

### **Plant architecture and vegetation structure: two ways for insect herbivores to escape parasitism**

**Abstract.** Interactions between herbivorous insects and their parasitoids take place in a highly structured and complex environment. Habitat structure can be an important factor affecting ecological interactions between different trophic levels. In this study the influence of plant architecture and surrounding vegetation structure on the interaction between the tansy leaf beetle, *Galeruca tanacetii* L. (Coleoptera: Chrysomelidae), and its egg parasitoid, *Oomyzus galerucivorus* Hedqvist (Hymenoptera: Eulophidae), was investigated on two small spatial scales in the field. It was expected that tall and structurally complex plants or vegetation represent an enemy-free space for the herbivore by turning host search more difficult for the parasitoid. On the scale of individual plants, plant height had a positive influence on herbivore oviposition and egg clutch height a negative impact on parasitism. Additionally, probability of oviposition of the beetle was higher on simple plants than on plants with ramifications, while the parasitoid remained unaffected by the degree of ramification. On the microhabitat scale ( $r = 0.1$  m around an oviposition site), both height and density of the vegetation affected beetle egg deposition positively and egg parasitism negatively. The herbivore and its parasitoid, therefore, were influenced in opposite ways by habitat structure on both spatial scales investigated, suggesting the existence of an enemy-free space for the herbivores' eggs on high plant individuals as well as in high and complex vegetation. This study contributes to recognise the importance of structural components of the environment for interactions among different trophic levels.

**Key words:** Chrysomelidae · enemy-free space · *Galeruca tanacetii* · environmental heterogeneity · oviposition site · plant architecture · *Oomyzus galerucivorus* · structural complexity · vegetation structure

## Introduction

Host-parasitoid interactions do not take place in a homogeneous but in a highly structured and complex environment (Casas and Djemai 2002). The structure of individual plants and the vegetation structure of habitat patches in general can influence the movement of herbivores (Crist *et al.* 1992), their decision to enter a habitat (Cronin 2003), their duration of stay (Bach 1984), their abundance (Anthes *et al.* 2003, Dennis 2004, Raghu *et al.* 2004) and their mortality (Kaitaniemi *et al.* 2004). Structure can, however, also indirectly influence herbivorous insects *via* their natural enemies. On the scale of individual plants, Andow and Prokrym (1990) and Lukianchuk and Smith (1997) showed that a complex plant architecture did not only reduce the probability that egg parasitoids found host eggs, but it also functionally reduced the parasitoids' searching time corresponding to the complexity of the plant. Gingras *et al.* (2002) drew the same conclusions from modelling the influence of plant architecture on parasitism rate and from validating this in three natural tritrophic systems. Also on larger spatial scales vegetation structure influenced the probability that hosts and patches with hosts were found (Kemp and Simmons 1978, Price *et al.* 1980, Finke and Denno 2002) as well as the abundance of their natural enemies (Langellotto and Denno 2004). The importance of structural complexity for host-parasitoid interactions, however, has only recently started to be investigated (Casas and Djemai 2002, Cronin 2003, Meiners and Obermaier 2004, Tschanz *et al.* 2005, Riihimäki *et al.* 2006).

Potential hosts of parasitoids can avoid parasitism by preferring oviposition sites where parasitoids are rare or absent (Quicke 1997). The use of such an 'enemy-free space' was defined by Jeffries and Lawton (1984) as 'way of living that reduces or eliminates a species' vulnerability to one or more species of natural enemies' and was shown to exist for several systems (Berdegue *et al.* 1996, Hopkins and Dixon 1997, Gratton and Welter 1999, Heisswolf *et al.* 2005). Regarding habitat structure, herbivores may make use of enemy-free space by oviposition on architecturally complex plants or within structurally complex vegetation where the risk of parasitism may be reduced.

