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Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem

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Abstract Herbivores shape plant communities through selective foraging. However, both herbivore selectivity and the plant's ability to tolerate or resist herbivory may depend on the density of herbivores. In an alpine ecosystem with a long history of grazing, plants are expected to respond to both enhanced and reduced grazing pressures, and the interaction between plant traits and changes in species abundance are expected to differ between the two types of alteration of grazing regime. To understand the mechanisms behind species response, we investigated the relationship between sheep selectivity (measured in situ), plant traits and experimentally derived measures of change in species abundance as a response to the enhancement (from low to high density) or cessation (from low to zero density) of sheep grazing pressure over a six-year time period for 22 abundant herb species in an alpine habitat in south Norway. Sheep selected large, late-flowering herbs with a low leaf C/N ratio. Species that increased in abundance in response to enhanced grazing pressure were generally small and had high root/shoot ratios, thus exhibiting traits that reflect both resistance (through avoidance) and tolerance (through regrowth capacity) strategies. The abundance of selected species remained stable during the study period, and also under the enhanced grazing pressure treatment. There was, however, a tendency for selected species to respond positively to cessation of grazing, although overall responses to cessation of grazing were much less pronounced than responses to enhanced grazing. Avoidance through short stature (probably associated with increased light availability through the removal of tall competitors) as well as a certain amount of regrowth capacity appear to be the main mechanisms behind a positive response to enhanced grazing pressure in this study. The plant trait perspective clearly improves our insight into the mechanisms behind observed changes in species abundance when the disturbance regime is altered.

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Introduction

Herbivore selectivity and the plant's ability to tolerate or resist herbivory are basic predictors for changes in plant community composition (Augustine and McNaughton 1998). Herbivore selectivity is a scale-dependent process (Senft et al. 1987) at local scales determined by plant quality, such as the contents of nutrients, especially nitrogen, in summer (Coley et al. 1985; Villalba and Provenza 1999; Pérez-Harguindeguy et al. 2003). Less-preferred species, which are protected through low digestibility,

secondary metabolites, morphological traits (e.g., thorns, spines), or through avoidance strategies such as short stature (Coley et al. 1985; Agrawal and Fishbein 2006), normally increase in abundance with herbivory (Augustine and McNaughton 1998). In addition, selectivity depends on the type and density of the herbivore as well as on plant community composition (Augustine and McNaughton 1998; Kausrud et al. 2006). Small herbivores (in terms of both species and life stage) are, for instance, more selective than large herbivores (with the same digestive system), and selectivity normally decreases with herbivore density (Demment and Van Soest 1985; Choquenot 1991; Mobæk et al. 2009). If herbivore densities increase to such an extent that high-quality forage becomes scarce, less-preferred species may also be affected by grazing to an extent that their abundances decline (Augustine and McNaughton 1998; Westoby 1999).

Herbivore selectivity, plant tolerance (the ability to regrow/reproduce after damage; Strauss and Agrawal 1999) and plant resistance (reduction of herbivore preference or performance; Strauss and Agrawal 1999) are all associated with several morphological and physiological plant traits (Fig. 1; Coley et al. 1985; Strauss and Agrawal 1999). Thus, species-specific predefined plant traits provide a route to understanding the mechanisms behind species' responses to grazing (Lavorel et al. 1997; McIntyre et al. 1999; Weiher et al. 1999). The literature on the effects of grazing on plant communities and the relationship between

