



# Gourmets or gourmands? – Diet selection by large ungulates in high-alpine plant communities and possible impacts on plant propagation

Karl Hülber\*, Siegrun Ertl, Michael Gottfried, Karl Reiter, Georg Grabherr

*Department of Conservation Biology, Vegetation and Landscape Ecology, Institute of Ecology and Conservation Biology, University of Vienna, Althanstrasse 14, A-1090 Vienna, Austria*

Received 14 January 2004; accepted 30 September 2004

## KEYWORDS

Central Alps;  
Climate change;  
Long-distance  
dispersal;  
Seed;  
Endozoochory

## Summary

Megaherbivores have a considerable impact on species composition and structure of natural plant assemblages at the alpine/nival ecotone of the Alps, but their role as dispersal vectors has scarcely been investigated. This study examined the diet selection of free-ranging ungulates on high-alpine swards with special focus on their potential for endozoochoric dispersal. Grazed areas and fenced control plots were investigated by a point-framing method.

Results show that the foraging behaviour of ungulates in high-alpine swards is selective. Flowers and fruits are preferred to leaves. Accordingly, an increase in long-distance dispersal events of alpine vascular plants by grazing ungulates can be predicted. Preferential feeding on the conspicuous flowers of herbs rather than on graminoid inflorescences causes a more pronounced reduction of seed numbers in herbs. We therefore suppose the enhancement of long-distance dispersal to be higher for graminoids. The impact of herbivores on plant migration processes must therefore be considered when changes in alpine plant assemblages are to be assessed.

© 2004 Elsevier GmbH. All rights reserved.

## Zusammenfassung

Großherbivore haben beträchtlichen Einfluss auf Artenzusammensetzung und Struktur von Rasen und Rasenfragmenten am alpin/nivalen Ökoton der Alpen. Ihre Rolle als Ausbreitungsvektoren ist allerdings nur unzureichend untersucht. Gegenstand dieser Studie ist die Nahrungswahl von Paarhufern (Schafe, Ziegen, Gamsen) auf alpinen Silikatrasen mit dem Hauptaugenmerk auf deren endozoochorem Ausbreitungspotential für Diasporen. Vegetationsstruktur und Artengarnitur wurden im Rahmen von Ausschlussflächenexperimenten erhoben.

\*Corresponding author. Tel.: +1 4277 54377; fax: +1 4277 9542.  
E-mail address: [hueb@pflaphy.pph.univie.ac.at](mailto:hueb@pflaphy.pph.univie.ac.at) (K. Hülber).

Die Ergebnisse der Studie zeigen, dass Paarhufer bei der Nahrungssuche auf alpinen Rasen sehr selektiv vorgehen, wobei Blüten und Früchte den Blättern vorgezogen werden. Dadurch kann eine Steigerung der Anzahl der Fernausbreitungsereignisse angenommen werden. Die zumeist auffälligen Blüten von Dikotylen werden gegenüber den Infloreszenzen der „Grasartigen“ bevorzugt aufgenommen. Eine überproportionale Verringerung der Zahl reifer Diasporen bei dikotylen Arten ist die Folge, wodurch für „Grasartige“ relativ höhere Steigerungen erfolgreicher Ausbreitungsereignisse durch Tiere zu erwarten sind. Bei der Beurteilung von Migrationsprozessen von Pflanzen im Hochgebirge sollte der Einfluss von Megaherbivoren daher berücksichtigt werden.

© 2004 Elsevier GmbH. All rights reserved.

## Introduction

During the last decades, upward migration of vascular plant species has been observed throughout the Alps (Hofer, 1992; Grabherr, Gottfried, & Pauli, 1994, 2001; Pauli, Gottfried, & Grabherr, 1996). Changes in the macro- and microclimatic situation are assumed to be the most important driving forces (Callahan, Maxwell, Molau, Oechel, & Panikov, 1996; Gottfried, Pauli, & Grabherr, 1998). It is still under debate whether the migration abilities of plant species can keep pace with the shifting template of suitable habitats. Fast migration rates and colonisation of new areas in primary succession, following deglaciation events, can only be accomplished with long-distance dispersal, which mostly requires sexual propagules (Pijl, 1972; Molau & Larsson, 2000). Vegetative reproduction and clonality (Stüfer, Erschbamer, Huber, & Suzuki, 2001) prevail in alpine regions under stable conditions (Körner, 1999; Grabherr, Gottfried, Gruber, & Pauli, 1995). However, under strong disturbance regimes (e. g. rapid climate changes), seed dispersal will probably become more important (Marchand & Roach, 1980).

In regions above the treeline most species are wind-dispersed (Marchand & Roach, 1980), with the proportion of anemochorous taxa increasing with altitude (Reisigl & Pitschmann, 1958). At the alpine/nival ecotone only very few species have morphological traits adapted to animal dispersal (Müller-Schneider, 1986).

Alpine ecosystems in the Alps are in general naturally grazed (Lovari, 1985; Körner, 1999), but wild ruminants have largely been replaced by human livestock (Körner, 1999; Austrheim & Eriksson, 2001). This change might also affect the endozoochoric migration rates (Poschlod, Bakker, Bonn, & Fischer, 1996) of alpine plants. However, the impact of herbivory by vertebrates decreases with elevation (Urbanska & Schütz, 1986; Galen, 1990).

Obligatory bud preformation of alpine plants in the preceding year (Körner, 1999) and the harsh climatic environments with low soil-nutrient contents, which require high maternal investment in sexual reproduction (Urbanska & Schütz, 1986), restrict compensatory responses to grazing damages. Seed predation is a major force modifying seed traits and dispersal behaviour (Harper, Lovell, & Moore, 1970; Janzen, 1969, 1971). Moreover, repeated grazing of arctic plants influences the biomass partitioning (Kleunen, Ramponi, & Schmid, 2004) and production of tillers and sexual reproduction (Chapin, 1980; Archer & Tieszen, 1986). However, the effects on reproductive traits (flower and seed reproduction) cannot be predicted from their vegetative response (Damhoureyeh & Hartnett, 1997).

