

Connectivity counts – disentangling effects of vegetation structures on the searching movement of a parasitoid through manipulative experiments

Abstract. The heterogeneous structure of habitats can have a negative impact on the host and prey location process of foraging natural enemies. In this study, we examined in the laboratory which elements of complex vegetation structure influence the searching movement of parasitoids. The effects of three structural parameters of the vegetation were evaluated independently in bioassay arenas without hosts. Dried grass stems were arranged according to the natural situation in different setups with low and high vegetation densities, heights and connectivities. We used the egg parasitoid *Oomyzus galerucivorus* (Hymenoptera, Eulophidae) as model organism, for which we know from previous fieldwork that tall and dense vegetation reduces parasitism success while increasing egg deposition of the host. Further, host egg clutches are preferentially situated close to the tips of plants in the field. The laboratory assays revealed that high stem density decreased the walking time of the parasitoids on the ground, but increased the propensity to fly between stems. Tall stems increased the time spent walking on them and walking time was almost proportional to grass stem length. No difference was observed in the number of contacts with grass stems in all investigated setups, in contrast to the likelihood of reaching the upper part of the stems. Fewer wasps reached the middle and upper part of grass stems in the high connectivity setup. Thus, laying eggs at the tip of long grass stems in dense vegetation is an adaptive strategy for the host, because this type of vegetation structure is the one which maximises the number of connection points between plant parts. The connection points disorient wasps, which lose time, reverse their direction or fly away.

Key words: egg parasitoid · habitat complexity · movement patterns · *Oomyzus galerucivorus* · physical vegetation characteristics · plant canopy · vegetation structure · walking behaviour

Introduction

A variety of physical and chemical properties of plants, on which hosts or prey are present, directly influence the mobility of natural enemies (Price *et al.* 1980, Coll *et al.* 1997, Romeis *et al.* 1998). In particular physical vegetation traits, as for example plant architecture, are known to affect the movement behaviour and searching activity of parasitoids and predators in either positive or negative ways (Grevstad and Klepetka 1992, Frazer and McGregor 1994, Weisser 1995, Clark and Messina 1998, Legrand and Barbosa 2003). The architecture of single plants influences notably enemies that are small in size such as parasitoids (Price *et al.* 1980, Gardner and Dixon 1985, Stadler and Völkl 1991). Several studies specifically investigated the host finding behaviour of parasitoids using artificial plant models varying in their degree of structural complexity (Andow and Prokrym 1990, Lukianchuk and Smith 1997, Gingras and Boivin 2002, Gingras *et al.* 2002). Other studies used natural plants to analyse the effect of plant architecture on foraging success of parasitoids (Cloyd and Sadof 2000, Gingras *et al.* 2003). All of the above-mentioned studies on parasitoids demonstrated that a high degree of plant structural complexity has a negative impact on foraging efficiency.

So far, the majority of studies dealing with the influence of physical plant traits on movement patterns of parasitoids concentrated on the architecture of single plants (but see Gols *et al.* 2005, Romeis *et al.* 2005). In contrast, the structure of the environment, e.g. a habitat patch, and its influence on natural enemy movement is often neglected in investigations of parasitoid-host and other arthropod interactions (Casas and Djemai 2002). Within a habitat the vegetation structure is often assumed to be entirely homogenous, but the structural complexity of patches may vary strongly in their degree of complexity (Meiners and Obermaier 2004, Langellotto and Denno 2004, Tschanz *et al.* 2005). Vegetation structure may significantly alter predator-prey interactions simply by modifying the movement tracks of predators (Kareiva and Perry 1989, Vohland 1996). Consequently, the movement ability of an insect depends on behavioural traits and vegetation structure, because both interact and lead to distinct movement patterns (Neuvonen 1999, Goodwin and Fahrig 2002). This may affect the time predators or parasitoids spend on a plant and subsequently the co-occurrence of natural enemies and their victims (Casas and Djemai 2002 and references therein).

