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INDUCTION OF PLANT SYNOMONES BY OVIPOSITION OF A PHYTOPHAGOUS INSECT

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Abstract—Earlier investigations of host habitat location in the egg parasitoid *Oomyzus gallerucae* have shown that oviposition of the elm leaf beetle (*Xanthogaleruca luteola*) induces the field elm (*Ulmus minor*) to emit volatiles that attract the egg parasitoid. In this study we investigated the mechanism of this induction by testing the effects of differently treated elm leaves on *O. gallerucae* in a four-arm olfactometer. First we investigated which sequence of the herbivore oviposition behavior is necessary for the synomone induction. The following major sequences were observed: (1) Prior oviposition, the gravid female gnawed shallow grooves into the leaf surface. (2) After gnawing upon the leaf surface, the female attached about 20–30 eggs with oviduct secretion in the grooves. We experimentally mimicked the shallow grooves on the leaf surface by scratching the leaf surface with a scalpel (= scratched leaves). Volatiles from such scratched leaves did not attract the egg parasitoid. However, as soon as eggs with oviduct secretion, or only oviduct secretion, was applied to these scratched leaves, they emitted attractive volatiles. Application of oviduct secretion and eggs on undamaged leaves did not elicit release of attractive synomones. Thus, an elicitor is located in the oviduct secretion, but becomes active only when the leaf surface is damaged. Jasmonic acid is known as a mediator of plant responses induced by feeding of herbivorous arthropods, and we demonstrate that it mediates production of elm synomones that attract *O. gallerucae.* The plant's reaction to oviposition was systemic, and leaves without eggs near leaves with eggs emitted attractants.

Key Words—Egg parasitoids, tritrophic level interactions, synomones, plant defense, systemic induction, oviposition, jasmonic acid, *Ulmus minor*, elm leaf beetle, *Oomyzus gallerucae.*

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INTRODUCTION

Parasitoids and predators of herbivorous insects are known to utilize volatile infochemicals emitted by plants under herbivore attack during host location (Turlings et al., 1990, 1991; Dicke, 1994; Mattiacci et al., 1994; Du et al., 1996; Turlings and Benrey, 1998). Studies of the mechanisms of induction of plant synomones by feeding of herbivores provided knowledge of the elicitor (regurgitate, volicitin), the mediator of response within the plant (jasmonic acid), the induced volatiles themselves, and the specificity of plant response (Turlings et al., 1993; Boland et al., 1995; Mattiacci et al., 1995; Alborn et al., 1997; Karban and Baldwin, 1997; De Moraes et al., 1998; Du et al., 1998; Paré and Tumlinson, 1998). Not only may feeding of an herbivorous arthropod induce release of plant synomones, but also oviposition of an herbivorous insect can induce the plant to emit volatiles that are attractive to an egg parasitoid. Meiners and Hilker (1997) have shown that oviposition of the elm leaf beetle *Xanthogaleruca luteola* Muller (Coleoptera, Chrysomelidae) induces leaves of the field elm (*Ulmus minor* Miller) to emit volatiles that are attractive to the egg parasitoid *Oomyzus gallerucae* (Hymenoptera, Eulophidae). The aim of this study was to investigate the mechanism of this plant synomone induction by oviposition.

We investigated the following questions: (1) When does the gravid female release the synomone elicitor during oviposition? (2) By which means does the gravid female apply the elicitor to the leaf surface? (3) Does jasmonic acid mediate synomone induction by oviposition as it does by feeding of herbivorous arthropods? (4) Does the plant respond systemically to an oviposition? Do elm leaves without eggs emit attractive volatiles, if they are near leaves with eggs?

In order to study questions 1 and 2, we at first watched the oviposition behavior of *X. luteola.* The gravid female removed some plant tissue from the undersurface of a leaf with its mouthparts. The female never bit completely through the leaf tissue, but just scratched the surface by gnawing shallow grooves. After gnawing these grooves, the female glued its eggs to the scratched surface. The egg glue was a secretion from the oviduct (Meiners, personal observations). This oviposition behavior suggested the following possible explanations for the induction process: (A) Removal of plant tissue by gnawing upon the leaf surface prior to each oviposition may induce the induction of synomones attractive to the egg parasitoid. We investigated whether mimicking this gnawing by artificial damage induces the synomone emission. (B) If such artificial damage of the leaf surface does not elicit the emission of synomones, a chemical from the egg surface or from the oviduct secretion might be the inducing factor. In that case transferring eggs or just oviduct secretion into artificially scratched grooves on the undersurface of elm leaves might induce the leaves to emit volatiles that attract the egg parasitoid. (C) If a chemical from the egg

surface or from the oviduct secretion is the elicitor of the induction process, the damage of leaf surface prior to oviposition might be redundant for the inductive process. To investigate whether damage of the leaf surface is necessary or not for the induction, we transferred freshly oviposited eggs to intact elm leaves and tested the attractiveness of such treated leaves to *O. gallerucae.*

