Sheep grazing and dynamics of alpine plants in a landscape-scale experiment

Marianne Evju

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Av og til

må noe vare lenge

Rolf Jacobsen, MERE FJELL

PREFACE

In 2001, Gunnar Austrheim called and asked if I would like to do field work on a newly established sheep grazing project in Hol. Being stuck in an office, copying and sending faxes all day long, I did not hesitate. During the course of the summer, Gunnar said to me: "You should do a PhD within this project". And so I did. With Rune Halvorsen and Atle Mysterud also on the team, we managed to get funding from the Norwegian Research Council for a three-year PhD-project (Project 153601/V40), and a fourth year was provided by the Natural History Museum, University of Oslo.

As things turned out, the PhD-project lasted for six years instead of four, but "having kids is an excellent opportunity to collect more data in the field". I am grateful to you, Rune, Gunnar and Atle, for being so enthusiastic and encouraging supervisors, providing quick but thorough feedback on manuscripts and other issues. Having such a team of supervisors has been both inspiring and frustrating – inspiring as you have all very different approaches to the same subject, and frustrating for the very same reason. Nevertheless, I have learned a lot about research from all of you. Thanks also to Knut Rydgren, for your valuable help with the population dynamics studies, and for arranging the matrix modelling workshop at exactly the right stage in my PhD-cycle.

I would also like to thank colleagues at the Botanical Museum for making my six years here so pleasant, and especially to the small and variable group of ecologists with whom discussions of methods, statistics and other small and large issues have been an important part of work. Special thanks to Anette Edvardsen, for sharing office, joys and frustrations the last two years, and for helping me with all small details in the final stages of thesis writing. Thanks also to Vegar Bakkestuen for taking time for discussions and reading manuscripts. I am also grateful to Wenche H. Johansen for help with providing literature.

Thanks to my numerous field colleagues at Minnestølen the seven summers that I have spent there, and to the Sveingard family for their hospitality during summers where babies were brought to the mountains. I am especially grateful to Synnøve Lindgren for helping me out with the population dynamics studies in 2003, when my oldest son was four weeks old. Your help was invaluable.

To my friends and family: thank you for patiently listening to my stories about sheep and plants, and for being supportive and encouraging when I needed it most. A special thanks to my good PhD-friends Mona, Marte and Trude, for sharing all these everyday PhD-life stories ☺

Last, but not the least: Audun, thanks for being patient and understanding these last months, and not to forget, the last six summers. And thanks to Tobias and Magnus, you are the best boys ever!

Oslo, December 2008

Marianne Evju

CONTENTS

ABSTRACT

Large herbivores such as sheep affect plants directly and indirectly through selective foraging, trampling, urination and defecation, thereby modifying intra- and interspecific interactions and altering resource availability for plants. Tolerance and resistance are the main means by which plants cope with herbivores. How herbivores change the relative abundance of tolerant and resistant species has large impact on long-term ecosystem productivity, and the possibility of using plant functional groups to make general predictions is currently a key topic. The ability to express tolerance and resistance will depend on herbivore selectivity and on grazing frequency and intensity, factors that are all dependent on herbivore density. Most studies of grazing focus on effects on the plant community composition, and either compare sites of contrasting herbivore densities or use small-scale exclosure experiments, thus comparing only two levels of grazing despite theories often predicting non-linear responses of plants to increasing grazing pressure. There is a need to compare more than two herbivore density levels, to link herbivore density to grazing pressure, and furthermore, to link plant responses to grazing with plant traits that can explain the mechanisms underlying changes in plant community composition.

This thesis presents studies of effects of sheep grazing on plants within the framework of a landscape-scale experiment covering 2.7 km^2 in a productive alpine ecosystem in southern Norway. The experiment was established in 2001, and the impact of three levels of sheep densities (high, low and zero), and more specifically of changing grazing regime (enhancement and cessation of grazing) on alpine herb species was investigated.

The experimental densities of sheep corresponded to low (low sheep density) and moderate (high sheep density) grazing pressure. Selected herb species, as determined by a combination of biomass and nutrient quality of the plants, did not in general respond negatively to enhanced grazing pressure. Rather, grazing response was related to both plant height and root/shoot ratio, i.e. avoidance through low stature combined with capacity for regrowth was the main mechanism behind a positive response to enhanced grazing pressure.

