

Mother's choice of the oviposition site: balancing risk of egg parasitism and need of food supply for the progeny with an infochemical shelter?

Abstract. Oviposition site selection of herbivorous insects depends primarily on host plant presence which is essential for offspring survival. However, parasitoids can exploit host plant cues for host location. In this study, we hypothesised that herbivores can solve this dilemma by ovipositing within high plant diversity. A diverse plant species composition might represent an 'infochemical shelter', as a potentially complex volatile blend can negatively affect the host location ability of parasitoids. We examined this exemplarily for the egg-laying response of the generalist leaf beetle, *Galeruca tanaceti*, in relation to (1) host plant availability and (2) plant species diversity in the field. Further, we investigated the effect of odours from mixed plant species compositions on (3) leaf beetle oviposition site selection and on (4) the orientation of its specialised egg parasitoid, *Oomyzus galerucivorus*. In the field, egg clutch occurrence was positively related to the presence and quantity of two major host plants, *Achillea millefolium* (yarrow) and *Centaurea jacea*, and to the number of herbaceous plant species. In two-choice bioassays, female beetles oviposited more frequently on sites surrounded by an odour blend from a diverse plant species composition (including yarrow) than on sites with a pure grass odour blend. In the presence of yarrow odour and an odour blend from a diverse plant mixture (including yarrow) no difference in the oviposition response was recorded. Experienced parasitoid females were attracted to yarrow odours, but showed no response when yarrow odours were offered simultaneously with odours of a non-host plant. In conclusion, it could be shown in laboratory bioassays that the parasitoid responds only to pure host plant odours but not to complex odour blends. In contrast, the herbivore prefers to oviposit within diverse vegetation in the field and in the laboratory. However, the laboratory results also point to a priority of host plant availability over the selection of a potential 'infochemical shelter' for oviposition due to high plant diversity.

Key words: *Galeruca tanaceti* · *Oomyzus galerucivorus* · insect herbivore · egg deposition · egg parasitoid · vegetational diversity · infochemical shelter

Introduction

The oviposition strategy of insects is a result of a complex trade-off between a variety of factors which can be conflicting, as for example, host plant availability, predation risk, larval mobility and host finding capability (Thompson 1988, Scheirs and De Bruyn 2002, Janz 2002). Herbivore mothers may face the dilemma of hiding their eggs from parasitoids on the one hand and providing hatching larvae with food plants on the other. While host plant presence is essential for herbivores, volatile host plant cues can provide parasitoids with valuable information during host search (for reviews see Dicke and van Loon 2000, Hilker and Meiners 2006). In contrast, high plant and plant odour diversity might hinder parasitoids from detecting these cues (Price *et al.* 1980, Sheehan 1986). In this study, we address the issue of how insect herbivores might adjust oviposition site selection relative to host plant presence and plant diversity with respect to offspring needs and natural enemy avoidance.

A diverse plant assemblage can affect the behaviour, reproduction and survival of herbivorous insects in several ways. For instance, a heterogeneous plant species composition in vegetationally diverse habitats can offer alternative host plants, alter predator communities and/or modify host-finding mechanisms of immigrating herbivores (reviewed in Kareiva 1983, Bernays and Chapman 1994, Finch and Collier 2000). Studies of the influence of host and non-host plants, specifically on oviposition behaviour, were mostly performed in agricultural settings for pest control reasons. Thus, they were conducted to detect an antagonistic effect of non-host plants on egg deposition (Andow 1991, Hooks and Johnson 2003, Finch *et al.* 2003, Bird and Krüger 2006). In contrast, little is known about the effect of vegetational diversity on egg deposition in natural habitats and the way herbivores might employ plant diversity for their own purpose. Moreover, it has been reported for various phytophagous insects that general (host) plant volatiles are decisive cues for orientation, host plant acceptance and oviposition (e.g. Bernays and Chapman 1994). However, how odour blends emitted from a diverse plant species community influence the oviposition decision of herbivores has received little attention.

The oviposition decision of phytophagous insects might be affected by both vegetational features and the pressure to escape their predators and parasitoids. Previous studies have demonstrated that natural enemies directly influence oviposition

site selection for several insect species (diamondback moth: Fox and Eisenbach 1992, whitefly: Nomikou *et al.* 2003, leafminer: Videla *et al.* 2006). In heterogeneous environments, the presence of host plants intermingled with non-host plants may hamper searching behaviour and reduce host-finding success of natural enemies (Langer 1996, Prefecto and Vet 2003, Gols *et al.* 2005). For specialist parasitoids, it has been argued that their abundance and effectiveness is reduced in diverse habitats (Sheehan 1986, Andow 1991). In general, chemical cues used during host location may be disrupted in habitats with a diverse plant species composition (Price *et al.* 1980, Sheehan 1986). For instance, non-host plants may emit volatiles, which repel parasitoid wasps (*Trichogramma* spp.: Romeis *et al.* 1998, ichneumonid spp.: Gohole *et al.* 2003, braconid and ichneumonid spp.: Wäckers 2004, Gohole *et al.* 2005, pteromalid spp.: Sanon *et al.* 2006). Volatiles released by non-host plants may also mask the odour of the host plants for parasitoids, as has been shown for tachinid flies parasitising sawflies (Monteith 1960). So far, the phenomenon of odour masking was described mostly for herbivore species (flea beetle: Tahvanainen and Root 1972, Colorado potato beetle: Thiery and Visser 1986, aphids: Nottingham *et al.* 1991, pollen beetle: Mauchline *et al.* 2005). Contrary to the above-mentioned investigations Dicke *et al.* (2003) did not detect an overall effect of volatiles from neighbouring plants on the behaviour of a predatory mite towards volatiles of plants harbouring prey.

