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Altitudinal differences in herbivory on montane *Compositae* species

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Abstract To test whether the range of montane *Compositae* species may be restricted to higher sites because of greater herbivory levels in the lowlands, we transplanted six species, combining them in three species pairs each consisting of a rare montane and a widespread species. Individuals of all species were planted at four sites of different altitude ranging from the lowlands to the subalpine Mt. Brocken in the Harz mountains, Germany. Food choice experiments with three mollusc species indicated that the montane plant was more palatable in the species pair *Senecio hercynicus*/*S. ovatus*, but the widespread plant was more palatable in the species pair *Petasites albus*/*Tussilago farfara*. In the third pair (*Cicerbita alpina*/*Mycelis muralis*), neither species was preferred. In the field, species-specific herbivory levels differed in their amount, in their interaction with plant phenology and in their effect on mortality. They only partially reflected the laboratory food choice results. We found clear differences between the lowest and the highest site for all species, but a continuous decrease in herbivory with altitude was only detected in three of the six species.

Keywords Plant distribution · Molluscs · *Cicerbita alpina* · *Petasites albus* · *Senecio hercynicus*

Introduction

Herbivory affects the performance and population dynamics of plants in many different ways. Its main effect can be considered to be negative, involving the loss of photosynthetically active, nutrient-rich plant tissue or storage organs. For several plant species, differential losses to herbivores have been found to occur along

abiotic environmental gradients of different scales (e.g. Cates 1975; Lincoln and Langenheim 1979; Louda 1983; MacGarvin et al. 1986; Louda et al. 1987; Louda and Rodman 1996; Palmisano and Fox 1997). In plants characterized by high acceptability and/or low tolerance to generalist herbivores in the field, herbivory may be involved in the restriction of the geographic range to a part of their climatically potential range.

In particular, biotic interactions should be considered in the study of montane and alpine plant species whose elevational occurrence is characterized by a diffuse lower altitudinal limit. These limits are only seldom satisfactorily explained by climatic factors alone. A hypothesis generally put forward is that highland plants experience a higher loss in storage carbohydrates due to the increase of respiration rate at higher temperatures. However, this hypothesis has only been supported in a few cases (e.g. Mooney and Billings 1961, 1965; Mooney 1963; Stewart and Bannister 1974; Graves and Taylor 1988; Bruelheide and Lieberum 2001). In contrast to direct climatic control of the upper limits of lowland plants, Woodward (1988) suggested that the lower altitudinal limits of upland vegetation are controlled by temperature-sensitive competition. However, herbivory, interacting with competition, may be an equally important biotic site factor. Along an altitudinal gradient, we assume that the habitat conditions for generalist invertebrate herbivores, particularly molluscs, become less favourable with increasing elevation; thus reducing herbivore pressure on plant species in general. The low-herbivory conditions of montane sites may provide a refuge for montane plant species which would grow well or even better at low elevations without herbivory.

Mollusc-plant interactions are good systems for investigating the effects of generalist herbivores on their host plants, because they can be investigated easily in the laboratory and in the field and can be successfully manipulated by a simple experimental design. Not surprisingly, molluscs, important consumers that influence plant community composition by selective herbivory, have been the subject of many field experiments (e.g.

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Kelly 1989; Reader 1992; Hulme 1994, 1996; Ehrlén 1995; Hanley et al. 1995; Clear Hill and Silvertown 1997; Bruelheide and Scheidel 1999; Edwards and Crawley 1999). Under field conditions, mollusc activity is dependent on various weather parameters in a complex manner, especially on temperature and water vapour pressure deficit (Crawford-Sidebotham 1972). In Central European mountains, increasing altitude is accompanied by prolonged rainy periods, which promote slug activity and thus exert an antagonistic effect to the decreasing temperature. However, the lower abundance of slugs in regions of harsher climate remains to be proved (Keller et al. 1999) and there has not yet been any attempt to study altitudinal patterns in mollusc abundance under otherwise comparable site conditions. Some indications of decreasing performance with increasing altitude have been found for the snail *Arianta arbustorum* (Baur and Raboud 1988).

The damage to a particular plant species will only be responsive to the decline in the activity of generalist herbivores with increasing altitude if the plant is highly palatable in general. Although the palatability of a particular plant species varied little when fed to different mollusc species (Jennings and Barkham 1975; Rathcke 1985; Scheidel and Bruelheide 1999a) or even to different generalist herbivores (Grime et al. 1996; Wardle et al. 1998; Hendriks et al. 1999), there were strong differences in palatability between plant species. Most Compositae species tested have been found to be highly palatable to molluscs in food choice experiments (Getz 1959; Grime et al. 1968, 1996; Briner and Frank 1998; Hendriks et al. 1999; Scheidel and Bruelheide 1999a). Members of this plant family are therefore particularly appropriate for testing the hypothesis that montane sites provide a refuge from herbivory. This high palatability of Compositae species is remarkable because many species contain secondary metabolites with possible deterrent effects, for example bitter-tasting sesquiterpene lactones (Frohne and Jensen 1992). These compounds may affect mollusc behaviour less than that of insects: e.g. albopetasine from *Petasites albus* reduced food consumption in the beetle *Oreina cacaliae*, but not in *Arianta arbustorum* (Hägele et al. 1996).

The Compositae-mollusc system has already been used to test the refuge hypothesis at high altitudes. Bruelheide and Scheidel (1999) transplanted the montane meadow plant *Arnica montana* to three sites at different elevations. Using a similar experimental design, we investigated additional montane Compositae: *Cicerbita alpina*, *Petasites albus* and *Senecio hercynicus*. Each species was compared to a widespread and closely related one of similar physiognomy (*Mycelis muralis*, *Tussilago farfara* and *S. ovatus*, respectively), resulting in three species pairs. We compared the leaf palatability of each pair to three mollusc species in laboratory food choice experiments. Phenology and herbivore damage to transplants of all six species were assessed at four localities between the lowlands and the subalpine Mt. Brocken in the Harz mountains, Germany, over an entire vegetation period.

The study focused on the following questions:

1. Are montane Compositae species more palatable than their widespread relatives?
2. Is there a general herbivory gradient of decreasing defoliation with increasing altitude?
3. Do the species studied benefit from herbivore enclosure under field conditions?
4. Does the shift in timing of plant phenology and herbivore activity between high and low altitude change plant damage levels?

Materials and methods

The plants

Cicerbita alpina/*Mycelis muralis*

C. alpina (L.) Wallr. occurs in the Harz mountains at its northernmost outpost in the Central European part of its range, which extends from the Pyrenees to the Carpathians and northern Apennines. In the Harz mountains, it has a lower altitudinal limit at about 530 m above sea level (a.s.l.) (Vogel 1981), although the plant may grow well in lowland gardens (Hegi 1987). *Cicerbita* colonizes slightly shaded forest slopes and edges and subalpine vegetation dominated by tall perennial herbs, characterized by sufficient water and nutrient supply and high air humidity, up to 2200 m a.s.l. in the Alps (Hegi 1987). In contrast to *Cicerbita*, the related *M. muralis* (L.) Dum. (synonym of *C. muralis* Wallr.) is widespread through most parts of Europe and occurs from sea level up to about 1140 m in the Alps (Oberdorfer 1994). *Mycelis* is a plant of shaded or semi-shaded locations, usually with high air humidity and nutrient-rich soils, often associated with natural or anthropogenic disturbance.

