by cutting the petiole of a leaf from the plant with a razor blade. Individual petioles, with an attached leaf, were inserted into a 6 ml vial with either the test solution or distilled water as control. One leaf of each plant was assigned to the treatment and the other to the control to reduce variation between treatments ($N = 5$).

Volatiles from Uninfested Lima Bean Leaves That Had Been Exposed to Volatiles from T. urticae-Infested Conspicuous Leaves. The petiole of uninfested, detached leaves was inserted into a 6-ml vial with either an aqueous solution of the protein synthesis inhibitor cycloheximide (10 $\mu\text{g/ml}$) or distilled water. After 3 hr, 300 *T. urticae* females were placed on each of five uninfested, water-treated leaves or uninfested, cycloheximide-treated leaves. After 1 day, the volatiles emitted from these leaves were collected and analyzed with GC-MS.

To confirm that water-treated leaves and cycloheximide-treated leaves were equally infested by *T. urticae*, we counted the number of *T. urticae* eggs on each leaf. This was done in a separate experiment as follows. We prepared cycloheximide-treated and water-treated leaves as described above ($N = 29$). After 3 hr, we made a 1 \times 1-cm-square barrier with a thin tanglefoot line on the surface of a leaf, and put one female in the square. After 24 hr, we measured the number of eggs in the square. The mean number of eggs was not significantly different between cycloheximide-treated and water-treated leaves (cycloheximide: $11.6 \pm \text{SE} = 0.60$, water: 10.3 ± 0.78 ; independent *t*-test $P = 0.187$). As the number of eggs is proportional to the amount of feeding (S. Yano, personal communication), the result shows that the cycloheximide-treatment did not significantly affect the feeding of *T. urticae* females.

Two water-treated leaves, each infested with 300 *T. urticae* females for 1 day, and three uninfested water-treated leaves and three uninfested cycloheximide-treated leaves were introduced into an airtight 7-l glass container. The container was placed into a climate-controlled room at $25 \pm 2^\circ\text{C}$ and with a photoperiod of 16 hr. Care was taken to ensure that the spider mites on the infested leaves did not invade the uninfested leaves (see Arimura et al., 2000a for the details of the

experimental design). Under these conditions, uninfested leaves were exposed to volatiles from the infested leaves for 1 day (HIPV-exposed leaves). In the control experiment, two uninfested water-treated leaves were used instead of the infested leaves in the above setup. The exposed leaves were named “ULV-exposed leaves,” where “ULV” stands for “uninfested leaf volatiles.” Volatile compounds emitted by the exposed leaves were collected and analyzed with GC-MS, as described above.

Volatiles Emitted from Odor-Exposed Leaves That Were Subsequently Infested by T. urticae. In this experiment, we investigated the effect of previous exposure to HIPV on the emission of volatiles and attraction of predators in response to subsequent spider mite infestation. All the leaves used had their petioles in distilled water. Two infested leaves (300 female spider mites per leaf, 1-day post-infestation—odor source) and five uninfested leaves were introduced into an airtight 7-l glass container for 1 day. For the control experiment, two uninfested leaves were used as the odor source. Volatiles from exposed leaves were collected immediately after the exposure, as well as 1 or 3 days after the exposure, and then analyzed with GC-MS.

We prepared five leaves exposed to volatiles from *T. urticae*-infested leaves (HIPV-exposed leaves) and five leaves exposed to volatiles from uninfested leaves for 1 day (ULV-exposed leaves). Subsequently, 50 *T. urticae* females were placed onto each odor-exposed leaf. Volatile compounds released from the infested leaves were collected 1 and 3 days after the introduction of *T. urticae* and analyzed with GC-MS.