The polyphagous tansy leaf beetle, *Galeruca tanaceti* L. (Coleoptera: Chrysomelidae), deposits its egg clutches in late autumn mainly on dry stalks of non-

host plants within mesoxerophytic grassland sites where the egg clutches then hibernate. There, the eggs are exposed to *Oomyzus galerucivorus* Hedqvist (Hymenoptera: Eulophidae), the only egg parasitoid of *G. tanaceti* in the study area. It was expected that a high and complex plant architecture and vegetation structure – which may both impede host finding by the parasitoid – provides enemy-free space for the egg clutches of the herbivore. Plant architecture was previously defined by the size, heterogeneity and structural complexity of the plant (plant form) (Andow and Prokrym 1990, Gingras *et al.* 2002). In this study, this definition was extended to larger spatial scales and plant architecture and vegetation structure were categorised due to their height (height of the structure) or their structural complexity (number of ramifications, vegetation cover or stalk number; Table 1).

In order to more completely understand the role of structure for host-parasitoid interactions, it was asked whether (1) the probability of herbivore oviposition increases and (2) the probability of parasitism decreases with increasing height and structural complexity on the respective spatial scale.

## **Material and Methods**

### **Study system**

The study was conducted on extensively managed meadows and mesoxerophytic grassland sites in diverse successional stages within the ‘Hohe Wann’ nature reserve (Northern Bavaria, Germany, 50°03'N, 10°35'E). The size of the nature reserve is approximately 1000 ha.

The tansy leaf beetle, *Galeruca tanaceti*, is polyphagous and feeds on species of the families Asteraceae, Brassicaceae, Caryophyllaceae, Dipsacaceae, Liliaceae, Lamiaceae, Polygonaceae and Solanaceae (Lühmann 1939, Pevett 1953, Obermaier and Zwölfer 1999). In the study area, one of the main host plants of *G. tanaceti* is yarrow, *Achillea millefolium* L. (Asterales: Asteraceae), (Meiners and Obermaier 2004), but larvae can also be found feeding on *Centaurea jacea* L. (Asterales: Asteraceae) and *Salvia pratensis* L. (Lamiales: Lamiaceae).

In autumn, females of the tansy leaf beetle deposit their egg clutches on vertical structures within the herbaceous vegetation layer, mostly on grass and other non-host plants (E. Obermaier, personal observations), where the egg clutches then hibernate (Meiners *et al.* 2006). The gravid females are unable to fly and have to walk up the plant structures for oviposition. After hatching in April-May, the larvae have to find suitable host plants in the surrounding of the oviposition site where they feed for about three weeks until pupation (Obermaier and Zwölfer 1999). After pupation, the adults can be found from early June onwards before they enter a reproductive diapause in mid-summer.

The eulophid wasp *O. galerucivorus* parasitises different *Galeruca* species (Sinacori and Mineo 1993), however, its main host in Germany is the tansy leaf beetle. *O. galerucivorus* parasitises the egg clutches of its host shortly after beetle oviposition in autumn. The parasitoid larvae hibernate in the host eggs and adults emerge next spring (Meiners *et al.* 2006). The 1.5 mm long egg parasitoids search at close range for host egg clutches by walking up and down vertical structures within the vegetation and using chemical contact cues from the host faeces (Meiners *et al.* 1997 and unpublished data).

### **Parameters investigated on the individual plant scale**

Plant architecture and vegetation structure were examined on two grassland sites called Schafhof and Prappach. The two sites were similar in most aspects as they showed sufficiently high densities of ovipositing females, a moderate density of the main host plant, *A. millefolium*, comparable slopes, the same biotope type (semiarid grassland), were located at approximately the same altitude (Schafhof 280 m, Prappach 300 m above NN) and are only 1900 m apart from each other. 100 (Schafhof) or 40 (Prappach) random points were selected on aerial photos of the two sites using the Geographical Information Software Arc View GIS 3.2 (ESRI, Redlands, California). In the field, the random points were addressed with a portable GPS. At 60 (Schafhof) or 20 (Prappach) of the random points the point was shifted to the nearest plant with an egg clutch of *G. tanaceti* and this plant and egg clutch were selected for investigation. The remaining random points per site were investigated as controls without egg clutches. From all selected plants with egg clutches as well as from random plants at

control points egg clutch height (if available), plant height, pattern (simple/ramified) and number of ramifications were recorded.