Petasites albus/*Tussilago farfara*

P. albus (L.) Gaertn. occurs from Western Europe to the Altai mountains. In the Harz mountains, small populations can be found from 250 m upwards, but the most vigorous populations occur between 400 and 600 m a.s.l. Whereas *P. albus* is mainly restricted to montane sites, the related species *T. farfara* L. is widespread through Europe and occurs in the study area from the lowlands up to the top of Mt. Brocken. Both species sometimes occur together as pioneer species on sporadically disturbed soils of montane road verges and brook or river banks. *Petasites* occurs also in nutrient-rich forest slopes and edges and in high montane vegetation dominated by tall herbs, whereas *Tussilago* colonizes more open disturbed sites, even on abandoned arable land. Both species are characterized by nearly equally sized leaves and a very early flowering time.

Senecio hercynicus/*S. ovatus*

S. hercynicus Herborg occurs from eastern France to the Carpathians and northern Greece (Herborg 1987). In the Harz mountains, the lower distribution boundary is at about 550 m a.s.l., whereas *S. ovatus* (P. Gaertn., Mey and Scherb.) Willd. can be found from about 100 m a.s.l. upwards. *S. ovatus* also has a Central to Southeastern European range. Both species colonize forest clearings, forest road verges and abandoned grassland. They can be distinguished by phenological, morphological and biochemical characteristics. Although the shoots emerge nearly simultaneously at about the end of April, *S. hercynicus* grows much faster and flowers in the middle of June about 5 weeks earlier than *S. ovatus* (Herborg 1987). We mainly used the different phenological development and the form of leaf insertion to distinguish these two species.

Food choice experiments

Each plant species was tested in food choice experiments using three abundant mollusc species: two slugs [*Arion lusitanicus* (Mabille) and *Deroceras agreste* (L.), nomenclature after Schaefer (1994)], collected in the New Botanical Garden of Göttingen at 170 m a.s.l., and one snail, *Arianta arbustorum* (L.), collected from a road verge near Göttingen at 160 m a.s.l. Species identification was based on external appearance after Quick (1960), Runham and Hunter (1970) and Stresemann (1992). *D. agreste* and *A. arbustorum* are widespread from the lowlands to subalpine altitudes. *Deroceras* individuals occurred at all plots in the transplantation experiment, whereas *Arianta* was found from the lowlands up to the montane sites. *Arion lusitanicus* is still spreading through Europe and was found only at the lowest plot, although this species has already expanded its range into the Harz mountains.

Young individuals of *Deroceras* (mean live weight of approximately 0.2 g) and *Arianta* (mean shell diameter of about 1.1 cm) were kept individually in 9-cm petri dishes with 5 ml of water. *Arion lusitanicus* (mean live weight of 2.6 g) was kept individually in 9-cm plastic pots filled up to the middle with wet sand and covered with a perforated plastic film. The experiments were carried out in the greenhouse of the New Botanical Garden in Göttingen under shaded conditions at maximum relative humidity with natural day length and a temperature range between 15°C at night and 25°C during the day. The experiments using the slug species were conducted in June, whereas *Arianta* was fed at the beginning of September 1999 when young individuals were abundant in the study area. In September, young leaves of lateral shoots were used to minimize differences in leaf age between the experiments which may influence palatability (e.g. Grime et al. 1970; Cates 1980).

We harvested fully expanded non-senescent leaves of the test species from native populations in the Harz mountains. Discs (diameter: 20 mm) cut from the leaves avoiding strong ribs at the basal half were used for feeding. The slugs were not starved prior to the experiment. Each slug was offered two discs of each of the two test species of a species pair for about 24 h. On the following day we assessed the leaf area consumed by placing the discs on graph paper and determining the area of the holes. For calculation of each species' percentage of the total leaf area consumed the values of both discs were summed. Fifteen simultaneous replicates were conducted.

Transplantation experiment

Seeds of *Cicerbita*, *Mycelis*, *S. hercynicus* and *S. ovatus* were collected in the Harz mountains between 400 and 700 m a.s.l. in 1998. In August, they were sown in soil in the New Botanical Garden in Göttingen. In March 1999, single plants were potted up in 11-cm plastic pots containing a loamy garden soil.

From *Petasites* and *Tussilago* we used rhizomes of plants growing in the Harz mountains at about 400 m a.s.l. They were collected in March 1999 and planted into 16-cm plastic pots including garden soil.

Between the beginning of April and the beginning of May 1999, 16 pots of each species were transferred to four sites at different elevations. The lowest site was an abandoned meadow in the New Botanical Garden in Göttingen (170 m a.s.l.), slightly shaded by trees growing along a small brook nearby. The second site was an abandoned meadow in a small valley near Bad Lauterberg at the southern border of the Harz mountains (400 m a.s.l.). This north-facing plot was shaded by the edge of a spruce forest. The third plot was located in a small clearing dominated by *Phalaris arundinacea* in a spruce/alder forest near Braunlage in the Harz mountains at 575 m a.s.l. The highest plot was established in the Botanical garden at the top of Mt. Brocken at about 1130 m a.s.l. This plot had a sparse vegetation consisting of *Calluna vulgaris*, *Galium hercynicum* and some grasses and was surrounded by a dense subalpine vegetation of *Calamagrostis villosa* and *Senecio hercynicus*.

The 96 pots were randomly placed in a regular 0.8 m×0.8 m grid, with 12 pots in each row. The plants were left in the pots to minimize edaphic differences between the sites. Immediately after transplantation, eight plants of each species were randomly selected and caged using polyethylene nets (mesh width of 1.6 mm, to a height of 50 cm, buried 10 cm deep in the soil) which were fixed to three wooden rods. The cages surrounded an area with a diameter of about 30 cm around the plants from which slugs were to be excluded. Slugs found inside the cages during the vegetation period were removed.

On the Mt. Brocken plot preliminary observations revealed almost no slug damage. Therefore, at this site the caging experiment was only conducted with *S. hercynicus*. We used only eight uncaged individuals of the other five species.

The plots were visited about every 10–20 days until the end of the vegetation period at the end of October. On each sampling date, the number of developed non-senescent leaves per plant and the amount of damage to them were assessed. Leaf damage was calculated by estimating the percentage of the area consumed for each leaf as up to 10%, 25%, 50%, 75% or 100%, summing the mean values (5%, 12.5% and so on) and dividing the sum by the plant's leaf number. Plants which were found to be completely destroyed on a sampling date were given a mean damage value of 100% per leaf.