Selective feeding occurs when the relative frequency of a particular food resource differs between the diet and the environment (Chesson, 1978). A large number of studies give evidence of the selective feeding behaviour of ungulates (Crocker, 1959; Jefferies, Klein, & Shaver, 1994; Mulder & Harmsen, 1995; Körner, 1999; Mulder, 1999), especially sheep (Arnold, 1987; Watt & Gibson, 1988; Miller, Geddes, & Mardon, 1999). The diet selected is a result of the animals' preferences (Hodgson, 1979), their ability to reach the preferred food and limitations based on the sward type (Grant et al., 1985).

Most information about grazing behaviour and its consequences are derived from studies on artificial vegetation or lowland pastures (e. g. Newman, Parsons, & Harvey, 1992; Parsons, Newman, Penning, Harvey, & Orr, 1994; Thornley, Parsons, Newman, & Penning, 1994; Watt, Treweek, & Woolmer, 1996; Chen et al., 2002). The structure of these pastures can be very patchy with more heavily grazed, short cut areas interrupted by tall clusters around faeces or unpalatable plants. On high-alpine swards, grazing-dependent changes in structure are mostly not noticeable at first glance.

Though many studies have been performed in Northern Europe (see [Mulder & Harmsen, 1995](#) for an overview), investigations on diet selection in the alpine belt of the Alps are very rare (e. g. [Onderscheka, 1974](#); [Perle & Hamr, 1985](#); [Diemer, 1996](#)). Results from other vegetation types cannot be applied to alpine ecosystems without restrictions, because the foraging decisions of grazing ungulates are too complex to be completely understood ([Parsons et al., 1994](#)). This study is designed to estimate the impact of free-ranging ungulates (mainly sheep) on high-alpine swards, with special focus on the effects on the sexual reproductive organs of vascular plants. In particular, we address the following questions: (1) Are there differences in vegetation structure between moderately grazed and ungrazed parts of high-alpine swards? and (2) Is the foraging behaviour of ungulates on high-alpine swards in the Alps selective? Thereupon, we discuss the potential of megaherbivores for long-distance dispersal of plant species due to their grazing selections.

## Methods

### Study area

The study was conducted on the southern slopes of Mount Schrankogel (3497 m a.s.l.; Stubai Alps, Tyrol, Austria). This mountain is built up of siliceous bedrock material and surrounded by an intensively glaciated environment. Its location at the northern margin of the Central Alps provides a continental, cool temperate, nemoral climate ([Walter & Lieth, 1960–1967](#)). Annual precipitation (< 2000 mm) is comparatively low ([Pitschmann, Reisigl, Schiechtl, & Stern, 1970](#)) due to the shelter effects of mountain ranges to the north of the Schrankogel. The investigations were conducted at the uppermost closed swards, mainly determined by *Caricion curvulae* associations ([Grabherr & Mucina, 1993](#); [Dullinger, 1998](#)). For a detailed description of the vegetation at the alpine/nival ecotone see [Pauli, Gottfried, and Grabherr \(1999\)](#).

The investigation area (ca. 500 ha) is part of a pasture system for about 400 free-ranging sheep

and 50 goats. Livestock stays in the area from July to late September. The most intensive grazing period with the highest number of animals lies between the end of August and the end of September (pers. comm. local shepherd). In August, some cattle graze in the vicinity of the lowest site for 2 weeks. Some chamois also feed on the sites.

### Data collection

Three study sites with largely homogenous vegetation (representing the most common vegetation types grazed by megaherbivores) were established ([Table 1](#)). On each site, 10 plots of 1 m<sup>2</sup>—five exposed to grazing, five fenced control quadrates—were installed. The quadrates were arranged in a 3 m × 3 m plot, where the centre and four corner quadrates were sampled with a point-framing method. The corners of each quadrate were anchored using aluminium tubes for exact repositioning. A grid frame strung with a net consisting of 100 meshes, i.e. 10 × 10 crossings, was used as the sampling scheme (compare [Levy & Madden, 1933](#); [Watt & Gibson, 1988](#); [Griffin, 1989](#); [Brower, Zar, & Ende, 1990](#)). It was adjusted in a horizontal position over the quadrates. By dropping a pin vertically at every sample point, all hits on vascular plants were recorded with species name, distance to the surface and a specification of the part of the plant hit (generative or vegetative).

Observations were carried out at the beginning of July, August and October 2001. Due to bad weather conditions only three of the five pairs of quadrates on each site could be recorded in October.

### Data analysis

All statistical analyses are based on comparisons between fenced plots and their corresponding control plots. To test for differences in number of hits as a measure of sward density, Mantel–Haenszel tests were applied to 2 × 2 × k cross tables, calculated with the number of records of generative and vegetative plant parts, respectively, with site as a stratification variable. The point-framing method with 100 sample points allows for

**Table 1.** General description of the study sites used for enclosure experiments on Mount Schrankogel

	Vegetation	Altitude (m)	N-coordinate	E-coordinate
Site 1	<i>Festuca halleri-poa alpina</i> association	2610	47°1.932'	11°5.743'
Site 2	<i>Caricetum curvulae</i>	2700	47°2.061'	11°5.606'
Site 3	<i>Caricetum curvulae</i>	2820	47°2.258'	11°5.584'

Vegetation characterisation follows [Dullinger \(1998\)](#).

estimations on percentage accuracy. For these estimations and subsequent comparisons of generative versus vegetative plant parts only sample points with no hit on generative plant parts were regarded as vegetative.

