

Original article

Altitudinal gradients of generalist and specialist herbivory on three montane Asteraceae

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Abstract

Different functional types of herbivory on three montane Asteraceae were investigated in natural populations in central Germany to test the hypothesis that herbivory is decreasing with altitude. Generalist herbivory was assessed as leaf area loss, mainly caused by slugs, and, in *Petasites albus*, as rhizome mining by oligophagous insect larvae. Capitules were found to be parasitized by oligophagous insects in *Centaurea pseudophrygia* and by the specialist fly *Tephritis arnicae* in *Arnica montana*. Only the damage to leaves of *P. albus* showed the hypothesized decrease with increasing altitude. No altitudinal gradient could be found in the leaf and capitule damage to *C. pseudophrygia*. In *A. montana*, capitule damage increased with increasing elevation. The data suggest that abundance and activity of generalist herbivores are more affected by climatic conditions along altitudinal gradients than specialist herbivores. In all probability, specialist herbivores depend less on abiotic conditions than on their host's population characteristics, such as host population size.

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1. Introduction

Plant range boundaries are the result of various abiotic and biotic factors that prevent the successful completion of the life cycle of a plant species outside its geographical range. This is also true in the case of montane and alpine species which do not occur in the lowlands. The hypothesis that the warmer lowland climate leads to higher respiratory losses of storage carbohydrates has often been referred to, but has been tested in only a few plant species (e.g. Stewart and Bannister, 1974; Graves and Taylor, 1988; Larigauderie and Körner, 1995; Atkin et al., 1996; Arnone and Körner, 1997; Bruelheide and Lieberum, 2001). However, the results of these studies generally showed a great acclimation potential of plants from higher altitudes. Most other abiotic site factors become more favourable for plant growth with decreasing altitude and therefore cannot directly cause range limits of highland plants at lower altitudes.

However, lowland conditions may disproportionately favour competitors, herbivores or pathogens which then re-

duce the fitness of the highland species. Grime (2001) presumed that herbivory decreases with increasing environmental harshness. The most important climatic variable that causes the harshness at higher altitudes is temperature which decreases with elevation. Molluscs as important consumers of plants may be affected negatively by decreasing temperatures (e.g. Baur and Rabaud, 1988), but may also benefit from increasing precipitation and reduced evapotranspiration at high elevations. The hypothesis that the abundance of slugs is generally lower in harsher climatic regions has yet to be proved (Keller et al., 1999).

We are also aware of only a few studies on herbivores other than molluscs along altitudinal gradients that could demonstrate a decrease in herbivore activity with increasing altitude. The damage to *Polemonium viscosum* by aphids and ungulates was lower at 4000 m than at 3530 m in the Rocky Mountains (Galen, 1990). Predispersal seed predation by oligophagous lepidopteran and dipteran larvae in Swedish *Bartsia alpina* populations was lower at 900 m than at 400 m (Molau et al., 1989). Herbivory damage to *Sanguisorba tenuifolia* in Japan reached clearly lower levels at 980 m than at 4 m (Suzuki, 1998). Kelly (1998) found decreasing aphid damage to *Solidago macrophylla* between 800 and 1550 m in

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the White Mountains (New Hampshire). Transplant experiments with several Asteraceae in the Harz Mountains, Germany, revealed decreasing levels of leaf area loss from the lowlands to montane and subalpine sites (Bruehlheide and Scheidel, 1999; Scheidel and Bruehlheide, 2001).

However, there are also studies that found no increasing herbivory with decreasing altitude. Olofsson (2001) reported similar densities of mammalian herbivores in a meadow at 450 m and in a snowbed at 600 m. However, without herbivore exclosure, the biomass of transplanted tall herbs decreased during 3 years in the snowbed but not in the meadow. In natural populations of *Arnica montana* (Scheidel and Bruehlheide, 1999) and *Senecio* sp. (Scheidel and Bruehlheide, 2001) in the Harz Mountains, no altitudinal gradient in the leaf damage could be detected. Other observations indicated that there was no linear altitudinal trend in herbivory. For example, Diemer (1996) found no altitudinal gradient (2600–3310 m) in leaf and flower damage to the alpine *Ranunculus glacialis*. In England, Randall (1986) reported maximum attack rates on seed capsules of *Juncus squarrosus* at 300 m where nearly all of the seeds were eaten by the larvae of the moth *Coleophora alticolella*. Above 300 m, seed predation decreased because of low larval densities due to more unfavourable climatic conditions. Below 300 m, there was also a decrease due to an increasing parasitoid attack to the larvae. Similarly, Virtanen and Neuvonen (1999) found that the parasitoid attack to the larvae of the moth *Epirrita autumnata* changed with altitude, however, one parasitoid species was most abundant at lowest altitudes and one species preferred the highest altitudes.