To assess mollusc activity, five ceramic tiles (20 cm×20 cm) were placed in the centre and the four corners of each plot on bare ground with their unglazed side upwards. A 9-cm petri dish filled on each sampling date with 5 g beer-soaked wheat bran was laid on each tile. This bait was covered by a second ceramic tile held at a distance of 1.8 cm by four wooden cubes at the corners. On each sampling date, the mucus trails that crossed a line running parallel to the tile's edge were examined. Mollusc activity was expressed as proportion of summed width of all trails to the total length of the line divided by the number of days between the sampling dates.

In the case of the *Senecio* species pair we were able to compare the results of the transplantation experiment to the damage levels of both species growing together in nearly equal amounts at six sites in the Harz mountains between 530 and 800 m a.s.l. At each site, we assessed the damage to five randomly chosen shoots of 50 stands of each species between the end of June and the beginning of July in 1999 and 2000. For each shoot, we estimated the percentage of leaf area removed for the leaf halfway up the height of the shoot.

Statistical analysis

All statistics were performed using SAS 6.02 (SAS Institute 1987). Tests of departure from the Gaussian distribution were made according to Shapiro Wilk (using PROC UNIVARIATE). Changes in damage and leaf number over time for the different sites and species compared was analysed by univariate repeated-measures ANOVA (PROC GLM, SAS Institute 1987) with sites, treatments and the species compared as the between-subject factors and time as the within-subject factor (Ende 1993). For the field observations on *Senecio* species a three-way ANOVA was performed with site and time as independent factors (PROC GLM). The sign test was performed after Bortz et al. (1990, pp. 256–257).

Results

Food choice experiments

Only in the *Senecio* pair did we find indications of a preference for the montane species (Fig. 1). The two slug species clearly preferred *S. hercynicus*, whereas *Arianta* did not show any preference and consumed nearly equal proportions of both species.

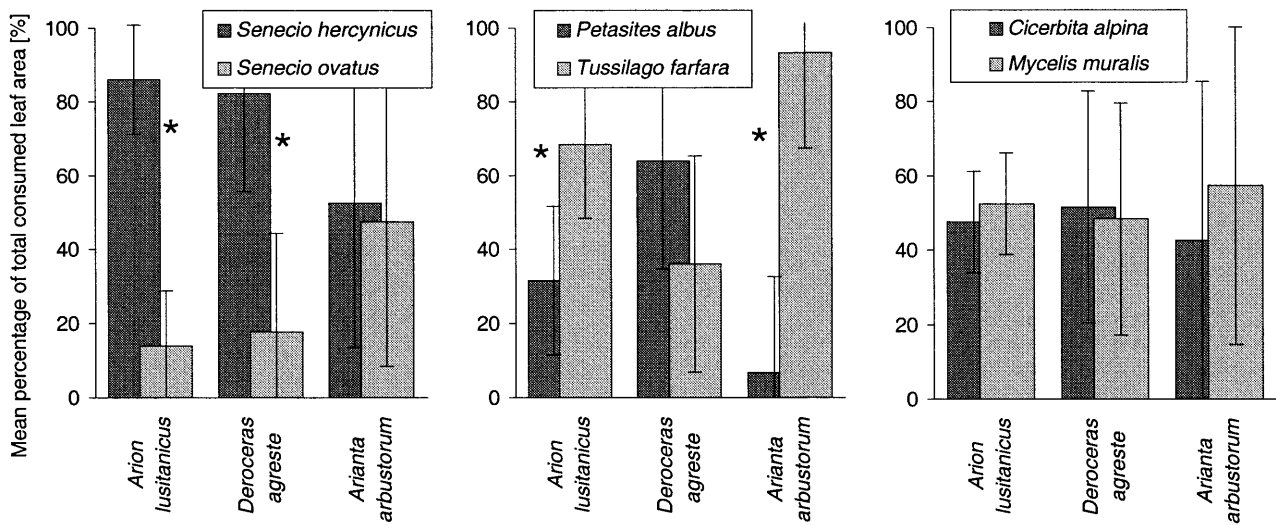


Fig. 1 Mollusc preferences in the food choice experiments ($n=15$ for each plant species). Error bars indicate SD. Asterisks indicate significant differences between consumption within a species pair according to the sign test (Bortz et al. 1990: in at least 11 of the 15 comparisons molluscs preferred the same species, $P<0.05$)

When fed with *Petasites* and *Tussilago*, *Arion lusitanicus* and *Arianta arbustorum* significantly preferred the widespread species, *Tussilago*, whereas *Deroceras* consumed greater amounts of *Petasites*, although this preference was not statistically significant. When *Cicerbita*

and *Mycelis* were offered, slug feeding revealed no preference in any case.

Transplantation experiment

In all three species pairs, significant differences in leaf damage to the transplants between the montane and the widespread species could be found (Table 1, Fig. 2). In two pairs, these differences corresponded to the palatability in the laboratory test. In the *Senecio* pair, the transplanted

Table 1 Results of repeated-measures two-way ANOVA on the effects of site, species and time on mean percentage of leaf area consumed (damage, %) and mean leaf number of uncaged plants only (leaf number). Mean damage and leaf number were calculated for five nearly simultaneous sampling dates (date I: 5 May in Göttingen, 6 May in Bad Lauterberg, 11 May in Braunlage and Mt. Brocken; date II: 1 June in Göttingen and Bad Lauterberg,

4 June in Braunlage and Mt. Brocken; date III: 1 July in Göttingen, 6 July in Bad Lauterberg, 28 June in Braunlage, 5 July on Mt. Brocken; date IV: 4 August in Göttingen, 2 August in Bad Lauterberg, 12 August in Braunlage, 9 August on Mt. Brocken; date V: 2 September in Göttingen, 7 September in Bad Lauterberg, 8 September in Braunlage and Mt. Brocken)