We investigated the movement patterns of *Oomyzus galerucivorus* Hedqvist (Hymenoptera: Eulophidae) a specialised egg parasitoid of the polyphagous leaf beetle *Galeruca tanaceti* L. (Coleoptera: Chrysomelidae). In general, the probability of leaf beetle oviposition increases in patches with high stem density in the field (Meiners and Obermaier 2004, Randlkofer *et al.* unpublished data). Earlier field studies further revealed that a dense and complex vegetation structure reduces the parasitism success of the egg parasitoid on a small spatial scale ($r = 0.1$ m) (Obermaier *et al.* in press, Obermaier *et al.* unpublished data). Furthermore, leaf beetle egg clutches, which are deposited high up on the plants used for oviposition are less likely parasitised (Obermaier *et al.* 2006). In the present laboratory study, we classified vegetation structure by the three structural parameters ‘density’ (number of plant stems per unit area), ‘height’ (plant size) and ‘connectivity’ (number of branchings within plants or direct contacts between different plant individuals). The classification of these three vegetational parameters was chosen with respect to a previous characterisation of the architecture of single plants (Andow and Prokrym 1990, Gingras *et al.* 2002). The impact of each individual parameter on the movement patterns of *O. galerucivorus* females was experimentally investigated in bioassay arenas. Thereby, we aimed at gaining insight in mechanisms potentially acting in the field.

Specifically, we asked in our study (1) whether a high degree of structural complexity constricts the movement of the egg parasitoid, and thus, decreases the searching activity within structures of high complexity or on plant parts relevant for host encounter and (2) whether it is possible to single out one structural parameter that has the strongest influence on the movement patterns.

Material and methods

Life-history of *Oomyzus galerucivorus*

O. galerucivorus is known to parasitise several species of *Galeruca* throughout Europe (Sinacori and Mineo 1993). The main host of the specialised egg parasitoid in Germany is *Galeruca tanaceti*, a polyphagous leaf beetle. In autumn, the leaf beetle

females oviposit well above the ground on dried vertical plant structures, mostly on non-consumable grass stems, within the herbaceous vegetation layer (Scherf 1966, Obermaier *et al.* 2006). Shortly after their deposition *O. galerucivorus* parasitises the leaf beetle eggs. The parasitoid larvae hibernate in the host eggs and adults emerge next spring. As the leaf beetle is an univoltine species, the adult parasitoids have to outlast 5-6 months until host eggs are available (Meiners *et al.* 2006).

Study insects

Parasitoids were reared from *G. tanaceti* egg masses collected in the nature reserve 'Hohe Wann' in Northern Bavaria, Germany. Egg clutches were kept separately in glass vials (10 ml, 32 x 24 mm) in a climate chamber at 20°C, 60% RH and L18:D6 photoperiod to initiate the eclosion of the parasitoids. Afterwards the parasitoids were transferred in a climate chamber with 10°C, 70% RH and L18:D6 until testing. The animals were provided with honey water as food and moist filter paper within the rearing Petri dishes. Females and males were separated shortly before the behavioural observations to ensure that females had the chance to mate.

Field investigation on oviposition height of the herbivore

The field investigation was conducted in the nature conservation area 'Hohe Wann' on a dry grassland site in Lower Franconia, Germany, in autumn 2006. In the surrounding of 50 random points the nearest egg clutch of the leaf beetle, *G. tanaceti*, was selected and the height of the egg clutch as well as the maximal height of the plant where the egg clutch was attached to, was recorded. The relationship between egg clutch height and maximal plant height was analysed with Pearson correlation after testing the data for normal distribution.

Laboratory experiments

Experimental design

The base of the test arenas (24×24 cm) consisted of floral foam covered with filter paper. Dried grass stems (*Dactylis glomerata* L., Poaceae), with the top part cut off and blades removed, were used to build 6 different types of vegetation structures. Dried, non-consumable grasses are the preferred oviposition substrate of the leaf beetle host of *O. galerucivorus* and the main component of the vegetation in the habitat at the time of host search. To vary the complexity of the vegetation structure, arena designs with a low or high degree of vegetation density, with a short or tall height of grass stems, or with low or high connectivity were created. In the centre of each arena one grass stem was placed and around it four concentric circles with a spacing of 2 cm were drawn. Thus, the inner circle had a diameter of 2 cm, whereas the outermost circle had a diameter of 16 cm. Within these circles the grass stems were dispersed equally in distance (Fig. 1).