In the present study, we investigate the influence of host and non-host plants, especially their odours, on oviposition site selection by the polyphagous leaf beetle, *Galeruca tanacetii* L. (Coleoptera: Chrysomelidae) and on the behavioural response of an egg parasitoid. *G. tanacetii* commonly deposits its egg clutches in autumn on plants it does not feed upon, mostly on dried grass stems that are well above the ground in grassland communities (Scherf 1966, Meiners *et al.* 2006). The eggs are subject to parasitism by the specialised egg parasitoid *Oomyzus galerucivorus* (Hymenoptera: Eulophidae). Previous studies have shown that dense and tall vegetation reduces the risk of parasitism and might therefore provide ‘enemy-free space’ for the leaf beetle (Meiners and Obermaier 2004, Obermaier *et al.* 2006 and unpublished data). Here, we argue that a vegetationally diverse environment might provide an ‘infochemical shelter’ for leaf beetle eggs. Thus, we ask (1) whether beetles choose oviposition sites on the basis of food plant presence and quantity; (2) if plant species diversity influences oviposition site selection; (3) how odour blends originating from host plants, non-host plants and diverse plant mixtures influence oviposition site selection

of the leaf beetle; (4) whether an enhanced plant odour complexity hampers the orientation of the specialised egg parasitoid.

Material and methods

Life-history of *G. tanacetii*

The polyphagous tansy leaf beetle *Galeruca tanacetii* L. (Coleoptera: Chrysomelidae) feeds on species of the families Asteraceae, Brassicaceae, Caryophyllaceae, Dipsacaceae, Liliaceae, Lamiaceae, Polygonaceae and Solanaceae (Lühmann 1939, Pevett 1953, Obermaier and Zwölfer 1999). The female leaf beetles oviposit in autumn on dry vertical grassy structures (Scherf 1966, Obermaier *et al.* 2006, Meiners *et al.* 2006). Food plants are rarely used for oviposition. Females oviposit about once a week after being fed *ad libitum* at 22°C in the laboratory (B. Randlkofer, personal observation). The gravid females are unable to fly and have to walk up the plant structures during the search of egg deposition sites. Hibernation takes place in the egg stage. In the following spring the beetle larvae hatch and three weeks later pupation occurs within leaf litter on the ground or in the soil. The emerging adults enter a reproductive diapause until September (Siew 1966, Meiners *et al.* 2006). The eggs are laid in clutches and are subject to parasitism by the specialised egg parasitoid, *Oomyzus galerucivorus* (Hymenoptera: Eulophidae). The egg parasitoid parasitises the egg clutches of its host shortly after their deposition in autumn. The parasitoid larvae hibernate in the host eggs and adults emerge the following spring.

Fieldwork

Study area

Field studies were conducted in autumn 2004 in Northern Bavaria, Germany (latitude 50°03', longitude 10°35'), in the nature reserve 'Hohe Wann', which is characterised by high proportions of semi-arid grassland (Elsner 1994). Three sites ranging from

1300 to 12000 m² that were similar in most aspects were chosen for the investigation. All three sites showed sufficiently high densities of ovipositing females and similar biotope type (semi-arid grassland) with comparable vegetational structure and plant species composition. The sites were unmown (site 1 and 2) or grazed by sheep occasionally (site 3).

Analysis of host plant presence and plant species composition with respect to leaf beetle egg deposition

Vegetational analyses were conducted within microhabitats ($r = 0.1$ m) around egg clutches (oviposition plots) and within microhabitats without egg clutches (control plots). Oviposition and control plots were selected randomly with random points generated using a geographic information system (GIS, ESRI™ ArcView 3.2, Redlands, USA). A handheld GPS device (Garmin® GPS 12 Personal Navigator®, Garmin International Inc., Olathe, USA) was used to locate these random points within each study site. A sample of 60 oviposition plots and 50 control plots was analysed at sites 1 and 3, whereas a sample of 32 control and 33 oviposition plots was analysed at site 2. At two study sites (sites 1 and 2), samples of oviposition plots represented all occurring egg clutches within the sites. Due to constraints in time and manpower, it was not possible to sample an equal number of oviposition and control plots for all investigated sites. At site 3, sampling had to be restricted to a subset of 60 oviposition plots because of its large area and the exceedingly high number of egg clutches. Within the sampling plots, most herbaceous plants present were identified to species and the remaining to genus. Grasses were not differentiated by species, but pooled as one category. The percentage plant cover was recorded for all occurring plant species. The percentage cover of all herbaceous plant species, except grasses, was pooled into the variable 'total forb cover'.

To study the influence of vegetational composition on parasitism, egg clutches remained at the study sites for at least one additional week after initial sampling to ensure maximal parasitisation. Then, all egg clutches were collected and their degree of parasitism was determined in the laboratory. Unexpectedly, parasitism rates were very low. Therefore no statistical analysis concerning the influence of vegetation parameters on parasitism could be performed.

Bioassays

Plant odours and oviposition site selection

Olfactometer bioassays were used to test how plant odours derived from different plant species compositions influence the selection of oviposition sites of *G. tanacetii* females. Olfactometer bioassay arenas were developed wherein the beetles could perceive the plant odour bouquet, but they had no direct access to the plants (Fig. 1). The test plants were taken from semi-arid grassland sites in the nature reserve ‘Hohe Wann’, Northern Bavaria, Germany. Plants were taken from natural beetle habitats to keep test conditions as close as possible to field conditions. For the test of the effect of diverse plant species composition on oviposition site selection, whole sods were dug and transferred to clay pots (diameter = 18 cm). Sods consisted of at least four different herbaceous plant species, including *Achillea millefolium* (Asteraceae) (a preferred beetle food plant) and *Thymus vulgaris* (Lamiaceae) (a non-food plant), with a maximum of eight different species all surrounded by grasses. To test the effect of pure grass odour on oviposition site selection, complete tussocks of the grass species *Koeleria pyramidata* (Poaceae) were transferred to clay pots. This grass species frequently occurs at the study sites, and female leaf beetles commonly use their stems for egg deposition. In order to obtain a pure yarrow odour blend, single flowering plants were dug and planted in groups of four to five plants in one pot.

