CHAPTER 4

Enemies in low places – insects avoid winter mortality and egg parasitism by modulating oviposition height

Abstract. Oviposition site selection in insects is essential in terms of low egg mortality, high offspring survival and therefore a high reproductive output. Although oviposition height could be a crucial factor for the fitness of overwintering eggs, it has rarely been investigated. In this study the oviposition height of a polyphagous leaf beetle, *Galeruca tanaceti* L., in different habitats and at different times of the season was examined and its effect on egg clutch mortality was recorded. The leaf beetle occurs as an occasional pest on several agricultural plants. It deposits its eggs within herbaceous vegetation in autumn. Eggs are exposed to numerous biotic and abiotic mortality factors summarised as egg parasitism and winter mortality. Oviposition height of the leaf beetle was not uniform, but changed significantly with the structure of the habitat and during the season. Mean oviposition height per site (70.2 ± 4.9 cm) was significantly higher than mean vegetation height (28.4 ± 2.4 cm). Height of plants with egg clutches attached and oviposition height were significantly positively correlated. The results suggest that females try to oviposit as high as possible in the vegetation and on the plants selected. In accordance with this, the probability of egg parasitism and of winter egg clutch mortality significantly declined with increasing oviposition height. A preference of *G. tanaceti* for oviposition sites high up in the vegetation might therefore have evolved due to selection pressures by parasitoids and winter mortality.

Key words: abiotic factors · Chrysomelidae · enemy-free space · *Galeruca tanaceti* · oviposition site · plant-animal interactions · *Oomyzus galerucivorus*

Introduction

Being immobile, insect eggs are the most vulnerable and endangered of all developmental stages (Hilker 1994). The selection of the optimal oviposition site can be essential for female fitness (Scheirs and De Bruyn 2002, Scheirs *et al*. 2004) and should be optimised in terms of a high offspring survival and low egg mortality.

Egg mortality of herbivorous insect eggs can be caused, for example, by parasitoids (Obermaier *et al*. 2001), predators (Ikeda and Nakasuji 2002), pathogens (Kellner 2002) or abiotic factors (Madrid and Stewart 1981, Smitley *et al*. 1998). Oviposition site selection in general can be triggered by various factors such as previous egg load of the host plant and future host plant supply (Mappes and Makela 1993, Nomakuchi *et al*. 2001), future larval performance (Kouki 1993), plant quality (Kouki 1991), plant architecture (Gingras *et al*. 2003), surrounding vegetation structure (Meiners and Obermaier 2004) and microclimate (Kopper *et al*. 2000).

Host plant height was examined in several studies as a factor potentially determining the choice of oviposition site or number of eggs laid (Hopkins and Whittaker 1980, Bjorkman *et al*. 1997, Nomakuchi *et al*. 2001, Agrawal and Van Zandt 2003). However, oviposition height within the host plant was only rarely investigated (Leite *et al*. 1999, Satoh 2002). There are no studies at all on oviposition height *per se* that exclude the effect of host plant characteristics simply changing with plant height. The effect of oviposition height on egg survival due to effects of winter mortality (Smitley *et al*. 1998) or parasitism (Wang *et al*. 1997) and the resulting selection pressures responsible for spatial patterns of egg distribution are very rarely examined as well.

The polyphagous tansy leaf beetle, *Galeruca tanaceti* L. (Coleoptera: Chrysomelidae), can occur as pest on potato, cabbage, beans, dahlia and other cultural plants (Lühmann 1939, Heinze 1974). The females oviposit at different heights on dry stalks of grasses or herbs of mostly non-host plants during autumn (Prevett 1953, Meiners and Obermaier 2004). An egg clutch contains on average 64.9 ± 1.3 eggs (Obermaier, unpublished data). The species overwinters in the egg stage and egg clutches stay on the plants for up to 7 months until hatching of the larvae in April (Obermaier and Zwölfer 1999). During this time, the eggs are exposed to numerous biotic and abiotic mortality factors. While the egg parasitoid *Oomyzus galerucivorus*

Hedqvist parasitises the eggs mainly from September to November, the eggs have to face detrimental abiotic factors, pathogen attack and predation throughout the whole winter. The effect of abiotic factors, pathogens and predation on egg survival can be conveniently described as winter mortality. We examined the variability of the oviposition height of *G. tanaceti* in space and time and proposed several hypotheses with ecological and evolutionary explanations for the observed patterns. A sub-set of these hypotheses was tested in the field. Specifically, we wanted to know whether oviposition height might be associated with vegetation height, egg parasitism or winter mortality. The following questions were asked: (1) Is there a standard uniform oviposition height for *G. tanaceti*, independent of the time of season and habitat? (2) Is egg clutch mortality related to oviposition height? (2a) Does winter mortality of egg clutches change with oviposition height? (2b) Does egg parasitism change with the height of the oviposition site?