### **Parameters investigated on the microhabitat scale ( $r = 0.1$ m)**

Around the egg clutch points as well as around the control points different measures of vegetation structure were recorded within a circle of 0.1 m radius. The average height (i.e. the weighted mean vegetation height after Sundermeier 1999) and the maximal height of the herbaceous layer were measured. The number of plant stalks was counted and the vertical cover of herbs, grasses and open ground was estimated. The horizontal vegetation cover was estimated in 0.1 m steps from 0 m up to 1.0 m using a white wooden board as background (Sundermeier 1999). Additionally, the occurrence of *A. millefolium*, the main host plant of *G. tanaceti*, was registered.

As the parasitoids may not only be influenced by vegetation structure but also by the density of host egg clutches, egg clutch abundance of *G. tanaceti* was further determined in three radii of 1 m, 1.5 m and 2 m around the random points with egg clutch occurrence.

Finally, the focal egg clutches from the studied egg clutch points were collected from the two sites at the end of October and were kept outdoors in the shade until the end of November. Then they were put singly in vials that were sealed with a fine net and kept for several weeks at room temperature until beetle larvae and adult parasitoids had hatched. The net was sprayed with water every three days to prevent egg clutches from drying out.

Parasitism was registered as incidence, i.e. whether at least one parasitoid had hatched from the egg clutch. To estimate the rate of parasitism per clutch, egg clutches of the site Schafhof ( $n = 60$ ) were dissected after parasitoids had hatched. Rate of parasitism was calculated as number of parasitoids hatched or completely developed within the eggs divided by the total number of eggs per egg clutch.

## Statistical analysis

The influence of structural parameters was analysed using multiple logistic regressions (Jongman *et al.* 1995, Hosmer and Lemeshow 2000) or multiple linear regressions (Sokal and Rohlf 1995). Prior to analysis, collinearity of habitat variables was eliminated by principal components analysis.

To evaluate the goodness-of-fit of the logistic regression models the coefficient of determination  $R^2$  after Nagelkerke (1991) was considered. ROC (receiver operating characteristic) plots, i.e. the area under the resulting plot (area under curve = AUC), were used to determine the classification accuracy of the model (Zweig and Campbell 1993, Guisan and Zimmermann 2000, Bonn and Schröder 2001). AUC values vary from 0.5 (determination by chance) to 1.0 (perfect classification). For model validation on the scale of the microhabitat, models were calculated for each site separately and then externally validated with the data of the other site (Fleishman *et al.* 2003, Schröder and Reineking 2004). The success of the validation was measured using again the AUC value (Bonn and Schröder 2001, Manel *et al.* 2001).

Multiple linear regressions were used to analyse the effect of structural parameters on rate of parasitism. In this case all variables were tested for normal distribution prior to analysis and all variables consisting of percentage values were arcsin-transformed (Sokal and Rohlf 1995). As above, collinearity of variables was avoided by principal components analysis. All procedures were calculated with the software package SPSS 14.0 (SPSS Inc. 2006).

## Results

### Plant architecture: Herbivore oviposition

Plant architecture was characterised by plant height and plant structural complexity (Table 1). Oviposition probability significantly increased with increasing plant height (coefficient = 5.593,  $P_{\text{variable}} = 0.001$ , Fig. 1A) and was higher on simple plant stems than on plant stems with ramifications (coefficient = 0.973,  $P_{\text{variable}} = 0.094$ )

