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ORIGINAL ARTICLE

Response of the parasitoid *Telenomus podisi* to induced volatiles from soybean damaged by stink bug herbivory and oviposition

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Egg parasitoids have a short time frame in which their host eggs are suitable for parasitism, and in several systems these parasitoids respond to plant volatiles induced by oviposition on the plant (either in isolation or in combination with feeding damage) as a means of finding suitable hosts. It is known that the parasitoid of pentatomid eggs *Telenomus podisi* responds to damage done to soybeans by female *Euschistus heros*, its preferred host. In this study our aim was to determine the type of *E. heros* damage to soybean (herbivory, oviposition or a combination of both) necessary for attraction of *T. podisi*. In a Y-tube olfactometer the parasitoid has shown to respond to the undamaged plant over clean air and herbivory-damaged plants over undamaged plants. However, the parasitoids did not respond to the treatments where oviposition occurred, either in isolation or in combination with herbivory. Analysis of volatile blends revealed that herbivory plus oviposition damage to soybean induced a volatile blend different to those induced when herbivory or oviposition occurred separately. These results, along with other results from this system, suggest that *T. podisi* uses plant volatile cues associated with female *E. heros* damage in order to be present when *E. heros* lays its eggs, and thus ensure its resource is optimal for parasitism.

Keywords: Pentatomidae; Scelionidae; infochemical detour; tritrophic interactions

Introduction

Parasitoids of herbivore eggs have evolved responses to the subtle changes in plant chemistry caused by herbivore oviposition in order to successfully find their hosts (reviewed by Hilker and Meiners 2006). The elicitor in the oviduct secretion of one herbivore has been partially characterized (Hilker et al. 2005), and there is evidence that it affects systemic jasmonate-mediated responses (Hilker et al. 2002; Mumm et al. 2003). However most studies have been concerned with insects that make an oviposition wound in order to lay their eggs, so the secretion from the oviduct is in direct contact with internal plant tissues. In contrast, egg deposition by stinkbugs (Pentatomidae) does not involve obvious mechanical damage to the plant during the act of oviposition, so the mechanism of volatile induction is a result of either cell death and the hypersensitive response (Hilker and Meiners 2002), or of chemical elicitors present in the egg, or the egg-plant binding substance. For instance, in the bean-*Nezara viridula* system, a combination of oviposition and adult feeding is necessary for attraction of the parasitoid *Trissolcus basalis* (Colazza et al. 2004a, 2004b), suggesting that oviposition on its own does not cause reliable changes in the volatile profile that parasitoids

can exploit. Furthermore some species of egg parasitoid have specific responses to damage by specific species (Mumm et al. 2005), suggesting there is variation in the effects of different kinds of damage in different systems, which is probably due to different effects of herbivore oviposition in the activation of plant defence.

In the soybean system it has been shown that the parasitoid of pentatomid eggs *Telenomus podisi* Ashmead (Hymenoptera, Scelionidae) responds to plant volatiles induced by feeding damage caused by *Euschistus heros* (F.) (Hemiptera, Pentatomidae) (Moraes et al. 2005). In Y-tube olfactometer bioassays *T. podisi* has shown to spend more time in odour fields of soybean damaged by nymphs or females of *E. heros*. However in the cited study the type of damage responsible for attraction of *T. podisi* was not compared with oviposition or oviposition plus herbivory damage at that time. Since in the bean-*N. viridula* system a combination of oviposition and adult feeding is necessary for parasitoid attraction (Colazza et al. 2004a), in this study our aim was to characterize how different types of damage to soybean oviposition, herbivory or a combination of the two caused by *E. heros* affect attraction of *T. podisi*. We also determined changes in volatile compounds

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that might be responsible for this attraction, and might indicate which metabolic pathways are affected by stink-bug oviposition and herbivory.

Materials and methods

Plant and insect rearing

Soybean (var. BR16) seeds were obtained from the Embrapa Soybean Research Center (Londrina, PR, Brazil). The seeds were germinated on damp paper, and after three days, transplanted to pots with soil and kept in growth chambers (LAB-LINE Instruments, INC Melrose Park, ILL), at $27 \pm 1^\circ\text{C}$ and 80% relative humidity. All plants used in the experiments were in the V3 physiological stage (Fehr et al. 1971).