Material and methods

Study system

The study was conducted in the nature conservation area 'Hohe Wann' in Lower Franconia, Germany, in autumn and winter of 2001/2002 and 2005. Due to the high time requirement for conducting phenological studies, only three sites were investigated at the same time. The three sites chosen for investigation were similar in most aspects so that a comparison of the oviposition phenology between them seems to be justified. All three sites showed sufficient high densities of ovipositing females, a moderate density of the main host plant, *Achillea millefolium* (Asteraceae), comparable slopes, the same biotope type (semi-arid grassland), are located at approximately the same altitude (Prappach: 300 m, Schafhof 280 m and Rauchberg 343 m above NN) and are only 909-2190 m apart from each other. They differ, however, in their inclination. The site Prappach has a north-west orientation, the sites Schafhof and Rauchberg are south oriented. The study was conducted on sub-squares (size 1100-2800 m^2) of all three sites. The largest site (Schafhof) was additionally used to study egg parasitism and winter mortality of *G. tanaceti* on a small spatial scale. Additionally, eleven similar semi-arid grassland sites in the same study area were selected for an investigation of oviposition height and vegetation structure at different sites.

The leaf beetle *Galeruca tanaceti* is a univoltine species distributed throughout Europe and in the East Palaearctic region, Near East and North Africa (Fauna Europaea Web Service 2004, version 1.1, http://www.faunaeur.org). It is therefore exposed to a wide range of abiotic conditions ranging from environments which are snow-free throughout winter to ones which have a much more prolonged cover of snow (e.g. Sweden, Finland) than the study sites in southern Germany.

The egg parasitoid *Oomyzus galerucivorus* parasitises egg clutches of its host shortly after oviposition of the host in autumn. The parasitoid larvae hibernate in the host eggs and adults emerge next spring. The 1.5 mm long egg parasitoids search for host egg clutches by walking up and down vertical structures within the vegetation (Meiners, unpublished data).

Phenology of oviposition height

On the three grassland sites selected the oviposition height of *G. tanaceti* was recorded over the oviposition season from September until December. Every 4 days the oviposition height of 18 egg clutches per site was measured as vertical height. All egg clutches at each date were marked, so that newly oviposited eggs could be distinguished. Only these were used for the investigations and a random sample of 18 egg clutches was also measured. With this method we also ensured a representative range of oviposition heights. We used the sample size of 18 egg clutches per date and per site because this was the largest estimated common sample size possible to collect on each of the three sites over a longer period of time. Since one female deposits only one egg clutch per week, it is usually difficult to find sites featuring enough newly oviposited egg clutches for permanent monitoring. By choosing an interval of four days to search for new laid egg clutches we were also able to investigate the current rate of parasitism at the same time. After mid-November newly laid egg clutches were searched for after longer time intervals, however, the collected eggs were also not older than four days. Mean vegetation height of the three sites was recorded by measuring vegetation height in 10 randomly selected squares within each site once during the oviposition period in October.

Oviposition and vegetation height at different field sites

On 11 dry grassland sites oviposition height was recorded for 20 randomly selected egg clutches per site. For each of the egg clutches the total height of the plant to which it was attached was also measured. Mean and maximal vegetation height was measured in fifteen 0.25 m^2 squares per site.

Parasitism and oviposition height

Selection of egg clutches

In October/November we investigated the influence of oviposition height on egg parasitism. For the study of egg parasitism we created 60 random points on an aerial photo of the grassland site *via* the spatial analyst module of the ArcView GIS software package (ESRI, Redlands, California). In the field, the random points were located with a GPS (Garmin). The egg clutch nearest to the obtained point was selected by the nearest neighbour method and marked with a stick. In all of the 60 randomly selected plant individuals, oviposition height was recorded as vertical height from the ground to the egg clutch. Afterwards, the egg clutches were harvested and transferred to the laboratory.