To estimate the impact of conspicuousness of flowers on diet selection, we tested the number of hits on herb (including dwarf shrubs) and graminoid flowers during main blossom. Differences in frequencies of graminoid and herb inflorescences were tested with Chi-Square tests for  $2 \times 2$  contingency tables. Differences in sward heights were tested with Mann–Whitney–*U* tests for non-parametric data.

All statistical tests were performed using the program SPSS 9.0.

## Results

A total of 16,078 hits were registered during the observation period in 2001. The average numbers of hits/m<sup>2</sup> are listed in Table 2. There is a remarkable increase in the number of hits from July to August and a significant decline from August to October on all sites. Grazed plots show a significantly stronger decline ( $p < 0.001$ , Chi-squared test) in number of hits than fenced ones.

### Generative versus vegetative plant parts

Figure 1 illustrates differences in the number of hits on generative and vegetative plant parts between grazed and corresponding enclosure plots. The differences between treatments increased from July to October, but the changes are much stronger for generative plant parts. However, only in October is the number of hits on generative plant parts significantly lower ( $p < 0.001$ , Mantel–Haenszel test) in grazed than in fenced quadrates. The proportions of sample points with hits on generative organs are shown in Table 3. In contrast to the nearly constant level of inflorescence abundance between the second and third observations in fenced plots, a clear decline was detected on grazed quadrates.

A comparison of the heights of generative plant parts only revealed significant differences ( $p = 0.025$ , Mann–Whitney–*U* test) between grazed and fenced plots in October (see Table 4).

### Herb versus graminoid flowers

Hits on generative organs of monocotyledons and dicotyledons were split into three height classes with equal interval distribution. In August, the number of hits on inconspicuously flowering monocotyledons is about equal in both grazed and fenced plots, whereas for dicotyledons the number of hits in the second and third height classes is significantly reduced on grazed plots ( $p = 0.002$ , Chi-Square test; Fig. 2). The number of hits on generative parts strongly declines towards the end of the vegetation period in both monocotyledons and dicotyledons. In October, grazing led to a similar reduction in inflorescence heights of both mono- and dicotyledons (Table 5) (Fig. 3).

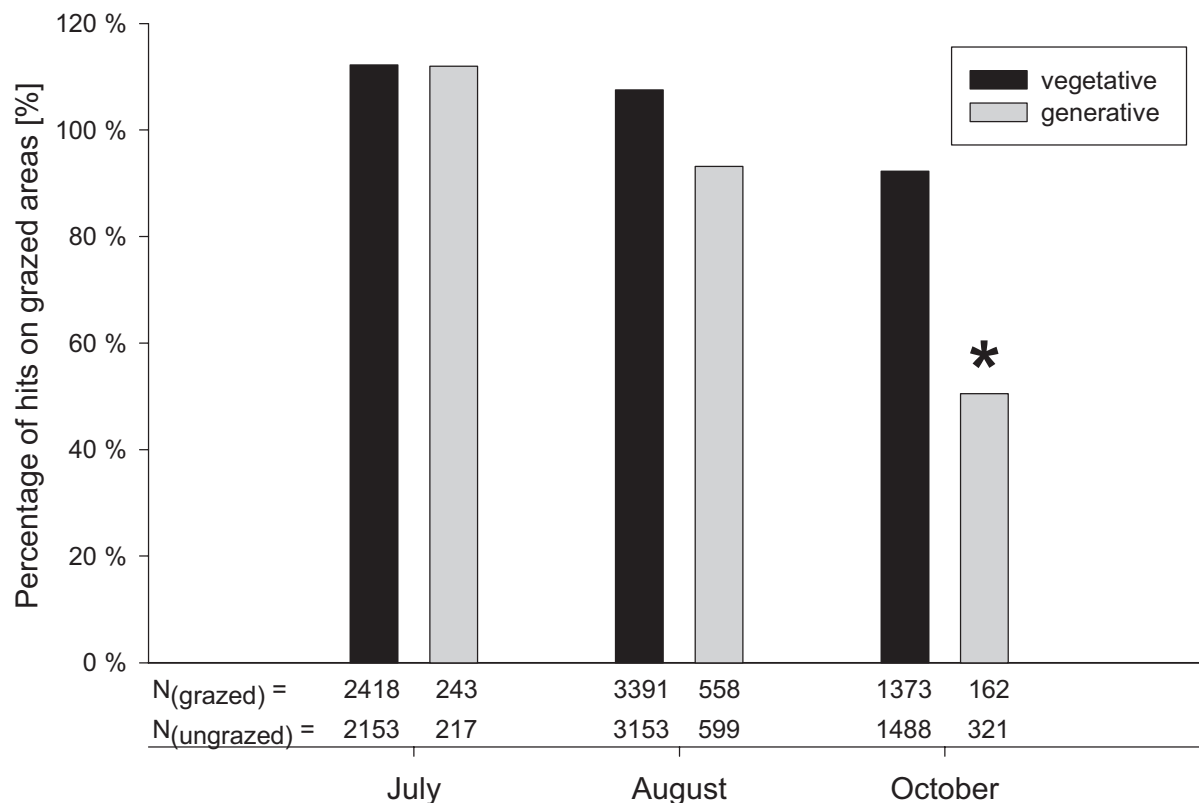
## Discussion

Densities of swards, expressed as the number of hits of a vertically dropped pin in a regularly distributed pattern, show clear seasonal variation (Table 2). An increase until August is followed by a considerable decline, which is partially caused by natural senescence. However, the decline on unfenced quadrates is about 65% more pronounced. The differences in development coincide with the different numbers of sheep browsing at the sites, which indicates grazing as one driving force for changes in vegetation structure.