grazing frequency and plant traits is already large and is growing (see review in Díaz et al. 2007). Plants with positive responses to grazing are frequently found to be short in stature (Díaz et al. 2001; Cingolani et al. 2005; Díaz et al. 2007); i.e., they most probably increase in abundance by avoiding grazing (resistance strategy). Traits related to the tolerance strategy have also been found to be positively related to grazing response; e.g., Díaz et al. (2001) and Cingolani et al. (2005) found that the response to grazing was positively correlated with specific leaf area (SLA). SLA is, in turn, positively correlated with growth rate (Garnier 1992), and is therefore an indicator of regrowth capacity (Weiher et al. 1999). However, the relationship between grazing response and plant traits seems to depend upon the grazing regime (Bullock et al. 2001), site productivity (Pakeman 2004), and regional climatic conditions (Vesk and Westoby 2001; de Bello et al. 2005). Furthermore, few grazing studies that incorporate data on plant traits use an experimental approach (but see Bullock et al. 2001), which complicates the use of change in species abundance as a measure of grazing response, as it is difficult to quantify the effect of different herbivore densities, and the use of paired sites (grazed vs. ungrazed) rather than true experiments with controlled herbivore densities may conceal nonlinear responses of species and plant traits to increased grazing (Westoby 1999).

In an alpine ecosystem, the majority of species are long-lived and short-statured compared to other ecosystems (Bliss 1971; Billings 1974, 1987). Scandinavian alpine ecosystems have a long history of grazing (Austrheim and Eriksson 2001), and so plants are expected to respond to both enhanced and reduced grazing pressures. The interaction between plant traits and change in species abundance can be expected to differ between the two types of altered grazing regimes. In a previous study, we investigated the effect of sheep grazing on changes in plant species abundance over a short-term scale (four years; Austrheim et al. 2008). To understand the mechanisms behind the responses of species, here we investigate the relationship between herbivore selectivity, plant traits and responses to increasing or decreasing grazing pressure after six years of altered grazing regime, within an established landscape-scale experiment of sheep-grazing effects in an alpine ecosystem.

For the most abundant plant species, we calculated three indices: (a) a selectivity index (SI), (b) a grazing response index (GR), and (c) an index of response to cessation of grazing (CR). Data on 15 plant traits covering regeneration mode, morphology and leaf chemistry were collected. Sheep are highly selective herbivores with a preference for herbs (Bowns and Bagley 1986; Hæggström 1990). As we found that selectivity for dwarf shrubs and variation in
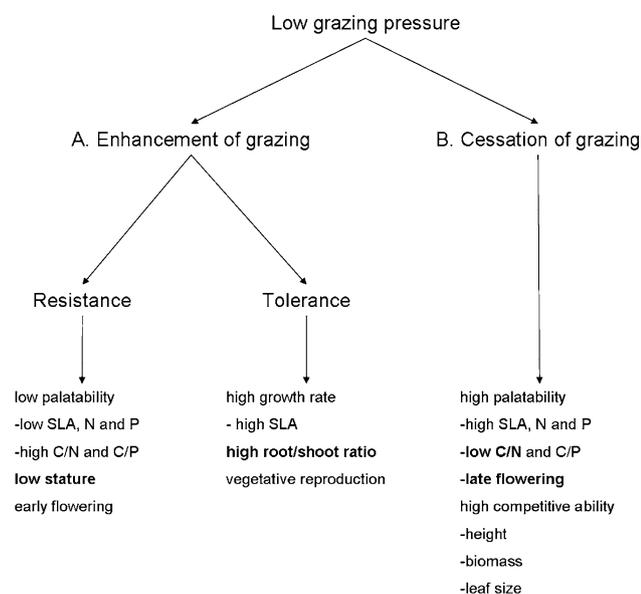

Fig. 1 Plant traits associated with a positive response (in terms of abundance change of plants) in an experimental design with enhancement or cessation of grazing pressure, depending on the main strategy of the species' response to grazing: resistance or tolerance. Traits in *bold* are found to be significant predictors of response to altered regime in this study