Euschistus heros individuals were obtained from a laboratory colony started from adults collected from soybean fields near the Embrapa Genetic Resources and Biotechnology Laboratory, Brasília, DF, Brazil ($15^\circ 47' \text{S}$ and $47^\circ 55' \text{W}$). Bugs were reared in 8-l plastic containers (100–150 insects/container) on raw peanuts (*Arachis hypogaea*), soybeans (*Glycine max*), sunflower (*Helianthus annuus*), fresh green beans (*Phaseolus vulgaris*), and water at $26 \pm 1^\circ\text{C}$ and 65% r.h. under a 14 light:10 dark photoperiod (light, 06:00–20:00 h) in a controlled environment (CE) room. The food supply was renewed three times per week. A 15-cm² piece of plastic mesh (~40 mesh) was placed against the inner wall of each container as an oviposition substrate and shelter for the bugs. To obtain virgin females, insects were sexed after their imaginal molt and cuticular hardening (ca. 24 h after molting), and maintained separately from males until use in experiments (*E. heros* becomes sexually mature 7–10 days after the imaginal molt).

Telenomus podisi were reared in angled-neck 25 cm² plastic tissue culture flasks (ICN Biomedicals, Irvine, CA, USA) on *E. heros* eggs in the same environmental conditions described for *E. heros*, but in a separate CE room. A droplet of pure honey was supplied in each flask as a food source.

Preparation of plants for experiments

The soybean plants were subjected to the following different types of damage by adults of *E. heros* in order to evaluate attraction of *T. podisi* and the resulting changes in the volatile chemistry of the plant: (i) Herbivory+oviposition: Five sexually mature, mated *E. heros* females, 12–15 days in the adult stage, were placed on the plant to feed and oviposit; (ii) Herbivory: Five virgin (2–5 days) *E. heros* females were placed on the plant to feed; and (iii) Oviposition: Five mated (12–15 days) *E. heros* females were placed on the plant after having removed their stylet with dissection scissors (in this treatment there was occasional mortality of females before the bioassays, in which case the dead individual was replaced). The treated and control (undamaged) plants were placed in micropore

plastic bags (bread bags), which allow gas exchange and do not accumulate humidity, until use in experiments. Just before the bioassays all insects were removed from the plants to avoid attraction to insect semiochemicals (Conti et al. 2004). Previous studies showed that *T. podisi* begins to respond to soybean only after the fourth day of damage by *E. heros* (Moraes et al. 2005). Therefore, all bioassays and chemical analyses were carried out using plants on/or after the fourth day of damage.

Bioassays

An acrylic block with a Y-shaped cavity (27.5×21.0 cm), sandwiched between two glass plates was used as the bioassay arena (Moraes et al. 2005). The trunk of the apparatus measured 8 cm and each arm measured 7 cm. Charcoal-filtered, humidified air was passed through the system at 300 ml/min through each arm in a push-pull system. The behaviour of the insect was monitored by CCD camera (Sony SPT M324CE) fitted with a 12.5–75.0 mm/F1.8 zoom lens) coupled to the SACAM software (Jorge et al. 2005) to register behavioural parameters. A single *T. podisi* female was introduced at the base of the Y-tube and observed for 10 min, and the first choice and residence time in each arm were recorded by the software. If the parasitoid entered one arm of the Y-tube and remained for 20 sec, a first choice was recorded. Each individual was used only once.

The following bioassays were carried out: *T. podisi* response to undamaged soybean vs. filtered humidified air ($n = 73$); *T. podisi* response to damaged soybean by herbivory+oviposition vs. undamaged soybean ($n = 91$); *T. podisi* response to damaged soybean by herbivory vs. undamaged soybean ($n = 72$); and *T. podisi* response to damaged soybean by oviposition vs. undamaged soybean ($n = 70$). All bioassays were carried out after four or five days damage to the plant.

Aerations and soybean volatile analyses

Soybean plants, treated as above, were aerated for collection of volatiles in a push-pull system. Plants were aerated during the fourth to seventh day of damage, with a sample taken every 24 h. Super Q (50 mg, 80–100 mesh, Alltech, PA, USA) was used as the adsorbent, secured in glass tubes with glass wool. The volatiles were eluted using 500 μl of *n*-hexane, and concentrated under a stream of N_2 to 200 μl .