The present contribution is based on the hypothesis that higher herbivory at lower altitudes causes the absence of montane plant species in the lowlands. To test whether or not there is a changing herbivory pressure even over a relatively small altitudinal gradient (300–700 m), observational studies were conducted in natural populations of three Asteraceae (*Arnica montana*, *Centaurea pseudophrygia*, *Petasites albus*) in the Harz Mountains. The plant species were widespread over the studied altitudinal gradient. Leaf area losses were mainly caused by polyphagous slugs; whereas the rhizomes of *P. albus* and the capitules of *P. albus* and *C. pseudophrygia* were parasitized by oligophagous insects. In contrast, the flower heads of *A. montana* were exclusively attacked by the monophagous fly *Tephritis arnicae*.

The main hypothesis of our study was that the damage by invertebrate herbivores decreases with increasing altitude. Another hypothesis was that this trend differed between polyphagous and oligophagous herbivores.

2. Materials and methods

2.1. Study area

The Harz Mountains in central Germany are mainly built up by palaeozoic rocks and rise from about 200 to 1142 m

(Mt. Brocken). They cover an area of more than 2000 km² with a maximum extension of about 90 km from northwest to southeast. There are clear altitudinal climatic gradients (Glässer, 1994). The mean annual temperature is at about 8 °C at the western foothills of the mountain range at 200 m and decreases by 0.55 K per 100 m altitude resulting in 2.8 °C at the top of Mt. Brocken. The growing season with mean daily temperatures > 8 °C is about 200 days at the western border of the Harz Mountains and 97 days on Mt. Brocken. The annual precipitation amounts to 840 mm at the western border and 1600 mm on Mt. Brocken.

The plant populations studied were located mainly in the south-western part of the mountain range between their lower altitudinal range limit (about 300 m) and an upper limit at about 700 m. Most investigations were carried out in 1999.

2.2. Study species

2.2.1. *Petasites albus* (L.) Gaertn

Petasites albus occurs in Europe from Spain to Russia and further east to the Altai Mountains. In central Europe, except for the Baltic Sea coast, most populations are found at altitudes higher than 200 m. The species is widespread in the Harz Mountains. Here the lowest stands grow at about 300 m. Most populations are found in montane forests, tall-herb communities, road verges and riverbanks and have a large extension due to clonal fragmentation of the rhizomes. The plant is functionally dioecious and flowers in March–April, i.e. before leaf expansion. Seeds are dispersed by wind in May. In summer, *P. albus* forms dense stands due to its large 15–30 cm tall leaves.

2.2.2. *Centaurea pseudophrygia* C.A. Meyer

Centaurea pseudophrygia occurs from central Europe to the southern Ural Mountains. In central Germany, most populations are found at submontane and montane altitudes, in mown or abandoned meadows and at road verges. In the southern parts of the Harz Mountains, the lowest populations are located at about 300 m. The shoots of this hemicryptophyte attain a height of more than 1 m. Flowering period starts at the beginning of July and continue until the first autumn frosts. Seeds are dispersed from the beginning of August onwards.

2.2.3. *Arnica montana* L.

Arnica montana grows in Europe from France to Russia. In central Europe, a large proportion of the lowland populations have disappeared during the last 50 years, mainly due to more intensive land use. In the Harz Mountains, the species is found in submontane and montane meadows above 350 m. The hemicryptophyte produces numerous rosettes. However, only a minor fraction develops a flowering shoot of about 50 cm height in June and July, with 1–5 flower heads. Seed dispersal is finished in mid-August.

2.3. Leaf damage

Damage to fully expanded non-senescent leaves was assessed as percentage leaf area loss in 10% intervals as the most precise visual estimation in the field. Damage to *Petasites albus* leaves was investigated at 214 sites at road verges (300–780 m) within 3 weeks in July and August 1999. As in all three study species, the sample sites were chosen in the spring, before the first damage measurements, with respect to their accessibility and an even distribution over the altitudinal range investigated that was as large as possible. In some large populations, several sites were sampled that were separated by at least 50 m from each other. At each *P. albus* site a sample of about 50 green leaves was taken around a randomly determined center. We assessed the leaf area loss of the 10 most severely damaged leaves at each site. Consequently, the assessed damage levels do not reflect the population mean but the average damage of the upper 20% quantile, in the following referred to as maximum leaf area loss. Eight of these sites were visited at intervals of about 2 weeks from May to October 1999 to assess the seasonal course of damage to fully expanded non-senescent leaves during the whole vegetation period.