Hatching of parasitoids

All egg clutches collected from the site (n=60) were put singly into vials, closed with a very fine net and kept for several weeks at room temperature until parasitoids hatched. The net was sprayed every three days with water to prevent egg clutches from drying out. Parasitism was registered as incidence. If at least one parasitoid had hatched from the clutch it was categorised as incidence (1), if no parasitoid had hatched it was a non-incidence (0).

Dissection of egg clutches

All eggs of the 60 egg clutches were additionally dissected in the laboratory to calculate the rate of parasitism per egg clutch. In order to achieve this, the number of parasitoids hatched, number of viable parasitoids within the egg shells and total egg number per clutch were counted.

Winter mortality and oviposition height

In December, 135 plants with egg clutches of *G. tanaceti* were marked with yellow tape at the Schafhof site. Egg clutches on herbs and grasses were tested in the same proportions. The tape was applied to a stalk next to the stalk with the egg clutch, to avoid any change in the stability of the plant. The height of the egg clutch was recorded as vertical height from the ground and as length of the stalk up to the egg clutch. Additionally, plant type (grass/herb), number of ramifications and oviposition substrate (leaf, flower, etc.) was recorded. Marked egg clutches were searched for again in April, after a long and deep cover of snow on the site during winter. In some cases it was difficult to relocate the markings because heavy snow cover had destroyed many plants and eggs and some marking indicators could not be found. Thus eggs clutches were searched for within a radius of 50 cm around the site of the tape mark for 4 minutes. After this time the egg clutch was categorised as either a) found on a plant or b) found on the ground or c) as disappeared (= destroyed).

All egg clutches were transferred to the laboratory. Five eggs per egg clutch were dissected. If a fully developed beetle larva had been found in at least one of the eggs we categorised the egg clutch as ‘survived’ (1). If the egg clutch had disappeared in the field or if a fully developed beetle larvae could not be found during dissection, the egg clutch was categorised as ‘not survived’ (0).

Statistical analysis

The change in oviposition height of *G. tanaceti* over the season (12 dates in the space of time 10/2-12/1) on three different sites was tested with ANCOVA (Crawley 2002). Differences between sites were tested by the site term. Differences between slopes of the regression lines by the date x site interactive term and differences of the slope from zero were tested by the date term. All single correlations were tested with the Pearson correlation coefficient, group differences between two groups were investigated with the paired t-test, after testing for normal distribution. The influence of oviposition height on parasitism and winter mortality of egg clutches was tested by multiple logistic regression (Hosmer and Lemeshow 1989, Jongman *et al*. 1995, see also Meiners and Obermaier 2004). Models were accepted only if forward and backward logistic regression methods resulted in the same combination of habitat variables. In order to evaluate the goodness-of-fit of the habitat models the coefficient of determination R^2 after Nagelkerke (1991) was considered. Influence of oviposition height on rate of parasitism per egg clutch was tested by multiple regression. All procedures were calculated with the software package SPSS 10.0.

Results

Phenology of oviposition height

Oviposition height was recorded on three sites over the whole oviposition period (Fig. 1). Oviposition height of the three sites differed significantly (F_{site} = 937.61, P = 0.001, n = 18). The slopes of the regression lines of all sites also differed significantly from zero (F_{date} = 124.759, P = 0.001, n = 18) and oviposition height declined over the season (B_{date} = -2.192, SE = 0.196, T = -11.170, P = 0.001) with the same slope for all three sites, since the site-by-date interaction was not significant ($F_{site\ x\ date}$ = 0.920, P = 0.399). The three studied sites differed in mean vegetation height (mean height ± SD): Rauchberg: 0.31 m ± 0.21 m, Schafhof: 0.31 m ± 0.17 m, Prappach: 0.59 m ± 0.25 m. The ungrazed Prappach site with the highest mean vegetation height also showed the highest oviposition height.