Compounds were identified by gas chromatography-mass spectrometry (GC-MS), using a quadrupole mass analyser (Shimadzu GCMS-QP-2010, Kyoto, Japan), and with a TRB-5 column (30 m, 0.25 mm ID, 0.25 μm film thickness, Teknokroma, Barcelona, Spain) on a temperature program of $50^\circ\text{C}/2$ min, $15^\circ\text{C}/\text{min}$ to $250^\circ\text{C}/5$ min and helium as the carrier gas. Ionization was by electron impact (70 eV, source temperature 250°C). Tentative identification was

carried out by comparing mass spectra and retention indices of compounds against mass spectral databases or to spectra in the literature. Identifications were confirmed by comparing mass spectra and KI values against those from authentic standards injected under the same conditions.

Quantitative analysis was carried out by GC-flame ionization detector (FID-250°C) using a DB-5 column (30 m, 0.25 mm ID, 0.25 µm film thickness, J&W Scientific, Folsom, CA, USA) on a temperature ramp of 50°C/2 min, 15°C/min to 250°C/5 min and helium as the carrier gas in a Shimadzu 17A GC (Kyoto, Japan). Amounts released by the plant in each 24 h period were calculated in relation to the area of the internal standard (IS, (*E*)-2-octen-1-ol, 30 µg/ml).

Statistical analyses

The choices of the parasitoid in the bioassays were analysed by logistic regression, and estimation of the probability (p) of choosing the test odour. The model fitted contained a block term for the different days on which replicates were carried out, and a factor for the side (left or right) on which the test odour was presented to control for this variability. The hypothesis of no preference (proportion choosing each odour = 0.5) was tested by means of a χ^2 Wald test. The proportions of the total bioassay time spent in each odour field were analysed by Wilcoxon's matched-pairs test after arcsine transformation of the data.

The total amount of volatiles daily produced in each treatment (converted to natural logarithms) were compared by means of a repeated measures split-plot ANOVA, fitting treatment as the explanatory variable. Degrees of freedom in the lowest (time) stratum were corrected using Greenhouse and Geisser's (1959) epsilon statistic to account for patterns of unequal correlation amongst days. The blends produced on each of the four days of aeration were compared by means of multivariate log-ratio compositional analysis (Aitchison 1986). This analysis allows comparisons of entire blends, assessing the contribution of individual compounds to the blend as a whole. It has recently been applied to the analysis of plant and insect volatile blends (Pareja et al. 2007a, 2007b). Each compound was expressed as a proportion of the total, and then this proportion as the natural logarithm of the ratio with respect to the IS. These values were then analysed using MANOVA to determine the overall effect of treatment, and linear discriminant analysis for determining the contribution of individual compounds in separating the treatments. Before all analyses were carried out the compounds known to be produced in large quantities by *E. heros* (Pareja et al. 2007a) were removed from the dataset, since they could affect the interpretation of results.

Sources of compounds

Super Q (80/100 mesh) was purchased from Alltech (PA, USA). The sources of chemicals were as follows: (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, (*Z*)-3-hexen-1-ol, α -pinene, camphene, β -pinene, 6-methyl-5-hepten-2-one, limonene and methyl salicylate (Sigma-Aldrich, Steinheim, Germany); (*Z*)-3-hexenyl acetate, hexyl acetate, nonanal, (*Z*)-3-hexenyl butyrate, benzothiazole, dodecanol (TCI-America, Portland, USA); (*E,E*)- α -farnesene was provided by J. Aldrich (Beltsville, MD, USA); (*E,E*)-4,8,12-trimethyltrideca-1,3,7,11-tetraene (TMTT) was synthesized from (*E,E*) farnesol by oxidation to their corresponding aldehyde followed by Wittig methylenation and was provided by M. Birkett (Rothamsted Research, Harpenden, UK).

Results

Bioassays

On first choice *T. podisi* showed a tendency to prefer undamaged soybean over clean air (63% choosing the arm with soybean), although this was marginally non-significant (Figure 1). However the proportion of time spent in the odour field with undamaged soybean was significantly higher than that for clean air (Figure 2). Herbivory-damaged soybean was more attractive to the parasitoid than undamaged soybean (64% of responders choosing the arm with herbivory-damaged soybean) when measured by first choice (Wald $\chi^2 = 5.02$, $p = 0.025$, Figure 1). However oviposition (45% of responders, Wald $\chi^2 = 0.15$, $p = 0.746$) and herbivory + oviposition (54% of responders, Wald