plant traits for graminoids were generally low (M. Evju, unpublished data), we focused our study on the 22 most common herb species. Three related issues at the interface between sheep selectivity, plant traits and vegetation change are addressed. Initially, we investigate how sheep selectivity is related to plant traits. More specifically, a grazer such as a sheep is expected to prefer tender leaves with a high specific leaf area (SLA), high nutrient content, but low C/N and C/P contents (Coley et al. 1985; Pérez-Harguindeguy et al. 2003). Secondly, we study the relation between species response to enhanced grazing pressure and plant traits that express grazing tolerance/resistance strategies (Fig. 1). If tolerance is the main strategy for coping with grazing in this ecosystem, we predict that enhanced grazing pressure should be reflected in positive responses of species with traits such as high root/shoot ratio and high relative growth rate (positively correlated with SLA). In contrast, if resistance is the most important strategy, a positive response to enhanced grazing pressure should be expected for species with traits such as low palatability (low nutrient content, high C/N content), low stature and early flowering time. As grazing and trampling also brings about the creation of gaps and openings in the vegetation, we predict that enhanced grazing pressure will also favor small-seeded species (Bullock et al. 1995; Bullock 2000) and species with a high capacity for vegetative reproduction (Oksanen and Ranta 1992; Vandvik 2004). Thirdly, we study the relationship between species response to cessation of grazing and plant traits (Fig. 1). We predict that species that increase in response to cessation of grazing will have high competitive abilities (tall, large-leaved species), as such plants benefit from reduced disturbance. Furthermore, reduced gap creation due to reduced herbivory activity is predicted to favor large-seeded species over small-seeded ones (Grime and Hillier 2000).

Methods

Study area

The study was carried out in Hol municipality, Buskerud county, south Norway (between 60°40′–60°45′N and 7°55′–8°00′E). Mean annual temperature is −1.5°C, with the mean temperature in January being −10.8°C and in July 8.9°C, and mean annual precipitation is approximately 1,000 mm (M. Evju, unpublished data). The bedrock consists of meta-arkose (Sigmond 1998), and the soil is moderately base rich (Austrheim et al. 2005). The vegetation predominantly consists of dwarf-shrub heaths interspersed with grass-dominated meadows (Rekdal 2001). A large enclosure covering ca. 2.7 km^2 was set up in the low alpine zone (1,050−1,300 m a.s.l.) in 2001 on a mainly south-facing hillside. The enclosure was split into nine parallel subenclosures, each covering ca. 0.3 km^2 and spanning the altitudinal gradient.

The subenclosures were grouped into three blocks, each with three subenclosures. The treatments—no sheep, low sheep density (25 sheep per km^2) and high sheep density (80 sheep per km^2)—were assigned to subenclosures in each block at random, in accordance with block-wise randomized designs. Such sheep densities are within the range of sheep densities normally encountered in alpine habitats of Norway (Mysterud and Mysterud 1999). The first experimental grazing season was 2002. Grazing lasted from the last week of June to the last week of August or the first week of September in all years.

Sheep grazing has a long history in Scandinavian alpine systems (Austrheim and Eriksson 2001), and sheep were indeed present, although at low densities, prior to the establishment of the experiment (A. Mysterud, pers. obs.). As the smallest changes in plant abundance during 2001–2007 took place in the low sheep density treatment (Austrheim et al. 2008), we interpreted this treatment as being close to a continuation of previous grazing regimes.

Field methods

In 2001, 180 permanent vegetation plots, each 0.5 × 0.5 m^2, were established; 20 per subenclosure. The plots were placed according to a random, stratified protocol to ensure a balanced distribution between altitudinal levels and main vegetation types (dwarf-shrub heaths, lichen ridges, graminoid-dominated snow-beds, and alpine meadow communities with varying cover of *Salix* spp.; Austrheim et al. 2005, 2008). The abundance of all vascular plants was recorded in 2001 and 2007 using the subplot frequency (presence–absence in 16 subplots of 0.125 × 0.125 m^2) in each of the 180 plots as a measure of abundance. A total of 104 vascular plant species were present in the plots in 2001 (Austrheim et al. 2005), and 107 in 2007 (G. Austrheim and M. Evju, unpublished data).