To investigate question 3, the effect of jasmonate treatment of elm leaves upon the egg parasitoid was studied. Jasmonates are well known as mediators or signal transducers which activate numerous diverse wound-induced responses in different plants (Farmer and Ryan, 1992; Creelman and Mullet, 1997; Karban and Baldwin, 1997), and induce volatile emissions in some plants (Boland et al., 1995). We studied whether treatment of an elm twig with jasmonic acid mimics the effect of an egg deposition of the elm leaf beetle on elm leaves by inducing the release of volatiles that attract *O. gallerucae.*

Our study of question 4 is based on the knowledge of systemic transport of damage-induced signals in plants (Sticher et al., 1997). Feeding damage by herbivores can induce volatiles in plants that are emitted both from the damaged area and from undamaged parts of the plant (Dicke and Sabelis, 1988; Dicke et al., 1990a,b; Turlings et al., 1990, 1995; Steinberg et al., 1993; Agelopoulos and Keller, 1994a,b; McCall et al., 1994; Röse et al., 1996; De Moraes et al., 1998; Du et al., 1998). We wanted to find out in this study whether the emission of volatile synomones from elm leaves was restricted to those leaves on which eggs of *X. luteola* were deposited or if a signal was systemically transported within an elm twig so that leaves without eggs were induced to produce volatile synomones affecting host location in *O. gallerucae.*

METHODS AND MATERIALS

Plants and Insects. Elm twigs (*Ulmus minor*) from the lower part of a tree were cut from June to September in the botanic garden of the Freie Universität Berlin and kept at 20°C, 16L : 8D, and 2000 lux. Adults and eggs of *X. luteola* were collected from 1996 to 1998 in the environs of Montpellier and Perpignan (southern France) and in Pamplona (northern Spain). All stages of *X. luteola* were kept at 20°C and 16L : 8D. Adults and larvae were fed leaves of *U. minor.* Emerging adult *O. gallerucae* were held at 10°C and 16L : 8D and transferred to 20°C several days before testing. They were fed diluted honey. Only experienced female parasitoids with prior contact with host eggs were studied. These females encountered host eggs two days prior to the experiments for a period of 24 hr (Meiners and Hilker, 1997).

General Bioassay Procedures. All experiments were conducted with elm twigs with 15–20 leaves that were treated on the day of cutting. All treated twigs were tested only 72 hr after treatment, since twigs with eggs are known to

emit attractive volatiles for up to 72 hr after egg deposition (Meiners and Hilker, 1997). During the period before testing, the twigs were kept in water at 20°C, 16L : 8D, and 2000 lux. The effect of odor of differentially treated elm twigs was studied in a four-arm airflow olfactometer (for details see Vet et al., 1983; Meiners and Hilker, 1997). Odorless, humidified air was offered in three odor fields (control) to a female parasitoid, while the fourth field of the olfactometer contained air that had passed through a glass cylinder with one test elm twig. The test twigs were standing with the cut stem in water. One female parasitoid was allowed to walk within the exposure chamber of the olfactometer for a period of 600 sec. Her residence time in each of the four odor fields was recorded. After testing three to seven parasitoid females, the odor source was changed. For each bioassay, a total of 18–36 parasitoids was tested. The observations were recorded with help of the Noldus Observer program 3.0 (Wageningen, The Netherlands).

Bioassays to Determine When and How the Female Deposits Synomone Elicitor. In order to elucidate when and how the herbivore female deposits the synomone elicitor, the effects of volatiles from differently treated elm twigs on the parasitoids were tested in the following procedures: (1) All intact elm leaves of a twig with 15–20 leaves were scratched with a sharp scalpel to mimic the elm leaf beetle's removement of plant tissue before egg deposition. Each leaf got a scratch 0.5–1 cm long on its undersurface that just damaged the surface. (2) Freshly oviposited egg masses (20) were removed cautiously from elm leaves and afterwards transferred onto leaves of a twig that had never carried an egg mass before, but were scratched as described above. One egg mass was transferred to each scratched leaf of a twig. Each egg mass was directly placed onto the scratch of the leaf. (3) Ten gravid female elm leaf beetles were dissected, and the oviducts were transferred to a glass slide and subjected to mild pressure from a blunt scalpel. The secretion issuing from the oviducts was smeared into the scratches of each leaf of the test elm twig. (4) Freshly oviposited egg masses (15–20) were removed cautiously from elm leaves and one egg mass was transferred to the underside of an undamaged leaf of another elm twig that never carried eggs before.