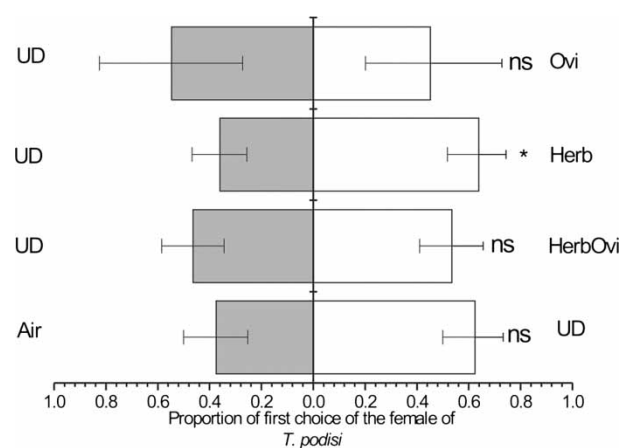


Figure 1. First choice of the parasitoid *T. podisi* to soybean (var. BR16) subjected to different damage treatments in Y-tube bioassays. The preference for the undamaged plant was marginally non-significant ($\chi^2 = 3.82$, $p = 0.051$), while the preference for the herbivory-damaged plant over the undamaged plant was significant ($\chi^2 = 5.02$, $p = 0.025$). The bioassays testing the response to oviposition-damaged ($\chi^2 = 0.15$, $p = 0.746$) and herbivory + oviposition damaged plants ($\chi^2 = 0.30$, $p = 0.585$) over undamaged plants were not significant. Analyses of preference were carried out by logistic regression, and a Wald χ^2 statistic to assess significance.

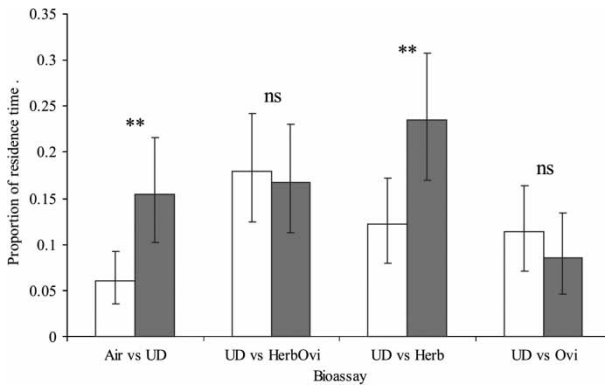


Figure 2. Proportion of residence time of the parasitoid *T. podisi* in odour fields during Y-tube bioassays testing responses to soybean (var. BR16) subjected to different damage treatments. The preference for the undamaged plant (UD) over clean air was significant ($W=883$, $p=0.009$, sample size = 73), as was the preference for the herbivory-damaged (Herb) plant over the UD plant ($W=838$, $p=0.007$, sample size = 72). The preferences for the oviposition-damaged (Ovi) plant ($W=1038$, $p=0.231$, sample size = 70) and the herbivory + oviposition-damaged (HerbOvi) plant ($W=1947$, $p=0.566$, sample size = 91) over the UD plant were not significant. Analyses by means of a Wilcoxon's matched-pairs test. ** $0.01 > p > 0.001$. Total bioassays time = 10 m.

$\chi^2 = 0.30$, $p = 0.585$) damage to soybean did not cause attraction of *T. podisi*. When the proportion residence time was analysed, *T. podisi* only showed a preference for the herbivory treatment over the undamaged soybean (Figure 2), in accordance with that observed for its first choice.

Volatile analysis

The total amount of volatiles released did not differ between treatments and showed a drop on the fifth day, which was similar between treatments (Figure 3). The chemical analysis of the extracts obtained from soybean plants subjected to each of the four treatments (undamaged plants, herbivory, herbivory + oviposition and oviposition damage) did not present any qualitative differences in the compounds identified by GC-MS (Figure 4). Some compounds (mainly the green leaf volatiles-GLVs, (*E*)-2-hexenal, (*E*)-2-hexen-1-ol, and (*Z*)-3-hexenyl acetate, some terpenes, like α -pinene and β -pinene, and the hydrocarbon decane were released in higher quantities on the fourth day of damage, and decreased from the fifth day onward.