I studied the detailed life history of two herb species, the tall, grazed *Geranium sylvaticum* and the low stature, non-selected *Viola biflora*, to explore how they coped with the three grazing levels. Contrasting responses to high sheep density and no sheep were predicted for the two species, the tall *G. sylvaticum* expected to benefit from cessation of grazing and the low stature *V. biflora* predicted to benefit from presence of herbivores. By following individual plants from 2002 through 2007, population-level consequences of different sheep densities were evaluated. Grazing increased clonal reproduction rates of *G. sylvaticum*, but at the same time reduced growth compared to ungrazed plants. However, the proportion of the populations that was grazed was low in all years (6−14% and 2−6% in the high and low sheep density treatments, respectively), and no differences in population growth rate (λ) between sheep grazing treatments were detected. The *V. biflora* populations that were exposed to sheep appeared to have more favourable conditions for growth than the population protected from sheep, but no effect of sheep grazing treatment was found on λ of this species either. However, in years with high levels of grazing by sheep and rodents, λ of *V. biflora* was suppressed. Between-year variations in λ were large for both species, and the pattern of variation was similar, strongly suggesting that external factors other than sheep grazing controlled between-year variation in vegetation.

The experimental sheep densities did not substantially change plant community or population dynamics on the six-year time scale included in this study, suggesting no negative impact on ecosystem productivity. The long history of grazing in Scandinavian alpine ecosystems, combined with long-lived plant species and moderate grazing pressure, is likely to explain the small changes, and variable climatic conditions seemed to overrule effects of grazing. Furthermore, effects of sheep on other herbivores in the ecosystem (rodents, invertebrates) may contribute to the lack of consistent results.

LIST OF PAPERS

This thesis is based on the following four papers, which will be referred to in the text by their Roman numbers:

I: Evju, M., Mysterud, A., Austrheim, G. and Økland, R. H. 2006. Selecting herb species and traits as indicators of sheep grazing pressure in a Norwegian alpine habitat. *Ecoscience* 13: 459-468.

II: Evju, M., Austrheim, G., Halvorsen, R. and Mysterud, A. 2008. Grazing responses in herbs in relation to herbivore selectivity and plant traits in an alpine ecosystem. Submitted to *Oecologia*.

III: Evju, M., Halvorsen, R., Rydgren, K., Austrheim, G. and Mysterud, A. 2008. Effects of sheep grazing and temporal variability on population dynamics of the clonal herb *Geranium sylvaticum* in an alpine habitat. Manuscript.

IV: Evju, M., Halvorsen, R., Rydgren, K., Austrheim, G. and Mysterud, A. 2008. Population dynamics of *Viola biflora*, a small, non-selected herb in a sheep grazing experiment. Manuscript.

INTRODUCTION

Herbivores regulate the structure of plant communities through selective foraging, trampling, urination and defecation (Pastor and Naiman, 1992, Jefferies et al., 1994, Hobbs, 1996, Augustine and McNaughton, 1998), resulting in alteration of resource availability, changing of the physical environment, and changing of inter- and intraspecific interactions. 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). Selectivity depends on the type and density of the herbivore as well as on plant community composition, i.e. on availability of forage (Augustine and McNaughton, 1998, Kausrud et al., 2006). At local scales, herbivore selectivity is determined by plant quality such as nutrient content and digestibility (Coley et al., 1985, Pérez-Harguindeguy et al., 2003) in combination with plant quantity (bite size; Crawley et al., 2004).

Tolerance and resistance denote two main strategies for plants to cope with herbivores, collected under the umbrella term defence, which is defined as "any trait that confer a fitness benefit to the plant in presence of herbivores" (cf. Strauss and Agrawal, 1999). Tolerant species are able to regrow and/or reproduce after a grazing event. They are characterised by having high relative growth rate, high photosynthetic rate, high branching/tillering rates, high leaf production, short leaf lifespan or low apical meristem (e.g. McIntyre et al., 1999, Strauss and Agrawal, 1999). Resistant species, on the other hand, avoid grazing through low digestibility, content of secondary compounds, morphological attributes such as thorns or spines, or through temporal or spatial unavailability (e.g. low stature; Coley et al., 1985, Seldal et al., 1994, Strauss and Agrawal, 1999). How herbivores change the relative abundance of selected and resistant species is, however, often difficult to predict, but has large impact on long-term ecosystem productivity, as selected species are more easily decomposed (Coley et al., 1985, Grime et al., 1996, Cornelissen et al., 1999), promoting positive feedback of nutrient cycling in the system (Frank and Groffman, 1998, Frank et al., 2000).