Bioassay to Determine If Jasmonic Acid is the Inducer. An induction experiment was carried out with jasmonic acid as possible inducer (question 3). Elm twigs with undamaged leaves were supplied with a 0.05% aqueous Tween solution containing 1 μmol/ml and 0.01 μmol/ml, respectively, of racemic (±)-jasmonic acid (Sigma, Germany) through the cut stem of the test twig. After a period of 72 hr, the effects of volatiles from these twigs were tested with *O. gallerucae.* In order to examine whether feeding damage of leaves interacts with the jasmonic acid, twigs were exposed in a further induction experiment to feeding by 20 elm leaf beetles each during the 72-hr period of jasmonic acid treatment (concentration 1 μmol/ml).

Bioassay to Determine If Induction is Systemic. To test if the induction of

volatiles was restricted to the damaged leaves or if it extended systemically over undamaged leaves of the same twig, we conducted two bioassays: (1) We took a twig that carried (15–20) leaves with one egg mass per leaf for 72 hr and 15–20 immediately adjacent leaves without eggs. The leaves with eggs were removed and the remaining twig with leaves that had never carried eggs was tested. (2) To exclude that volatiles from leaves with eggs adsorb to neighboring leaves without eggs and make these attractive, we offered the lower part of an elm twig (15–20 leaves) to females of gravid elm leaf beetles for feeding and oviposition in a Plexiglas cylinder and prevented the beetles from contact with the upper part (15–20 leaves) by the use of a partition plate (Figure 1). This plate also prevented an air exchange between both parts of the twig. Thus, attractive volatiles from leaves with eggs could not adsorb to leaves without eggs on the same twig. After an oviposition period of 72 hr, the twig was cut into two pieces and the upper part was tested for an emission of attractive volatiles in the four-arm olfactometer.

Statistical Analyses. Data were statistically evaluated by a two-way analysis of variance to analyze homogeneity of durations of stay within field sectors of the olfactometer (factor 1) and homogeneity of samples of each assay (factor 2). If durations of stay within the field sectors of the olfactometer differed significantly from homogeneity, durations of stay within each of the four field sectors were compared to each other by the Scheffé test (Bortz, 1993).

RESULTS

Bioassays Determining When and How Induction Occurs. Mimicking the gnawing of the beetle prior to oviposition by removing leaf surface tissue with a scalpel did not induce an odor in the elm leaves that attracted *O. gallerucae* in the four-arm olfactometer (two-way ANOVA; factor 1: test and control sectors, $df = 3$, $F = 1.148$, $P = 0.338$; factor 2: odor sources, $df = 5$, $F = 0.009$, $P = 0.999$) (Figure 2a). The transfer of freshly laid elm leaf beetle eggs into artificially produced grooves on the undersurface of elm leaves induced the emission of volatiles in the leaves and significantly influenced residence time of parasitoids in the test odor field (two-way ANOVA and Scheffé test; factor 1: test and control sectors, $df = 3$, $F = 4.828$, $P = 0.003$; factor 2: odor sources, $df = 5$, $F = 0.016$, $P = 0.999$) (Figure 2b). Application of oviduct secretion of gravid *X. luteola* females to artificially scratched grooves on the undersurface of test leaves was sufficient to elicit emission of volatiles that attract and arrest the parasitoids in the test odor field of the olfactometer (two-way ANOVA and Scheffé test; factor 1: test and control sectors, $df = 3$, $F = 6.331$, $P = 0.001$; factor 2: odor sources, $df = 6$, $F = 0.077$, $P = 0.998$) (Figure 2c). However, odor of a test elm twig with undamaged leaves to which freshly laid eggs of *X. luteola* had been transferred