Two predatory mite “choice” experiments were conducted in a Y-tube olfactometer. Individual *Phytoseiulus persimilis* mites were offered a choice between (a) uninfested leaves vs. HIPV-exposed leaves that were subsequently infested by 80 *T. urticae* females for 1 day, or (b) uninfested leaves vs. ULV-exposed leaves that were subsequently infested by 80 *T. urticae* females for 1 day. In the center of the Y-tube olfactometer, was an iron, Y-shaped wire (for details of the olfactometer setup, see Takabayashi and Dicke, 1992). Leaf volatiles, in air cleaned with activated charcoal, were pushed into each of the arms of the olfactometer at a flow rate of 2.5 l/min. Adult female predatory mites that had been starved for 1 day were individually positioned at the beginning of the iron wire. When the predator reached the end of one of the arms of the olfactometer, the choice was recorded. The maximum time that each individual was allocated for reaching the end of an arm was 5 min. After every five mites, the alternate odor sources were swapped to the other arm to adjust for potential asymmetries in the experimental arena. Individual predators were used only once, and a total of 30 predators were used in 1 day. Each experiment was replicated on at least three different days, each with different odor sources and predatory mites. The test was performed in a climate-controlled room at $25 \pm 2^\circ\text{C}$ and $70 \pm 10\%$ RH. The distribution of the predators over two odor sources was analyzed with a binomial test to determine whether the distribution was significantly different from a 1:1 distribution. Fisher’s

exact probability test was used to determine the significant differences between the distributions of predators over the two odor sources for different experiments. All experiments were done from October 2000 to August 2001.

RESULTS

Volatiles from Uninfested Lima Bean Leaves That Had Been Exposed to Volatiles from T. urticae-Infested Conspecific Leaves. Infested water-treated leaves released more (*E*)- β -ocimene, linalool, DMNT, MeSA, and TMTT than infested cycloheximide-treated leaves, which emitted only trace amounts of these volatiles (Figure 1a). Conversely, both HIPV-exposed cycloheximide-treated leaves and

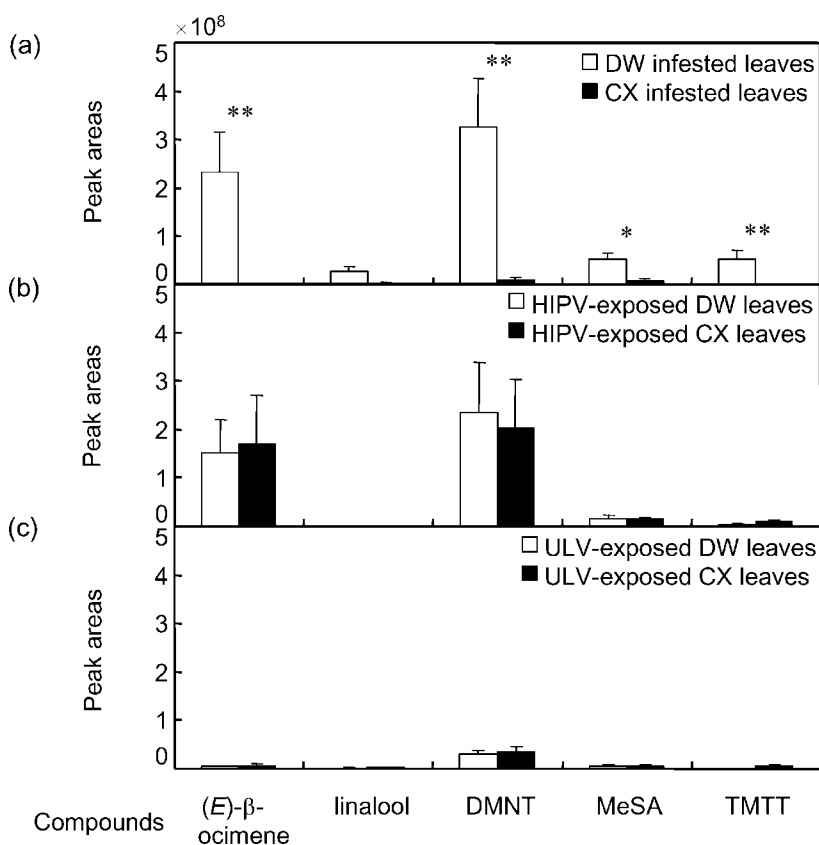


FIG. 1. The effect of cycloheximide on the production of volatiles by (a) *T. urticae*-infested leaves, (b) HIPV-exposed leaves, and (c) ULV-exposed leaves (ion intensities per leaf; mean \pm SE). * = $P < 0.05$, ** = $P < 0.01$.