Whether ruminants provide successful endozoochoric dispersal or destroy the seeds depends strongly on the degree of maturity of these seeds and therefore on the season. Foraging of mature seeds can increase the number of long-distance dispersal events, whereas earlier removal of inflorescences must be detrimental for propagation of plants. In August, the number of inflorescences on grazed areas is only a little lower than on fenced quadrates. Until October the abundance of flowers

**Table 2.** Average number of hits on vascular plants/m<sup>2</sup> in the enclosure experiments on Mount Schrankogel 2001

	Site 1		Site 2		Site 3	
	Grazed	Fenced	Grazed	Fenced	Grazed	Fenced
July	219	210	174	142	183	164
August	242	245	305	283	291	272
October	147	188	188	185	177	229



**Figure 1.** Number of hits on vegetative and generative plant parts of grazed plots as percentages of the corresponding values in enclosure areas (= 100%). Statistically significant differences ( $p < 0.001$ , Mantel-Hänszel test) between hits on generative plant parts of fenced and grazed plots were detected only in October.

**Table 3.** Averaged percentages of sample points of 1 m<sup>2</sup>-plots with at least one hit on inflorescences

	July (%)	August (%)	October (%)
Fenced plots	13	33	29
Grazed plots	15	30	16

**Table 4.** Heights of hits on inflorescences (mean  $\pm$  SE measured in cm) between grazed and fenced 1 m<sup>2</sup>-plots were tested for significance with Mann-Whitney-U test

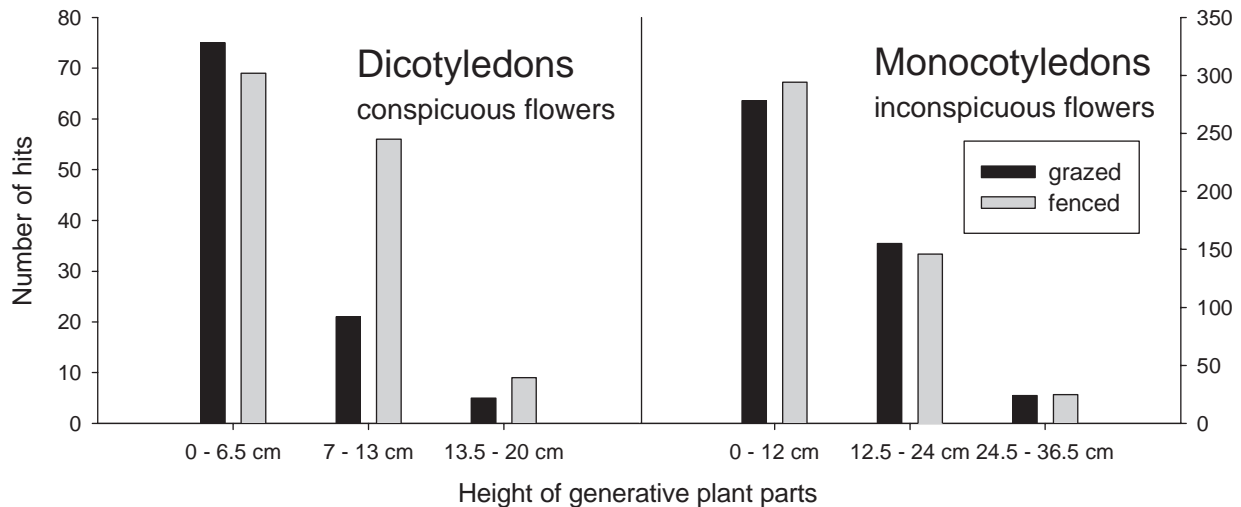
	Grazed	Fenced	<i>p</i>
July	7.7 $\pm$ 0.25	7.5 $\pm$ 0.26	n.s.
August	10.9 $\pm$ 0.26	10.8 $\pm$ 0.28	n.s.
October	8.1 $\pm$ 0.38	9.0 $\pm$ 0.26	0.025

Non-significant differences are marked n.s.

and fruits remained stable when grazers were excluded, but was cut to one half under grazing pressure. In the same period, the number of hits on leaves decreased only by approximately 15%. Moreover, inflorescences in fenced plots were significantly taller. Hence, the establishment of enclosure areas enhanced the development of sexual repro-

ductive organs disproportionately, indicating that ungulates feed selectively on generative organs.

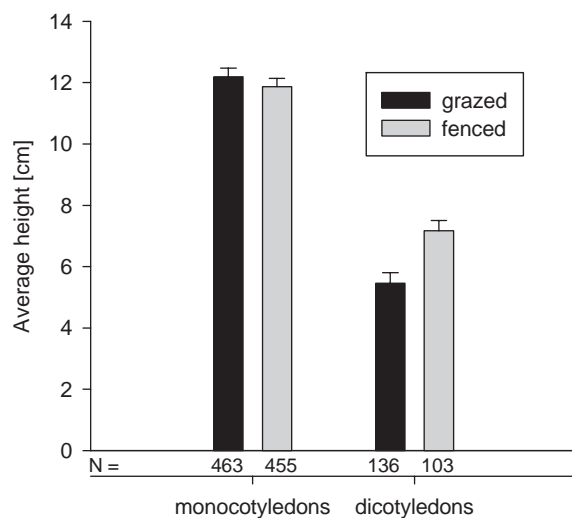
Vascular plant species differ widely in density, food quality and nutrient status (Parsons et al., 1994). Jefferies et al. (1994) suggested that plant-herbivore relations are controlled by nutritional pulses. Díaz, Noy-Meir, and Cabido (2001)



**Figure 2.** Height class distribution of generative parts in August 2001. Classes are partitioned in equal intervals. Statistically significant differences ( $p = 0.002$ , Chi-square test) between grazed and fenced quadrates were only detected for dicotyledons.