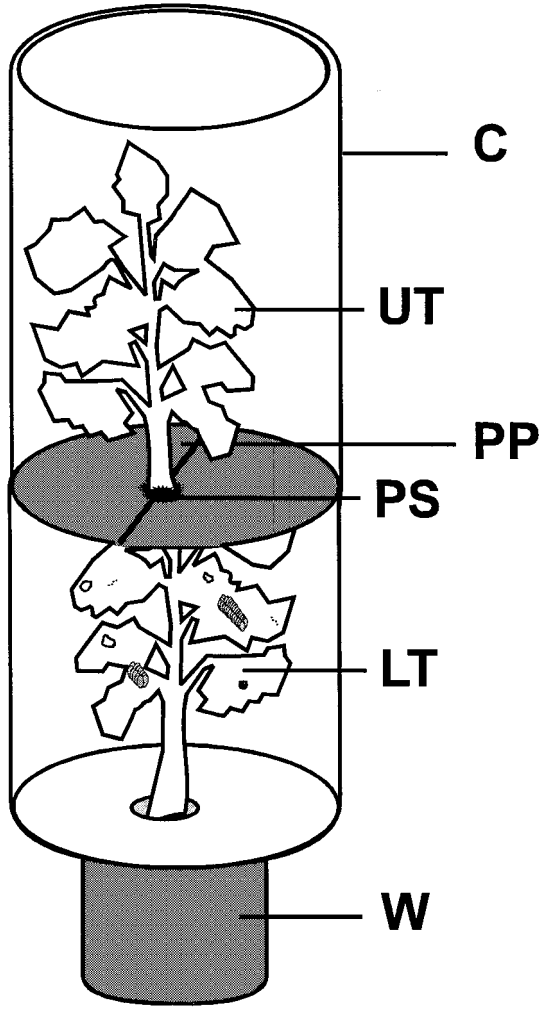

FIG. 1. Induction chamber for systemic induction of elm leaves. C, Plexiglas cylinder; PP, partition plate; W, water supply; LT, lower part of test twig; UT, upper part of test twig. Length of cylinder: 50 cm, diameter (15 cm). The lower and upper parts of the test twig were about 20 cm long.

did not affect the parasitoids behavior in the olfactometer (two-way ANOVA; factor 1: test and control sectors, $df = 3$, $F = 0.316$, $P = 0.814$; factor 2: odor sources, $df = 4$, $F = 0.005$, $P = 0.999$) (Figure 2d).

Bioassays Determining Whether Jasmonic Acid is the Inducer. Intact elm

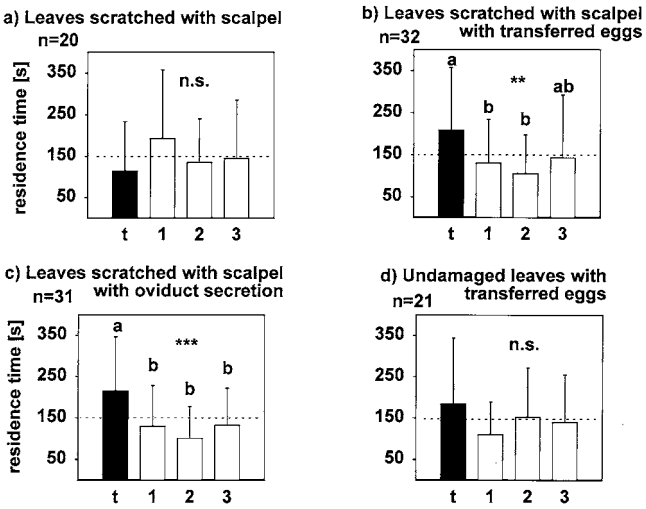

FIG. 2. Responses of females of the egg parasitoid *Oomyzus gallerucae* to volatiles from elm leaves that experienced different (mimics of) sequences of oviposition by the elm leaf beetle. Mean values and standard deviations of residence times of parasitoid females in test and control fields of a four-arm olfactometer. Each parasitoid female was observed for 600 sec; t = field with test elm twig odors; 1, 2, 3 = three fields with control air. Treatments: (a) leaf tissue removed with scalpel, (b) leaf tissue removed with scalpel and eggs transferred into the grooves, (c) Leaf tissue removed with scalpel and oviduct secretion smeared into the grooves, (d) elm leaf beetle eggs transferred onto intact elm leaves. Two-way analysis of variance: n.s., not significant; $^{**}P < 0.01$; $^{***}P < 0.001$. Scheffé test: different letters indicate significant ($P < 0.05$) differences.