All herbs that were initially present in at least 10% of the plots were included in the study of plant traits. During the recording of vegetation in the field, *Pyrola minor* and *P. rotundifolia* were treated as one taxon (*Pyrola* spp.), as were *Hieracium alpinum* and *Hieracium* sp. (*Hieracium* spp.). Additionally, *Potentilla erecta* (8.9%), *Leontodon autumnalis* (7.8%) and *Alchemilla* sp. (4.4%) were included despite exhibiting slightly lower frequencies than 10% due to their potential importance as sheep diet constituents. Two taxa were only determined to genus level (*Alchemilla* sp. and *Taraxacum* sp.). The final dataset consisted of 22 taxa (Table 1, Table S3 in the "Electronic supplementary material"), which are hereafter referred to as species. Nomenclature follows Lid and Lid (2005).

Table 1 Selectivity (SI), the proportion of sites at which it was recorded that the species was grazed; response to enhanced grazing pressure (GR), the relative change in abundance of species in the high sheep density treatment compared to the low sheep density treatment from 2001 to 2007; and the response to cessation of grazing (CR), the relative change in abundance of the species in the no sheep density treatment compared to the low sheep density treatment from 2001 to 2007

Species	SI	GR	CR
Alchemilla alpina	0.13	0.18	−0.02
Alchemilla sp.	0.40	−0.83	−1.06
Bistorta vivipara	0.11	0.10	−0.09
Euphrasia wettsteinii	0.00	−1.05	0.07
Geranium sylvaticum	0.43	−0.48	0.13
Hieracium spp.	0.60	−0.03	0.04
Leontodon autumnalis	0.35	4.21	0.22
Melampyrum sylvaticum	0.19	−2.36	−0.02
Omalotheca norvegica	0.62	−0.34	0.25
Omalotheca supina	0.13	1.22	0.32
Potentilla erecta	0.31	−0.31	−0.20
Pyrola spp.	0.13	0.39	0.21
Ranunculus acris	0.42	−0.29	0.32
Rumex acetosa	0.48	0.12	−0.24
Saussurea alpina	0.68	−0.15	0.02
Sibbaldia procumbens	0.19	0.15	−0.47
Solidago virgaurea	0.64	−0.37	0.49
Taraxacum sp.	0.49	1.23	0.44
Trientalis europaea	0.01	−0.05	−0.20
Veronica alpina	0.06	−0.46	0.07
Viola biflora	0.03	−0.20	−0.07
Viola palustris	0.00	1.40	−0.11

A total of 15 traits covering regeneration mode, morphology and leaf chemistry were collected for each species (Table 2). In accordance with recommendations by Cornelissen et al. (2003), traits were measured on individuals that were judged as being healthy, typical, fully grown and with developed fruits, that were preferably located in well-lit environments, and were not strongly affected by herbivores or pathogens. To ensure an unbiased sampling of individuals, the following sampling protocol was used: each subenclosure with no sheep was divided into three compartments, one low altitude, one mid altitude and one high altitude, so that the total number of compartments was nine. The midpoint of each compartment was determined from a map and located using a GPS (see Fig. 2). For each species fulfilling the criteria above, the individual that was located closest to the midpoint of the compartment was selected for sampling. For each species, one compartment was randomly selected in order to sample two individuals, so that the total number of individuals sampled per species was ten. If a species was absent from a

compartment, another compartment was randomly selected for additional sampling. As plant height can be highly variable, we measured 20 individuals per species for this trait by sampling the two individuals closest to the compartment midpoint.

From each sampled plant individual, two relatively young, fully expanded leaves were collected and pressed. Then the entire ramet was dug up, soil was removed carefully, and the ramet was divided into belowground parts, aboveground parts, and reproductive structures, which were kept separately in paper bags in a dry place. Traits were measured following the protocol of Cornelissen et al. (2003); Table 2. For each species and trait, the average of the values recorded for all sampled individuals was used (see Table S1 in the "Electronic supplementary material"). For *Pyrola* spp. we used trait values for *P. minor*, and for *Hieracium* spp. we used trait values for *H. alpinum*, as these were the only ones for which data on traits were available. Trait sampling was carried out in August 2004.

Statistical analyses

A selectivity index (SI) was made based on observational data of sheep foraging in the study area in 2002 (Kausrud et al. 2006), in which vegetation data were collected from 500 sites where sheep were observed to graze. Selectivity was defined as the proportion of sites in which it was recorded that the species in question was observed to be grazed.