The oviposition olfactometer bioassay arenas consisted of plastic trays (50 cm × 32 cm × 7 cm) (Fig. 1). The trays had two circular openings (diameter = 14 cm) covered with fine gauze (mesh size = 0.5 mm). In the centre of the gauze, 5 senesced grass stems (height = 35 cm) were inserted and served as an oviposition substrate for the leaf beetle females. Grass stems were renewed prior to the beginning of each trial. The edges of the arenas were painted with liquid Teflon[®] (Dyneon[™]) to prevent the beetles from escaping. The floor of the plastic tray was covered with tissue paper and sprayed with water twice a day to ensure a moist environment during the experiment. The plastic trays were placed on top of two plexiglass cylinders containing pots with different plant compositions. In each of the 5 to 9 arenas, 5 gravid females were released. The average egg deposition rate per female is not more than one egg clutch consisting of about 60 eggs per week (B. Randlkofer, personal observation). Therefore, the test individuals were allowed to oviposit on three consecutive days from 10 am to 6 pm. On each test day, beetles were distributed at random across the bioassay arena. The

arena was cleaned with ethanol and water after testing. No food was provided within the test arenas, but during 6 pm to 10 am the females were kept in rearing plastic boxes and allowed to feed on yarrow leaves. Beetles were collected in the field (semi-arid grassland sites near Bamberg and Bayreuth, Northern Bavaria, Germany). Experiments were conducted in a green house from September to October of 2004 and 2005.

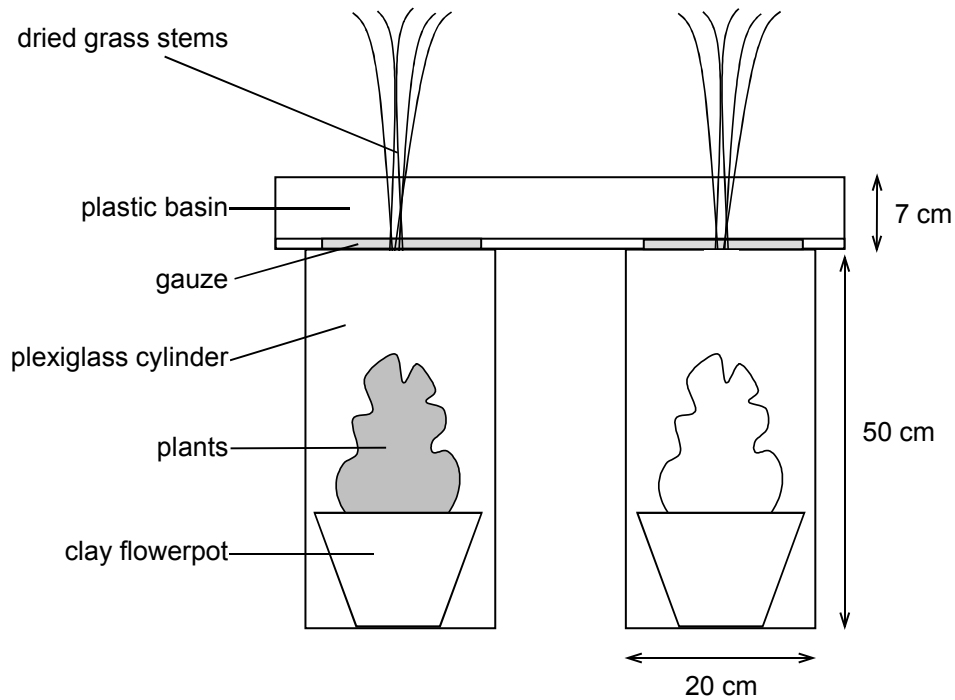


Fig. 1. Side view of the oviposition olfactometer arena used for two-choice tests with gravid *G. tanacetii* females and different plant species compositions.

Plant odours and parasitoid orientation

Parasitoids were reared from *G. tanacetii* egg masses collected in the field in the North of Berlin. After hatching from eggs the parasitoids were kept in a climate chamber (20°C and L18:D6 photoperiod) without plants. Adult parasitoids were reared in Petri dishes with moist filter paper and were provided with honey water as food.

Test parasitoids were trained *via* sensitisation. Sensitisation has been defined by Papaj and Prokopy (1989) as the gradual increase in responsiveness to a stimulus with repeated exposure to that stimulus. Prior to the bioassays, *O. galerucivorus*

females were placed in an exsiccator together with the plant material used for testing for a period of 24 h. Plant material consisted of leaves of thyme (*T. vulgaris*) or yarrow (*A. millefolium*). Individuals tested to the thyme and yarrow odours simultaneously were exposed only to yarrow odours prior to the tests. Plant leaves without any host excretions such as frass were used because the parasitoids frequently encounter clean host plants in the vicinity of host eggs. Naïve wasps were handled exactly like sensitised ones, but they were kept in exsiccators without plant material. Whole leaves from each plant species with a fresh weight of 200 mg were used. The cut ends of the leaves were sealed with Parafilm M[®] to ensure that no volatiles were released from the wounds. Thyme leaves were taken from commercially available plants, whereas yarrow leaves were collected from the lawn adjacent to the building housing the Department of Applied Zoology/Animal Ecology, Freie Universität Berlin, Germany.