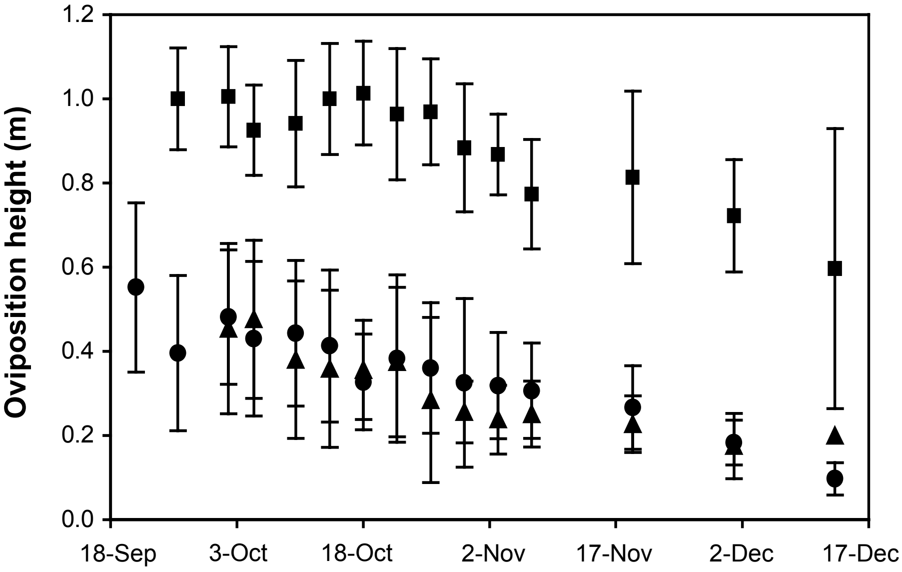

Fig. 1. Development of the oviposition height during the oviposition period of *G. tanaceti* at three sites in autumn ($R_{corrected}$ = 0.779; F_{date} = 124.759; P_{date}= 0.001; F_{site} = 937.610; P_{site} = 0.001; *n* = 18). Only eggs newly deposited up to each date were used for the calculation. Sites examined were Prappach (■), Rauchberg (▲) and Schafhof (●). Mean values and standard deviation are given.

Oviposition height in different habitats

There was a significant positive correlation between mean oviposition height and mean maximal vegetation height for 11 dry grassland sites (r_P = 0.641, *P* = 0.034, *n* = 11). There was no significant correlation of mean oviposition height and mean vegetation height (r_P = 0.493, *P* = 0.123, *n* = 11). Oviposition height seemed to increase with increasing maximal vegetation height of sites. Additionally, mean oviposition height was significantly higher than mean vegetation height (t = 9.65, *P* < 0.001, *n* = 11), but did not differ significantly from mean maximal vegetation height (t = 0.794, ns, *n* = 11) (Fig. 2).

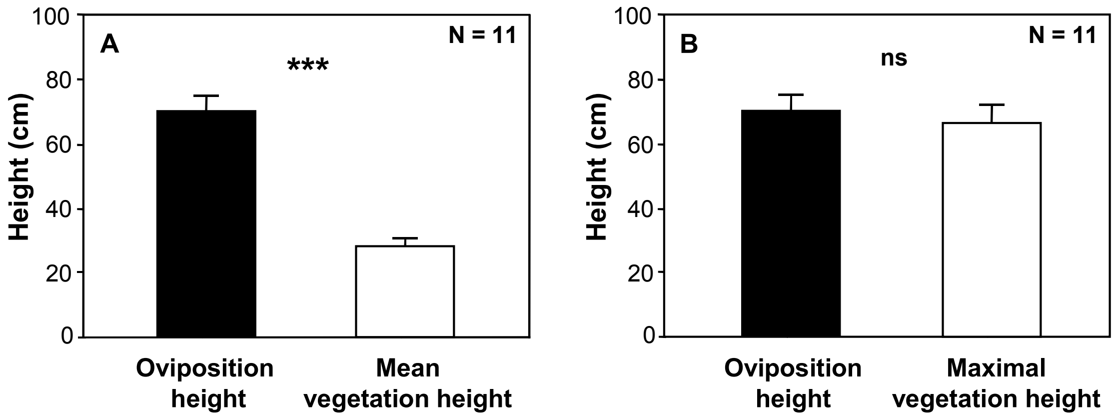

Fig. 2. (A) Mean oviposition height of *G. tanaceti* versus mean vegetation height at different sites (t = 9.65, $P < 0.001$, $n = 11$). (B) Mean oviposition height versus maximal vegetation height at different sites (t = 0.794, ns, $n = 11$). Different letters indicate significant different means. Illustrated are mean and standard error.