We calculated the response to increased grazing pressure (grazing response; GR) for each species as the relative abundance change in the high sheep density treatment compared to the low sheep density treatment from 2001 to 2007:

$$\text{GR} = \log_2\left(\frac{\bar{X}_{\text{High 07}}}{\bar{X}_{\text{High 01}}}\right) - \log_2\left(\frac{\bar{X}_{\text{Low 07}}}{\bar{X}_{\text{Low 01}}}\right)$$

where $\bar{X}_{\text{High 07}}$ is the average abundance (over all 60 plots in that treatment) of species X in the high-density treatment in the year 2007, etc. Correspondingly, we calculated the response to cessation of grazing (CR) for each species as the relative change in abundance from 2001 to 2007 in the no sheep treatment compared to the low sheep treatment:

$$\text{CR} = \log_2\left(\frac{\bar{X}_{\text{No07}}}{\bar{X}_{\text{No01}}}\right) - \log_2\left(\frac{\bar{X}_{\text{Low07}}}{\bar{X}_{\text{Low01}}}\right)$$

A GR/CR of 1 would thus imply that the species doubled its abundance in response to enhanced grazing pressure or cessation of grazing, respectively, and conversely a GR/CR of −1 would imply that the species reduced its abundance by 50% when the grazing regime was altered. Values of GR/CR close to zero would indicate that abundance changes due to changing the grazing regime were small.

Table 2 Plant traits included in the study

No	Code	Variable	Unit	Comments
1	SM	Seed mass	mg	Weight of individual seeds, estimated by weighing batches of 10–100 oven-dry seeds from each ramet, dried at 80°C for 48 h. Literature studies were used to obtain data for some species (see Table S1 in the "Electronic supplementary material")
2	SN	Seed number		The number of seeds per ramet, either counted directly or estimated using the number of seeds per fruit and multiplying with the number of fruits. Literature studies were used to obtain data for some species (see Table S1 in the "Electronic supplementary material")
3	ALR	Allocation to reproduction		The proportion of the aboveground biomass allocated to reproductive structures (including peduncles, flowers, fruits and seeds)
4	FFD	First flowering day		Data on Julian day for first flowering were compiled from Molau et al. (2005). For species missing from this dataset, we estimated FFD using a regression model with data on flowering period from Lid and Lid (2005) and FFD for the remaining species
5	PLH	Plant height	cm	The shortest distance between the upper boundary of the photosynthetic tissue on the plant and ground level for rosette plants based on rosette leaves
6	LS	Leaf size	mm^2	The one-sided projected area of a single leaf, including the petiole. Measured using image analysis software on scanned dried-and-pressed leaves
7	AGB	Aboveground biomass	mg	The oven-dry mass of the entire aboveground portion of the ramet, dried at 80°C for 48 h
8	BGB	Belowground biomass	mg	The oven-dry mass of the entire belowground portion of the ramet, dried at 80°C for 48 h. For species with interconnected ramets, the belowground biomass of the ramet in question was calculated using the ramet's proportion of total (all ramets) aboveground biomass
9	RS	Root to shoot ratio		The ratio of the oven-dry weight of belowground biomass to the aboveground biomass
10	VR	Vegetative reproduction		The proportion of individuals interconnected to other ramets
11	SLA	Specific leaf area	mm^2 mg^{-1}	Leaf size divided by the oven-dry weight of the leaf, dried at 80°C for 48 h
12	N	Nitrogen content	%	12–15: Leaf content. Analyses were performed at the Soil Science Laboratory, the Swedish University of Agricultural Sciences, using ICP/MS (Elan 6100, PerkinElmer, Norwalk, CT, USA) and an elemental analyzer (PerkinElmer). Between two and four samples of dried leaves were analyzed for each species
13	P	Phosphorus content	%	
14	C/N	Ratio of carbon to nitrogen content		
15	C/P	Ratio of carbon to phosphorus content		