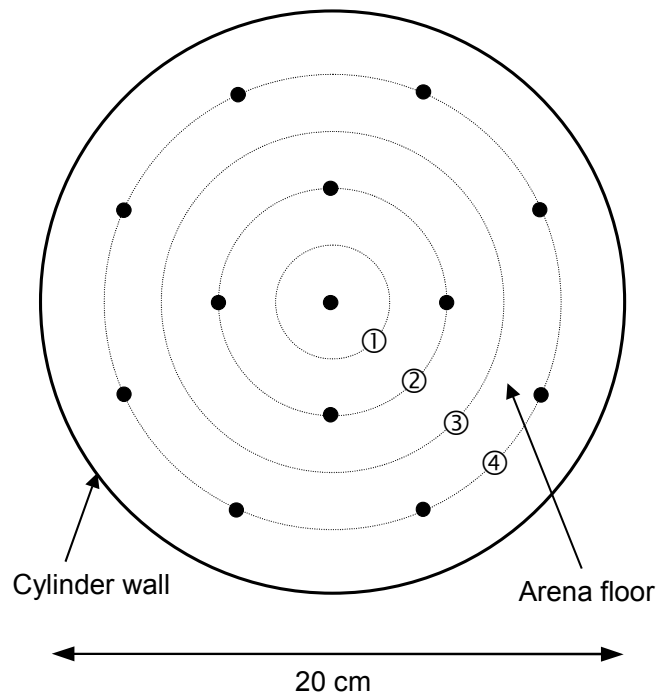


Fig. 1. Schematic representation of the bioassay arena (top view) for observations of the searching behaviour of *O. galerucivorus* in different vegetation structure types. Numbers and dotted lines indicate circles where the grass stems were arranged according to the chosen design. Black dots = position of dried grass stems (here for the low density design).

For the low density design 13 grass stems were used in total (circle 2: 4 stems, circle 4: 8 stems), whereas for the high density design 51 grass stems were used in total (circle 1: 5, circle 2: 10, circle 3: 15, circle 4: 20). Thus the high density design had about four times more stems than the low density design. In order to test the influence of height on the movement patterns of the egg parasitoid, short and tall grass stems were used (short height: 15 cm, tall height: 45 cm). The effect of connectivity was tested in arenas with high stem density and an equal stem height of 45 cm. Connections (length ca. 1.5 cm) between the grass stems were inserted by using bast fibres at three different heights (8, 23 and 38 cm). In the low connectivity design, 10 connections in total per level between two single grass stems were randomly tied (circle 1: 1 connection, circle 2: 2 connections, circle 3: 3 connections, circle 4: 4 connections). In the high connectivity design 50 connections in total per level were tied between grass stems, i.e. each grass stem within a circle was connected *via* bast fibres with its neighbour. Overall, in the high connectivity design a total of 150 connections were created, whereas in the low connectivity design a total of 30 connections were created.

All arenas were covered with a plexiglass cylinder with a diameter of 20 cm and with a height of 50 cm. A lid with very fine plastic gauze (mesh size 0.5 mm) was used to close the cylinder at the top. Experiments were conducted under uniform illumination provided by a full spectrum plant lamp (60 W light bulbs, General Electric Company) simulating daylight conditions. The light bulbs were covered with translucent parchment paper to dampen the brightness of the lamps.

Behavioural observations

In all experiments female parasitoids were mated, fed and naïve with respect to experience with vegetation structures and oviposition. The test individuals were 7-34 days old. At this age female parasitoids used for rearing were observed to successfully parasitise leaf beetle eggs in a long-day light cycle (B. Randlkofer unpublished data). The female parasitoids were released singly on the floor in the centre of the arena and each female was only used once. Their behaviour (walking, flying, resting and grooming) and their position (floor, stems, cylinder wall) inside the arena were recorded for 5 minutes. Every stem contact was registered, which implied that a

parasitoid had either walked up a grass stem or had landed on it after a short flight. In order to specify the position of the parasitoids on stems, the 45 cm long grass stems were subdivided into three 15 cm sections (lower, middle and upper section). Before the first parasitoid was released into the arena, the floor was sprayed with water, which was repeated in regular intervals. After each completed observation the arena was rotated for 90 degrees to avoid the influence of potential side effects. Two corresponding arena designs (e.g. low and high density) were usually used during the same time span and after 5 consecutive observations the arena types were exchanged between the two observers. The observations were recorded using the Noldus Observer programme 3.0 (Noldus Information Technology, Wageningen, The Netherlands). Experiments were undertaken in a constant temperature room during daytime from 9:30 a.m. and 16:00 p.m. The average abiotic test conditions were 22 ± 2 °C, 71 ± 6 % RH, 1013 ± 7 hPa.