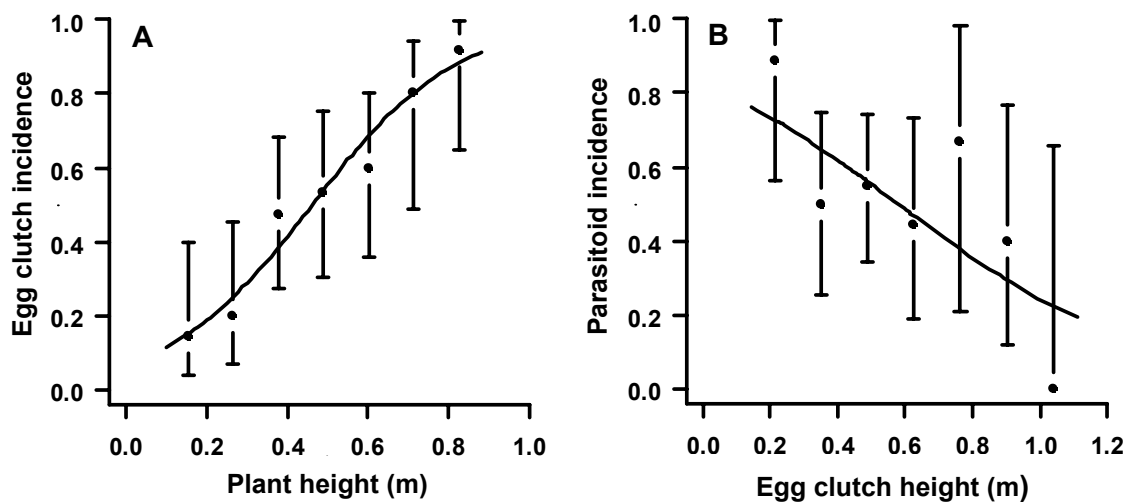
( $R^2_{\text{Nagelkerke}} = 0.334$ ,  $P_{\text{model}} = 0.001$ ,  $AUC = 0.799$ ,  $P_{AUC} = 0.001$ ,  $n = 100$ ). The second variable added to the fit of the overall model was therefore included. The variable ‘number of ramifications’, in contrast, was excluded by the analysis. Therefore, beetle females used mainly high plants for oviposition, but did additionally show a slight preference for plants with low plant structural complexity.

**Table 1.** Overview on structural parameters studied on the two spatial scales for their effect on egg distribution of *G. tanacetii* and parasitism by *O. galerucivorus*. Structural parameters were categorised according to the height of the respective structure and the structural complexity of the plant or habitat patch (after Gingras *et al.* 2002, modified for the different scales). Parameters, which are correlated significantly within a scale, are indicated by an asterisk (\*) and are combined by principal component analysis to the factor vegetation structure.

Scale	Structural parameters studied	
	Height	Complexity
<b>Individual plant</b>	<ul style="list-style-type: none"> <li>• Plant height</li> <li>• Egg clutch height</li> </ul>	<ul style="list-style-type: none"> <li>• Number of ramifications</li> <li>• Patterns of ramifications (simple/ramified)</li> </ul>
<b>Microhabitat (<math>r = 0.1\text{ m}</math>)</b>	<ul style="list-style-type: none"> <li>• Height of herbaceous layer * (mean/maximum vegetation height)</li> </ul>	<ul style="list-style-type: none"> <li>• % Vertical cover of herbs, grasses and open ground</li> <li>• % Horizontal vegetation cover *</li> <li>• Number of stalks *</li> </ul>

### Plant architecture: Parasitism

The height at which an egg clutch was deposited had a significantly negative impact on its probability of being parasitised by *O. galerucivorus* (coefficient = -0.027,  $R^2_{\text{Nagelkerke}} = 0.095$ ,  $P = 0.047$ ,  $AUC = 0.637$ ,  $P_{AUC} = 0.07$ ,  $n = 60$ , Fig. 1B). Egg clutch height thereby was significantly positively correlated with plant height ( $r_p = 0.97$ ,  $P = 0.001$ ,  $n = 50$ ). In contrast, both measures of structural complexity, i.e. the pattern and the number of ramifications per plant, were removed by the multiple logistic regression model and had no significant influence on parasitism. Therefore, only egg clutch height influenced parasitism on the scale of the individual plant.