**Table 5.** Number of hits on buds, flowers and seeds in three height classes in October 2001

Height class	Dicotyledons			Monocotyledons		
	0–6.5 cm	7–13 cm	13.5–20 cm	0–12 cm	12.5–24 cm	24.5–36.5 cm
Grazed	11	3	0	123	23	2
Fenced	32	11	1	212	64	1



**Figure 3.** Average height of monocotyledons and dicotyledons measured in August 2001. Error bars represent standard errors. Differences between grazed and fenced quadrates were only significant in dicotyledons ( $p < 0.001$ , Mann–Whitney- $U$  test).

and Mulder and Harmsen (1995) confirm a higher consumption of herbs despite their low abundance in various grassland types. Herbs are regarded

as more nutrient-rich (Bulmer & Diemer, 1996; Tolvanen & Henry, 2000) than the dominant graminoids. In arctic and alpine environments flowering inflorescences of some herbs, and especially seeds and fruits, are remarkably nutrient-rich (Jefferies et al., 1994). Järvinen (1987) and Mulder and Harmsen (1995) argue that reproductive organs rather than leaves are more intensively preyed on by different kinds of herbivores, with the degree of browsing damage related to the size or number of inflorescences (Ehrlén, 1997).

However, diet selection of grazing herbivores cannot be explained by intake rates alone (Parsons et al., 1994). Sheep cover much longer distances during grazing than it is necessary to meet their physiological demands (Parsons et al., 1994). Black, Kennedy, and Colebrook (1987) emphasise that foraging selections are determined by sensory factors such as taste or odour. Newman et al. (1992) even presume a preference for rarity or novelty in food intake. In contrast to the inconspicuous, wind-pollinated grass blossom, the flowers of herbs in alpine regions are mostly quite large and attractive (Körner, 1999). Together with the prolonged flowering time (Arroyo, Armesto, & Villagran, 1981), these traits can be interpreted as



an adaptation to low frequencies of pollinator visitations (Totland, 2001). However, this flowering syndrome not only attracts insects for pollination, but also predatory mammals (Hainsworth, Wolf, & Mercier, 1984; Black et al., 1987; Molau, Eriksen, & Knudsen, 1989). In August, the time of main flowering, we observed a significantly higher grazing pressure on herb flowers. In October, when nearly all flowers had matured to inconspicuous seeds, the number of hits on monocotyledons and dicotyledons was about equal. Due to preferential foraging on flowers, the seed yield of herbs is reduced to a larger extent than that of graminoids, which consequently have a higher chance of being eaten as matured seed. Hence, different responses of functional plant groups can be expected not only due to climatic changes (e. g. Winkler & Herbst, 2004), but also due to changes in herbivory intensity with low competitive species (most herbs) being more constraint by pre-dispersal seed predation (Szentesi & Jermy, 2003) than dominant species (mostly graminoids).

Additionally, the average height of herb flowers on grazed areas is lower than on fenced ones. Flowers that are highly exposed above surrounding vegetation, are more accessible for selective feeding and therefore have a higher risk of being grazed. Thus, herb fruits are less elevated in grazed areas. Reduced height of inflorescences and increased obstruction by enveloping leaves consequently lead to lower wind-dispersal distances for respective diaspores (Tackenberg, 2001, 2003).

The migration of alpine plants can be limited by their dispersal abilities (Miles, 1972; Andersen, 1989; Peart, 1989; Malanson & Armstrong, 1996; Jakobsson & Eriksson, 2000; Turnbull, Crawley, & Rees, 2000). Most of the seeds are dispersed within a few metres of their mother plant. Long-distance dispersal events are very rare and stochastic, but of great significance for the colonisation of new areas (Marchand & Roach, 1980; Pitelka & Plant Migration Workshop Group, 1997; Clark, Silman, Kern, Macklin, & Lambers, 1999; Higgins & Richardson, 1999; Cain, Brook, & Strand, 2000; Molau & Larrson, 2000; Greene & Calogeropoulos, 2001).

Alpine and nival plants of the Alps produce many seeds with rather limited biomass (Urbanska & Schütz, 1986). On the other hand, seed mass is correlated with recruitment success (Howe & Smallwood, 1982; Jakobsson & Eriksson, 2000). The undirected transport by wind, the main dispersal vector, reduces the likelihood of meeting a safe site, especially for small seeds (Bonn & Poschlod, 1998). The rarity of safe sites may therefore be an explanation for the high quantities of seeds. Andersen (1989) claims that the impact of

seed loss on plant population size can be considered as a function of density of safe sites.

Müller-Schneider (1986) classified the vascular plant species of Graubünden (Switzerland) according to their dispersal vectors. Applying these data to the species of our investigation area, we found almost 20% (9 species out of 50) being facultatively dispersed by endozoochory. Thus, considerable numbers of viable seeds in the dung can be assumed.

Survivorship of seeds after ingestion by large herbivores varies with animal and plant species (e.g. Janzen, 1984); however, endozoochoric seed dispersal by livestock is a common phenomenon. Welch (1985) reported over 20 plant species germinating from sheep dung collected in heather moorland in Scotland, detecting more graminoid than dicotyledonous seedlings, though most species with frequency less than 10% of seedlings. Pake-man, Digneffe, and Smal (2002) identified 37% of the species recorded in the vegetation germinating in dung samples of sheep. Characteristics of these species include small seed size and the capability of forming a persistent seed bank.