Studies of effects of grazing in alpine and arctic habitats are abundant. However, how herbivores affect vegetation has mainly been addressed using small-scale exclosure experiments (e.g. Moen and Oksanen, 1998, Olofsson, 2001, Grellmann, 2002), or by comparing areas with contrasting herbivore densities (e.g. Olofsson, 2006, Bråthen et al., 2007, Ims et al., 2007). The effect of different densities of herbivores on plants has rarely been examined experimentally on large spatial scales (Bullock et al., 2001). Using spatial contrasts of ‘highly grazed’ and ‘less grazed’ areas might, however, conceal non-linear responses of plant species to increasing grazing pressure (Westoby, 1999). The ability of plants to express tolerance or resistance, or the magnitude of defence offered by these strategies, are not constants, but will depend upon both herbivore selectivity (Augustine and McNaughton, 1998) and the frequency and intensity of grazing (del-Val and Crawley, 2005), factors that are all partly dependent upon herbivore density. Tolerance may be a viable strategy if grazing frequency and intensity are low enough to ensure that the plant has resources available for regrowth, and the opportunity for regrowth is also linked to environmental conditions such as soil nutrients and moisture (Hobbs, 1996). Furthermore, at high herbivore densities, high-quality forage may become scarce, and less-preferred resistant species may be grazed to such an extent that their abundance decline (Augustine and McNaughton, 1998). Consequently, the same species can respond both positively and negatively to increased grazing pressure (Stohlgren et al., 1999, Pakeman, 2004).

To evaluate the consequences of herbivores in terms of plant community composition and long-term ecosystem productivity, it is important to know what grazing pressure different herbivore densities correspond to, i.e. how frequent are the most palatable species grazed? Within an experimental design, control with herbivore densities provides an opportunity for assessing grazing pressure on the landscape scale.

Plant functional traits and grazing studies

In an effort to increase our understanding of mechanisms behind species’ responses to grazing, a plant functional traits approach has been adopted (Lavorel et al., 1997, McIntyre et al., 1999, Weiher et al., 1999, McIntyre and Lavorel, 2001). Plant functional traits can be defined as morphological, physiological or phenological traits which impact plant fitness indirectly via their effects on growth, reproduction and survival (Violle et al., 2007). Some studies have found that species that respond positively to increased grazing pressure are of low stature and have high specific leaf area (SLA; Díaz et al., 2001, Cingolani et al., 2005b), i.e. possessing strategies related both to resistance (avoidance through low stature) and tolerance (regrowth capacity, correlated with SLA). Mechanisms behind grazing response seem, however, to depend upon season of grazing. Bullock et al. (2001) found that under summer grazing, grazing response was positively related to gap colonising ability, whereas under winter and spring grazing, species which were selected by sheep increased in abundance. Furthermore, the relationship between grazing response and plant traits is also dependent on site productivity (Pakeman, 2004) and regional climatic conditions (Vesk and Westoby, 2001, Vesk et al., 2004, de Bello et al., 2005). Within a study system, however, plant traits can be useful for understanding responses to a given change in grazing regime, provided that the set of traits included in the analysis is large enough (Klimešová et al., 2008).

Few studies exist that evaluate the link between grazing response and plant traits in alpine systems (de Bello et al., 2005), and the link has rarely been examined by use of experimental designs with controlled densities of herbivores (see Bullock et al., 2001). I used *in situ* measurements of sheep selectivity and plant traits to investigate the mechanisms behind abundance change of common herbs in response to enhancement and cessation of grazing. In ecosystems in which low levels of grazing has been the prevailing regime for a long period of time, such as the alpine (Austrheim and Eriksson, 2001), both enhanced and reduced grazing pressure is expected to trigger abundance change of plants. However, the mechanisms behind abundance change are expected to differ. Cessation of grazing could be expected to benefit tall, large-leaved species that have high competitive ability. In contrast, species that increase in abundance in response to enhancement of grazing could be predicted to be either tolerant (i.e. with a high regrowth capacity) or resistant (e.g. low digestibility, low stature).

Grazing and plant population studies

Grazing can affect different stages of the life cycle of a plant species differently. Seedlings are expected to be more susceptible to grazing than adult plants (Crawley, 1997). Large individuals are, however, often selected over small by the herbivores (e.g. Ehrlén, 1995b, Knight, 2004). Grazing can reduce individual survival (Ehrlén, 1995b) or growth (Knight, 2004). Grazing can also reduce seed output in the population, through direct consumption of inflorescences (Hunt, 2001a, b, Lennartsson and Oostermeijer, 2001, Brys et al., 2004), or through a general size-reduction of the plants (Bastrenta, 1991, Ehrlén, 1995a, Knight, 2004).