The response of naïve (control) female wasps and experienced (sensitised) ones with volatiles from one of two different plant species was tested in a static four-chamber olfactometer. The olfactometer was made of acrylic glass consisting of a cylinder (4 cm high × 19 cm in diameter) divided into four chambers (Steidle and Schöller 1997), which contained a moistened filter paper each (4 cm in diameter). The plant material used for testing was placed only in one of the chambers, while the other three chambers were left without any odour source. A walking arena (1cm high × 19 cm in diameter) was placed on top of the cylinder. This arena was composed of a rim of acrylic glass with plastic gauze (mesh size 0.5 mm) glued on one side and the other side was covered with a glass plate. In the static four-arm olfactometer, parasitoids search actively for host plant and/or host eggs when they encounter the synomone (innate or trained odour). Because the odour from the odour source under the test field also diffuses to the adjacent fields in the walking-arena, the parasitoids do not experience a sharp border between odour fields, but an odour gradient. As a consequence the parasitoids are expected to stay longer in the control fields adjacent to the test field containing an attractive odour rather than in the most distant control field. Therefore the fields adjacent to the test field were treated as buffer zones between the test and the most distant control field. The behaviour of the parasitoids in the buffer zones was not included in the analysis (see also Ninkovic *et al.* 2001, Collatz *et al.* 2006). The experiments were performed at 20-24°C, 64-74% RH. Diffuse light from a 60 W light bulb covered with glassine paper provided uniform illumination of the olfactometer. Female parasitoids were observed for a total of 5 min. For statistical

analysis, only the first minute of each observation was considered as the tested individuals showed habituation to the offered odours over the complete observation period. A total of 16-30 females were tested in each assay.

All observations were recorded using the Noldus Observer programme 3.0 (Noldus Information Technology, Wageningen, The Netherlands). Females that walked for less than 2.5 min were discarded from the data analysis.

Statistical analysis

The Mann-Whitney U-test was used to compare the percentage cover of host plants of *G. tanacetii* in oviposition and control plots. Multiple variable logistic regression models were used to predict the probability of egg deposition by *G. tanacetii* depending on the vegetational variables recorded in the field (Hosmer and Lemeshow 1989). Generally, logistic regression is a statistical technique that predicts the probability of a dichotomous dependent variable (here egg clutch presence or absence) using a combination of continuous independent predictor variables. We calculated pairwise Spearman rank correlations between the variables ‘number of plant species’, ‘host plant cover’ and ‘total forb cover’ to control for a sufficient degree of independence. In the development of logistic regression models, only one variable of a pair of variables that show a correlation of $r_s \geq 0.7$ should be included (Fielding and Haworth 1995). Correlations that appeared in our data set ranged from 0.24 to 0.57. Therefore these variables were retained and employed simultaneously in the calculation of logistic regression models. To develop the regression model, the backward stepwise regression method was used. This method incorporates all predictor variables at the beginning of the analysis and then eliminates them from the model in an iterative process. The fit of the model is tested after the elimination of each variable to ensure that the model still adequately fits the data. When no more variables can be eliminated from the model, or the improvement from one step to the next is negligible, the analysis is complete. The goodness-of-fit of the habitat models was determined by considering the coefficient of determination R^2 after Nagelkerke (1991), which ranges from 0 to 1. In order to measure the classification accuracy of the models irrespective of a particular threshold, the Receiver Operating Characteristic curve (ROC-curve) (Hanley and McNeil 1982, Hanley and McNeil 1983) and the resulting Area Under Curve (AUC-value) was used.

The AUC-value provides a measure of the diagnostic accuracy of the model (Zweig and Campbell 1993) and varies from 0.5 (determination by chance: null-model) to 1.0 (perfect classification) (Zweig and Campbell 1993, Bonn and Schroeder 2001); see also Meiners and Obermaier 2004). All analyses concerning the logistic regression were performed with SPSS 13.0 for Windows.

The Wilcoxon matched-pairs test (Sokal and Rohlf 1995) was used to compare the number of egg depositions in the two-choice olfactometer tests. The comparison of the residence time of naïve and experienced *O. galerucivorus* females in the test field and the control field of the four-chamber olfactometer was also performed with the Wilcoxon matched-pairs test. For both tests, we used STATISTICA for Windows, StatSoft Inc., 1999, Tulsa, USA.

Results

Host plant availability and oviposition site selection

The occurrence of host plants was significantly different between oviposition and control plots at all three study sites. At least one of the host plant species of *G. tanacetii* (*A. millefolium* and *C. jacea*) occurred significantly more often in oviposition plots than in control plots. At site 1, host plants were present in 72% of the oviposition plots compared to 49% in the control plots ($\chi^2 = 6.27$, $df = 1$, $P = 0.012$). At site 2, host plants were present in 97% of the oviposition plots compared to 78% in the control plots ($\chi^2 = 8.72$, $df = 1$, $P = 0.003$). At site 3, host plants were present in 94% of the oviposition plots, compared to 64% in the control plots ($\chi^2 = 9.31$, $df = 1$, $P = 0.002$). Overall, 50-80% of control plots were occupied by either one or both of the host plant species, whereas 70-100% of the oviposition plots were occupied by host plants.