To study the leaf damage in *Centaurea pseudophrygia*, 72 grassland sites (300–680 m) were investigated at the beginning of the flowering period within 2 weeks in July and August 1999. Within large meadow populations, several sites were sampled that were separated from each other by at least 50 m. The sample at each site comprised of 20 randomly chosen shoots growing in an area of about 5 m in diameter. For each shoot, we estimated the leaf area loss of two leaves inserted at one-third and two-thirds of the shoot length.

2.4. Rhizome damage

In *Petasites albus* also, herbivore damage to the rhizomes was studied at 161 sites at road verges (295–695 m) at the beginning of the flowering period in March 2000. The sites were mainly the same as for the investigation of leaf damage. Each site included an arbitrarily chosen area of 1×1 m where the *P. albus* rhizomes reached a total length of several meters. Twenty cross-sections were prepared in different older rhizome pieces at a distance of at least 2 cm from an apical bud. Twenty cuts were made in younger rhizomes less than 1 cm behind an apical bud. Most of the older rhizomes were probably more than 1 year old; whereas the younger pieces had been produced in the previous vegetation period. The percentage of cuts falling in a rhizome sector mined by herbivores was assessed.

2.5. Capitule damage

To assess the herbivore damage to the flower heads of the study species, single capitules or, in *Petasites albus*, entire capitulescences were harvested from natural populations. In contrast to the sampling of leaf and rhizome damage, only

one sample comprising of at least 12 capitules or capitulescences was taken at a site. Within 2 days after cutting, the flower heads were carefully dissected in the laboratory looking for signs of herbivore damage.

Flower heads of *P. albus* were investigated in two parts of the growing season 1999. During seed development in the spring, the damage to single flower heads was investigated at 15 sites at road verges, randomly chosen from the sites visited for the estimation of leaf damage with respect to an even distribution between 300 and 680 m. During senescence in the autumn, whole capitulescence buds from the same sites were dissected.

In *Centaurea pseudophrygia* and *Arnica montana*, flower head herbivory was measured as percent heads per site with signs of parasitic infestation ('attack rate'), as percent seeds from all seeds of the flower head which showed parasite damage and as the sum of parasite larvae and pupae per flower head. Flower heads of *C. pseudophrygia* were randomly chosen within 18 grassland populations at 290–670 m. These were randomly chosen from the populations known from the estimation of leaf damage. At most sites, the damage to flower heads that were in flower on the respective observation date was assessed at three dates from the beginning of the flowering period in July to the beginning of September.

Randomly selected flower heads of *A. montana* from nine grassland populations at 370–680 m were investigated during anthesis between the end of June and the middle of July 1999. For this species, we did not differentiate between sample dates because of the short flowering period. Since the study sites were clearly separated from neighbouring *Arnica* stands, it was easily possible to quantify the population size by estimating the total number of flowering shoots.

2.6. Data analysis

All calculated parameters were tested for normal distribution (proc univariate, Shapiro-Wilk-statistics, SAS Institute, 2000). In general, Pearson's (r^2) correlation was computed. For data that were not normally distributed Spearman's (r_s^2) rank correlation was calculated (proc corr, SAS Institute, 2000). Nevertheless, figures also show parametric regression lines for non-normally distributed data (see Figs. 1 and 5). The effect of altitude on the damage to *Petasites* leaves during the vegetation period was tested for each sample date with sequential Bonferoni correction according to Holm (1979). Differences in damage level between leaves inserted at different heights and rhizomes of different age were tested with a *t*-test for paired comparisons (proc means, SAS Institute, 2000). Seasonal differences were tested with ANOVA with subsequent single post-hoc comparisons according to Scheffé (proc glm, SAS Institute, 2000). In all tests, the significance level was $\alpha = 0.05$.