| Source of variation | df | <i>Cicerbita alpina</i> / <i>Mycelis muralis</i> | | <i>Petasites albus</i> / <i>Tussilago farfara</i> | | <i>Senecio hercynicus</i> / <i>S. ovatus</i> | | |
|---------------------|---------|--------------------------------------------------|-------------|---------------------------------------------------|-------------|----------------------------------------------|-------------|---------|
| | | F | F | F | F | F | F | |
| | | Damage | Leaf number | Damage | Leaf number | Damage | Leaf number | |
| Site | 3 | 9.58** | 3.76* | 29.36** | 19.27** | 33.42** | 6.51** | |
| Species | 1 | 5.37* | 239.42** | 16.69** | 16.49** | 6.52* | 7.50** | |
| Time | 4 | 14.88** | 16.46** | 23.86** | 13.46** | 18.14** | 15.81** | |
| Time×site | 12 | 3.01** | 1.50 | 3.82** | 6.80** | 4.60** | 5.37** | |
| Time×species | 4 | 1.04 | 20.45** | 2.61* | 1.88 | 1.31 | 3.78** | |
| Date I→II | Time | 1 | 22.49** | 49.43** | 87.15** | 39.13** | 17.71** | 33.96** |
| | Site | 3 | 3.72* | 1.96 | 14.19** | 2.65 | 3.89* | 2.46 |
| | Species | 1 | 1.13 | 31.78* | 0.19 | 1.06 | 0.16 | 1.55 |
| Date II→III | Time | 1 | 0.50 | 1.29 | 0.00 | 0.35 | 0.26 | 18.39** |
| | Site | 3 | 2.10 | 5.68** | 0.45 | 3.70* | 1.79 | 3.49* |
| | Species | 1 | 0.56 | 4.03* | 2.53 | 1.27 | 3.86 | 5.37* |
| Date III→IV | Time | 1 | 3.44 | 7.79** | 2.96 | 0.08 | 3.22 | 14.71** |
| | Site | 3 | 1.45 | 0.91 | 0.40 | 1.64 | 1.69 | 7.57** |
| | Species | 1 | 1.36 | 17.26** | 0.21 | 0.13 | 0.11 | 7.08* |
| Date IV→V | Time | 1 | 1.45 | 9.73** | 0.00 | 0.01 | 5.34* | 2.88 |
| | Site | 3 | 0.78 | 1.01 | 1.10 | 2.35 | 1.79 | 2.70 |
| | Species | 1 | 0.01 | 1.87 | 0.15 | 1.96 | 3.51 | 0.64 |

* $P<0.05$, ** $P<0.01$

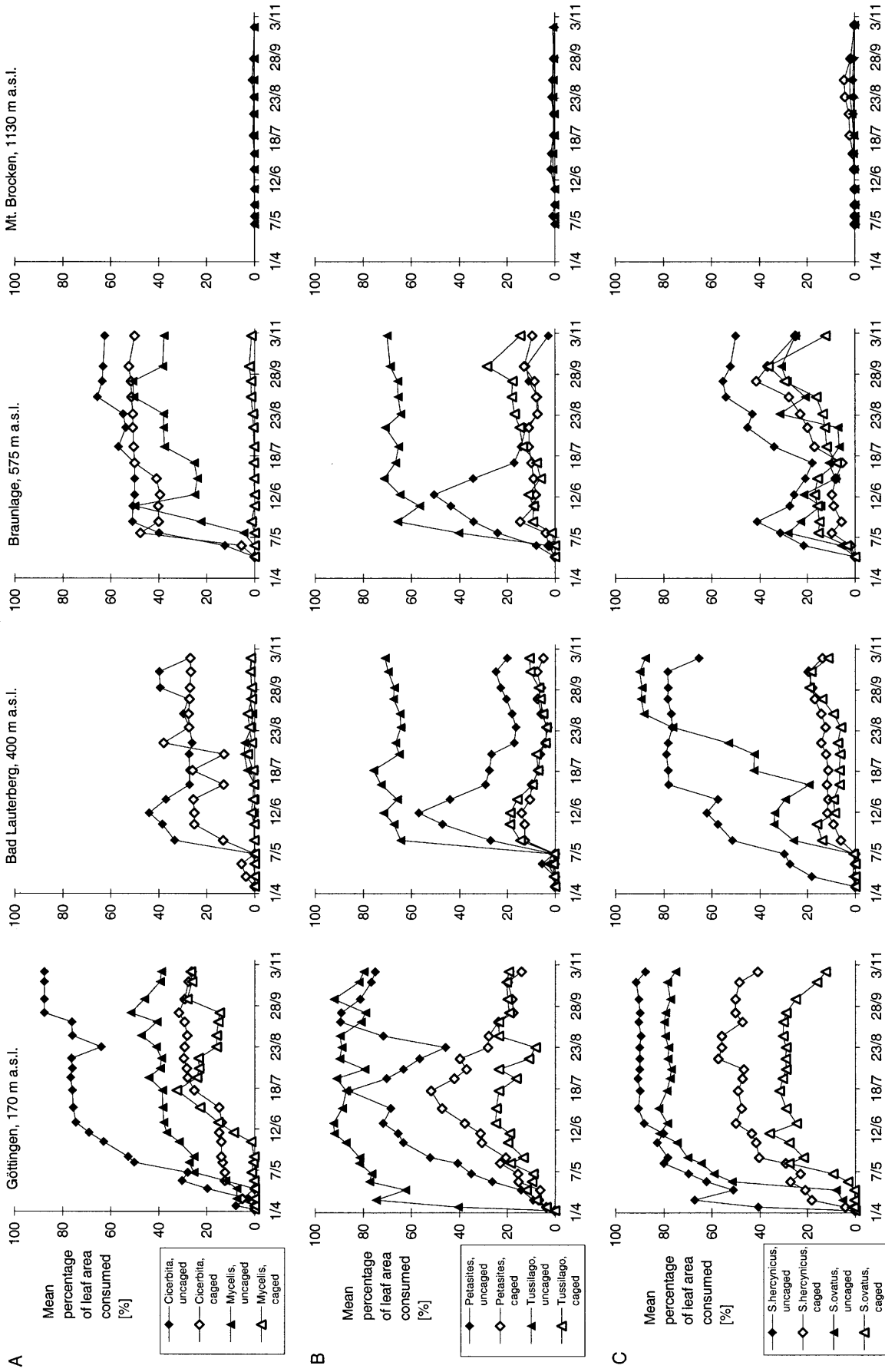


Fig. 2 Herbivore damage to the transplants: mean percentage of leaf area consumed for the species pairs **A** *Cicerbita alpina*/*Mycelis muralis*, **B** *Petasites albus*/*Tussilago farfara*, **C** *Senecio hercynicus*/*S. ovatus* at the experimental sites, from transplant date in April or May until the end of October

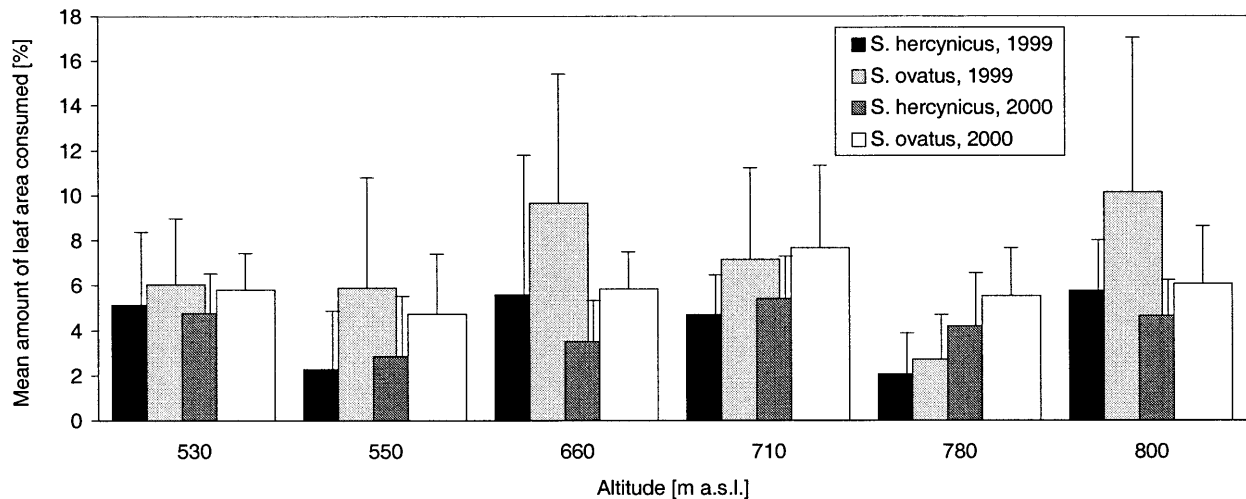


Fig. 3 Herbivore damage to native mixed populations of *S. hercynicus* and *S. ovatus* in 1999 and 2000: mean amount of leaf area consumed from leaves halfway up the shoot, at six localities in the Harz mountains between 530 and 800 m a.s.l. ($n=50$ different stands for each site). Error bars indicate SD