Compositional analysis of the volatile blends revealed significant separation of the blends of the four treatments on all four days of aeration (for days four to seven respectively: $F_{42,36} = 1.85$, $p = 0.030$; $F_{57,37} = 2.06$, $p = 0.011$; $F_{48,39} = 2.54$, $p = 0.002$; $F_{57,34} = 2.61$, $p = 0.002$). Interestingly the herbivory + oviposition damage dissociated from both the herbivory and the oviposition treatments in all analyses, indicating that the combination of these two types of damage produces a volatile blend different

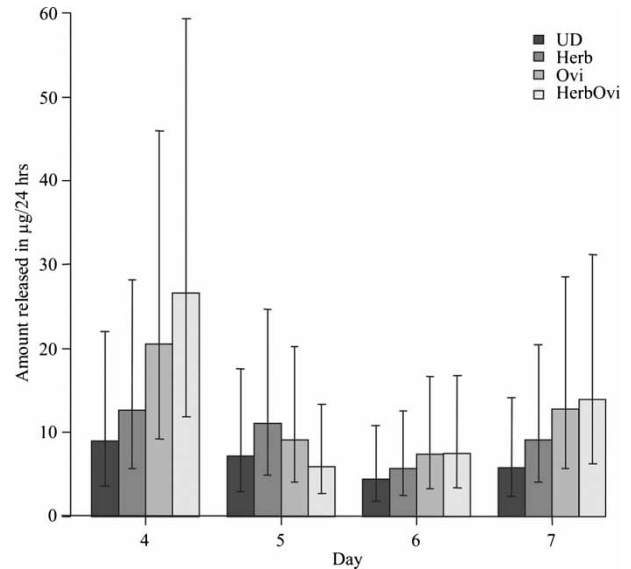


Figure 3. Total amount (in μg) of volatiles released in each treatment in each 24 h period, over four days of aeration (mean and 95% confidence interval). The decrease over the four days was significant ($F_{2,1,60,92} = 6.99$, $p = 0.002$), but the effect of treatment was not ($F_{3,34} = 0.70$, $p = 0.561$), and the decrease was similar between treatments (interaction term $F_{6,30,60,92} = 0.81$, $p = 0.574$). Degrees of freedom involving time are corrected for unequal correlations between days.

from the individual types of damage (Figure 5). Several compounds repeatedly associated to the different treatments (Figure 5). Damage by herbivory was associated to high relative proportions of (*Z*)-3-hexenyl acetate. The herbivory + oviposition treatment was characterised by a higher relative presence of (*E*)-2-hexenal and (*Z*)-3-hexen-1-ol. On the fourth and seventh day 4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT) was also associated to this treatment. The compositional analysis showed that (*E,E*)- α -farnesene appeared to be strongly associated to both herbivory and oviposition damage.

Discussion

Telenomus podisi responds to soybean damaged by adult female herbivory, but not to soybean plants on which eggs have been laid, either in isolation, or in combination with herbivory damage. For an egg parasitoid this result is counter-intuitive, since it is expected that the parasitoid would respond to cues more directly associated to its host (the eggs). Furthermore it contrasts with another pentatomid egg parasitoid system, where it has been shown that a combination of egg deposition and feeding damage is necessary for attraction of the parasitoid *Trissolcus basal* (Colazza et al. 2004a). Thus at first inspection it would appear that in the soybean-*E. heros*-*T. podisi* system volatiles do not serve as an 'early herbivore alert' (Hilker and Meiners 2006). However, for this tritrophic system, there is growing evidence that feeding damage could be a more reliable indicator of fresh