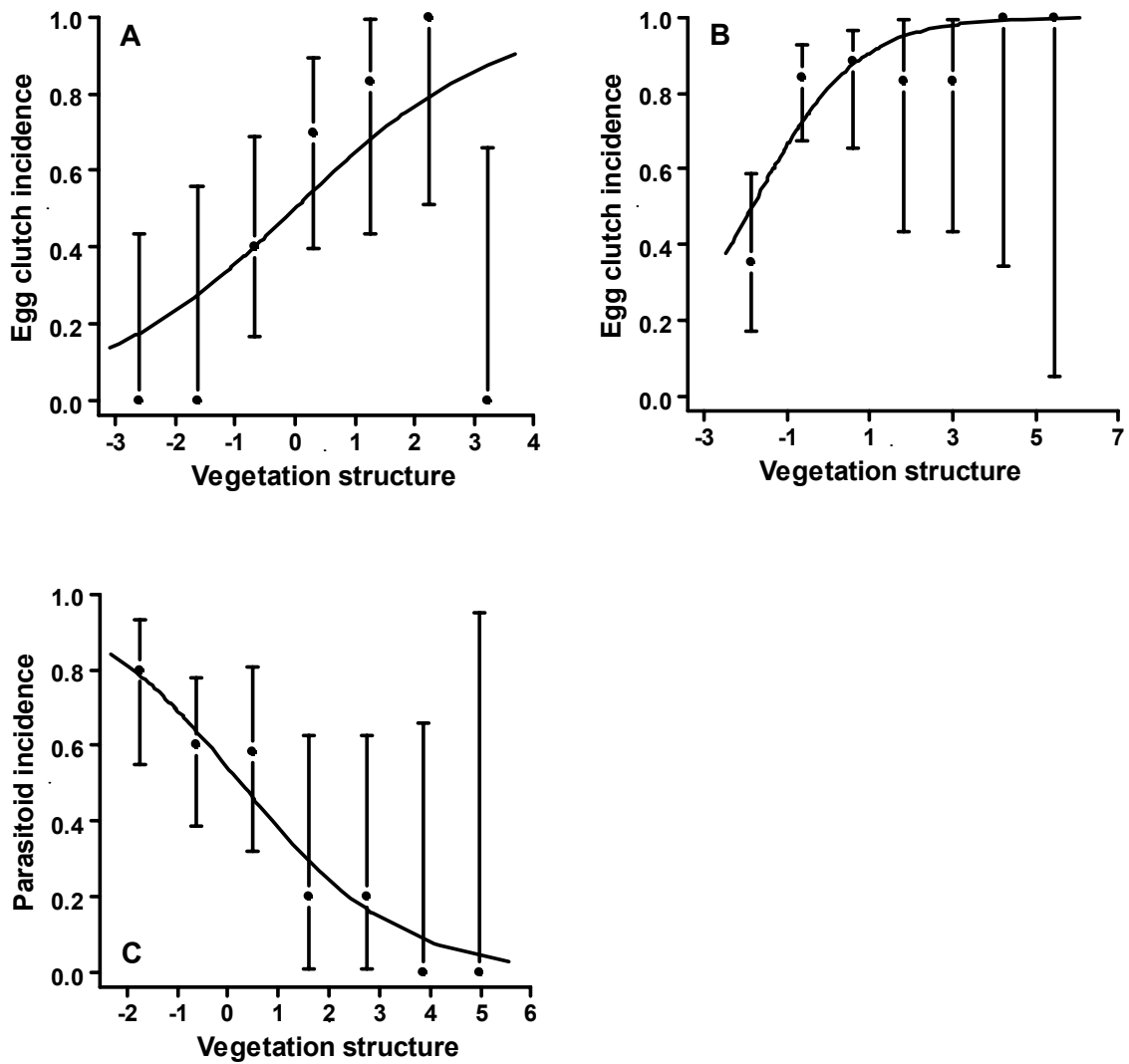
**Fig. 1.** Oviposition of *G. tanaceti* (A) and parasitism by *O. galerucivorus* (B) at different plant (A) and egg clutch (B) heights. Plotted are the mean  $\pm$  95 % CI of egg clutch or parasitoid incidences (circles with bars) and the predicted probability of egg clutch or parasitoid incidence (line) calculated by the logistic regression models.  $n = 100$  plants (A),  $n = 60$  plants with egg clutches (B).

