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

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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.

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, Gemsen) auf alpinen Silikatrasen mit dem Hauptaugenmerk auf deren endozoochorem Ausbreitungspotential für Diasporen. Vegetationsstruktur und Artengarnitur wurden im Rahmen von Ausschlussflächenexperimenten erhoben.

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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.

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 & Larrson, 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 (Croker, 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.; Stubaier Alpen, 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^2 — five exposed to grazing, five fenced control quadrates — were installed. The quadrates were arranged in a 3 m $\times$ 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 $\times$ 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 $2 \times 2 \times k$ 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 exclosure experiments on Mount Schrankogel

	Vegetation	Altitude (m)	*N*-coordinate	*E*-coordinate
Site 1	*Festuca halleri-poa alpina* association	2610	47°1.932′	11°5.743′
Site 2	*Caricetum curvulae*	2700	47°2.061′	11°5.606
Site 3	*Caricetum curvulae*	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 2×2 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^2 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 exclosure 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^2 in the exclosure 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

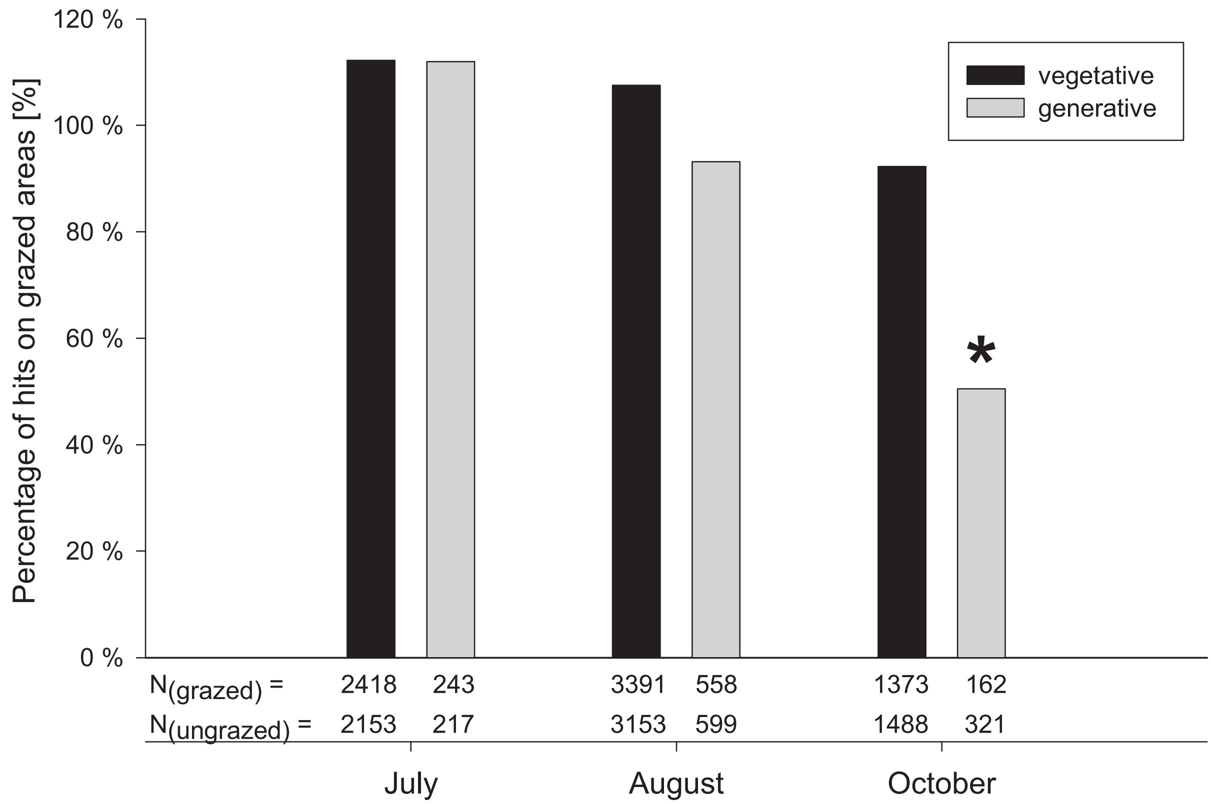

Figure 1. Number of hits on vegetative and generative plant parts of grazed plots as percentages of the corresponding values in exclosure areas (= 100%). Statistically significant differences ($p<0.001$, Mantel–Hänszel test) between hits on generative plant parts of fenced and grazed plots were detected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