Although these investigations have not been carried out in alpine environments, one can presume that these findings are also valid for alpine vegetation. Seeds with similar morphological traits should not be destroyed in the digestive tract of sheep that easily. The strategy of many alpine species to produce huge numbers of small seeds enhances the probability of a successful endozoochoric transport. Thus, grazing leads to a reduction of dispersed seeds, because not all seeds are consumed at maturity and not all of them survive the passage through the digestive tract. However, the amount of long-distance dispersed seeds should be augmented if we take into account the long distances covered by ungulates during their daily circles (Parsons et al., 1994).

To summarise, the impact of grazers on community structure at the alpine/nival ecotone could be proved, although grazers were excluded for only one growing season. The very precise point-framing method revealed a very selective feeding behaviour of large herbivores. Furthermore, grazing ungulates, especially sheep, potentially increase the number of long-distance dispersal events. This enhancement will be very species-specific due to the selectivity of food intake and digestion. Because of the great importance of long-distance dispersal of seeds in plant migration processes (Marchand & Roach, 1980; Pitelka & Plant Migration Workshop Group, 1997; Clark et al., 1999; Higgins & Richardson, 1999; Cain et al., 2000; Greene & Calogeropoulos, 2001), the impact of

megaherbivores should not be ignored when triggering factors of changes in the composition and patterning of plant assemblages in alpine regions of the Alps are to be assessed.

## Acknowledgements

We are grateful to Andreas Beiser, Nina Habermann and Christian Keusch for their assistance in the field. Thanks also go to Manuela Winkler and Stefan Dullinger for useful comments and for reviewing an early draft. The Austrian Academy of science funded this research project (MAB-6/23), which is part of the Man-and-Biosphere Programme.

## References

- Andersen, A. N. (1989). How important is seed predation to recruitment in stable populations of long-lived perennials. *Oecologia*, *81*, 310–315.
- Archer, S., & Tieszen, L. L. (1986). Plant response to defoliation: hierarchical considerations. In Gudmundson, O. (Ed.), *Grazing research at northern latitudes* (pp. 45–59). New York: Plenum Publishing Corporation.
- Arnold, G. W. (1987). Influence of the biomass, botanical composition and sward height of annual pastures on foraging behaviour by sheep. *Journal of Applied Ecology*, *24*, 759–772.
- Arroyo, M. T. K., Armesto, J. J., & Villagran, C. (1981). Plant phenological patterns in the Andean cordillera in central Chile. *Journal of Ecology*, *69*, 205–223.
- Austrheim, G., & Eriksson, O. (2001). Plant diversity and grazing in the Scandinavian mountains—patterns and processes at different spatial scales. *Ecography*, *24*, 683–695.
- Black, J. L., Kennedy, P. A., & Colebrook, W. F. (1987). Diet selection by sheep. In Wheeler, J. L., Pearson, J. L., & Robards, G. E. (Eds.), *Temperate pastures, their production, use and management* (pp. 331–334). Csiro/Australian Wool Corporation.
- Bonn, S., & Poschlod, P. (1998). *Ausbreitungsbiologie der Pflanzen Mitteleuropas*. Wiesbaden: Quelle und Meyer.
- Brower, J. E., Zar, J. H., & Ende von, C. N. (1990). *Field and laboratory methods for general ecology*. Dubuque, Iowa: Wm. C. Brown Publishers.
- Bulmer, P., & Diemer, M. (1996). The occurrence and consequences of grasshopper herbivory in alpine grassland, Swiss Central Alps. *Arctic and Alpine Research*, *28*, 435–440.
- Cain, M. L., Brook, G. M., & Strand, A. E. (2000). Long-distance seed dispersal in plant populations. *American Journal of Botany*, *87*, 1217–1227.
- Callahan, T. V., Maxwell, B., Molau, U., Oechel, W. C., & Panikov, N. S. (1996). Terrestrial ecosystems and feedbacks on climate change. In Wright, J. L., & Sheehan, C. W. (Eds.), *Arctic systems: natural environments, human actions, nonlinear processes* (pp. 68–82). Oslo: International Arctic Science Committee.
- Chapin, F. S. (1980). Nutrient allocation and responses to defoliation in tundra plants. *Arctic and Alpine Research*, *12*, 553–563.
- Chen, W., Scott, J., Blair, G., Lefroy, R., Hutchinson, K., King, K., & Harris, C. (2002). Diet selection and productivity of sheep grazing contrasting pastures. *Australian Journal of Agricultural Research*, *53*, 529–539.
- Chesson, J. (1978). Measuring preference in selective predation. *Ecology*, *59*, 211–215.
- Clark, J. S., Silman, M., Kern, R., Macklin, E., & Lambers, J. H. R. (1999). Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, *80*, 1475–1494.
- Crocker, B. H. (1959). A method of estimating the botanical composition of the diet of sheep. *New Zealand Journal of Agricultural Research*, *2*, 72–85.
- Damhoureyeh, S. A., & Hartnett, D. C. (1997). Effects of bison and cattle on growth, reproduction, and abundances on five tallgrass prairie forbs. *American Journal of Botany*, *84*, 1719–1728.
- Díaz, S., Noy-Meir, I., & Cabido, M. (2001). Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology*, *38*, 497–508.
- Diemer, M. (1996). The incidence of herbivory in high-elevation populations of *Ranunculus glacialis*: a re-evaluation of stress-tolerance in alpine environments. *Oikos*, *75*, 486–492.
- Dullinger, S. (1998). *Vegetation des Schrankogels*. Master thesis, University of Vienna, Vienna.
- Ehrlén, J. (1997). Risk of grazing and flower number in a perennial plant. *Oikos*, *80*, 428–434.
- Galen, C. (1990). Limits to the distribution of alpine tundra plants: herbivores and the alpine skipper. *Polemonium viscosum*. *Oikos*, *59*, 355–358.
- Gottfried, M., Pauli, H., & Grabherr, G. (1998). Prediction of vegetation patterns at the limits of plant life: a new view of the alpine–nival ecotone. *Arctic and Alpine Research*, *30*, 207–221.
- Grabherr, G., Gottfried, M., Gruber, A., & Pauli, H. (1995). Patterns and current changes in alpine plant diversity. In Chapin, F. S., III, & Körner, C. (Eds.), *Arctic and alpine biodiversity: patterns, causes and ecosystem consequences* (pp. 167–181). Berlin: Springer.
- Grabherr, G., Gottfried, M., & Pauli, P. (1994). Climate effects on mountain plants. *Nature*, *369*, 448.
- Grabherr, G., Gottfried, M., & Pauli, P. (2001). Long term monitoring of mountain peaks in the Alps. In Burga, C. A., & Kratochwil, A. (Eds.), *Biomonitoring: general and applied aspects on regional and global scales. Chapter C. Aspects of global change in the Alps and the high arctic region, Tasks for vegetation science 35* (pp. 153–177). Dordrecht: Kluwer Academic Publisher.