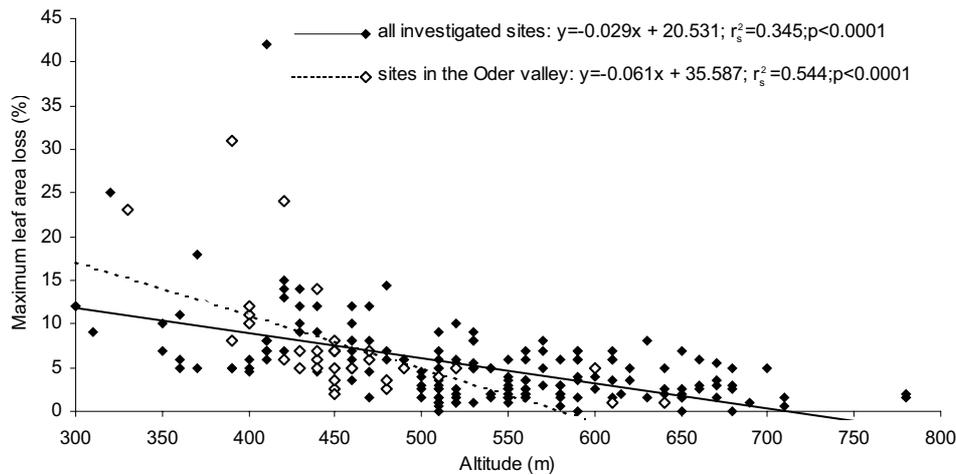


Fig. 1. Mean leaf area loss of the 10 most damaged leaves of *Petasites albus* at 214 sites (300–780 m). Each sample consisted of 50 fully expanded, non-senescent leaves. The Oder Valley sites were considered separately. Trend lines and equations refer to linear regression; r_s^2 and P refer to Spearman rank correlation.

3. Results

3.1. Leaf damage

In *Petasites albus*, the leaf area loss decreased significantly with increasing altitude (Fig. 1). All stands whose mean losses of the 10 most severely damaged leaves were higher than 10% were located at altitudes lower than 500 m. Up to 440 m, no stand exhibited less than 4% damage. In contrast, the four stands with completely undamaged leaves were found at altitudes higher than 500 m. A similarly significant correlation resulted from the locally restricted 35 stands in the NE–SW running Oder Valley (330–640 m). The patterns of leaf damage indicated that molluscs were the predominant herbivores. Individuals of several slug (*Arion* sp., *Deroceras* sp.) and snail species (*Arianta arbustorum*) were observed feeding on the leaves.

A tendency of decreasing leaf damage with increasing altitude was also found in eight of these stands, which were investigated over the whole vegetation period (Fig. 2). For all sample dates except for May 21st and July 5th a significant Spearman rank correlation ($P < 0.05$) between altitude and leaf area loss was found. During the first half of the growing season, up to the end of July, the leaf area loss remained below 12%. Only the plants at 330 m showed much greater damage levels, which reached about 30% in June. After the beginning of August, the curves diverged. The damage to the two highest plots remained below 10% until the end of the growing season. The three lowest plots reached damage levels of more than 50% in the autumn. Most plots did not show a continuous increase of the leaf damage with time, but intermittently declining values, when the production of new leaves surpassed the herbivore activity.

In contrast to *P. albus*, the leaves of *Centaurea pseudophrygia* showed no significant gradient in the herbivore damage with increasing altitude (Fig. 3). At all sites, however, the high-inserted leaves suffered lower damage

levels than the lower leaves (3.8% vs. 10.5%, on average; $P < 0.0001$).

Effects of insertion height could be found not only by the comparison of lower and higher inserted leaves. In addition, the leaf damage decreased slightly with increasing mean height of the sampled shoot groups, although this correlation was not significant. The shoot height, however, decreased significantly with increasing altitude (Spearman rank correlation; $r_s^2 = 0.085$; $P = 0.013$).

3.2. Rhizome damage

At most *Petasites albus* stands, less than 10% of the dissected younger rhizome pieces showed signs of mining by larvae of Lepidoptera and Carabidae; no altitudinal gradient existed (Fig. 4). The maximum damage was at 20%. The damage to the older rhizome pieces was significantly higher than that to the younger rhizome pieces (10.2% vs. 1.9%, $P < 0.0001$). At 16 sites, more than 20% of the cross-sections in older pieces revealed mining damage. As in the younger rhizome pieces, there was no significant decrease of the damage to older rhizomes with increasing altitude (Fig. 4).

3.3. Capitule damage

The dissection of flower heads of *Petasites albus* in spring 1999 did not reveal any signs of insect parasitization. However, some inflorescences suffered damage by molluscs, which grazed the leafy scales of the capitulescence axis and the flower heads, or ungulates, which consumed whole flowering shoots. In autumn, capitulescence buds were destroyed by rhizome-feeding larvae of Lepidoptera and Carabidae. Additionally, Enchytraeidae were found in the decaying material of attacked buds. The percentage of damaged buds ranged between 0% and 17%. There was no significant correlation between damage and altitude.