individuals of the more palatable montane species *S. hercynicus* were also more damaged, at least at the beginning of the growing season. However, the damage observed in native *Senecio* populations revealed an unexpected pattern differing from those in the food choice and the transplantation experiment (Table 2, Fig. 3). *S. ovatus* leaves suffered significantly higher losses than *S. hercynicus* at all sites and in both years, with additional significant interactions between species, site and time effects on the leaf damage.

In the *Petasites/Tussilago* pair, the more palatable widespread species, *Tussilago*, also suffered higher leaf area loss in the field. Although the two species did not differ in palatability, the *Cicerbita/Mycelis* pair showed the hypothesized higher damage to the montane species in the field.

The majority of the damage was caused by molluscs with typical damage patterns. Slugs and snails of several species and their mucus trails and faeces could be frequently found on all six plant species. In the first half of the growing season, mucus trails on the bait tiles at the Göttingen plot were more frequent in comparison to the montane sites on all sampling dates (Fig. 4). At the Mt. Brocken site, no mucus trail was ever observed. Insect herbivores partly contributed to the observed damage. For example, we observed chrysomelid beetles on *Senecio* leaves in Braunlage. In *Mycelis* the damage often consisted of many small holes in the leaves, which were probably not exclusively caused by mollusc feeding.

In all species pairs leaf damage differed significantly between sites along the altitudinal gradient (Table 1). However, these significances mainly resulted from high damage levels at the Göttingen plot compared to negligible leaf loss at the Mt. Brocken site. The damage to the plants at the two montane sites revealed intermediate levels with damage levels either decreasing with altitude

Table 2 Results of three-way ANOVA on the effects of *Senecio* species, site and year on leaf damage to the native mixed populations of *Senecio hercynicus* and *S. ovatus*

| Source of variation | df | MS | F |
|---------------------|------|---------|----------|
| Species | 1 | 1434.45 | 130.96** |
| Site | 5 | 328.62 | 30.00** |
| Time | 1 | 72.03 | 6.58* |
| Species×site | 5 | 46.69 | 4.26** |
| Species×time | 1 | 75.00 | 6.85* |
| Site×time | 5 | 203.02 | 18.54** |
| Species×site×time | 5 | 25.42 | 2.32* |
| Error | 1176 | 10.95 | |

* $P<0.05$, ** $P<0.01$

(*Senecio* sp.), showing no difference (*Petasites/Tussilago*) or, surprisingly, being higher at higher altitude (*Cicerbita/Mycelis*). In the native *Senecio* populations studied, there was a considerable variability between the sites, but no indication of an altitudinal gradient (Fig. 3).

Mortality (Fig. 5) reflected the general pattern of leaf damage. At the Mt. Brocken site all plants were still alive at the end of the vegetation period, whereas in Göttingen more than half of the uncaged plants of all species except *Mycelis* were killed during the vegetation period. The montane sites showed intermediate survival rates, but the differences between species were remarkable. At both montane sites, most uncaged *Tussilago* plants died. Additionally, in Bad Lauterberg most uncaged *Senecio* plants were killed. In Braunlage, *Senecio* survived better, whereas *Cicerbita* suffered particularly high mortality.

On average, caging resulted in a reduction of the leaf area consumed by more than 50% in most species in early summer (Fig. 2). In all species except *Cicerbita*, the cage effect on leaf area loss was statistically significant (Table 3). In most cases, caging reduced the mortality to a maximum of two out of eight plants (Fig. 5).

There were significant effects of time on the leaf damage to the uncaged plants of each species pair (Table 1) and to all plants of each species (Table 3). However, testing the differences between certain sampling dates revealed significant time effects mainly between

Fig. 4 Mollusc activity in May and June, expressed as a mean proportion of the summed width of all mollusc trails to the total length of an 80-cm line running parallel to the tile's edges; and then divided by the number of days between the sampling dates ($n=5$ tiles for each site). Error bars indicate SD. Data for Bad Lauterberg are missing after the beginning of June because the tiles had been displaced by larger animals

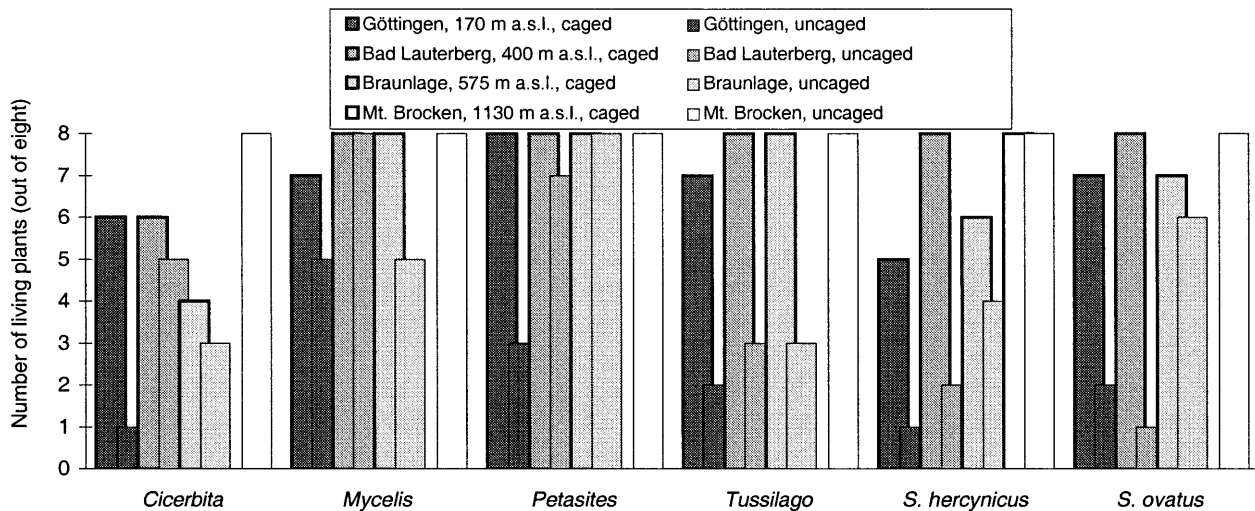
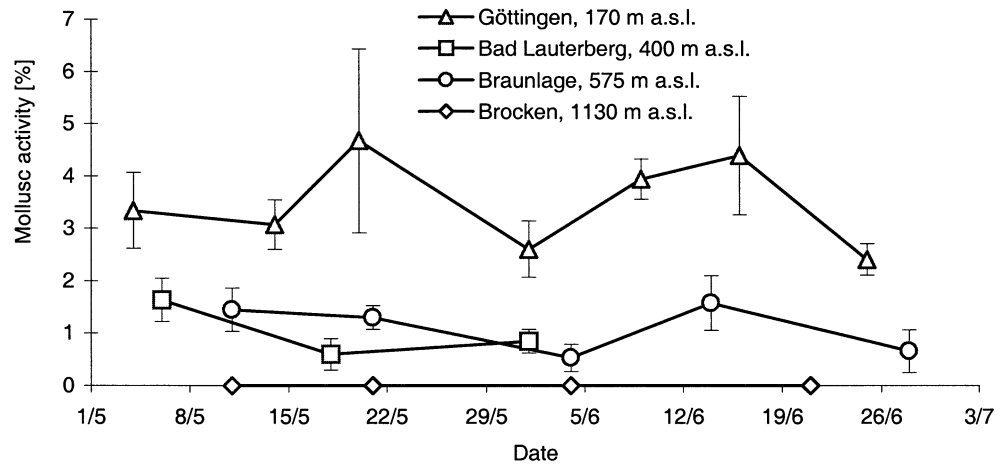