leaves that were supplied through the cut stem of the twig with jasmonic acid at a concentration of 1 μmol/ml emitted an odor that attracted *O. gallerucae* (two-way ANOVA and Scheffé test; factor 1: test and control sectors, $df = 3$, $F = 9.200$, $P = 0.001$; factor 2: odor sources, $df = 3$, $F = 0.023$; $P = 0.995$) (Figure 3a). The 100-fold lower concentration of jasmonic acid (0.01 μmol/ml) did not cause emission of attractive volatiles (two-way ANOVA, factor 1: test and control sectors, $df = 3$, $F = 2.012$, $P = 0.118$; factor 2: odor sources, $df = 5$, $F = 0.041$, $P = 0.999$) (Figure 3b). Neither did elm leaves that were damaged by feeding of adult beetles and supplied through the cut stem of the twig with jasmonic acid at the high concentration of 1 μmol/ml emit an odor that attracted *O. gallerucae* (two-way ANOVA; factor 1: test and control sectors, $df = 3$, $F = 1.597$, $P = 0.196$; factor 2: odor sources, $df = 8$, $F = 0.037$, $P = 0.999$) (Figure 3c).

Tests for Systemic Induction. The odor of leaves without eggs that were

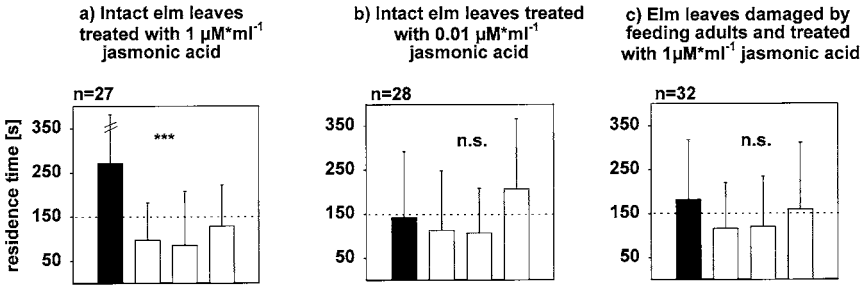

FIG. 3. Responses of females of the egg parasitoid *Oomyzus gallerucae* to volatiles from elm leaves treated by different concentrations of jasmonic acid through the cut stem of a twig for 72 hr. Mean values and standard deviations of residence times from females of *O. gallerucae* in test and control fields of a four-arm olfactometer. The observation period per female parasitoid was 600 sec; t = field with test elm twig odors; 1, 2, 3 = three fields with control air. Treatments: (a) intact elm leaves treated with jasmonic acid at a concentration of 1 μmol/ml, (b) intact with elm leaves treated with jasmonic acid at a concentration of 0.01 μmol/ml, (c) elm leaves that were damaged by adult feeding during 72 hr and simultaneously treated with jasmonic acid at a concentration of 1 μmol/ml. Two-way analysis of variance: n.s., not significant; ***$P < 0.001$. Scheffé test: different letters indicate significant ($P < 0.05$) differences.

immediately adjacent on the same twig to leaves with eggs prolonged the parasitoids' residence time in the test odor field of the olfactometer (two-way ANOVA and Scheffé test; factor 1: test and control sectors, $df = 3$, $F = 4.544$, $P = 0.005$; factor 2: odor sources, $df = 2$, $F = 0.020$, $P = 0.980$) (Figure 4a). The odor of undamaged leaves of the upper part of a twig, whose leaves on the lower part experienced egg deposition and feeding, significantly attracted *O. gallerucae* (two-way ANOVA and Scheffé test; factor 1: test and control sectors, $df = 3$, $F = 5.683$, $P = 0.001$; factor 2: odor sources, $df = 5$, $F = 0.022$, $P = 0.999$) (Figure 4b).

DISCUSSION

The results of our studies clearly show that the oviduct secretion of the elm leaf beetle contains an elicitor inducing elm leaves to produce volatiles that are attractive to the egg parasitoid *O. gallerucae*. The elicitor from the oviduct secretion is inactive when it contacts only the intact uninjured leaf surface. However, when the surface of the leaf is slightly damaged and oviduct secretion is applied to the damaged tissue, the elicitor becomes active. Neither artificial damage nor damage by feeding of nonovipositing elm leaf beetles induces elm leaves to produce synomones that attract *O. gallerucae* (see also Meiners and Hilker,