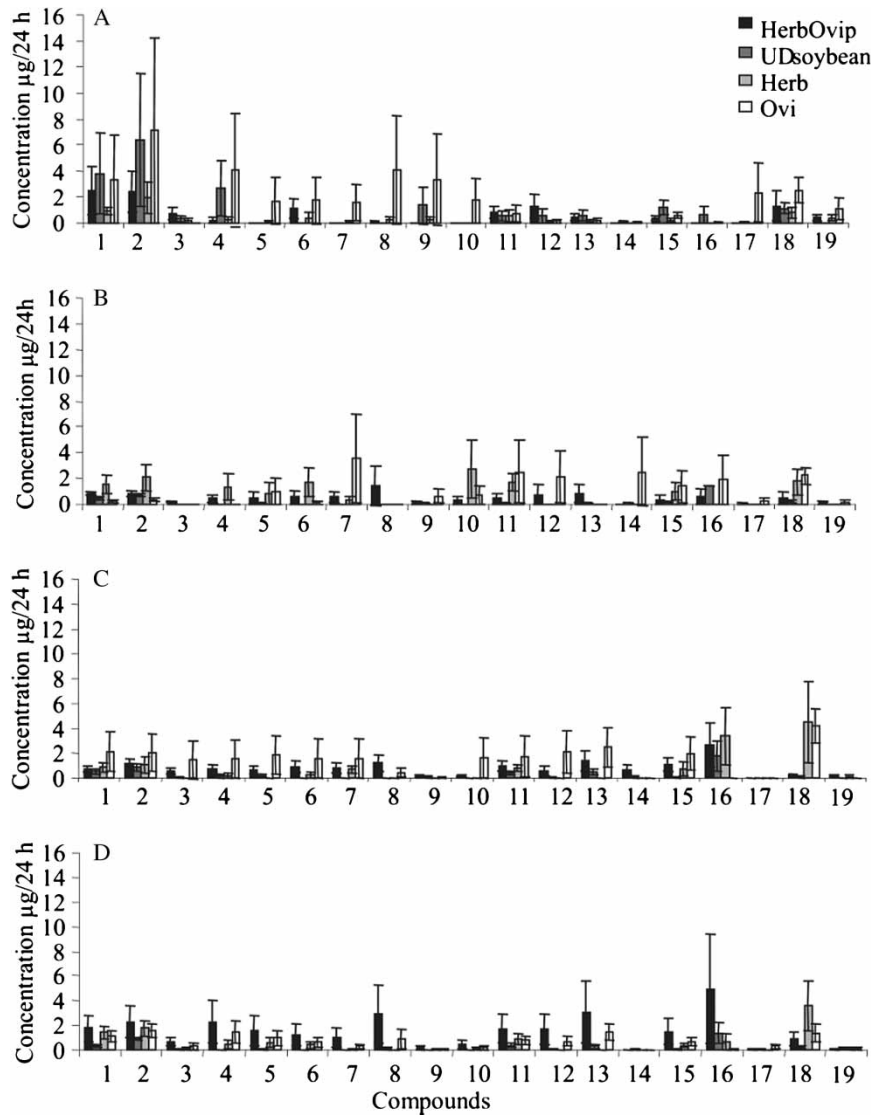


Figure 4. Qualitative and quantitative (mean \pm error standard) comparison of the volatiles blend released by soybean on the four days and different treatments: (A) Fourth day: Herbivory + oviposition (HerbOvi, $n = 7$); undamaged soybean (UD, $n = 8$); herbivory (Herb, $n = 6$); oviposition (Ovi, $n = 8$) (B) Fifth day: HerbOvi ($n = 6$); UD ($n = 8$); Herb ($n = 8$); Ovi ($n = 9$) (C) Sixth day: HerbOvi ($n = 9$); UD ($n = 7$); Herb ($n = 6$); Ovi ($n = 9$) (D) Seventh day: HerbOvi ($n = 9$); UD ($n = 8$); Herb ($n = 8$); Ovi ($n = 9$). Numbering of the compounds as follows: 1. (*E*)-2-hexenal; 2. (*E*)-2-hexen-1-ol; 3. (*Z*)-3-hexen-1-ol; 4. α -pinene; 5. camphene; 6. β -pinene; 7. 6-methyl-5-hepten-2-one; 8. decane; 9. (*Z*)-3-hexenyl acetate; 10. hexyl acetate; 11. limonene; 12. undecane; 13. nonanal; 14. (*Z*)-3-hexenyl butyrate; 15. methyl salicylate; 16. benzothiazole; 17. dodecanol; 18. (*E,E*)- α -farnesene; 19. 4,8,12-trimethyl-1,3,7,11-tridecatetraene (TMTT).

eggs than actual oviposition damage. By the time the volatile profile changes in response to oviposition (4 days) the eggs could be too old for parasitism, because *T. podisi*, like many Scelionidae (Orr et al. 1986), prefers eggs 24–48 h old (Borges et al., unpublished data). *Trissolcus basalis* also has a limited time frame for parasitism, but is slightly longer, since it can heavily parasitize eggs 72–96 h old (Colazza et al. 2004a).