Fig. 2 The study area, with subenclosures nested into blocks, and with three replicates of each sheep grazing treatment (no sheep, low and high sheep density). Twenty permanent plots (0.5 × 0.5 m^2) are located within each subenclosure. *Asterisks* refer to sampling sites for plant functional traits
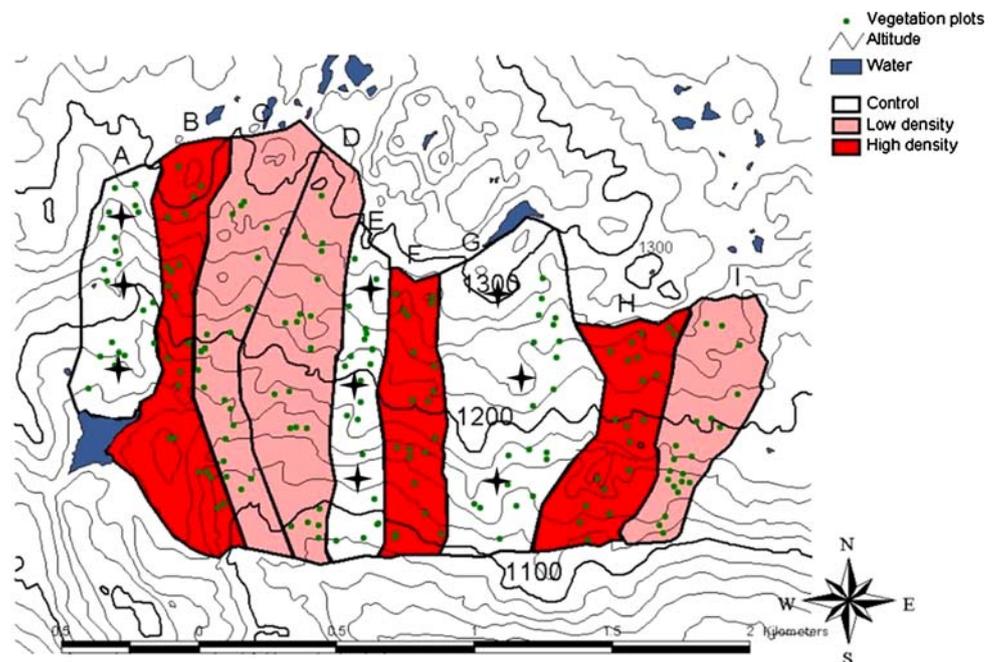
We used linear regression with forward selection of variables to investigate which plant traits were related to the selectivity index. We used F tests of residual deviance for model evaluation, and only included terms that significantly reduced deviance (at the $p < 0.05$ level). The resulting model is termed the "best model."

The relationship between GR and CR was investigated by calculating correlation coefficients (a negative correlation was predicted; i.e., that species that increase under enhanced grazing pressure decrease under reduced sheep grazing pressure and vice versa). Similarly, we investigated if GR and CR were related to sheep selectivity (SI). We then used linear regression to investigate how the response to enhanced grazing and cessation of grazing was related to plant traits, following the procedure above. For the best models, we tested the interaction between sheep selectivity and the plant traits included in the model.

Traits for which the observed values were strongly skewed to the left were log-transformed prior to the analyses. We did not include analyses of phylogenetic independent contrasts (PIC), as we found in a previous study that herb abundance and plant trait relationships in the study area were similar when using species or PICs (Austrheim et al. 2005). All analyses were performed with R Version 2.7.0 (R Development Core Team 2008).

Results

Sheep selectivity

The sheep selectivity index (SI) varied between 0.00 and 0.68 (Table 1). Single-trait correlations with SI are shown in Table S2 of the "Electronic supplementary material." Variation in selectivity was best explained by a combination of aboveground biomass, C/N content and first flowering day (Table 3a), with SI increasing as a function of both aboveground biomass and first flowering day but decreasing with increasing C/N.