Indirectly, however, large herbivores could positively affect individual plants, through increasing light availability by removal of tall neighbours, prevent accumulation of litter or creating vegetation gaps that facilitate germination and seedling establishment (e.g. Bullock et al., 1994, Lennartsson and Oostermeijer, 2001, Brys et al., 2004, Ehrlén et al., 2005). These individual effects manifest themselves at the population level through an effect on the population's vital rates, i.e. rates of survival, growth and recruitment. In order to assess grazing effects on a plant population, the whole life cycle therefore needs to be considered. The impact of grazing on a population will thereby depend on 1) which vital rates are affected, 2) how large are the changes in the vital rates and 3) how sensitive is the population growth rate to changes in these vital rates (Caswell, 2001, Knight, 2004).

A tall, herbivore selected species could be predicted to respond negatively to high levels of grazing and be favoured by cessation of grazing. In contrast, a low stature species that avoids grazing by large herbivores could be expected to be favoured by high levels of grazing but respond negatively to cessation of grazing as increased growth of tall neighbours would lead to reduced light availability.

I investigated these predictions by collecting demographic data over six years for two common herbs, a tall, grazed perennial (*Geranium sylvaticum*) and a low stature, non-selected perennial (*Viola biflora*). Using data on fates of individual plants, population-level consequences of different densities of sheep were evaluated and compared among species.

The alpine ecosystem as a study system

Alpine vegetation is characterised by the absence of trees and by dominance of plants of generally low stature (Billings, 1973, Körner, 1995), which represent few types of growth forms: low stature or prostrate shrubs, graminoids and perennial herbs (Billings and Mooney, 1968). Of these, herbs contribute the least to biomass, but the most to species richness (Körner, 1995). Due to a large variety of microhabitats, caused mainly by variation in depth and duration of snow cover, the structural and functional diversity among alpine plants is considered to be high (Körner, 2003, Austrheim et al., 2005, Choler, 2005). The majority of alpine plants are long-lived and possess means for clonal reproduction (Billings and Mooney, 1968, Billings, 1974). For some species life spans up to 300 years have been estimated (Morris and Doak, 1998, Forbis and Doak, 2004). Sexual reproduction is generally assumed to be of less importance, both because it is predicted that clonal species allocate less resources to sexual reproduction (Eriksson, 1989, Callaghan et al., 1992), and because of low temperatures that could limit pollination (Totland, 1997) and seed maturation (Stephensen, 1981). Several studies show, however, that seedlings are indeed abundant in alpine vegetation (e.g. Chambers, 1995, Welling and

Laine, 2000, 2002, Welling et al., 2004) and that establishment rates of seedlings are as high as in temperate regions (Forbis, 2003).

The main large herbivores in alpine ecosystems in Scandinavia are reindeer and sheep. Alpine areas in Norway have been used as livestock pastures for approximately 5000 years (Kvamme, 1988, Moe et al., 1988). Currently, more than 2 million sheep are released to unamended pastures each summer in Norway (Drabløs, 1997), and sheep is by far the most important livestock species in alpine areas in south Norway (Austrheim et al., 2008a). Sheep are highly selective herbivores, in general preferring herbs (Bowns and Bagley, 1986) over graminoids and shrubs (Nedkvitne et al., 1995). Small mammalian herbivores (rodents) are also abundant in alpine systems, and can strongly impact vegetation during population peaks (e.g. Andersson and Jonasson, 1986, Olofsson et al., 2004).

The sustainability of the current levels of sheep grazing in Norwegian alpine areas has been heavily debated (e.g. Högstedt and Seldal, 1998, Seldal and Högstedt, 2002, Seldal et al., 2003), but empirical evidence of the impact of sheep grazing is scarce (Mysterud and Mysterud, 1999). In 2001, a sheep grazing experiment was initiated in an alpine habitat in south Norway with the objective of finding methods to establish whether the sheep grazing regime in a given area is sustainable or not, through exploring the consequences of different sheep densities on vegetation (Austrheim et al., 2008b), small (Steen et al., 2005) and large (Mysterud and Austrheim, 2008) vertebrate herbivores, invertebrates (Mysterud et al., 2005), birds (Loe et al., 2007) and habitat use and selectivity of the sheep (Kausrud et al., 2006, Mysterud et al., 2007, Mobæk et al., 2008). In 2002, funding was ensured for a side project (three year PhD-funding to M. Evju, NFR project 153601/V40) to further investigate sheep grazing effects on plants.