Oviposition and control plots significantly differed in the percentage of *A. millefolium* and *C. jacea* plant cover. In oviposition plots, the mean percentage plant cover for both host plant species was between 6.4% and 13.4%, whereas control plot plant cover averaged between 2.3% and 8.0% (Fig. 2). At site 1, oviposition plots had an average host plant cover of $6.4 \pm 1.2\%$ (mean \pm SE) compared to control plots with

an average of $2.3 \pm 0.5\%$ ($U = 1076.5$, $P = 0.004$). At site 2, the mean percentage of host plant cover in oviposition plots was $11.1 \pm 2.1\%$ compared to control plots with a mean percentage of $6.8 \pm 1.6\%$ ($U = 977.0$, $P = 0.001$). At site 3, oviposition plots had an average of $13.4 \pm 1.4\%$ host plant cover compared to control plots with an average of $8.0 \pm 1.3\%$ ($U = 364.5$, $P = 0.031$). Overall, oviposition plots had a mean host plant cover that was about two times higher than control plots.

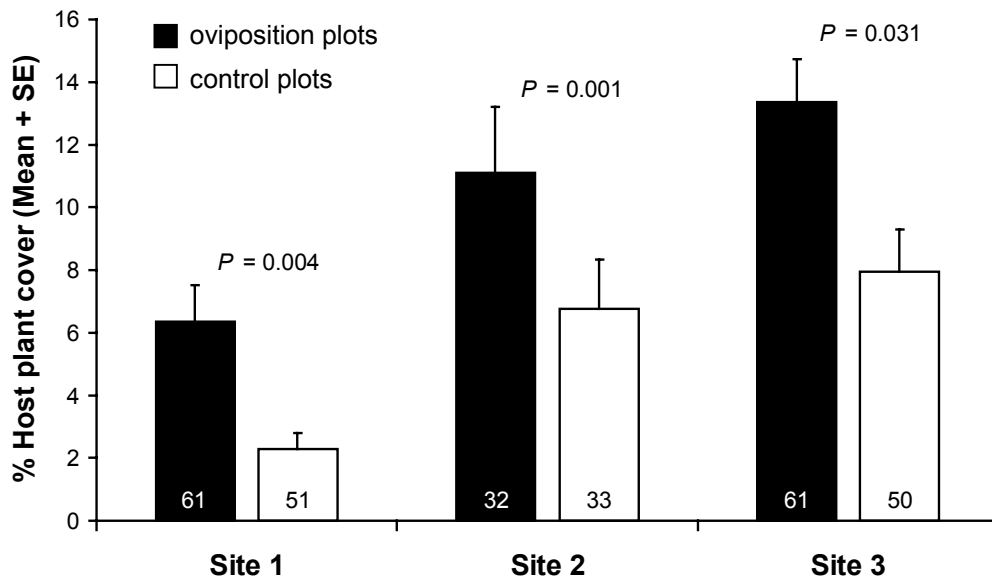


Fig. 2. Percentage plant cover of the two host plants *A. millefolium* and *C. jacea* (mean + SE) within oviposition plots and control plots for the three investigation sites. Numbers within bars indicate the sample size. *P*-values are shown for Mann-Whitney U-test comparing oviposition and control plots.

Plant species composition and oviposition site selection

The mean number of herbaceous plant species was significantly higher in plots with egg clutch occurrence than in plots without an egg clutch (Fig. 3). At site 1, oviposition plots contained on average 3.6 ± 0.2 (mean \pm SE) different herbaceous plant species, whereas control plots contained on average 3.0 ± 0.2 ($U = 1222.0$, $P = 0.047$). At site 2, oviposition plots had a mean of 4.3 ± 0.3 herbaceous plant species compared to control plots with a mean of 3.5 ± 0.3 ($U = 386.5$, $P = 0.059$). At

site 3, the mean number of herbaceous plant species was 6.4 ± 0.3 in plots with an egg clutch and 5.3 ± 0.3 in plots without an egg clutch ($U = 1052.5$, $P = 0.005$).

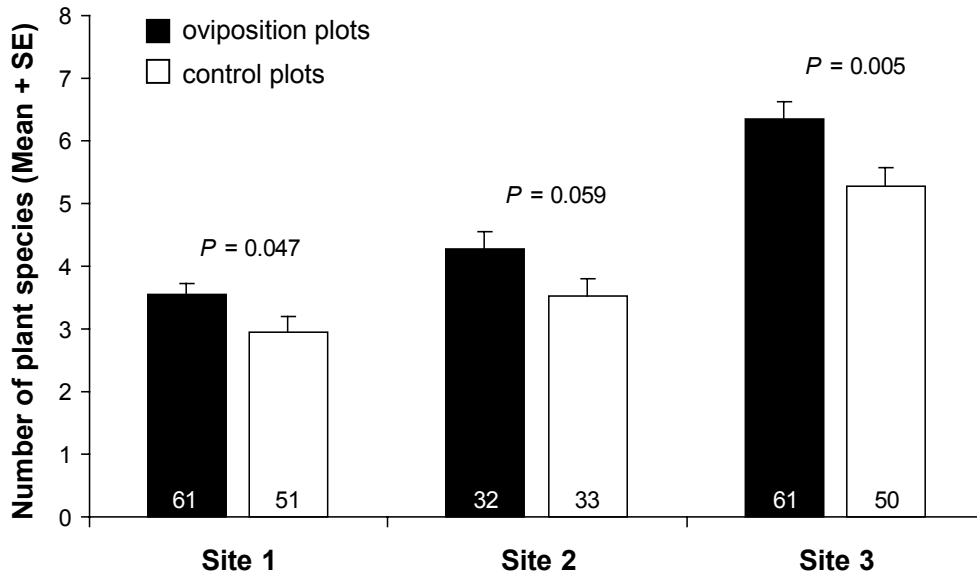


Fig. 3. Number of herbaceous plant species (mean + SE) occurring in oviposition plots and control plots for the three investigation sites. Numbers within bars indicate the sample size. P -values are shown for Mann-Whitney U-test comparing oviposition and control plots.