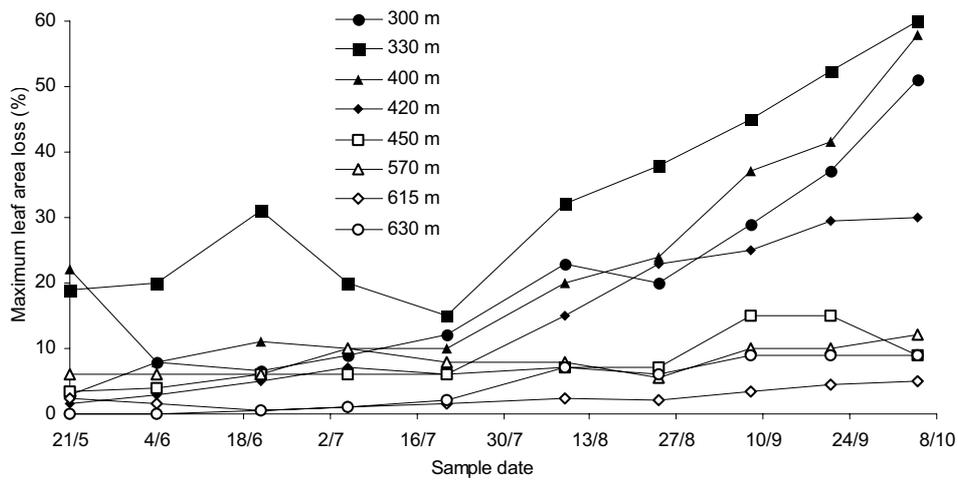


Fig. 2. Seasonal trend (mid-May to end October) in mean leaf area loss of the 10 most damaged leaves of *Petasites albus* at eight sites (300–630 m). Each sample consisted of 50 fully expanded, non-senescent leaves.

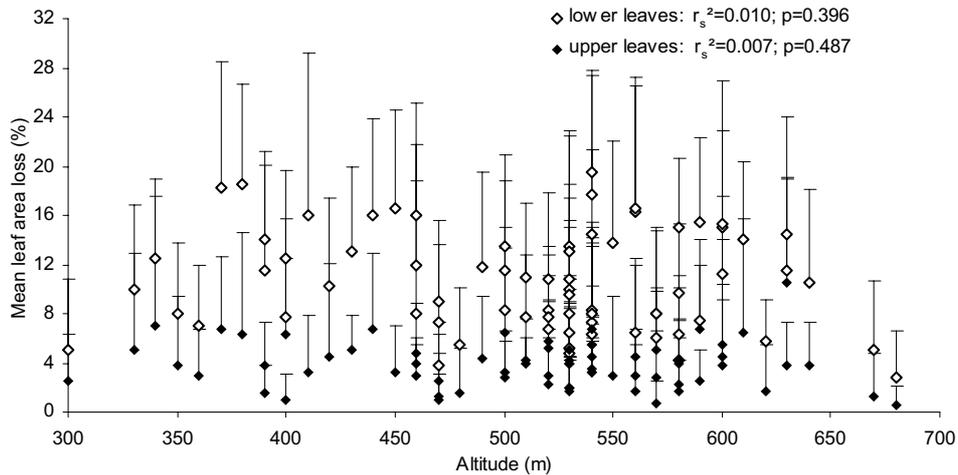


Fig. 3. Mean leaf area loss of stem leaves of *Centaurea pseudophrygia* at 72 sites (300–680 m), one-third and two-thirds up the stem. Error bars indicate standard deviation. r_s^2 and P refer to Spearman rank correlation.

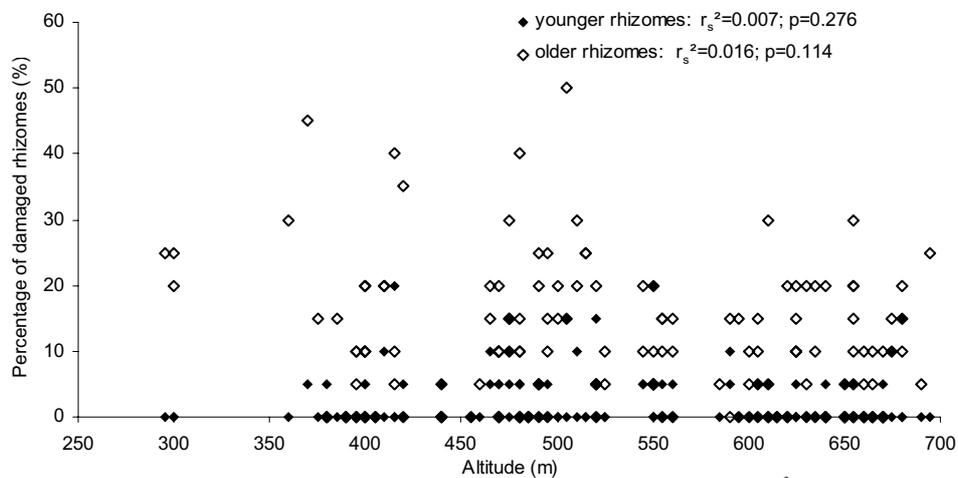


Fig. 4. Percentage of damaged 1-year old and older rhizome pieces of *Petasites albus* at 161 sites (295–695 m). r_s^2 and P refer to Spearman rank correlation.