Mode of movement (flying versus walking behaviour)

Two distinct categories were defined in order to distinguish what kind of influence the vegetation structures have on different modes of movement and thus, on the wasps' movement patterns. All observed individuals showing walking and/or flying behaviour during the observations were allocated either to the 'non-flying' or 'flying' category for each of the tested arena designs (Table 1). Flying wasps were defined either as individuals which showed flying behaviour, additionally to walking behaviour, while foraging or as individuals which flew to the wall of the cylinder and reentered the arena. Non-flying wasps were defined as individuals which did not fly at all during the 5 min of the experiments or which foraged for an undefined time by walking, then flew straight to the cylinder and stayed there. We interpreted this flight behaviour as a giving up decision, leading to a self-censoring. Only the walking time of 'non-flying' individuals was kept for further analyses of the time which the parasitoids actively spent searching within the arena.

The Mann-Whitney U-test was applied to analyse variations in the time the parasitoids spent walking on the floor, the stems or the different stem parts and the difference in the number of stem contacts. A survival analysis (Tarone-ware method) was carried out on the number of individuals walking up the stems, the time intervals being here the amount of time which the wasps spent in the lower, middle and upper

stem parts. Censoring was applied to the group reaching the top of stems, as we do not know whether these individuals would have moved up even further with longer stems.

Table 1. Number of ‘non-flying’ and ‘flying’ individuals for each of the tested arena designs. Flying wasps are defined as individuals which showed flying behaviour while foraging or flew to the wall of the cylinder and reentered the arena. Non-flying wasps are defined as individuals which did not fly at all during the 5 min of the experiments or which foraged for an undefined time by walking and then flew straight to the cylinder and stayed there.

	‘Non-flying’ individuals	‘Flying’ individuals
Low density – Short stems	38	20
High density – Short stems	32	12
Low density – Tall stems	26	19
High density – Tall stems	55	34
Low connectivity	21	14
High connectivity	21	14

Results

Height of host egg deposition

In the field, host egg clutches were generally located high above the ground, relatively close to the top of the plants chosen as egg deposition substrate. The average height of host egg clutches on plants was 56.3 ± 18.7 cm (mean \pm SD) compared to the mean height of these plants of 60.7 ± 18.7 cm (Fig. 2). This resulted in a mean distance of 4.4 ± 4.8 cm measured from an egg clutch to the top of the oviposition plant. Egg clutch height and absolute height of plants chosen for egg deposition was significantly correlated ($r_p = 0.967$, $P < 0.001$, $n = 50$).

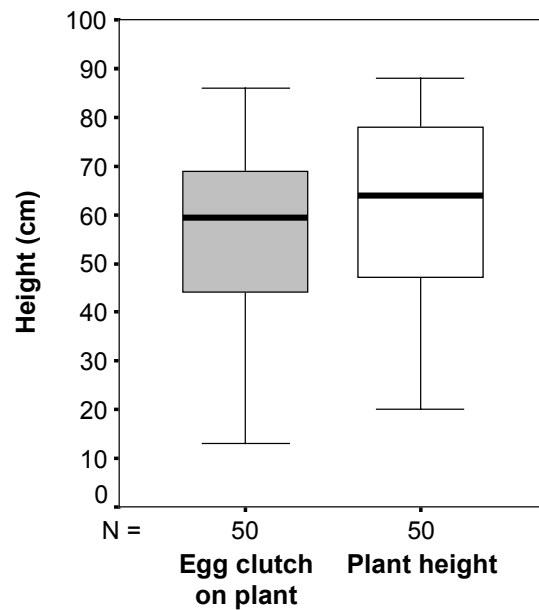


Fig. 2. Height at which host egg clutches were deposited on plants and the average height of these plants. The horizontal line within the box represents the median, the upper and lower border of the box are the 75th and 25th percentiles, respectively and the error bars show the non-outlier minimum and maximum.

Effect of density on parasitoid searching movement

In the laboratory, high stem density significantly decreased the time *O. galerucivorus* females spent walking on the floor compared to low stem density, irrespective of the length of the grass stems (short stems: $U = 334.5$, $P = 0.001$; tall stems: $U = 322.0$, $P < 0.001$, Fig. 3A). No difference in searching time was observed between the low or high density setup for tall grass ($U = 588.0$, $P = 0.199$, Fig. 3B). By contrast, the searching activity on short grass stems was significantly enhanced when offered in high density ($U = 212.5$, $P < 0.001$, Fig. 3B). However, stem density did not considerably influence the number of stem contacts, neither for short stems ($U = 558.0$, $P = 0.093$) nor for tall stems ($U = 676.0$, $P = 0.228$, Fig. 3C).