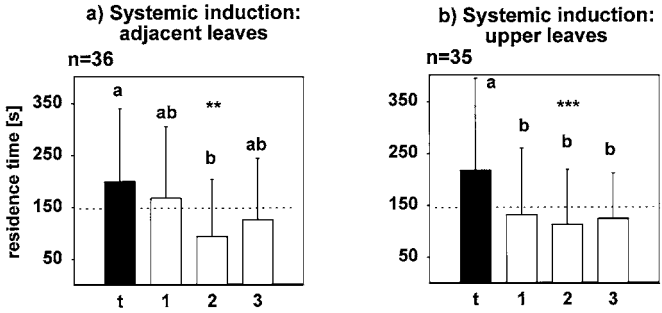

FIG. 4. Responses of females of the egg parasitoid *Oomyzus gallerucae* to volatiles from systemically induced elm leaves. Mean values and standard deviations of residence times from females of *O. gallerucae* in test and control fields of a four-arm olfactometer. The observation period per female parasitoid was 600 sec; t = field with test elm twig odors; 1, 2, 3 = three fields with control air. Two-way analysis of variance: $^{**}P < 0.01$; $^{***}P < 0.001$. Scheffé test: different letters indicate significant ($P < 0.05$) differences.

1997). Even though other plants are known to change concentrations of secondary metabolites in response to the kind of damage experienced (Baldwin, 1988, 1991; Tallamy, 1985), elm leaves do not change the volatile emission relevant for host searching of *O. gallerucae* in response to artificial damage and feeding of the elm leaf beetle.

While damage of elm leaves by elm leaf beetle feeding for food is a process lasting for hours and results in numerous holes in the leaf, gnawing by a female elm leaf beetle prior to oviposition removes only the leaf surface in less than a minute in order to make a trench for the eggs. We cannot exclude the possibility that the female also applies an elicitor through the mouthparts when scratching the grooves for her eggs. Several insects are known to release an elicitor through the mouthparts during normal feeding, and the induced plant synomones attract antagonists of the insect (Alborn et al., 1997; Mattiacci et al., 1994; Paré and Tumlinson, 1998; Turlings et al., 1993). We do not know which component(s) of the oviduct secretion elicit(s) the emission of synomones from elm leaves. Oviduct secretion of *X. luteola* needs to be chemically analyzed in the same way that the regurgitant of caterpillars has been investigated, resulting in detection of volicitin and β-glucosidase as the synomone elicitor (Alborn et al., 1997; Mattiacci et al., 1995).

Jasmonic acid applied to intact elm leaves at a concentration of 1 μmol/ml mediates the induction of synomones attractive to *O. gallerucae*. However, elm leaves that are exposed to both jasmonic acid and feeding elm leaf beetles did not emit an attractive odor, but leaves with this double treatment show features of senescence. Elm leaves that are treated with jasmonic acid, but are heavily

damaged by feeding of elm leaf beetles rapidly become senescent. High concentrations of jasmonic acid (10 μmol/ml) are known to induce senescence in different plant species (Boland et al., 1995). When both feeding and jasmonic acid affect the elm leaves, possibly senescence processes counteract the induction of volatiles in such quantities and qualities that they do not influence the host searching behavior of the egg parasitoid.

The inductive effect of jasmonic acid is known to be dependent upon the applied dose and the time lag after application (Bodnaryk, 1994; Boland et al., 1995; Baldwin, 1996; Miksch and Boland, 1996). Furthermore, many biotic and abiotic factors determine the intensity and quality of induced volatile emissions (Takabayashi et al., 1994; Turlings et al., 1998). In our study, elm twigs that were incubated in 1 μmol/ml jasmonic acid emitted attractive volatiles, while incubation at a concentration of 0.01 μmol/ml was not sufficient for the induction of attractive synomones. A concentration of 1 μmol/ml jasmonic acid induced volatile emission in leaves of various plant species (for example, in *Salix alba*, *Eucalyptus globulus*, and *Gingko biloba*) (Boland et al., 1995). The threshold concentration for inducing volatiles in *Phaseolus lunatus* and *Zea mays* was 0.1 μmol/ml jasmonic acid (Hopke et al., 1994). The time elapsed (72 hr) between application of jasmonic acid and the bioassay was the same period of time as that between egg deposition and bioassay of egg-containing elm leaves for their effects towards *O. gallerucae* (Meiners and Hilker, 1997).

The synomone-inducing effect of egg deposition on elm leaves acts systemically. When testing the effects of volatiles from egg-free leaves that are immediately adjacent to leaves carrying eggs, we did not exclude the possible adsorption of attractive volatiles from leaves with eggs. However, when testing the effects of egg-free leaves that are prevented from adsorption of volatiles from leaves with eggs on the same twig, the egg parasitoid is attracted by the egg-free leaves, indicating systemic induction of volatiles. This is the first study to show that oviposition of an herbivorous insect can cause a systemic plant response that affects the third trophic level.

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