Plant species composition, host plant quantity and oviposition site selection

When the variables ‘number of plant species’, ‘host plant cover’ and ‘total forb cover’ were included simultaneously in the calculation of logistic regression models, the variable ‘total forb cover’ was excluded from each model calculated for the three study sites. Instead, plant species diversity and host plant cover were the best predictors for oviposition site selection. The two variables ‘number of host plant species’ and ‘host plant cover’ showed a significant and positive influence on egg clutch occurrence for all three sites (Table 1). The probability of egg deposition increased with an increase in plant species diversity and percentage of host plant cover (site 1: $R^2_{\text{Nagelkerke}} = 0.151$, $P_{\text{model}} = 0.001$, $\text{AUC} = 0.673$, site 2: $R^2_{\text{Nagelkerke}} = 0.135$, $P_{\text{model}} = 0.031$, $\text{AUC} = 0.670$, site 3: $R^2_{\text{Nagelkerke}} = 0.159$, $P_{\text{model}} = 0.001$, $\text{AUC} = 0.696$, Table 1).

Table 1. Model characteristics for significant multivariate logistic regression models that comprise both the variables ‘number of plant species’ and ‘percentage of host plant cover’ (*A. millefolium* and *C. jacea*) for the investigated study sites. R^2_N = coefficient of determination after Nagelkerke; P_{model} = p-value of the model; AUC = Area Under Curve-value; P_{ROC} = p-value of the Receiver Operating Characteristic curve (ROC-curve); P_{Coeff} = p-value of the coefficient.

Site	R^2_N	P_{model}	AUC \pm SE	P_{ROC}	Variables included in model	Coefficient \pm SE	P_{Coeff}
1	0.151	0.001	0.673 \pm 0.050	0.002	Plant species diversity	0.233 \pm 0.136	0.088
					Host plant cover	0.101 \pm 0.041	0.013
2	0.135	0.031	0.670 \pm 0.068	0.018	Plant species diversity	0.336 \pm 0.174	0.053
					Host plant cover	0.044 \pm 0.027	0.095
3	0.159	0.001	0.696 \pm 0.051	0.001	Plant species diversity	0.243 \pm 0.103	0.018
					Host plant cover	0.051 \pm 0.021	0.018

Plant odours and oviposition site selection

Although a total of 520 *G. tanacetii* females were used for the bioassays, oviposition response was low for both experiments. In treatments with grass versus a diverse plant species composition, 32% of the 174 conducted trials had at least one egg deposition. Thus only 56 trials could be statistically analysed. In treatments with yarrow versus a diverse plant species composition, 25% of the 135 conducted trials had at least one egg deposition. Therefore 34 trials could be statistically evaluated.

When beetles could choose between an odour bouquet from a mixed plant species composition (four to eight different species of naturally occurring host plants and non-host plants) and pure grass odour, a significantly higher number of egg depositions occurred on dried grass stems located within the odour blend derived from the mixed plant species composition (Fig. 4A). On average, 0.77 ± 0.08 (mean \pm SE) egg clutches were deposited in the diverse odour environment compared to 0.45 ± 0.07 egg clutches in the grass only odour environment (Wilcoxon-test, $Z = -2.162$, $P = 0.031$). In contrast, when female leaf beetles were able to choose between an odour blend emanating from a mixed plant species composition (including *A. millefolium*) and the odour of their preferred host plant *A. millefolium*, 0.71 ± 0.09 egg clutches

were laid in the pure yarrow odour environment, whereas 0.47 ± 0.11 egg clutches were deposited in the odour environment originating from a diverse plant species composition (Fig. 4B). However, this tendency was not statistically significant (Wilcoxon-test, $Z = -1.241$, $P = 0.215$).

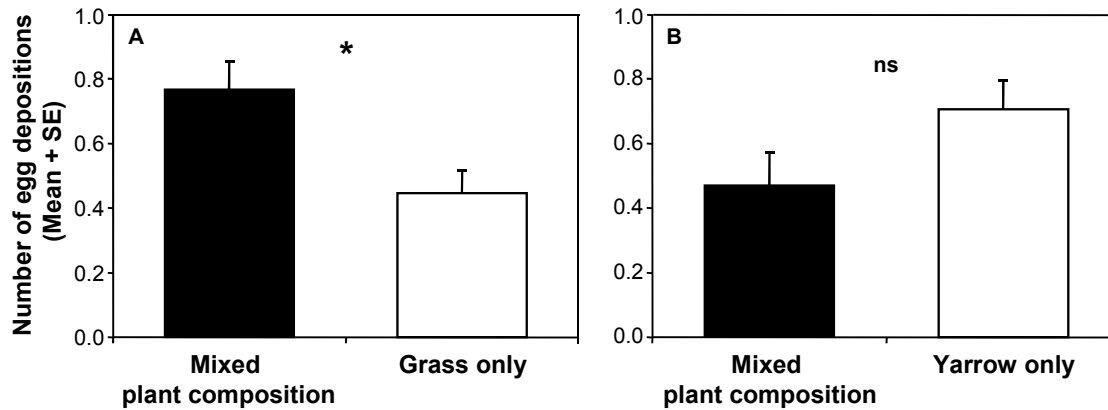


Fig. 4. Choice of egg deposition site of *G. tanacetii* females in response to plant odours emitted by different plant species compositions. (A) odour blends from a diverse plant species composition (four to eight different herbaceous plant species, including host plants) tested against odours from one grass species (*K. pyramidata*) (56 replicates). (B) odour blends from a diverse plant species composition (host plants included) tested against odours from the preferred host plant (*A. millefolium*) (34 replicates). Bars represent the mean number of egg depositions and the standard error. The asterisk indicates a significant difference at $P < 0.05$ between the number of eggs laid according to Wilcoxon matched-pairs test, ns = not significantly different.