Fig. 5 Number of plants (out of eight) which were still alive on a specific sampling date between the end of September and the beginning of October

Table 3. Results of repeated-measures two-way ANOVA on the effects of site, cage and time on mean percentage of leaf area consumed

| Source of variation | <i>Cicerbita alpina</i> <i>F</i> | <i>Mycelis muralis</i> <i>F</i> | <i>Petasites albus</i> <i>F</i> | <i>Tussilago farfara</i> <i>F</i> | <i>Senecio hercynicus</i> <i>F</i> | <i>S. ovatus</i> <i>F</i> |
|---------------------|-------------------------------------|------------------------------------|------------------------------------|--------------------------------------|---------------------------------------|------------------------------|
| Site | 3.50* | 3.70* | 20.97** | 6.78** | 19.21** | 11.05** |
| Cage | 0.99 | 4.15* | 7.26** | 23.82** | 22.58** | 6.91* |
| Time | 15.90** | 5.47** | 13.99** | 22.57** | 17.42** | 17.27** |
| Time×site | 1.70 | 1.85* | 2.29** | 3.39** | 2.93** | 3.47** |
| Time×cage | 0.43 | 1.87 | 2.00 | 5.15** | 1.15 | 2.95* |
| Cage (date I→II) | 0.42 | 5.10* | 8.67** | 7.89** | 0.90 | 0.04 |
| Cage (date II→III) | 0.28 | 3.76 | 2.28 | 2.19 | 0.72 | 0.02 |
| Cage (date III→IV) | 2.20 | 0.51 | 0.26 | 2.50 | 0.51 | 1.10 |
| Cage (date IV→V) | 0.06 | 0.74 | 0.21 | 0.07 | 0.48 | 3.74 |

* $P < 0.05$, ** $P < 0.01$

the first and second tested date in May and June, respectively. In all species pairs, a site effect was significant only between dates I and II. In this period repeated-measures ANOVA also revealed the most significant changes in leaf number (Table 1). Later on, significant

changes in leaf area loss between the sampling dates occurred to a minor degree.

The altitudinal gradient is revealed more clearly when damage is related to the maximum damage observed for a certain species. In Fig. 6 the mean date when a

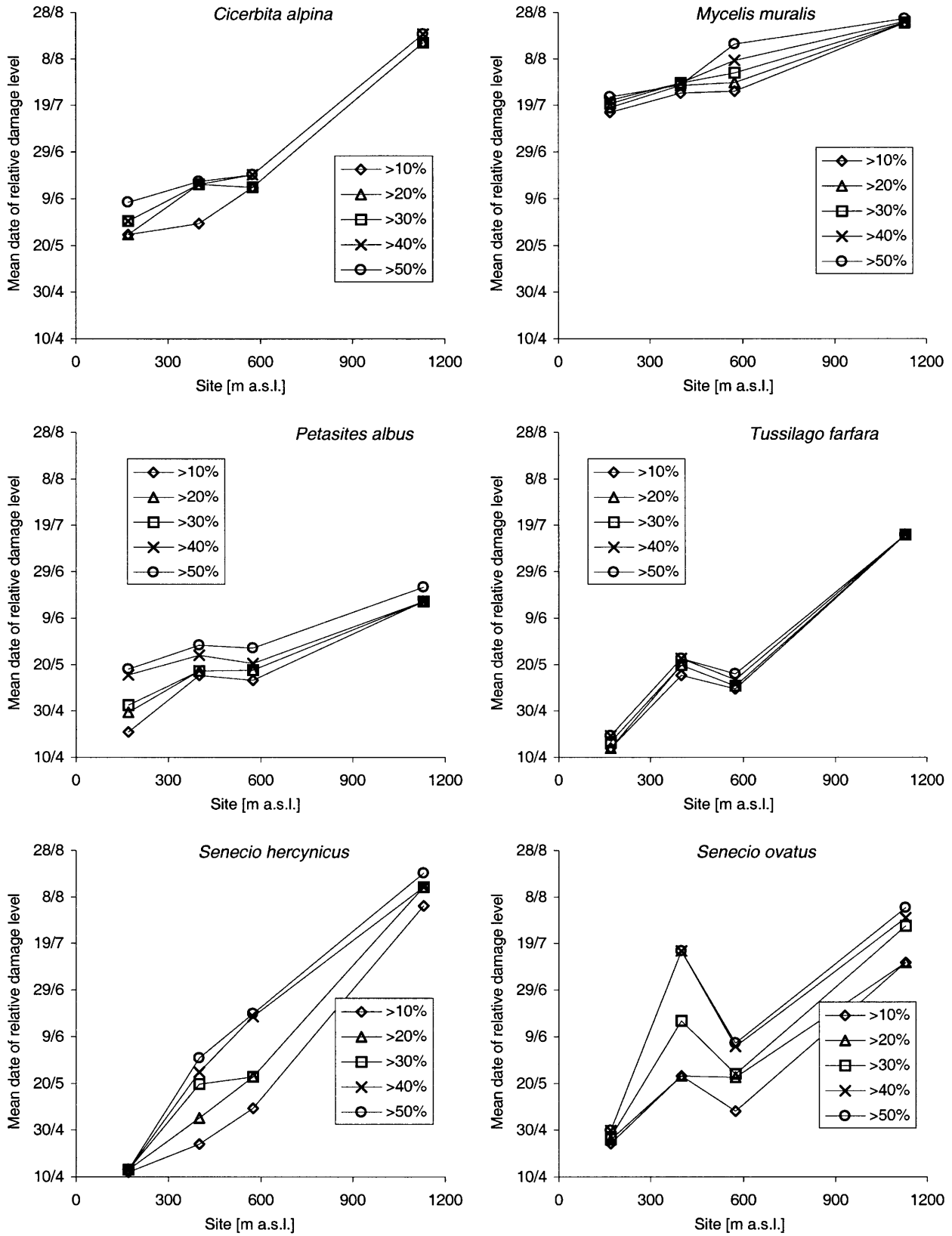


Fig. 6 Mean date when the relative leaf damage per plant of the uncaged individuals, calculated as percentage of the plant's maximum leaf damage, exceeded 10%, 20%, 30%, 40% and 50%