Objectives

The main aim of this thesis is to provide new insight into sheep grazing effects on plants in an alpine habitat, with a focus on herb species. In the framework of a landscape-scale experiment, the impact of three levels of sheep densities (high, low and zero), and more specifically, the impact of changing grazing regime (enhancement and cessation of grazing) on the dynamics of plant populations and communities is studied. The following questions are addressed:

- What grazing pressure do different levels of sheep densities exert on the vegetation, and can easily recordable variables such as plant height, flowering frequency and grazing frequency be used to monitor grazing pressure (Paper I)?
- Can plant traits be used to provide a mechanistic explanation of plant community dynamics in response to enhanced and reduced grazing pressure (Paper II)?
- How do different levels of sheep densities affect rates of growth, survival and reproduction, and thereby population dynamics, in a tall, competitive, grazed herb and in a low stature, non-selected herb (Papers III and IV)?

STUDY AREA

The study was carried out in a landscape-scale experiment of ecological effects of sheep grazing in an alpine ecosystem, located in Hol municipality, Buskerud county, south Norway (60° 40’−60° 45’ N, 7° 55’−8° 00’ E). In 2001, 17.3 km of standard sheep fencing (110 cm high) was set up, constituting an enclosure covering 2.7 km^2 in the low alpine and partly the middle alpine zone (1050−1300 m a.s.l.). The enclosure was divided into nine parallel sub-enclosures, each running from low to high altitude and covering ca. 0.3 km^2 (Fig. 1). A block-wise randomised design was applied to assign three replicates of three sheep densities; no sheep, low sheep density and high sheep density. The vegetation was mapped in 2001 by a professional grazing ecologist, who also assessed the value for sheep grazing (Rekdal, 2001). As the objective of the experiment was to investigate effects of current levels of sheep grazing in Norwegian alpine habitats, sheep densities were chosen to represent the range commonly occurring in mountain pastures in Norway. High sheep density was set to 80 sheep per km^2 of grazeable land (excluding water bodies, bogs and some other habitats dominated by moss, lichens and rocks) and low sheep density to 25 sheep per km^2. These densities are characterised by sheep owners as “high, but acceptable” and “intermediate/low”, respectively. Sheep are of the “Kvit norsk sau” breed, the most common breed in Norway (Drabløs, 1997). Ewes averaged 83 kg in spring, and lambs averaged 19 kg in spring and 42 kg in autumn (A. Mysterud, unpublished data). The first experimental grazing season was 2002. The grazing season lasted from the last week of June to the last week of August/first week of September all years, similar to the grazing season for free ranging sheep in mountain pastures in south Norway.

The vegetation in the study area was dominated by low shrubs (*Betula nana*, *Vaccinium* spp., *Empetrum nigrum*, *Salix* spp.) in a mosaic with grass-dominated meadows. Some scattered birches appeared in the low-lying areas, but the study area was located above the forest line. The bedrock consisted of meta-arkose (Sigmond, 1998), and the soil was moderately base-rich, especially in landscape depressions with seepage water (Austrheim et al., 2005). The study area was representative of relatively productive Norwegian alpine areas, with total standing crop in dwarf shrub and grassland communities averaging 332 and 160 g/m^2, respectively [G. Austrheim, unpublished data, note that values which have been previously published are underestimates (Mysterud and Austrheim, 2005, Kausrud et al., 2006, Mysterud and Austrheim, 2008)]. Climate data interpolated from weather stations surrounding the study area [kindly provided by the