### Vegetation structure in the microhabitat ( $r = 0.1$ m): Herbivore oviposition

On both study sites, the probability of oviposition by *G. tanaceti* significantly increased with increasing height and density of the vegetation structure around the oviposition site (Prappach: coefficient = 0.992,  $R^2_{\text{Nagelkerke}} = 0.225$ ,  $P = 0.007$ ,  $\text{AUC} = 0.775$ ,  $P_{\text{AUC}} = 0.001$ ,  $n = 40$ , Fig. 2A; Schafhof: coefficient = 1.360,  $R^2_{\text{Nagelkerke}} = 0.215$ ,  $P = 0.001$ ,  $\text{AUC} = 0.768$ ,  $P_{\text{AUC}} = 0.001$ ,  $n = 80$ , Fig. 2B). The factor ‘vegetation structure’ consisted of the parameters maximal and mean vegetation height, number of stalks and horizontal vegetation cover in 0.3 m height, i.e. beetle eggs were found more often in high and dense vegetation. As the model could be successfully cross-validated between both sites (Table 2), it seems to be of broader generality.

The probability that a *G. tanaceti* egg clutch was present was not correlated with the presence of the main host plant *A. millefolium* (yarrow) on the microhabitat scale. On the site Schafhof, yarrow was present in 91% of the investigated microhabitats, on the site Prappach in 50%.





**Fig. 2.** Oviposition of *G. tanaceti* (A + B) and parasitism by *O. galerucivorus* (C) in different vegetation structures (= factor composed of vegetation height (max, mean), % horizontal vegetation cover at 0.3 m height, and stalk number) on the microhabitat scale ( $r = 0.1$  m). Plotted are the mean  $\pm$  95 % CI of egg clutch or parasitoid incidences (circles with bars) and the predicted probability of egg clutch or parasitoid incidence (line) calculated by the logistic regression models at the sites Prappach,  $n = 40$  microhabitats (A), Schafhof,  $n = 80$  microhabitats (B) and Schafhof,  $n = 60$  microhabitats (C).

**Table 2.** Cross-validation of the logistic regression model explaining the egg distribution of *G. tanacetii* depending on microhabitat vegetation structure for the two sites Schafhof and Prappach. Models were parameterised with data from one site (training site, left column) and validated at the data from the other site (test site, first row). Given are AUC ( $\pm$  SE) and p-values of the validations.  $n = 80$  microhabitats (Schafhof) and  $n = 60$  microhabitats (Prappach).

Training\Test		Schafhof	Prappach
Schafhof	<b>AUC</b>	0.768	0.785
	<b>SE</b>	0.069	0.081
	<b>P</b>	0.001	0.01
Prappach	<b>AUC</b>	0.764	0.775
	<b>SE</b>	0.069	0.081
	<b>P</b>	0.001	0.01

### Vegetation structure in the microhabitat ( $r = 0.1$ m): Parasitism

Parasitism could be investigated only on the site Schafhof since none of the egg clutches collected on the second site was parasitised. There was a highly significant negative correlation between the probability of parasitism and the factor ‘vegetation structure’ around the oviposition site (coefficient = -1.154,  $R^2_{\text{Nagelkerke}} = 0.352$ ,  $P_{\text{model}} = 0.001$ ,  $AUC = 0.79$ ,  $P_{AUC} = 0.001$ ,  $n = 60$ , Fig. 2C). The factor ‘vegetation structure’ consisted of the same parameters as above. At the same time the probability of parasitism increased with increasing density of *G. tanacetii* egg clutches within a radius of 2 m around the oviposition site (coefficient = 0.431,  $R^2_{\text{Nagelkerke}} = 0.140$ ,  $P_{\text{model}} = 0.01$ ,  $AUC = 0.70$ ,  $P_{AUC} = 0.007$ ,  $n = 60$ ). The rate of parasitism of *G. tanacetii* egg clutches was also significantly negatively correlated with vegetation structure (coefficient = -0.162,  $R^2_{\text{corrected}} = 0.110$ ,  $P = 0.006$ ,  $n = 60$ ) and showed a tendency of a positive correlation with host density (coefficient = 0.064,  $R^2_{\text{corrected}} = 0.05$ ,  $P = 0.051$ ,  $n = 60$ ).