It is also known that general female damage to soybean is more attractive to *T. podisi* than male damage (Moraes et al. 2005), and that *E. heros* females preferentially oviposit on plants previously damaged by conspecific feeding (Laumann et al., unpublished data). These results suggest that in this system there is a variation of the infochemical detour

concept (Vet and Dicke 1992) mediated by the plant, in what would be ‘indirect infochemical detour’. In this way, *T. podisi* appears to be responding to plant volatile cues closely associated to adult *E. heros* females as a way of being present at the time, or just after, it lays its eggs. This adds to the cases of pure infochemical detour that have already been documented for parasitoids of pentatomid eggs (Colazza et al. 1999, 2004a; Borges et al. 2003; Conti et al. 2004). Colazza et al. (2004a) reported that *N. viridula* avoids laying eggs on the same plant on which it feeds, but, as mentioned above *E. heros* prefers to lay eggs of previously damaged plants (Laumann et al., unpublished data). *Euschistus heros* is not as generalist as *N. viridula*, preferring soybean (Panizzi 1997), and with *T. podisi* as its main

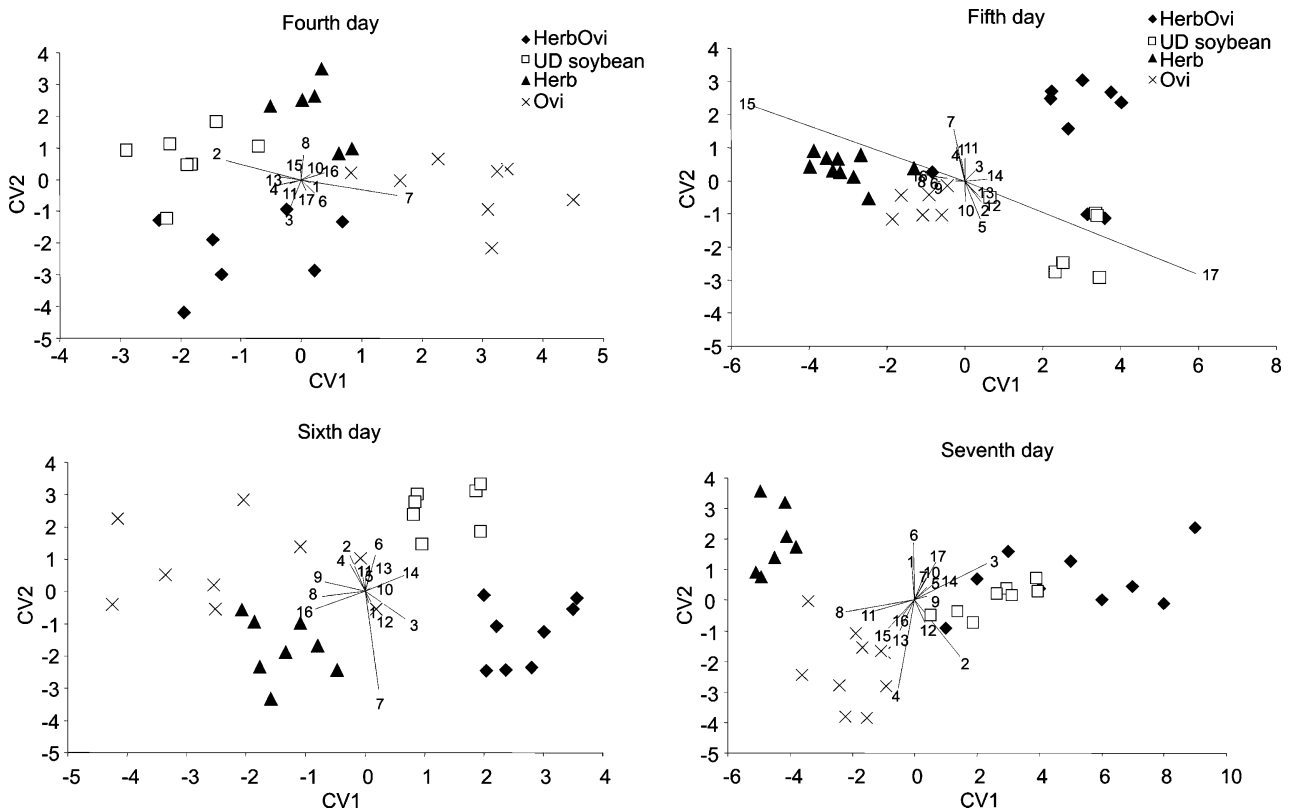


Figure 5. Discriminant analysis biplots showing separation of the four experimental treatments to soybean: Herbivory + oviposition (HerbOvi) damaged; undamaged (UD); herbivory (Herb) damaged; and oviposition (Ovi) damaged. The points represent the score for each replicate in the linear combination, and the lines are the loadings, which represent the importance of each compound in separating the treatments along the two dimensions (CV1 and CV2). With four treatments there are three canonical variates, but only the first two are presented because on each of the four days they represented approximately 90% of the variation. Numbering of the compounds as follows: 1. (*E*)-2-hexenal; 2. (*E*)-2-hexen-1-ol; 3. (*Z*)-3-hexen-1-ol; 4. α -pinene; 5. camphene; 6. β -pinene; 7. 6-methyl-5-hepten-2-one; 8. (*Z*)-3-hexenyl acetate; 9. hexyl acetate; 10. limonene; 11. nonanal; 12. (*Z*)-3-hexenyl butyrate; 13. methyl salicylate; 14. benzothiazole; 15. dodecanol; 16. (*E,E*)- α -farnesene; 17. 4,8,12-trimethyl-1,3,7,11-tridecatetraene.

parasitoid (Pacheco and Corrêa-Ferreira 2000). Therefore, this system appears to be more complex in the relationships among the individuals involved than those described for bean- *N. viridula*- *T. basalis* (Colazza et al. 2004b).

Since residence time was a more powerful indicator of the response of *T. podisi*, it is likely that the parasitoid uses volatiles as arrestant cues when foraging. Thus it appears that the parasitoid is finding the habitat where oviposition by *E. heros* is more likely and searching intensively within these areas.

The results presented here agree with those presented by previous work on induced plant responses to Pentatomidae egg-deposition (Colazza et al. 2004a, 2004b) in that oviposition in itself did not cause changes that are attractive to the parasitoid, and that the combination of egg-deposition and herbivory causes different changes in the volatile profile when compared to herbivory on its own. The studies differ in that here, the combination of herbivory and oviposition caused a switching-off in volatile signalling, since the parasitoid was not attracted. Also, in this study we found a clear differentiation