Oviposition height and height of plants on which egg clutches were attached were significantly positively correlated ($r_P = 0.934$, $P < 0.001$, $n = 220$) (Fig. 3). This implies that the higher the plants used for oviposition, the higher the oviposition site on the selected plants.

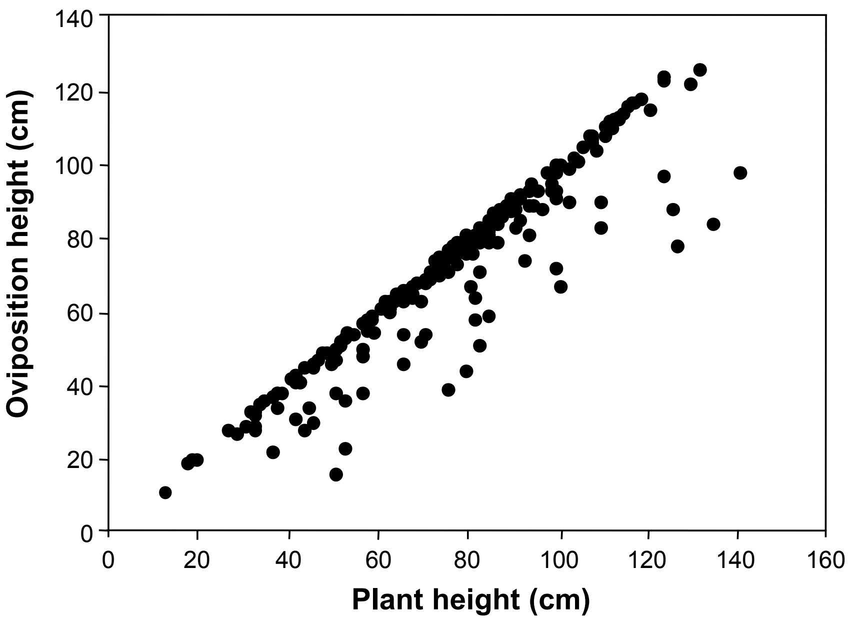

Fig. 3. Correlation of oviposition height with height of plants the egg clutches were attached to ($r_P = 0.934$, $P < 0.001$, $n = 220$).

Parasitism of egg clutches at different heights

The probability of an egg clutch being parasitised decreased significantly with increasing vertical height of the oviposition site above ground ($R^2_{Nagelkerke}$ = 0.095, P_{model} = 0.036, coefficient = -0.027, SE = 0.014, $P_{variable}$ = 0.047, n = 60) (Fig. 4). When the egg clutches were dissected for total rate of parasitism per egg clutch, results were similar. Rate of parasitism per egg clutch was significantly negatively correlated with oviposition height ($R^2_{corrected}$ = 0.051, F = 4.070, P_{model} = 0.048, coefficient = -0.006, SE = 0.003, $P_{variable}$ = 0.048, n = 60).

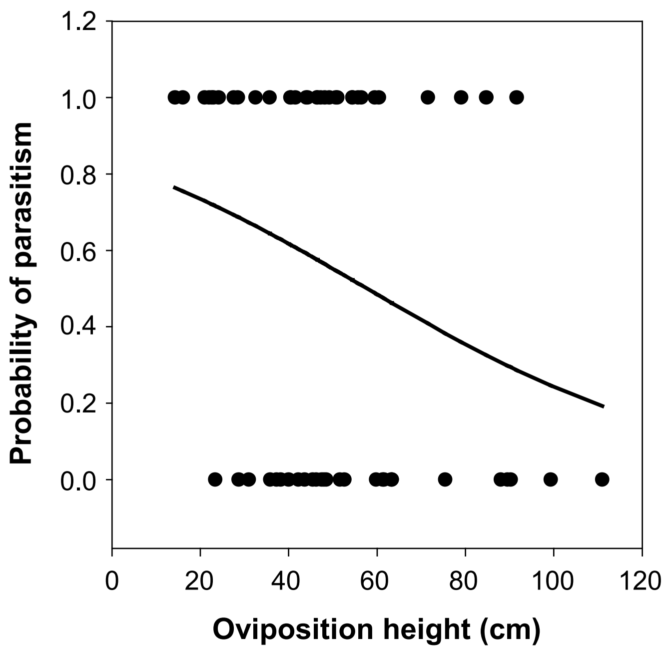

Fig. 4. Parasitism of the egg clutches of the leaf beetle *G. tanaceti* by the parasitoid *O. galerucivorus* at different oviposition heights. Plotted are the incidence of parasitism (●) and the predicted probability of the incidence of parasitism (—) calculated by the logistic regression model (n = 60 egg clutches).