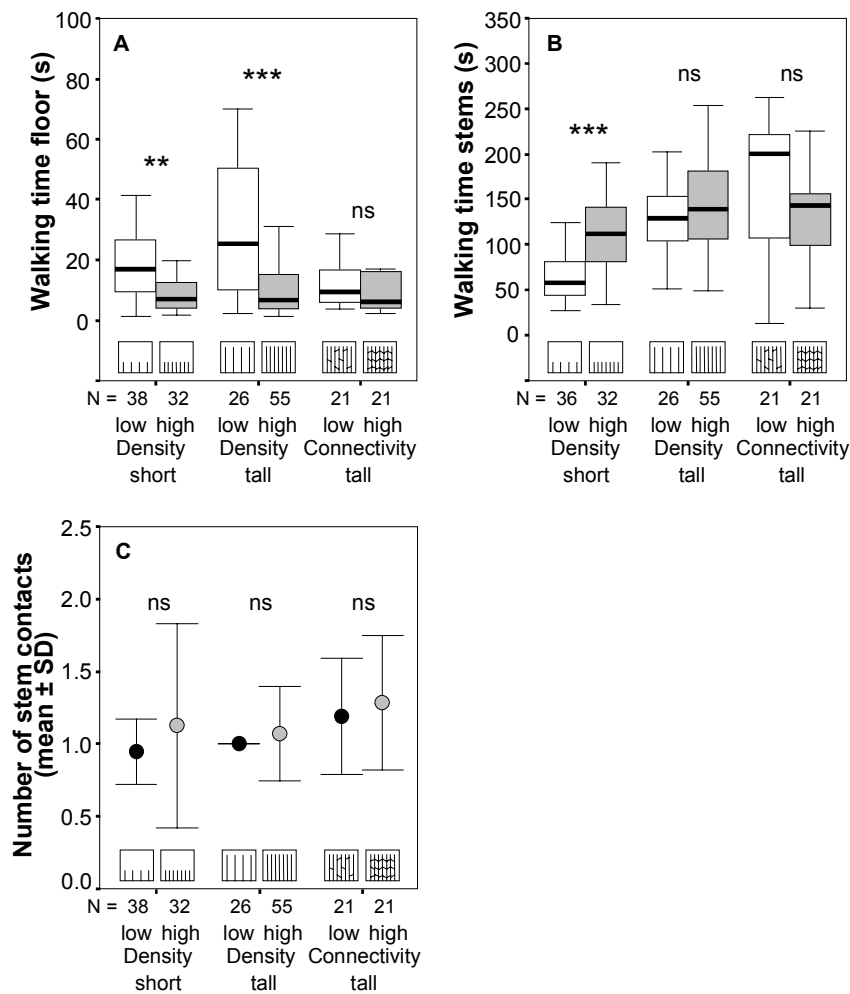


Fig. 3. Searching behaviour of *O. gallerucivorus* females in vegetation structures composed of short (15 cm) or tall (45 cm) grass stems at a low/high density or possessing a low/high degree of connectivity at an overall high density during the observation period of 300 s. Considered were only data of individuals which foraged within the arena by walking (= 'non'-flying individuals). (A) The total time, which the parasitoids spent walking on the floor or (B) on the stems. (C) Total number of stem contacts (mean \pm SD). 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 non-outlier minimum and maximum. Asterisks indicate a significant difference * at $P < 0.05$, ** $P < 0.01$ and *** at $P < 0.001$ according to the Mann-Whitney U-test (ns = no significant difference).

Table 2. Number of different types of events displayed by flying wasps.