for the first time in Göttingen (170 m a.s.l.), Bad Lauterberg (400 m a.s.l.), Braunlage (575 m a.s.l.) and Mt. Brocken (1130 m a.s.l.)

particular level of relative damage was exceeded is plotted against altitude. In three species, *C. alpina*, *M. muralis* and *S. hercynicus*, the 50% levels show a continuous increase of date with altitude. The gradient was steep and almost linear in *S. hercynicus*, whereas it was weak in *Mycelis*. The remaining three species do not show a continuous gradient because a particular level was exceeded slightly (*Petasites/Tussilago*) or distinctly (*Senecio ovatus*) earlier in Braunlage than in Bad Lauterberg.

Discussion

Only for one species pair were the results consistent with the first hypothesis, that montane species are generally more palatable than their widespread relatives. Although the montane *S. hercynicus* would be expected to be less palatable because its pyrrolizidine alkaloid content is 100 times higher than in *S. ovatus* (Herborg 1987, p. 75) and its leaf hairiness is more pronounced, it was preferred to *S. ovatus* in the food choice experiment. Correspondingly, *S. hercynicus* suffered higher damage than *S. ovatus* in the transplantation experiment over most of the growing season.

However, the damage levels to native *Senecio* populations, which were much lower than those to the transplants at the montane sites, showed an opposite pattern. The conclusion from these contradictory results is either that the transplantation experiment overestimated the herbivore pressure, e.g. because potted plants attracted herbivores more effectively, or that the observations on native populations underestimated the herbivore pressure, e.g. because the sites with common occurrences of both species represented exceptional refuges from herbivory. There are several reasons for relying more on the experimental results. In non-manipulative studies the observed herbivore damage is not only influenced by palatability but also strongly by accessibility. In the case of *Senecio*, the distance between resting sites at the ground and feeding sites on upper leaves increases with growth height. Additionally, hairy stems may act as a barrier against herbivore approach from the ground. Grime et al. (1970) studied snail contact to and ascension on vertical stems of several plant species. Except for two glabrous plant species, the mean height of snail climbing was reduced in comparison to polyethylene control stems. On the sampling date in early summer, the native stands of the more rapidly growing *S. hercynicus* were already flowering and were in general slightly higher than *S. ovatus*. Therefore, the leaves, which we examined halfway up the shoot, were also higher above the ground in *S. hercynicus*; this may have resulted in less damage. Similarly, Grime and Blythe (1969) found that snails mainly damaged the lower leaves of *Urtica dioica* and *Mercurialis perennis*. In contrast to the native *Senecio* individuals, the 1-year-old *Senecio* transplants were generally less tall. In these smaller plants the damage level was probably more closely related to leaf palatability and less affected by stem height.

As in the case of the *Senecio* pair, in the *Petasites/Tussilago* pair, the food choice results were consistent with the findings of the transplantation experiment, but in contrast, the montane species was less damaged. This contrasting pattern and the absence of a significant difference in palatability in the *Cicerbita/Mycelis* pair does not support the first hypothesis and indicates that high palatability may not be the crucial disadvantage of montane species at low altitudes in general.

The second hypothesis, of a general decrease in the herbivore pressure with increasing altitude, was supported by the results of the transplantation experiment. In all species studied, there was a significant site effect on the leaf damage. The main decrease occurred between 575 m and 1130 m a.s.l. where additional experimental sites would have been desirable. At the two montane sites, herbivory levels ranked between the lowland and the subalpine site, but did not differ consistently from each other as would have been expected from their respective altitudes.

These results indicate that site factors other than those that change directly with altitude may additionally affect herbivore pressure in a species-specific manner. In *Arnica montana*, Scheidel and Bruelheide (1999b) found that the large-scale altitudinal gradient of leaf damage is masked by small-scale factors, particularly by characteristics of the surrounding vegetation, which may attract herbivores searching for food (e.g. Rand 1999) or shelter (e.g. Boyd 1988). Reader (1992) found differences in the mortality of grassland perennials with intact or removed neighbours that did not reflect direct competitive effects but were indirect effects of the surrounding vegetation, which provided favourable habitat conditions for herbivores. At the three lower transplantation sites, the surrounding herbaceous vegetation reached a height of more than 1 m in summer, whereas at the Mt. Brocken site it remained much lower, which possibly further reduced herbivory there. However, to exactly evaluate associational effects, species composition of the surrounding vegetation may be important, as well as its height or density. In this context, the abundance of the test species themselves in the surrounding vegetation has to be considered. At the lower sites, outside their natural range, the transplants of the montane species form small patches isolated from native populations. Potential specialist herbivores may not be sustained by these outposts (e.g. Zabel and Tschardtke 1998), whereas the abundance of generalist herbivores, like molluscs, is less responsive to the presence of a single plant species. Furthermore, molluscs have been found to prefer mixed to pure diets (Speiser and Rowell-Rahier 1993) and therefore selectively consume the rarer species of their habitat (Cottam 1985).

Except for *Cicerbita*, caging significantly reduced leaf area loss in all tested species, as hypothesized. Although the enclosures could not prevent all damage, they reduced mollusc grazing considerably. The level of decrease in leaf loss and especially the reduced mortality in caged plants are clear indications of the negative effects that molluscs have on plant performance.