## **Discussion**

As insect herbivores depend primarily on their host plants for survival and reproduction, analyses of the abundances and distribution patterns of these plants have been the basis of many studies on herbivore-plant interactions (Bernays and Chapman 1994). Recently it has been emphasised, however, that this approach may be too restricted and habitats for insect herbivores have been defined too narrowly. In particular, non-consumable resources (structural elements) have been ignored (Dennis 2004). The present study is one of the first to examine effects of plant and vegetation structure *per se*, apart from effects of host plant availability usually correlated to (host) plant size and density, in the field. This is possible since the model organisms studied almost exclusively use dry structures of non-host plants for oviposition. The study reveals that plant architecture and vegetation structure cannot only influence distributions of herbivores or parasitoids, but even seem to have the potential to mediate interactions across different trophic levels (host-parasitoid interactions). Table 3 gives a schematic overview on the influences of plant and vegetation structure on the studied herbivore-parasitoid system for both spatial scales.

On the scale of the individual plant, plant architecture was defined as size and structural complexity of a plant (Table 1; after Andow and Prokrym 1990 and Gingras 2002). In the literature, structural complexity has been shown to affect herbivores (Raghu *et al.* 2004, Rudgers and Whitney 2006) as well as parasitoids (Andow and Prokrym 1990, Lukianchuk and Smith 1997). In several studies, host finding success in parasitoids was found to be higher on simple structured plants than on plants with complex structures (Andow and Prokrym 1990, Lukianchuk and Smith 1997, Gingras *et al.* 2002, 2003). Likewise, in large plants or complex canopies herbivores were better able to escape predation at least by some species of natural enemies (Heisswolf *et al.* 2005, Riihimäki *et al.* 2006).

In contrast to this, the structural complexity of the individual plant (number and patterns of ramifications) had no or only a slight influence on the egg distribution of the tansy leaf beetle and none on the probability of parasitism by *O. galerucivorus* in the present study. The beetle females were even more attracted by simple plant stems than by complex ones, possibly because they preferred high grass stems over smaller herbs with a higher complexity for oviposition. Therefore, another plant architectural

**Table 3.** Overview on the influence of plant architecture and vegetation structure on herbivore oviposition and parasitism of egg clutches of *Galeruca tanacetii* on two spatial scales. + denotes a significantly positive relationship, – a significantly negative relationship, n.s. means not significant. \* indicates variables summarised by PCA to the factor ‘vegetation structure’.

Scale	Variable	Herbivore oviposition	Parasitism
<b>Individual plant</b>	Plant height	+	
	Egg clutch height		–
	Number of ramifications	n.s.	n.s.
	Patterns of ramification (simple/ramified)	+	n.s.
<b>Microhabitat</b>	Maximum vegetation height *	+	–
	Weighted mean vegetation height *	+	–
	Number of stalks *	+	–
	Vertical cover by herbaceous plants, grass, open ground	n.s.	n.s.
	Horizontal vegetation cover		
	• 0.10 m	n.s.	–
	• 0.20 m	n.s.	–
	• 0.30 m *	+	–
	• 0.40 m	+	n.s.
	• 0.50 m	+	n.s.
	Factor ‘vegetation structure’ (PCA including all *)	+	–
	Host plant incidence	n.s.	n.s.
Egg clutch density		+	

trait, plant height, showed a strong positive influence on herbivore beetle oviposition and, being correlated with egg clutch height, a negative influence on the probability of parasitism. Supporting this, a previous study (Obermaier *et al.* 2006) showed that beetles selected the highest plants available for oviposition within the vegetation and oviposited as high as possible on the plants selected. As the egg parasitoid mainly searches for its host by running up vertical structures (T. Meiners, personal observation), ovipositing high up in the vegetation seems to help preventing the higher located egg clutches from being parasitised. Thus, choosing high oviposition sites on high plant individuals within the herbaceous vegetation may result in a higher selective advantage for individuals of this beetle species as ovipositing in complex structured plants.