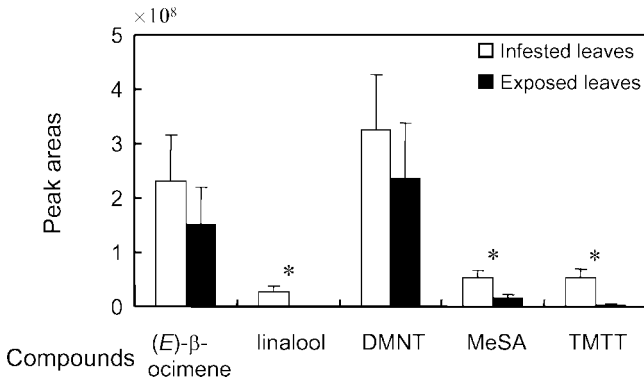


FIG. 2. Comparison of volatile emission rates from spider-mite infested leaves and leaves exposed to odors from spider-mite infested leaves (ion intensities per leaf; mean \pm SE). * = $P < 0.05$.

HIPV-exposed water-treated leaves released large amounts of these volatiles, and the amounts were not significantly different among treatments for any of the compounds (Figure 1b). Trace amounts of (*E*)- β -ocimene, DMNT, and MeSA were recorded in ULV-exposed water-treated leaves and ULV-exposed cycloheximide-treated leaves, and trace amounts of TMTT were recorded in only ULV-exposed cycloheximide-treated leaves (Figure 1c). Infested water-treated leaves emitted significantly more linalool, MeSA, and TMTT than HIPV-exposed water-treated leaves. (Figure 2).

Volatiles Emitted from Odor-Exposed Leaves That Were Subsequently Infested by T. urticae. All leaves used in the experiments had their petioles in distilled water. HIPV-exposed uninfested leaves released more (*E*)- β -ocimene, DMNT, and MeSA than ULV-exposed uninfested leaves just after the exposure (Figure 3). However, a rapid reduction in the amounts of these compounds emitted from HIPV-exposed uninfested leaves, except for MeSA, was observed 1 and 3 days after exposure (Figure 3).

One day after the introduction of *T. urticae*, HIPV-exposed leaves emitted more (*E*)- β -ocimene and DMNT than ULV-exposed leaves (Figure 4a). HIPV-exposed leaves still released larger amounts of those volatiles than ULV-exposed leaves 3 days after the introduction of *T. urticae*, but the differences were not statistically significant (Figure 4b).

More predators were attracted to HIPV-exposed infested leaves than uninfested leaves (Figure 5b), whereas the predators were equally distributed between ULV-exposed infested leaves and uninfested leaves (Figure 5a). The results of these two olfactometer experiments are significantly different (Fisher's exact probability test, $P = 0.007$).

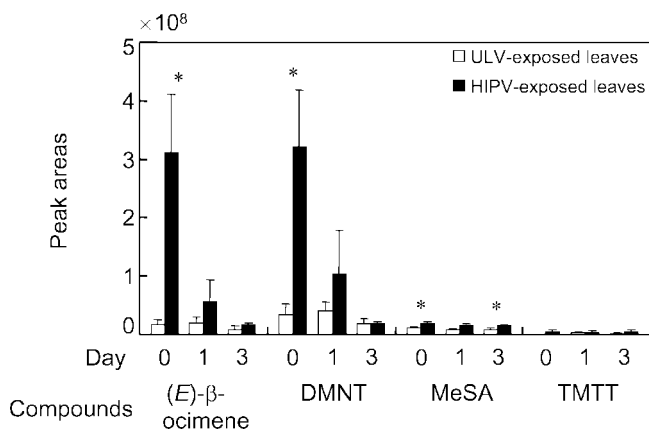


FIG. 3. Emission rates of volatiles emitted from odor-exposed leaves at 0, 1, and 3 days after exposure (ion intensities per leaf; mean \pm SE). * = $P < 0.05$.