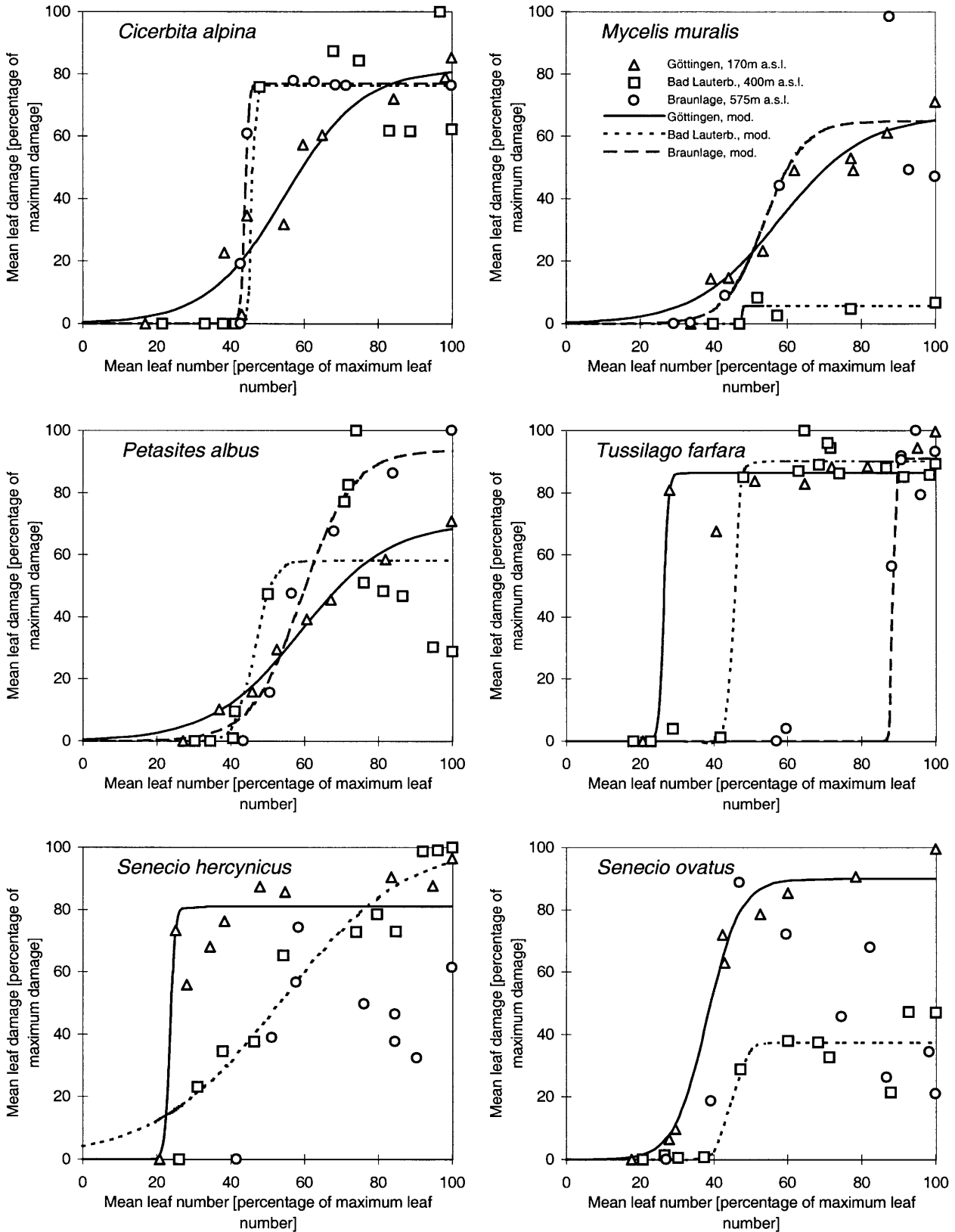


Fig. 7 Mean leaf damage per plant, calculated as percentage of the maximum leaf damage of the uncaged plants (see Fig. 2), plotted against mean leaf number of the caged plants calculated as percentage of their maximum mean leaf number, from the start of the experiment to the date of maximum leaf number. Trend lines

(*mod.*) show modelled sigmoid regression (Sigma Plot 4.0). The Mt. Brocken site is not considered because of generally low damage levels. In the *Senecio* pair, the regression model failed to predict the Braunlage data

The fourth hypothesis assumed that phenological shifts with changing altitude alter the probability of the coincidence of herbivore activity and plant sensitivity to damage. The period with largest increase in damage coincided with the largest increase in leaf number. Therefore, we focused on the interaction of damage and phenology by plotting the relative leaf damage versus the relative leaf number based on the maximum leaf number attained (Fig. 7). In *Tussilago*, *S. hercynicus* and *S. ovatus* relative damage developed more slowly than relative growth with increasing altitude. For example, the transplanted *S. hercynicus* specimens at the lowest site suffered 50% of maximum damage when only five leaves had developed on average (23% of maximum leaf number at this site, Fig. 7). At the higher sites, this relative damage value was reached when the plants had 11 (50%, 400 m a.s.l.), 12 (55%, 575 m a.s.l.) or 11 leaves (47%, 1130 m a.s.l.). A similar pattern was observed for *S. ovatus* and *Tussilago*.

This pattern was not confirmed for the other three species, in which damage and growth developed similarly at all altitudes (*Mycelis* and *Petasites*), or the high-elevation sites even showed more rapidly developing relative damage (*Cicerbita*). However, at the beginning of the vegetation period these species exhibited faster-developing relative damage at low altitude, i.e. at the Göttingen site. Although the absolute magnitude of relative damage in this period can be considered to be only small, it may have important consequences for plant growth. In spring, the small emerging plants with an easily accessible meristem at the soil surface may be destroyed by only a few bites. Even tall herbs that protect their leaves from slugs by achieving a high position above ground surface are exposed to slug damage during emergence in spring (Rathcke 1985). The delayed start of herbivore activity after emergence that was observed in some species at the montane sites may be of crucial importance for survival of this most vulnerable plant stage. A similar escape mechanism was found in the palatable morphotype of *Asarum caudatum* characterized by particularly early leaf and flower production, before maximum slug activity occurred (Cates 1975). In *Arnica montana*, severe mollusc damage in the spring led to high mortality (Bruehlheide and Scheidel 1999). Similarly, in both *Petasites* and *Tussilago* mortality due to defoliation occurred mainly in the spring. When completely defoliated in summer, transplants were able to regenerate themselves by frequent lateral shoot production from the rhizome and repeatedly produced new leaves. If the start of herbivore activity in the spring is more delayed with increasing altitude than plant emergence, a developmental head start in montane plants may contribute to escape from herbivory at montane elevations but not in the lowlands.

In general, montane species can be expected to emerge earlier in the spring because they have a lower temperature threshold for initiating leaf extension (Woodward et al. 1986). For the montane *A. montana* Bruehlheide and Scheidel (1999) showed that transplanted

individuals in the lowlands started growing very early in spring with a low subsequent growth rate in contrast to montane sites. The resulting disadvantageously long emergence period allowed severe slug attack on the young leaves. However, this expected difference between montane and lowland plants could neither be confirmed in our experiments (Fig. 7) nor be rejected unequivocally. A methodological drawback of the experiment was that the transplantation, which took place in April, was too late to allow the detection of differences before this date.

In our study no species pair behaved completely in accordance with all four hypotheses, even though the general decrease in damage to all six tested species with altitude indicates that montane sites may provide refuges from herbivory for plant species at risk. Montane species are handicapped by either high palatability or insufficient regeneration in the lowlands. Moreover, at higher elevations temporal decoupling of sensitive phenological phases from periods of high herbivore activity may promote survival of plants sensitive to mollusc herbivory.

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