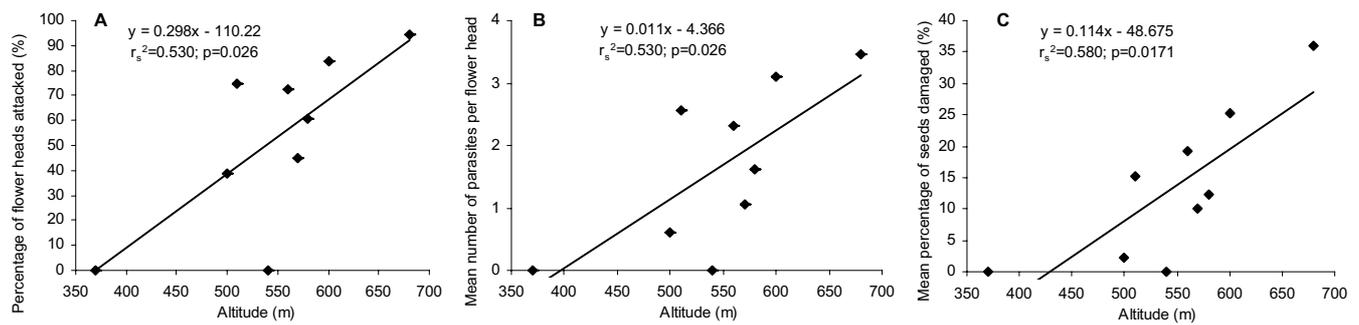


Fig. 5. Damage to flower heads of *Arnica montana* at nine sites (370–680 m) at one sample date during the flowering period. (A) Percentage of flower heads attacked; (B) mean number of *Tephritis arnicae* individuals (larvae and pupae) per flower head; (C) mean percentage of *Arnica montana* seeds predispersally damaged. Trend lines and equations refer to linear regression; r_s^2 and P refer to Spearman rank correlation.

The damage to flower heads of *Centaurea pseudophrygia* showed no altitudinal gradient on any sample date. However, there were significant seasonal differences. On the first sample date in the middle of July, only some days after the beginning of the flowering period, at most sites the attack rate was below 40% of the flower heads dissected. The level of parasitization at this date was significantly lower ($F = 12.27$; $P = 0.0001$) than in August and in September when at the majority of sites more than 50% of the flower heads were parasitized by several tephritid or lepidopteran species. Even comparably isolated, small *Centaurea* stands were attacked. Similarly, the mean number of parasites per flower head was lower on the sample date in July than in August and September ($F = 9.7$; $P = 0.0006$). The maximum number was about four individuals per head in August. The percentage of damaged achenes reached the highest values in August, with a maximum of about 50%. In July and September, significantly less achenes were damaged ($F = 12.56$; $P = 0.0001$).

In *Arnica montana*, a significant altitudinal gradient in flower head damage was found (Fig. 5A–C). However, in contrast to the damage to the leaves of *P. albus* (Fig. 1), increasing damage levels were found with increasing altitude. The capitules of the lowest sample site at 370 m were completely undamaged; whereas 95% of the heads collected at the highest site (680 m) showed signs of parasitization (Fig. 5A). In a manner similar to the attack rate, the number of parasite larvae and pupae per capitule increased significantly from 0 at 370 m to nearly 3.5 at 680 m (Fig. 5B). The damage per capitule specified as the percent seeds with obvious signs of herbivore damage also increased with increasing altitude (Fig. 5C). In all damaged heads, exclusively the *Arnica* specialist *Tephritis arnicae* (Diptera: Tephritidae) was found.

The *Arnica* populations sampled at higher altitudes consisted of several 100 to more than 1000 flowering shoots, whereas the two lowest sites and that at 540 m produced less than 50 flowering shoots in 1999 (Table 1). The *Arnica* population at the lowest site (370 m) was very small and isolated, probably insufficient to support a *Tephritis* population. The population at 500 m consisted of many more rosette shoots, however, with a very low flowering rate. Therefore,

the studied altitudinal gradient coincides with increasing population size, and percent flower head damage significantly increased with increasing population size ($r_s^2 = 0.749$; $P = 0.0026$).