Response to enhanced grazing (high vs. low density)

The relative change in abundance with high as compared to low sheep density (grazing response; GR) ranged from −2.4 (strong decrease) to 4.2 (strong increase; Table 1). No correlation was found between overall GR and SI ($r = 0.003$, $p = 0.989$, $n = 22$). Single-trait correlations with GR are shown in Table S2 of the "Electronic supplementary material."

The response to enhanced grazing pressure was best predicted by a combination of plant height and root/shoot ratio (Table 3). The relationship between grazing response and plant height was negative, implying that small plants increased and tall plants decreased when grazing pressure was enhanced. Conversely, grazing response was positively related to root/shoot ratio, so species with large roots relative to their shoots increased at high grazing pressures, while species with small roots decreased. There was no significant interaction between SI and either plant height or root/shoot biomass (results not shown). As the model was strongly influenced by two annual species with low root/shoot ratios, we also ran the analysis without these species. The resulting model included plant height as the only significant predictor variable ($F_{(1,18)} = 12.51$, $R^2_{\mathrm{adj}} = 0.377$, $p = 0.002$).

Response to cessation of grazing (no sheep vs. low density)

The relative change in abundance with no sheep versus low sheep density from 2001 to 2007 (response to cessation of grazing; CR) ranged from 0.49 (moderate increase) to −1.06 (moderate decrease; Table 1), and was thus generally smaller than the grazing response. No correlation between CR and selectivity was detected ($r = 0.202$, $p = 0.368$, $n = 22$), and there was no negative correlation between CR and GR ($r = 0.251$, $p = 0.260$, $n = 22$). Single-trait correlations with CR are given in Table S2 in the "Electronic supplementary material."

Response to cessation of grazing was best predicted by first flowering day (positive relationship; late-flowering species increased in response to cessation of grazing) and C/N (Table 3). No significant interaction was found between SI and either first flowering day or C/N content in leaves (results not shown).

Discussion

Alterations of grazing regimes affect the abundances of plants (Mulder 1999; Hester et al. 2006), but the mechanisms of plant responses, and how these relates to plant morphological and physiological traits, are often not explicitly quantified. We have examined the functional importance of species-specific plant traits related to herbivore selectivity, plant tolerance and resistance in order to explain grazing responses over a six-year period in an experimental design in an alpine habitat. We found that sheep select large, late-flowering herbs with low C/N ratios in leaves. This supports the hypothesis of Villalba and Provenza (1999), that selectivity can be viewed as a combination of intake rate and nutritional quality, given that late-flowering species are phenologically younger, and that early phenological stages of plants generally have higher nutritional quality in terms of available energy and protein (Albon and Langvatn 1992; Hebblewhite et al.

Table 3 Stepwise linear regression results

	LS est.	SE	p
(a) Sheep selectivity (SI)			
log(AGB)	0.149	0.020	<0.0001
C/N	−0.019	0.005	0.001
FFD	0.006	0.002	0.004
R^2_{adj}			0.785
(b) Response to enhanced grazing pressure (GR)			
log(PLH)	−0.563	0.133	0.0007
log(RS)	0.418	0.150	0.0005
R^2_{adj}			0.531
(c) Response to cessation of grazing (CR) as a function of plant traits ($n = 22$)			
FFD	0.015	0.004	0.003
C/N	−0.029	0.012	0.024
R^2_{adj}			0.372

LS est., Least squares estimate; *SE*, standard error; *AGB*, aboveground biomass; *C/N*, carbon/nitrogen ratio in leaves; *FFD*, first flowering day; *PLH*, plant height; *RS*, root/shoot ratio

2008). Small size and early flowering thus seem to be viable avoidance strategies in this alpine environment.

The question of herbivore selectivity and response of palatable versus unpalatable species to grazing is certainly a complex matter; reported patterns range from decreases in selected species (Anderson and Briske 1995; Díaz 2000; Bråthen and Oksanen 2001; Pakeman 2004), to no relationship (Cingolani et al. 2005), to increased abundances of selected species (Jónsdottir 1991; Bullock et al. 2001) with increased grazing pressure. We found no simple relationship between sheep selectivity and plant response to enhanced sheep densities. The link between selectivity and grazing response is indeed expected to be weak if selected species are tolerant to grazing (e.g., Bullock et al. 2001).