Plant odours and parasitoid orientation

When the response of the egg parasitoid *O. gallerucivorus* towards yarrow odours was tested, experienced females spent significantly more time in the test field than in the control field with pure air (Wilcoxon-test, $Z = 2.366$, $P = 0.018$, Fig. 5). Naïve females did not show a response towards yarrow odours (Wilcoxon-test, $Z = 1.111$, $P = 0.267$). Thus, experienced female parasitoids were attracted to the host plant odours whereas naïve ones were not. In contrast, neither naïve nor experienced parasitoids responded to odours of thyme, a non-host plant of *G. tanacetii* (Wilcoxon-test, naïve: $Z = 0.140$, $P = 0.889$; experienced: $Z = 0.085$, $P = 0.932$). When both plant species were offered simultaneously, neither parasitoids that had been sensitised in the presence of yarrow odours, nor naïve ones showed a longer residence time in the test field compared to the

control field (Wilcoxon-test, naïve: $Z = 0.110$, $P = 0.913$; experienced: $Z = 0.734$, $P = 0.463$).

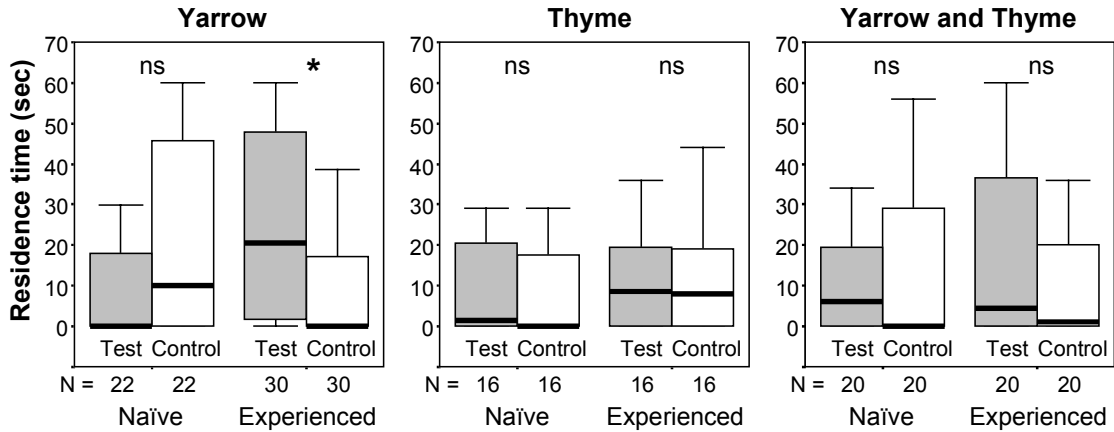


Fig. 5. Response of naïve and experienced *O. galerucivorus* females to host and non-host plant odours in a static four-chamber olfactometer during an observation period of 60 sec. Statistics are given for the Wilcoxon matched-pairs test evaluating the residence time of naïve or experienced females in the test field with plant odours compared to the control field with pure air. The horizontal line within the box represents the median, the upper and lower border of the box are the 75th and 25th percentiles, respectively and the error bars show the minimum and maximum. * = significant attraction at $P = 0.018$, ns = not significantly different at $P < 0.05$, N = number of tested individuals.

Discussion

The selection of appropriate oviposition sites can be a conflicting task for phytophagous insects, because they have to consider both the potential risk of egg predation and the future availability of food plants for their larvae (Thompson 1988, Jones 1991). In this study we primarily asked whether an ovipositing herbivore female can simultaneously ensure the protection of her eggs from natural enemies and the availability of larval host plants by taking advantage of a possible ‘infochemical shelter’ in diverse vegetation.

The egg is a relatively defenceless stage in insect development, but eggs possess a variety of protective agents to repel parasitoids, predators or pathogens (Blum and Hilker 2002). The most immediate mortality factor for the egg clutches of *G. tanacetii* is parasitism caused by the specialised egg parasitoid *O. galerucivorus*.

Parasitism rates can reach 90% (Meiners *et al.* 2006). A previous field survey (Meiners and Obermaier 2004) revealed that the presence of the host plant *A. millefolium* enhanced the probability of egg parasitism by *O. galerucivorus*. Furthermore, we have shown in the present study that experienced female parasitoids are attracted to odours from *A. millefolium*. The results of the previous field study and the present laboratory findings indicate that *O. galerucivorus* can exploit host plant volatiles for host location. The relevance of general host plant volatiles for the host finding process of insect parasitoids has been reported for ichneumonid and braconid wasps (Elzen *et al.* 1983, Benrey *et al.* 1997, Takabayashi *et al.* 1998, Roßbach *et al.* 2005). In the field, however, *G. tanaceti* females laid their egg clutches preferentially in the immediate vicinity of their main food plants (*A. millefolium* and *C. jacea*), which were present more often and in higher densities in oviposition plots compared to control plots within the investigated natural grassland habitats. By ovipositing close to the host plants *G. tanaceti* ensures ready access to nutritional resources for hatching larvae, despite the fact that their eggs may also be more subject to parasitism. In field cage experiments, the dispersal abilities of newly hatched larvae appeared to be quite low (Obermaier *et al.* unpublished data). Feeding larvae stayed on a once found food plant during all larval developmental stages and only moved to other plants when resources became depleted. In a previous laboratory study, the orientation of newly hatched *G. tanaceti* larvae towards volatiles released by host plants was tested in a bioassay (Müller 1999). In this study Müller (1999) excluded contact or visual stimuli and could show that naïve individuals used olfactory cues to detect and orient towards food plants.