Winter mortality of egg clutches at different heights

Of 135 markings attached to the stalks of egg clutches in autumn, 85 markings and 21 egg clutches belonging to the markings were found again in spring. Of the 21 egg masses successfully recovered, 13 were found on the ground and 8 on plants. 5 of 13 egg clutches found on the ground were no longer viable, as was 1 of 8 egg clutches found on plant structures. Winter egg clutch mortality decreased significantly with increasing vertical oviposition height above ground (winter mortality of egg clutches: $R^2_{Nagelkerke} = 0.77$, $P_{model} = 0.047$, coefficient = -0.029, SE = 0.015, $P_{variable} = 0.049$, $n = 85$) (Fig. 5).

Oviposition height was the only factor which significantly could explain winter mortality. The other variables tested, plant type (grass/herb), number of first order ramifications and oviposition substrate (leaf, flower, etc.) did not contribute to the model.

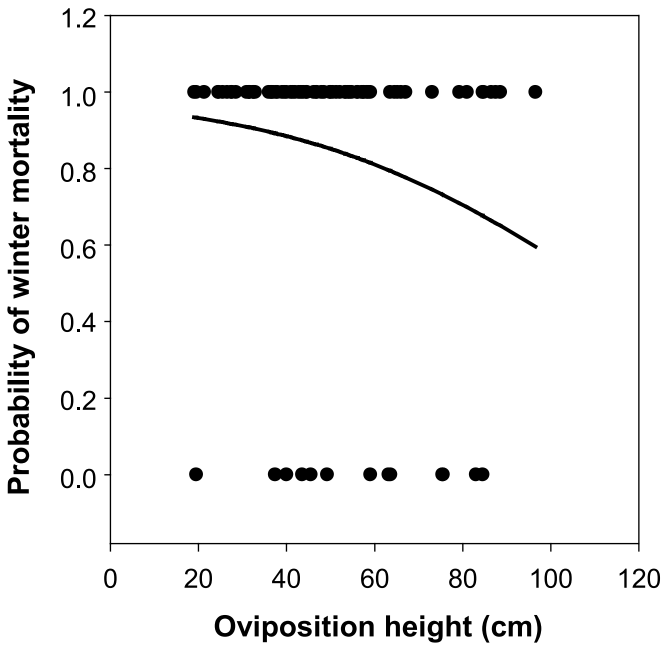

Fig. 5. Winter mortality of the egg clutches of the leaf beetle *G. tanaceti* at different oviposition heights. Plotted are the incidence of winter mortality (summarising mortality by pathogens and abiotic factors) (●) and the predicted probability of the incidence of winter mortality (—) calculated by the logistic regression model (n = 85 egg clutches).

Discussion

Oviposition height of *G. tanaceti* decreased significantly over the season and varied strongly over a range of sites examined. This suggests, in contrast to the observations of Scherf (1966), that this beetle species does not prefer a uniform standard oviposition height but that this parameter is extremely variable in time and space. Oviposition height seems to depend proximately on the vegetation height of the sites and the height of the individual plants selected for oviposition. The climatic conditions during the season, as well as the physiological state of the females, might further contribute to the actual height.

Oviposition height was highest at the beginning of the oviposition period and decreased later significantly to 80-40% of the initial height on all three sites examined. This could be interpreted as a declining ability of the gravid female beetles to climb high up the stalks. However, a comparison of the oviposition height at the different sites contradicts this hypothesis since at the end of the season at the site Prappach females oviposited as high as females at the other two sites at the beginning of the oviposition season in September. On the other hand, over the course of the oviposition period (autumn), the availability of high plant structures, attractive for oviposition by *G. tanaceti*, might decline because high structures at suitable places are either already occupied with previous egg clutches or become rarer by natural degradation during autumn (B. Randlkofer, personal observation).