- Grabherr, G., & Mucina, L. (1993). *Die Pflanzengesellschaften Österreichs. Teil II—Natürlich waldfreie Vegetation*. Fischer Verlag: Jena.
- Grant, S. A., Suckling, D. E., Smith, H. K., Torvell, L., Forbes, T. D. A., & Hogson, J. (1985). Comparative studies of diet selection by sheep and cattle: the hill grasslands. *Journal of Ecology*, *73*, 987–1004.
- Greene, D. F., & Calogeropoulos, C. (2001). Measuring and modelling seed dispersal of terrestrial plants. In Bullock, J. M., Kenward, R. E., & Hails, R. S. (Eds.), *Dispersal ecology* (pp. 3–23). Oxford: Blackwell.
- Griffin, G. F. (1989). An enhanced wheel-point method for assessing cover, structure and heterogeneity in plant communities. *Journal of Range Management*, *42*, 79–81.
- Hainsworth, F. R., Wolf, L. L., & Mercier, T. (1984). Pollination and pre-dispersal seed predation: net effects on reproduction and inflorescence characteristics in *Ipomopsis aggregata*. *Oecologia*, *63*, 405–409.
- Harper, J. L., Lovell, P. H., & Moore, K. G. (1970). The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, *1*, 327–356.
- Higgins, S. I., & Richardson, D. M. (1999). Predicting plant migration rates in a changing world: the role of long-distance dispersal. *American Naturalist*, *153*, 464–475.
- Hodgson, J. (1979). Nomenclature and definitions in grazing studies. *Grass and Forage Science*, *34*, 11–18.
- Hofer, H. R. (1992). Veränderungen in der Vegetation von 14 Gipfeln des Berninagebietes zwischen 1905 und 1985. *Bericht des Geobotanischen Institutes ETH. Stiftung Rübel*, *58*, 39–54.
- Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, *13*, 201–228.
- Jakobsson, A., & Eriksson, O. (2000). A comparative study of seed number, seed size, seedling size and recruitment in grassland plants. *Oikos*, *88*, 494–502.
- Janzen, D. H. (1969). Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution*, *23*, 1–27.
- Janzen, D. H. (1971). Seed predation by animals. *Annual Review of Ecology and Systematics*, *2*, 465–492.
- Janzen, D. H. (1984). Dispersal of small seeds by big herbivores: foliage is the fruit. *The American Naturalist*, *123*, 338–353.
- Järvinen, A. (1987). Microtine cycles and plant production: what is cause and effect? *Oikos*, *49*, 352–357.
- Jefferies, R. L., Klein, D. R., & Shaver, G. R. (1994). Vertebrate herbivores and northern plant communities: reciprocal influences and responses. *Oikos*, *71*, 193–206.
- Kleunen, van M., Ramponi, G., & Schmid, B. (2004). Effects of herbivory simulated by clipping and jasmonic acid on *Solidago canadensis*. *Basic and Applied Ecology*, *5*, 173–181.
- Körner, C. (1999). *Alpine plant life—functional plant ecology of high mountain ecosystems*. Berlin: Springer.
- Levy, B., & Madden, E. A. (1933). The point method of pasture analysis. *New Zealand Journal of Agriculture*, *46*, 267–279.
- Lovari, S. (1985). *The biology and management of mountain ungulates*. London: Croom-Helm.
- Malanson, G. P., & Armstrong, M. P. (1996). Dispersal probability and forest diversity in a fragmented landscape. *Ecological Modelling*, *87*, 91–102.
- Marchand, P. J., & Roach, D. A. (1980). Reproductive strategies of pioneering alpine species: seed production, dispersal and germination. *Arctic and Alpine Research*, *12*, 137–146.
- Miles, J. (1972). Experimental establishment of seedlings on a southern English heath. *Journal of Ecology*, *60*, 225–234.
- Miller, G. R., Geddes, C., & Mardon, D. K. (1999). Response of the alpine *Gentiana nivalis* L. to protection from grazing by sheep. *Biological Conservation*, *87*, 311–318.
- Molau, U., Eriksen, B., & Knudsen, J. T. (1989). Predispersal seed predation in *Bartsia alpina*. *Oecologia*, *81*, 181–185.
- Molau, U., & Larsson, E. L. (2000). Seed rain and seed bank along an alpine altitudinal gradient in Swedish Lapland. *Canadian Journal of Botany*, *78*, 728–747.
- Mulder, C. P. H. (1999). Vertebrates and plants in the arctic and subarctic: effects on individuals, populations, communities and ecosystems. *Perspectives in Plant Ecology, Evolution and Systematics*, *2*, 29–55.
- Mulder, P. H., & Harmsen, R. (1995). The effect of Muskox herbivory on growth and reproduction in an arctic legume. *Arctic and Alpine Research*, *27*, 44–53.
- Müller-Schneider, P. (1986). *Verbreitungsbiologie der Blütenpflanzen Graubündens*. Zürich: Veröffentlichungen des Geobotanischen Instituts der ETH, 85.
- Newman, J. A., Parsons, A. J., & Harvey, A. (1992). Not all sheep prefer clover: diet selection revisited. *Journal of Agricultural Science*, *119*, 151–178.
- Underschek, K. (1974). Ernährungsprobleme beim Gamswild. In Schröder (Ed.), *Tagungsbericht des 1. Internationalen Gamswild-Symposiums* (pp. 34–51). Oberammergau.
- Pakeman, R. J., Digneffe, G., & Smal, J. L. (2002). Ecological correlates of endozoochory by herbivores. *Functional Ecology*, *16*, 269–304.
- Parsons, A. J., Newman, J. A., Penning, P. D., Harvey, A., & Orr, R. J. (1994). Diet preference of sheep: effects of recent diet, physiological state and species abundance. *Journal of Animal Ecology*, *63*, 465–478.
- Pauli, H., Gottfried, M., & Grabherr, G. (1996). Effects of climate change on mountain ecosystems—upward shifting of alpine plants. *World Resource Review*, *8*, 382–390.
- Pauli, H., Gottfried, M., & Grabherr, G. (1999). Vascular plant distribution patterns at the low-temperature limits of plant life—the alpine-nival ecotone of Mount Schrankogel (Tyrol, Austria). *Phytocoenologia*, *29*, 297–325.
- Peart, D. R. (1989). Species interactions in a successional grassland. I. Seed rain and seedling recruitment. *Journal of Ecology*, *56*, 421–431.
- Perle, A., & Hamr, J. (1985). Food habits of chamois (*Rupicapra rupicapra* L.) in Northern Tyrol. In Lovari,