4. Discussion

The hypothesized decrease in the herbivore damage with increasing altitude was confirmed only for the damage to leaves of *Petasites albus*. In the damage to rhizomes and capitulescence buds, the same tendency occurred albeit without being significant. Single flower heads suffered no damage, although Merz (1994) reported *Trypeta zoe* as capitule parasite of *P. albus* and of several other Asteraceae with comparatively small flower heads in Switzerland.

For studying plants at their lower altitudinal range limit *P. albus* is a particularly appropriate species, because it is dispersed by rhizome fragments along road verges and riverbanks. Therefore, plants can be found to frequently colonize sites on the lower distribution boundary. The other two species studied are characterized by much less frequent dispersal events since the lowest populations of these red-list species (Garve, 1994) are known for a long time. Small populations at the distribution boundary have a higher risk of extinction due to factors other than herbivory and at the same time a lower probability of recolonization. Therefore, even in the case of a potentially herbivory-caused distribution limit, populations that show the maximum of herbivore damage that is tolerated can be expected to be quite rare. A further reason why lethal threshold levels of herbivore damage are not observed is that adult individuals are generally less sensitive to herbivory than seedlings. Lower altitudinal sites are not colonized by *Arnica montana* and *Centaurea pseudophrygia* probably due to high seedling mortality (Scheidel and Bruelheide, submitted for publication), even though adult plants suffer comparatively little damage. In contrast, *P. albus* is characterized by vegetative regeneration that tolerates much higher levels of herbivory.

There are other reasons, why a decreasing herbivory pressure with increasing altitude was not detected. Small-scale factors such as shoot height may influence the herbivory risk

Table 1
Estimated population size of the sampled populations of *Arnica montana* and land use of the grassland

Location	Altitude (m)	Number of rosettes	Number of flowering shoots in 1999	Land use
Brandesbach Valley	370	100	30	Fallow
Giepenbach Valley	500	10 000	10	Mown
Stiege, Selkenfeld	510	1000	500	Mown
Benneckenstein, road verge	540	10	5	Fallow
Hohegeiss, hotel	560	100	50	Fallow
Hohegeiss, ski slope	570	1000	200	Mown
Hohegeiss, Gretchenkopf	580	10 000	1000	Mown
Braunlage, Hasselkopf	600	10 000	10 000	Mown
St. Andreasberg, Jordanshöhe	680	1000	5000	Mown

of certain leaves. Hairy stems can act as a barrier against herbivores climbing up to the leaves, as discussed for *Hieracium laevigatum* (Bruehlheide and Scheidel, 1999) or *Senecio* sp. (Scheidel and Bruehlheide, 2001). In *Centaurea pseudophrygia*, shoot height decreased with increasing altitude. In the same plants, leaf damage tendentially increased with decreasing shoot height. This tendency may promote relatively high damage levels at high altitudes and mask elevational gradients of leaf damage assessed at a certain insertion height at the shoot. Therefore, it may be possible to find an altitudinal decrease in the leaf damage by eliminating effects of differing shoot height and investigating leaves at the same height above the ground.

Another explanation for missing relationships between damage level and altitude could be that altitudinal gradients are masked by phenological differences. Although there is no clear indication for this in our investigations of the flower head damage to *C. pseudophrygia*, it is possible that seasonal changes in the parasitization rate are shifted to later dates at higher elevations due to a delay in the plant and/or herbivore phenology. Similarly, leaf damage to *Sanguisorba tenuifolia* in Japan decreased in late summer, partly caused by the senescence of the old leaves and recruitment of new ones (Suzuki, 1998). Therefore, as discussed by Scheidel and Bruehlheide (2001), it may be misleading to assess the damage to different plants growing at differing altitudes on the same sample date without regarding phenological differences, particularly if these are paralleled by changes in plant palatability (e.g. Speiser and Rowell-Rahier, 1991). However, in the case of mollusc damage to *P. albus* leaves this problem may be of minor importance because at least the snail *Arianta arbustorum* consumed the leaves equally in spring and summer (Hägele and Rahier, 2001). In general, to gain more relevant data on leaf losses longitudinal monitoring should be preferred to snapshot estimates (e.g. Jackson et al., 1999).