of the blend of oviposition-damaged plants from control plants, unlike the other cited works. However, there is a difference in the size of the egg masses between the studies, which could be considered when comparing the results: in the study by Colazza et al. (2004a) *N. viridula* laid between 60 and 80 eggs in each mass, whereas *E. heros* laid 12–15 eggs in each mass and 1 or 2 egg masses per plant. In addition, these studies suggest that egg-laying activates metabolic changes in the plant in pathways that produce few volatile signals, but are capable of interacting with octadecanoid signalling either negatively (in this study) or positively (Colazza et al. 2004a, 2004b) in terms of parasitoid attraction. If oviposition activates salicylic acid-dependent responses there could be negative crosstalk with the jasmonate-dependent responses (Bostock 2005), leading to an inhibition of the attractive volatiles dependent on the latter pathway. An alternative explanation is that there is a chemical substance deposited along with the eggs that silences the jasmonate cascade. To determine this, further biochemical and physiological studies on soybean and on the oviduct secretion of *E. heros* are necessary.

However the correlations between compounds (measured by the angle between loadings in Figure 5) may suggest the relative activity of different biosynthetic pathways. (*E*)-2-Hexenal and (*E*)-2-hexen-1-ol had a tendency for being negatively correlated to each other (vectors in opposite directions on days six and seven in Figure 5). (*E*)-2-Hexenal was also associated to damage by feeding only and at the same time it had a very strong negative correlation with methyl salicylate and a strong positive correlation with 6-methyl-5-hepten-2-one. The corresponding six-carbon alcohol, (*E*)-2-hexen-1-ol, showed a positive correlation with methyl salicylate and a negative correlation with 6-methyl-5-hepten-2-one. Thus it would seem that the balance between (*E*)-2-hexenal and (*E*)-2-hexen-1-ol released by the plant (as well as 6-methyl-5-hepten-2-one) could be strongly influenced by the activity of the salicylate pathway. Furthermore the balance between these GLVs, methyl salicylate and 6-methyl-5-hepten-2-one could provide important information to *T. podisi* when foraging for a host. To confirm these results electroantennogram studies will be conducted with the total extracts and synthetic blends of the volatiles.

Overall it appears that oviposition-induced plant volatiles are not being used by *T. podisi* for finding host eggs. This parasitoid appear to have evolved responses very closely associated to female *E. heros*, that may be an adaptation from phoretic behaviour observed in others *Telenomus species* (Orr et al. 1986; Austin et al. 2005). The results presented here, and in previous studies, indicate that infochemical detour is the major strategy used by this parasitoid for location of habitats where stink bugs eggs are more likely to be found.

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