Moreover, the field investigations revealed that leaf beetle females prefer to oviposit in microhabitats with a higher host plant abundance and also within patches with a more diverse plant species composition. The number of herbaceous plant species recorded in oviposition plots significantly exceeded the number of herbaceous plant species in control plots for all three sites investigated. To our knowledge there exists only one other field study which evaluated the combined influence of host plant presence and plant species composition in a natural habitat on oviposition site selection (Kopper *et al.* 2000). Contrary to the results presented here, Kopper *et al.* (2000) did not find a preference for microhabitats with high plant diversity by a specialist nymphalid butterfly in a native tallgrass prairie. A more diverse plant species composition possibly implies a more diverse blend of volatiles in oviposition plots compared to control plots. In turn, a more complex odour blend derived from

oviposition plots might have a negative effect on the host location process of the egg parasitoid (Price *et al.* 1980, Sheehan 1986). The volatiles emitted from the non-host plants might interfere with the perception of the host plant odours. This phenomenon has been almost exclusively described for phytophagous insect species (e.g. Thiery and Visser 1986, Nottingham *et al.* 1991, Mauchline *et al.* 2005, but see Monteith 1960). In the olfactometer bioassays of our study, neither naïve nor experienced egg parasitoids were attracted to odours of a leaf beetle host plant (*A. millefolium*) when offered simultaneously with odours of a non-host plant (*T. vulgaris*). In contrast, there was a significant attraction of experienced but not of naïve parasitoids to the pure host plant odour. These results suggest that the egg parasitoid does not respond to the volatile cues emitted from the host plant of its host when the diversity of the volatile blend is enhanced by adding a non-host plant species, at least if it has not experienced this odour blend before. By ovipositing in microhabitats with a diverse plant species composition the leaf beetle might exploit the parasitoid's shortcomings in dealing with enhanced odour complexity for the benefit of its offspring.

For many monophagous as well as for polyphagous herbivorous insect species, it is well documented that host plant volatiles and plant odours in general play an important role in orientation to host plants and oviposition (for reviews see Visser 1986, Bernays and Chapman 1994, leaf beetle: Kalberer *et al.* 2005, diamondback moth: Couty *et al.* 2006). More specifically it was shown for several phytophagous insects that host plant odours alone enhance the rate of egg deposition (papilionid butterfly: Feeny *et al.* 1989, leafmining moth: Kagata and Ohgushi 2002, noctuid moth Srinivasan *et al.* 2006, seedcorn-fly: Gouinguéné and Städler 2006). We set out to determine whether plant odours guide beetle females of *G. tanaceti*, when selecting oviposition sites using a laboratory assay. We expected the bioassay to further reveal how leaf beetle females respond to odour blends of diverse plant compositions. In the two-choice oviposition olfactometer bioassays, gravid *G. tanaceti* females could choose between different plant odour blends offered as volatile environmental cues during egg deposition. The olfactometer test clearly showed that the female beetles responded during oviposition to the volatiles released by the plants. *G. tanaceti* preferred the odours of a diverse plant species mixture for oviposition, which always included food plants when tested against the odours of grass plants, which they mostly use as an oviposition substrate. However, in the presence of an odour blend originating from a diverse plant species composition and the simultaneously offered odour blend

emanating from only the host plant *A. millefolium*, the difference in the number of egg depositions was not statistically significant. Therefore the laboratory results, in contrast to the findings described from the field, point to a higher importance of host plant odour for the oviposition decision of the leaf beetle in comparison to plant diversity. This may be explained by different amounts of host plant biomass within the pots; in the pure host plant pots, 4-5 yarrow plants were included, whereas in the diverse plant species mixture on average one yarrow plant was present. The attraction of the pure host plant pot might have been stronger and could have confounded the effect of high plant diversity.

Despite that, it is possible that the increased number of egg clutches found in vegetation with higher plant diversity in the field does not represent an active choice of the leaf beetle females but rather a passive preference for diversity. An enhanced cover of host plants appears to be associated with an enhanced number of herbaceous plant species. At two of three field sites, a weak positive correlation between the variables 'host plant cover' and 'number of plant species' could be observed. Those two variables further showed a moderate positive correlation with the total cover of forbs at the three investigated sites. Nevertheless, when the three variables were incorporated in a logistic regression analysis, the variable 'total forb cover' was removed during the stepwise model calculation at all sites. The significant final 'best' logistic regression models retained only the two variables, 'number of plant species' and 'host plant cover' for each of the three investigated sites. The analysis revealed that the probability of an egg deposition increases with increasing plant diversity and host plant quantity. These two variables seem to be sufficient to describe egg clutch occurrence in the field, because the regression models could not be improved by adding the third variable at all three sites. In this study, we only surveyed the beetles' responses to plant volatiles. However, contact-arrestants present on host plants may also be released by contact with host plants (Dethier *et al.* 1960), which might hold responding beetle individuals in the vicinity of oviposition places. This would add another level of decision-making that remains to be studied to explain the oviposition preferences found in the field.

In conclusion, according to the laboratory experiments, host plant availability seems to be superior to the selection of a potential 'infochemical shelter' for oviposition due to high plant diversity. In spite of that, the field results indicated that both factors are important for oviposition site selection of *G. tanacetii*. However,

regardless of the mechanism(s) underlying oviposition location (i.e. an active choice of oviposition sites within high plant diversity versus a passive consequence of ovipositing close to host plants), oviposition within high vegetational diversity seems to represent a selective advantage for the leaf beetle. This could solve an herbivorous insect's dilemma of reducing egg parasitism and providing food for larvae at the same time.

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