Also, on the larger spatial scale it was hypothesised that high and complex vegetation structure might provide enemy-free space for insect herbivores. In several studies, vegetation height and structural complexity were shown to affect herbivore species richness (Stinson and Brown 1983), population density (Dennis 2004), habitat colonisation (Coll and Bottrell 1994), mate finding (Langellotto and Denno 2001) and host plant detection (Anthes *et al.* 2003). Regarding natural enemies the effect of vegetation structure varies. A previous study on two larger spatial scales showed either the same effect of vegetation structure on the occurrence of both, the beetle and the parasitoid or no effect on parasitism at all (Meiners and Obermaier 2004). An investigation on larval predation and egg parasitism in the shield beetle species *C. rubiginosa* revealed a higher predation risk of larvae on exposed host plants, but no influence on egg parasitism or oviposition site choice of the female beetles (Tschanz *et al.* 2005). On the other hand, in a meta-analysis, seven out of nine natural enemy guilds turned out to be most abundant under conditions of increased habitat complexity (Langellotto and Denno 2004).

In the present study, vegetation structure had a highly significant influence both on the egg distribution of the herbivore and on parasitism by *O. galerucivorus* within the microhabitat scale, i.e. in the close surroundings of the oviposition site. While beetle egg clutches were found more often in plots with high and dense vegetation, their risk of being parasitised was higher in low and loose vegetation as both occurrence and rate of parasitism were negatively correlated with height and density of the surrounding vegetation. The model explaining egg clutch occurrence depending on the factor ‘vegetation structure’ could be successfully cross-validated between two

study sites. High and dense ‘vegetation structure’, combining the parameters stalk number, horizontal cover and average and maximal vegetation height per plot, seemed to provide enemy-free space for the beetle females to hide their eggs from the parasitoids. This is in accordance with optimal oviposition theory, which predicts that females should oviposit at those sites that enhance the performance and survival chances of their offspring (Jaenike 1978, Thompson 1988, Thompson and Pellmyr 1991, Heisswolf *et al.* 2005). It is suspected that parasitoids show a shorter giving-up time and switch earlier to other patches in high and dense vegetation.

Additionally, the probability of parasitism was positively correlated with host density (positive density dependence), i.e. depositing too many eggs in dense vegetation may counteract the selective advantage of hiding eggs in dense vegetation. A positive density dependence of parasitism on this scale corresponds to earlier results on the sensory capabilities of a close congener of the egg parasitoid examined, *O. gallerucae*, which locates the microhabitat of its host by odours and contact cues (kairomones) of host faeces (Meiners and Hilker 1997). Also in *O. gallerucivorus* plots with high egg clutch density may increase the residence time of parasitoids and thus their probability of finding host eggs, as contact with beetle faeces may occur more frequently.

On both small spatial scales investigated in this study, the herbivore and its parasitoid differed in their patterns of oviposition, possibly linked to a reduced host finding success of the parasitoid in high or structurally complex plants and vegetation. Height and structural complexity of individual plants and of the herbaceous vegetation seem not only to influence oviposition patterns, but actually to mediate the host-parasitoid interaction. The structure and complexity of the environment therefore can have important implications for multitrophic level interactions, apart from the host plant.

## **Acknowledgements**

We are grateful to Boris Schröder for statistical advice. E. Obermaier thanks the bureau of women’s affairs of the University of Würzburg and the BMBF (MOSAIC-

project, code 01LN0007) for financial support. The authors thank the government of Lower Franconia for the permission to work in the nature reserve.

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