DISCUSSION

As pointed out by Dicke et al. (1990) and Bruin et al. (1995), there are two hypotheses to explain the volatile emissions from leaves that have been exposed to volatiles from infested leaves: (1) HIPV are detected by exposed leaves, which results in the production of volatiles (the production hypothesis), and (2) HIPV are adsorbed onto the surface of exposed leaves and subsequently re-emitted (the adsorption hypothesis). Since cycloheximide-treatment resulted in the suppression of the induced volatiles, lima bean leaves do not use preformed enzymes together with the relevant substrates, but require protein synthesis for the production of herbivore-induced volatiles. Moreover, cycloheximide-application did not affect the emission of volatiles from HIPV-exposed leaves. These data support the adsorption hypothesis. If adsorption and re-release were the only cause of the volatile emissions from HIPV-exposed leaves, the blend of volatiles when these leaves were treated with cycloheximide, would be expected to be similar to that of the volatiles from infested leaves. However, a difference in blend composition of volatiles from HIPV-exposed leaves and infested leaves was observed: *T. urticae*-infested leaves emitted linalool, but HIPV-exposed leaves did not. Different adsorption, or re-release, rates for different compounds may explain this difference.

It is important to note that the production and adsorption hypotheses are not mutually exclusive. HIPV-exposed leaves that were subsequently infested by spider mites (*T. urticae*) for 1 day released significantly larger amounts of volatiles than the ULV-exposed leaves with the same level of infestation. The difference in volatile emissions cannot be explained by higher emission rates from HIPV-exposed,

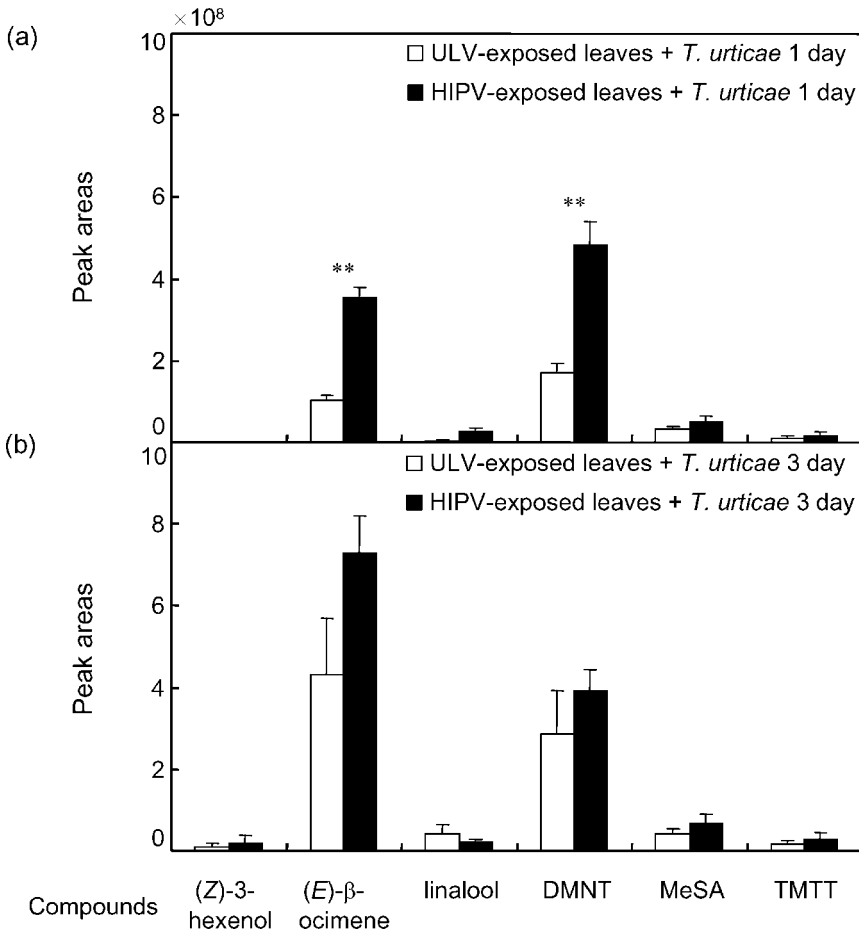


FIG. 4. Effects of odor exposure on the production of *T. urticae*-induced volatiles: (a) volatiles emitted from the exposed leaves one day after infestation and (b) volatiles emitted from the exposed leaves three days after infestation (ion intensities per leaf; mean \pm SE). ** = $P < 0.01$.