The comparison of oviposition height and vegetation height at different sites supported the second interpretation and revealed a significant positive correlation of oviposition height and maximal vegetation height. Furthermore, mean height of egg clutches was significantly higher than mean vegetation height and ranged at the height of the mean maximal vegetation height. Oviposition height was also significantly positively correlated with the height of the plants to which egg clutches had been attached. These results suggest that female beetles select oviposition sites high above the mean vegetation height and try to oviposit as high as possible within the vegetation and on the selected plants.

Beside the proximate factors which seem to influence oviposition height, such as available vegetation height, we wanted to investigate hypotheses on main selection pressures which might have induced herbivores to oviposit high up in herbaceous vegetation. Parasitism by the specialised egg parasitoid *Oomyzus galerucivorus* (the only egg parasitoid of *G. tanaceti* in this region) and mortality by abiotic factors, pathogens or removal by predators during winter, summarised as "winter mortality" were examined as the main mortality factors of the egg stage of the tansy leaf beetle. Both mortality factors were significantly reduced with increasing oviposition height above ground in the present study.

Parasitism significantly decreased with increasing oviposition height. 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 to prevent the higher located egg clutches from being parasitised. It might therefore represent a selection advantage for these eggs. Egg-parasitism of the European corn borer also was lower in the upper parts of corn plants (Wang *et al*. 1997). Gingras *et al*. (2002, 2003) showed that plant structure affected the host finding success of parasitoids which was higher on plants with a simple structure and low on plants with a complex structure. On certain microsites of plants mortality was reduced (Berdegué *et al*. 1996, Hopkins and Dixon 1997). According to the results of our study oviposition sites located high up in the vegetation might represent an enemy-free space as well.

Like parasitism, winter mortality in *G. tanaceti* eggs was lower when the oviposition site was located high up in the vegetation. It can therefore explain the preference for high oviposition sites by *G. tanaceti*. The result stands in contrast to the findings of two studies on winter mortality of eggs of the gypsy moth in the USA and Canada (Madrid and Stewart 1981, Smitley *et al*. 1998). There, due to the snow cover, eggs close to the ground have a higher chance of survival than eggs high above the snow. We, at present, are not able to solve the question as to why there is a higher survival from winter mortality factors at higher oviposition sites with currently available data. Field observations show that most stalks are still upright after the first heavy snow falls at the beginning of January (E. Obermaier, personal observation) and that original oviposition height therefore might still influence survival during the ongoing winter. Hypotheses for a higher survival of eggs laid higher in the vegetation include a possibly lower chance of deterioration of those egg clutches and higher temperatures high above the ground. Previously it had been shown that *G. tanaceti* prefers a sunny microclimate and therefore higher temperatures for oviposition (Meiners and Obermaier 2004).

Winter egg mortality in herbivorous insects can be caused by pathogens such as fungi (Fargues and Rodriguez 1980, Storey *et al.* 1991, Long *et al.* 1998, Tallamy *et al.* 1998), or bacteria (Robert *et al.* 1998), or by removal due to predators. The interaction of pathogens and abiotic factors (such as wind, heavy rain or snow) might enhance the deterioration and disappearance of most of the egg clutches fallen to the ground over the winter. Our data suggest that a significant higher proportion of egg clutches which remained on the stalks over the winter were viable, compared with those that had fallen to the ground ($\chi^2 = 14.09$, df = 1, $n = 21$, $P > 0.001$). Egg clutches found to be fed upon by arthropod predators in autumn were very rare (about 5% of the egg clutches were preyed upon in a recent investigation, Obermaier, unpublished data). Vertebrate predators, like birds, might also contribute to the high number of egg clutches disappearing completely from the ground. However, birds were shown to avoid the larvae of *Galeruca tanaceti* because they contain anthraquinones as a defence agent (Hilker and Köpf 1994). Since not only larvae, but also the eggs of *G. tanaceti* contain anthraquinones, they might be protected against vertebrate predators as well (Meiners *et al.* 1997).

Oviposition height in *G. tanaceti* is variable in time and space and probably dependent on vegetation height. The females seem to oviposit as high as possible in the herbaceous vegetation. Mortality caused by the main mortality factors of the eggs, 'egg parasitism' and 'winter mortality', summarising all mortality factors acting upon the egg clutches over the winter, is dependent on oviposition height and is significantly reduced with increasing oviposition height. High oviposition sites of *G. tanaceti* can therefore be explained by and have possibly evolved through reduced mortality, and may thus represent an enemy-free space.

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