Design	Stem to stem	Stem to floor	Stem to cylinder	<i>n</i> flying individuals
Low density – Short stems	4	5	12	20
High density – Short stems	8	6	6	12
Low density – Tall stems	6	3	19	19
High density – Tall stems	15	1	30	34
Low connectivity	2	0	15	14
High connectivity	10	3	4	14

Effect of height on parasitoid searching movement

Since in the field the highest probability of egg clutch encounter is close to the tips of grasses, we analysed the searching activity on different parts of the tall grass stems within low and high density. The walking time on the lower, middle and upper 15 cm of grass stems averaged between 30 and 50 seconds per section and was not significantly influenced by stem density (lower stem parts: $U = 640.5$, $P = 0.451$; middle stem parts: $U = 642.5$, $P = 0.541$; upper stem parts: $U = 579.5$, $P = 0.619$; Fig. 4). Thus, time spent searching within different parts appears to depend on the length of the stems.

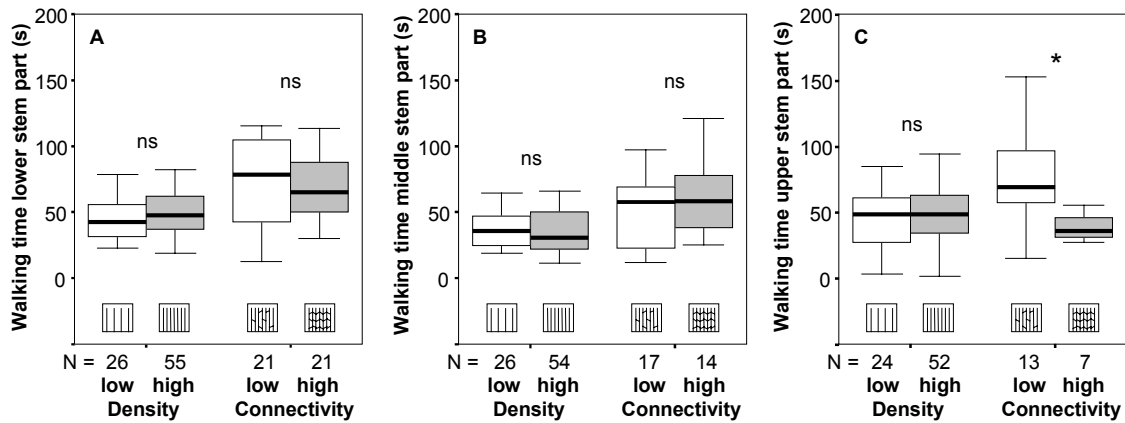


Fig. 4. Searching behaviour of *O. gallerucivorus* females in vegetation structures composed of 45 cm tall grass stems at a low/high density or low/high connectivity at an overall high density. Considered were data of individuals which foraged within the arena by walking (= ‘non’-flying individuals). The time, which the parasitoids spent walking on (A) the lower 15 cm, (B) the middle 15 and (C) the upper 15 cm of grass stems. 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 non-outlier minimum and maximum. The asterisk indicates a significant difference at $P < 0.05$ according to the Mann-Whitney U-test (ns = no significant difference).

Effect of connectivity on parasitoid searching movement

The wasps in the two connectivity designs tended to spend a larger amount of time in the lower and upper stem parts than the wasps of the two non-connectivity designs with tall grass stems. The time spent walking on different stem parts was approximately similar for the two connectivity designs, at least for the lower and middle stem parts (averaging between 60 and 80 seconds), and hence length dependent as in the non-connectivity/tall stems designs (Fig. 4). Fewer wasps reached the middle or upper part of tall grass stems within the two connectivity designs compared to the non-connectivity designs with tall grass stems. In high connectivity this effect was larger than in low connectivity. This resulted in a significantly reduced walking time on the upper stem part within the high-connectivity design in comparison to the low-connectivity design ($U = 20.0$, $P = 0.043$, Fig. 4). The wasps showing flying behaviour in the low-connectivity arena frequently left the vegetation structures by flying away from stems to the wall of the cylinder, as they did this in the non-connectivity/tall stems designs (Table 2). By contrast, wasps tended to fly often from stem to stem within the vegetation structures in the high-connectivity arena.

The survival analysis on the number of individuals crossing the different height levels (shown in Figure 4, for example 21, 14 and 7 individuals for the high connectivity setup) shows that females have difficulties reaching the top of stems in the high connectivity setup (Log rank test, Tarone-Ware method, Chi-squared = 3.081, $df = 1$, $P = 0.079$). The difference is very clear when comparing all three treatments (no, low and high connectivity, Chi-squared = 33.544, $df = 2$, $P < 0.001$).