The response to enhanced grazing pressure was best predicted by a combination of traits typical of resistance/avoidance (short plants increased in abundance when the grazing pressure was enhanced, while tall plants decreased) and tolerance (plants with high root/shoot ratios increased) strategies, despite the fact that alpine plants are generally small, and other studies have found plant height to be of minor importance for predicting grazing response in alpine areas (de Bello et al. 2005). Plant responses to enhanced grazing differed from responses to cessation of grazing, not only in terms of which of the traits were related to the response but also in terms of the magnitude of species-specific responses. Our results showed that species-specific responses to cessation of grazing were generally smaller than responses to enhanced grazing pressure. This can probably be partly explained by the relatively small difference in herbivore density between the no sheep and low sheep density treatments (0 vs. 25 sheep per km^2) compared to the low versus high sheep density treatments

(25 vs. 80 sheep per km^2). However, the results are also in accord with the findings of Olofsson (2006), who found that immediate responses to reduced grazing pressure (indirect effects of competition) are much slower than responses to increased grazing pressure (effects of foraging and trampling). We found indications of a positive effect of release from sheep grazing for selected species, due to the generally more positive responses of late flowering than early flowering species to cessation of grazing (see also Hellström et al. 2003; Louault et al. 2005), and the more positive responses of species with low C/N levels in leaves, with both of these traits being correlated with selectivity. We did not find evidence for an increase in tall competitive species at the expense of small, less competitive species, and no indication of a decrease in small-seeded species was found, contrary to our prediction. Regeneration traits were not related to response to enhanced grazing pressure either, and we suspect that the rate of gap creation by sheep may be low in comparison with other biotic factors such as rodent activity (Steen et al. 2005; Austrheim et al. 2008), contributing to this lack of effect.

Herbivore density relative to habitat productivity is a critical factor for evaluating grazing responses in general. The grazing pressure exerted by the sheep in our study area has previously been reported to be low to moderate (cf. Holechek et al. 1999) in the low and high sheep density treatments, respectively (Evju et al. 2006). Although herb species abundances responded to both enhanced and reduced grazing, changes in plant species composition were only moderately related to sheep grazing treatments after four (Austrheim et al. 2008) and six years (this study). In our study system, in which grazing has occurred since prehistoric times and the species pool is thus expected to be

adapted to grazing (Austrheim and Eriksson 2001), small changes in plant community structure are not unexpected (Milchunas et al. 1988; Milchunas and Lauenroth 1993), at least when the change in disturbance regime is not extreme. Detailed population-level studies of one of the tall, selected herbs in this study indicate a shift towards smaller individual plants and increased vegetative reproduction in the high sheep density treatment, but no detectable effects on the population growth rate (M. Evju, unpublished data). Thus, plasticity in phenotypic traits may be important to prevent changes in plant abundance as a response to a change in the grazing regime (e.g., Lennartsson 1997; Lennartsson et al. 1997). Additionally, year-to-year fluctuations in plant communities (Dodd et al. 1995) in alpine ecosystems strongly determined by local climatic conditions (Evju et al. 2006) as well as nonlinear species responses over time to changed grazing regime (Bullock et al. 2001; Austrheim et al. 2008) may weaken patterns of trait responses.

Conclusion

Growth forms are widely applied as functional groups when studying grazing effects (e.g., Olofsson 2006; Bråthen et al. 2007), but inconsistent responses to grazing within growth forms are not uncommon (Grellmann 2002; Austrheim et al. 2008). The plant trait perspective clearly improves our insight into mechanisms behind observed changes in abundance of species when the disturbance regime is altered. We found no evidence for a general decline in the abundances of selected species when herbivore densities were enhanced. Instead, we found that short-statured species were favored by increased grazing pressure, probably through a combination of avoidance of herbivores and reduced competition for light, and that capacity for regrowth (root/shoot ratio) was an important prerequisite for responding positively when grazing pressure was increased.

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