- S. (Ed.), *The biology and management of mountain ungulates* (pp. 77–84). London: Croom-Helm.
- Pijl, van der L. (1972). *Principles of dispersal in higher plants* (2nd ed.). Berlin: Springer.
- Pitelka, L. F., Plant Migration Workshop Group (1997). Plant migration and climate change. *American Scientist*, 85, 464–473.
- Pitschmann, H., Reisigl, H., Schiechtl, H. M., & Stern, R. (1970). Karte der aktuellen Vegetation von Tirol 1/100000. I. Teil: Blatt 6, Innsbruck-Stubaier Alpen. *Doc Carte Veget. Alpes (Grenoble)*, 8, 7–34+Karte.
- Poschlod, P., Bakker, J., Bonn, S., & Fischer, S. (1996). Dispersal of plants in fragmented landscapes. Species survival in fragmented landscapes. In Settele, J., Margules, C. R., Poschlod, P., & Henle, K. (Eds.), *Species survival in fragmented landscapes* (pp. 123–127). Dordrecht: Kluwer.
- Reisigl, H., & Pitschmann, H. (1958). Obere Grenze von Flora und Vegetation in der Nivalstufe der zentralen Ötztaler Alpen (Tirol). *Vegetatio*, 8, 93–129.
- Stüfer, J. F., Erschbamer, B., Huber, H., & Suzuki, J. I. (2001). The ecology and evolutionary biology of clonal plants: an introduction to the proceedings of Clone-2000. *Evolutionary Ecology*, 25, 223–230.
- Szentesi, A., & Jermy, T. (2003). Pre-dispersal seed predation and seed limitation in an annual legume. *Basic and Applied Ecology*, 4, 207–218.
- Tackenberg, O. (2001). Methoden zur Bewertung gradueller Unterschiede des Ausbreitungspotentials von Pflanzenarten. *Dissertationes Botanicae*, 347.
- Tackenberg, O. (2003). Modeling long-distance dispersal of plant diaspores by wind. *Ecological Monographs*, 73, 173–189.
- Thornley, J. H. M., Parsons, A. J., Newman, J., & Penning, P. D. (1994). A cost-benefit model of grazing intake and diet selection in a two-species temperate grassland sward. *Functional Ecology*, 8, 5–16.
- Tolvanen, A., & Henry, G. H. R. (2000). Population structure of three dominant sedges under Muskox herbivory in the high arctic. *Arctic, Antarctic and Alpine Research*, 32, 449–455.
- Totland, O. (2001). Environment-dependent pollen limitation and selection on floral traits in an alpine species. *Ecology*, 82, 2233–2244.
- Turnbull, L. A., Crawley, M. J., & Rees, M. (2000). Are plant populations seed limited? A review of seed sowing experiments. *Oikos*, 88, 225–238.
- Urbanska, K. M., & Schütz, M. (1986). Reproduction by seed in alpine plants and vegetation research above timberline. *Botanica Helvetica*, 96, 43–60.
- Walter, H., & Lieth, H. (1960–1967). *Klimadiagramm-Weltatlas*. Jena.
- Watt, T. A., & Gibson, C. W. D. (1988). The effect of sheep grazing on seedling establishment and survival in grassland. *Vegetatio*, 78, 91–98.
- Watt, T. A., Treweek, J. R., & Woolmer, F. S. (1996). An experimental study of the impact of seasonal sheep grazing on formerly fertilized grassland. *Journal of Vegetation Science*, 7, 535–542.
- Welch, D. (1985). Studies in the grazing of heather moorland in north-east Scotland IV. Seed dispersal and plant establishment in dung. *Journal of Applied Ecology*, 22, 461–472.
- Winkler, J. B., & Herbst, M. (2004). Do plants of a semi-natural grassland community benefit from long-term CO<sub>2</sub> enrichment? *Basic and Applied Ecology*, 5, 131–143.