uninfested leaves than from ULV-exposed, uninfested leaves, because the volatiles from HIPV-exposed leaves and ULV-exposed leaves were not different 1 day after exposure (Figure 3), and the difference of (*E*)- β -ocimene and DMNT release between infested ULV- and HIPV-exposed leaves at day 1 (Figure 4a) was significantly higher (Mann-Whitney *U* test: $P < 0.05$) than that between ULV- and HIPV-exposed leaves (Figure 3). Therefore, these data indicate that changes related to the biosynthesis of volatiles occurred in the HIPV-exposed leaves, which

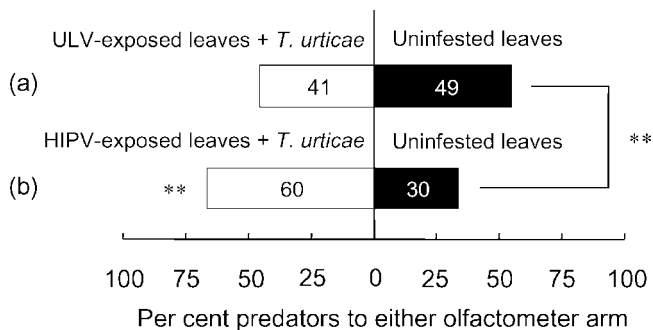


FIG. 5. The olfactory response of *P. persimilis* females to volatiles from odor-exposed leaves of different treatments, as determined in a Y-tube olfactometer: (a) uninfested leaves vs. HIPV-exposed water-treated leaves that were subsequently infested by 80 *T. urticae* females for 1 day, and (b) uninfested leaves vs. ULV-exposed water-treated leaves that were subsequently infested by 80 *T. urticae* females for 1 day. Asterisks besides the bar of choice (b) mean the significant difference between uninfested leaves and infested ULV-exposed leaves. Asterisks between the bars mean the significant difference in preference of predators between choice (a) and (b). ** = $P < 0.01$, Numbers in the bar segments represent the actual numbers of predators.

supports the production hypothesis. Recently, Engelberth et al. (2004) have reported that corn seedlings previously exposed to green leaf volatiles (GLV) from neighboring plants produced more jasmonic acid and volatile sesquiterpenes in response to mechanical damage and induction with caterpillar regurgitant than seedlings not exposed to GLV. The olfactometer bioassays showed that the infested HIPV-exposed leaves were also more attractive to the predatory mites than infested ULV-exposed leaves. This indicates that HIPV-exposed uninfested leaves produce more of the predator attractants when infested by spider mites than ULV-exposed uninfested leaves that are subsequently infested by spider mites. However, whether adsorbed volatiles might also contribute to the attractiveness of predatory mites by infested HIPV-exposed leaves remains unanswered.

One disadvantage of induced defense by plants is that there is a time lag between infestation and the induction of the defense. Maeda and Takabayashi (2001) studied the time course of HIPV-emission in *T. urticae*-infested kidney bean plants and found that the plants started to emit HIPV after there were approximately 50 (female) spider mites per leaf. They suggested that the indirect defense of HIPV by kidney bean plants might be induced after an increase of spider mites. Our present results (Figures 4 and 5) show that the time lag between infestation and volatile emission can be reduced by previous exposure to volatiles from conspecific neighbors. Mattiacci et al. (2001) reported analogous effects in cabbage plants that had been previously infested by the herbivore *Pieris brassicae*; when undamaged

leaves of previously infested cabbage plants were re-infested by conspecifics for a short time, such leaves were 10 times more attractive to the parasitoid *Cotesia glomerata* than recently infested leaves from plants that had not previously been infested.

In this paper, we have presented data in support of two possible ways in which undamaged plants, which are exposed to volatiles from infested conspecifics, become more attractive to predatory mites: (1) uninfested exposed leaves may recruit predators before being damaged, most likely through a passive process involving adsorption of predator-attractants, and (2) exposed plants increase their higher volatile emission rate as soon as they become infested by the herbivore species that infested their neighbors, through an active process. The latter phenomenon is likely to be important to HIPV-exposed plants, as it allows them to induce an indirect defense more intensively or at a faster rate than when they had not been exposed to the volatiles of their neighbors. Thus, a disadvantage of inducible defenses, i.e., the time delay between infestation and induction of a defense, may be attenuated by responding to volatiles from herbivore-infested neighbors. Our data add to the growing literature on infochemical-mediated interactions between damaged and undamaged plants (Dicke and Bruin, 2001 and references therein).

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