Discussion

Earlier field investigations in this parasitoid-host system showed that host egg clutches are deposited more frequently in patches with high stem density than compared to low density patches in the field (Meiners and Obermaier 2004, Randlkofer *et al.* unpublished data). Moreover, the success of *O. galerucivorus* to parasitise eggs is reduced within patches of tall and dense vegetation on a small spatial scale ($r = 0.1$ m) (Obermaier *et al.* in press). Host egg clutches are usually located close to the tips of plants, as confirmed by this study. The higher egg clutches are attached to plants, the lower is the probability of parasitism (Obermaier *et al.* 2006). In the present study, we aimed at gaining insight in the mechanisms responsible for this effect, focussing exclusively on the influence of vegetation structure. In the laboratory we reproduced situations in which we could assess the influence of three structural parameters, stem density, height and connectivity. In the following, we discuss these three aspects in turn by using an approach which considers a foraging wasp as a particle moving in a geometrically complex environment in which movement decisions can be taken at regular distance intervals, an approach which has a long history in statistical physics (Casas and Djemai 2002). From the parasitoid's point of view, the probability of reaching host eggs is equivalent to the probability to walk up to the top of tall plant stems in order to find host eggs within a given time period. Successful parasitism depends partly on the allocation of searching time to specific places within the habitat and the likelihood to encounter a host egg clutch on a plant might decrease with a shortened duration of the search (cf. Casas and Djemai 2002).

High stem density significantly reduced the time the parasitoids spent walking on the floor, but did not increase the number of stems visited, which was identical for all designs. Time limitations determined by the experimental conditions seemed not to be the reason for this finding. After reaching the top of grass stems, the individuals spent a considerable amount of time inspecting the tip of the stem, and commonly switched over to resting and grooming activities after some time. They did not move downwards. Individuals that showed flying behaviour within the arenas tended to move more frequently from stem to stem by flying in higher grass stem densities. This observed behaviour in the bioassay might partially explain the reduced efficacy of the parasitoid in dense vegetation under natural conditions.

Grass stem height has an effect on the time spent walking, but mainly a proportional effect: the higher the stem, the longer it takes. We showed that the number of stems visited is not influenced by height and that all females did reach the tip of the stems in the long stems design. Therefore, the extra time to cover the extra distance is not sufficient to explain the reduced parasitism success observed in the field on tall grasses. The reason is obviously not due to the grass height.

Connectivity between plant parts had a strong impact on the probability to reach the tip of the grass stems. This effect was larger in high connectivity than in low connectivity, which resulted in a significantly reduced walking time on the upper stem part within the high-connectivity design in comparison to the low-connectivity design. The connection points served sometimes as resting places. Sometimes, the wasps moved backwards.

Our manipulative experiments do not support findings of previous studies that investigated the movement behaviour of predatory arthropods, such as coccinellid beetles and spider mites, within artificially created plant canopies. In these experiments individual plants were arranged in a way that leaves between plants could touch and formed 'bridges' for the walking predators (Kareiva & Perry 1989, Skirvin & Fenlon 2003). Concordantly, these investigations report that bridges of touching leaves facilitated the movement of the carnivores within the plant canopy, allowing them to move more easily through the canopy and disperse faster. However, other investigations conducted in the field and the laboratory are in accordance with our results. For example, regarding the impact of plant density, Risch *et al.* (1982) detected that the foraging success of a predaceous lady beetle was reduced with increasing plant density in an intercropping study, because the beetles spent a high amount of time on

plants without prey. Moreover, strong effects of connectivity were observed in other manipulative studies. Investigations conducted with *Trichogramma evanescens* parasitising hosts on different cabbage species revealed that the degree of connectivity of individual cabbage plants had the strongest effect on host-finding success, which was in general lower on plants with complex structures (Gingras *et al.* 2002). The parasitism rate of a moth species on birch trees was diminished in structural more complex canopies of trees, too (Riihimäki *et al.* 2006). These observations were recently confirmed through computer simulations, which predicted that the proportion of plant canopy searched is mediated by the complexity of the vegetation structure, with a lower proportion of the canopy visited on more complex structured parts (Skirvin 2004).

In conclusion, it is advantageous for the leaf beetle host to place its eggs at the top of long stems not because of the length *per se*, but because long plant stems situated in highly dense vegetation ensures the presence of many connections between plant parts. The connections confuse the wasps, which either lose time, reverse their movement direction or fly away.

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