Table 3. Averaged percentages of sample points of 1 m^2-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 ± SE measured in cm) between grazed and fenced 1 m^2-plots were tested for significance with Mann–Whitney-*U* test

	Grazed	Fenced	*p*
July	7.7±0.25	7.5±0.26	n.s.
August	10.9±0.26	10.8±0.28	n.s.
October	8.1±0.38	9.0±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 exclosure areas enhanced the development of sexual reproductive 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)

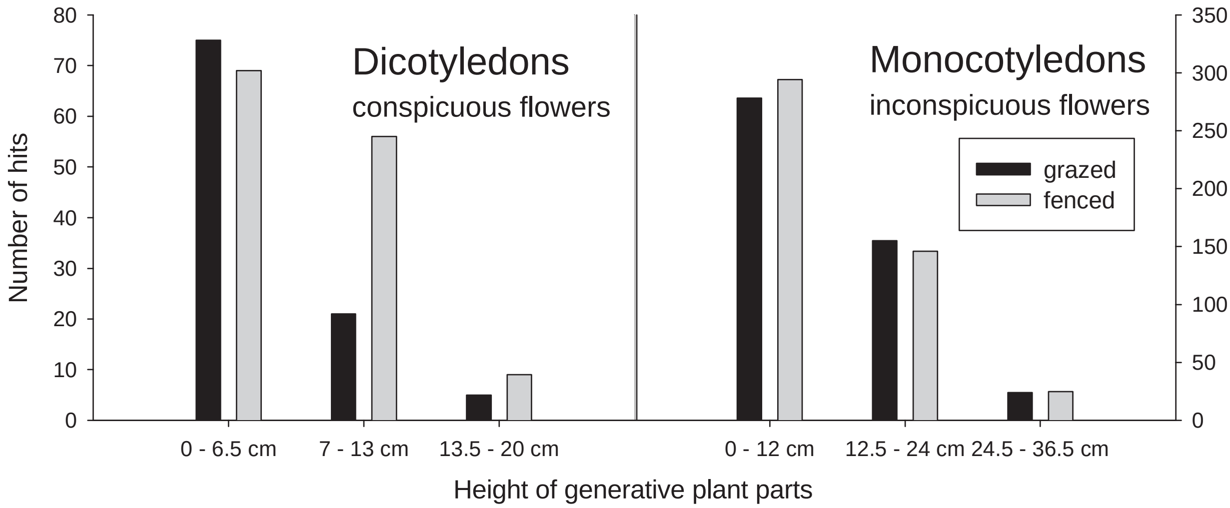

Figure 2. Height class distribution of generative parts in August 2001. Classes are partitioned in equal intervals. Statistically significant differences ($p = 0.002$, Chi-square test) between grazed and fenced quadrates were only detected for dicotyledons.

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

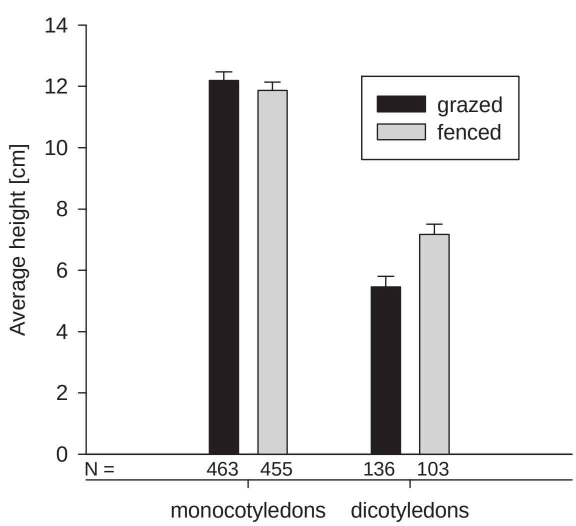

Figure 3. Average height of monocotyledons and dicotyledons measured in August 2001. Error bars represent standard errors. Differences between grazed and fenced quadrates were only significant in dicotyledons ($p < 0.001$, Mann–Whitney-*U* test).

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, Armnesto, & 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 facutatively 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. Pakeman, 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.

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