Another factor that may influence herbivore susceptibility is plant population size. For example, the probability that the large blue butterfly *Maculinea rebeli* occurred at *Gentiana cruciata* sites increased with increasing population size of the specialist's host plant (Kéry et al., 2001). Similarly, *Tephritis arnicae*, the only parasite found in *Arnica montana* flower heads in the study area, is highly specialized on *A. montana* (Merz, 1994). In small *Arnica* populations, mainly

occurring near to the lower altitudinal distribution limit, the parasite has to cope with a high probability of local extinction in years of low flowering due to late frosts, early mowing or grazing, and unknown factors causing high year-to-year variability in the flower production of *Arnica*. Therefore, close to distribution boundaries, decreasing host plant population size and smaller attack rates by specialist herbivores can be expected.

In contrast to *Tephritis arnicae*, the parasites of *P. albus* and *C. pseudophrygia* were generalist consumers. Our results give clear indications that altitudinal trends are different for generalist herbivores. Generalist herbivores can be expected to depend less on host phenology and population size (e.g. Zabel and Tschardt, 1998). Even the opposite tendency is possible: for a balanced uptake of nutrients and toxins generalists may prefer mixed over pure diets (Speiser and Rowell-Rahier, 1991; Bernays et al., 1994) and show some kind of 'neophilia' (Cook et al., 2000). In this case, rare species may be consumed over-proportionally. However, contrary results may be due to adaptation processes and preference shifts of the herbivores to the more frequent plant species. For example, Linhart and Thompson (1995) found a local adaptation of the snail *Helix aspersa* to certain terpenoid chemotypes of *Thymus vulgaris*. Speiser et al. (1992) discussed similar adaptations of the snail *Arianta arbustorum* to toxic compounds of *Adenostyles alliariae*.

What is the relevance of the observational data for a herbivory-caused distribution limit of the study species? In *P. albus*, we found an altitudinal gradient in the leaf damage in summer. However, the values remained quite low even at most lower elevation sites. This may be due to the comparatively low palatability of the species to molluscs (Scheidel and Bruehlheide, 2001), the most important herbivores of *P. albus* leaves in the study area. Similarly, in *C. pseudophrygia*, leaf herbivory remained low during the summer. Usually, losses of about 10% were reported from a wide variety of plant species and communities (Pimentel, 1988; Sand-Jensen et al., 1994), and this herbivory pressure should not prevent plants from growing.

In contrast to the usually low loss of leaf area, the damage to flower heads reaches very high levels, as has been found in many studies on predispersal seed predation: investigating 20 Asteraceae, Fenner et al. (2002) found the highest percentage of capitulum infestation in *Arctium minus* (46.5% of

the flower heads). Romstöck (1988) found a loss of 50%, on average, of the potential seed production in *Cirsium helenioides*. The proportion of insect damage to the flower heads of *Erigeron glaucus* reached a maximum of 100% in late summer (English-Loeb and Karban, 1992). On average, more than 50% of the fruits of *Silene alba* and *S. dioica* were parasitized (Biere and Honders, 1996). *Cerajocera tussilaginis* attacked up to 65% of all investigated *Arctium minus* flower heads (Straw, 1991).

However, there have been only very few attempts to quantify the effects of seed damage on subsequent life stages. For example, the population density of *Cirsium helenioides* was obviously not influenced by the flower head damage (Romstöck, 1988). In contrast, Louda (1982) and Kelly and Dyer (2002) were able to show a significant influence of flower head insects on seedling and young plant density of *Haplopappus squarrosus* or *Liatis cylindracea*, respectively. Besides quantitative effects on seed production there may be qualitative and genetical changes. For example, Molau et al. (1989) found the highest predation rate on *Bartsia alpina* capsules in the middle of the inflorescences. At the same time, flowers at this position showed the lowest outcrossing rate, resulting in an increase in the proportion of outcrossed seeds by seed predation.

Quantification of the effects of the herbivore damage to leaves, rhizomes or flower heads on the population dynamics of the study species was beyond the scope of this study. In any case, these investigations would have to be combined with experimental approaches (Louda, 1994), including transplantation or sowing experiments and manipulations of the density of different herbivore species. In perennial plant species, long-term investigations are needed to find possible bottlenecks caused by herbivory. Particularly, the damage to the seedling stage has to be quantified in sowing experiments as carried out by Scheidel and Bruelheide (submitted for publication) with *A. montana* and *C. pseudophrygia*. To compare the herbivory pressure at montane sites with the lowlands montane species should be transplanted to the lowlands or the damage should be assessed in closely related species that occur from the lowlands to montane sites (Scheidel and Bruelheide, 2001).

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