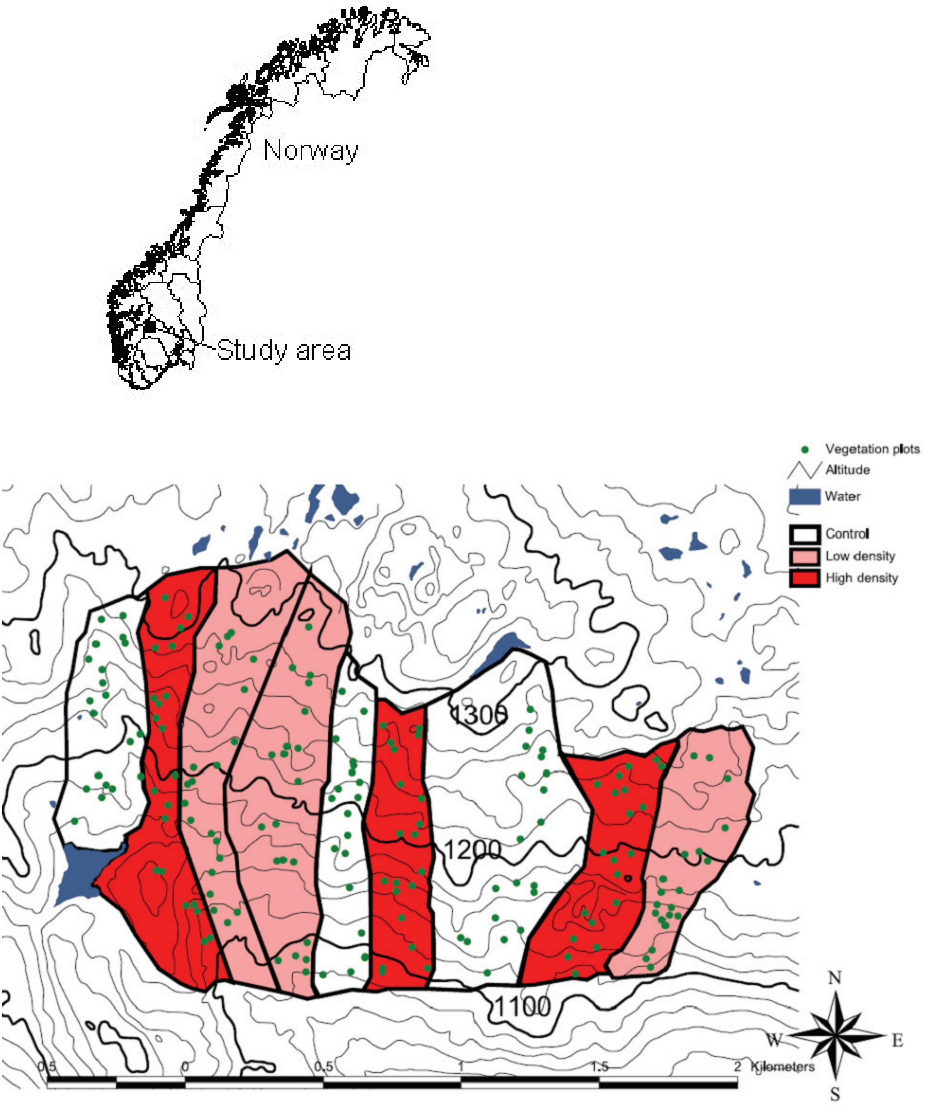

Figure 1. The experimental design, with three replicates of the treatments no sheep (control), low sheep density and high sheep density. Twenty permanent plots (0.5 × 0.5 m^2), in which plant abundance was measured, were located within each sub-enclosure.

Norwegian Meteorological Institute, see Tveito et al. (2005) for methods] gave an estimated mean annual temperature of −1.5 °C, with January temperature –10.8 °C and July temperature 8.9 °C (normal period 1961–90; interpolated data). The mean annual precipitation (normal period 1961–90; Førland 1993) was estimated (M. Evju, unpublished data) to be about 1000 mm (on the basis of interpolated data and one-year data from a weather station set up in the study area in 2007), but the estimate was uncertain because precipitation varies much over small distances in alpine areas.

Prior to the establishment of the grazing experiment, sheep densities were estimated to < 10 sheep per km^2 (A. Mysterud, pers. comm.). The area had been occasionally visited by individuals or small herds of reindeer (*Rangifer tarandus*) in spring, and moose (*Alces alces*) could enter the area while foraging at night (personal observation). As grazing in Norwegian alpine areas dates back to the Bronze Age (Kvamme, 1988, Austrheim and Eriksson, 2001), the experimental design was interpreted to represent two contrasting alterations of grazing regime; enhancement of grazing (the high sheep density treatment) and cessation of grazing (the no sheep grazing treatment), whereas the low sheep density treatment was considered to represent a continuation of previous grazing regime. This was supported by the finding of the smallest changes in plant community and single species in the low sheep density treatment after the establishment of the experiment (Austrheim et al., 2008b).

MATERIALS AND METHODS

In 2001, 180 plots measuring 0.5 × 0.5 m^2 were established, 20 per sub-enclosure, in a random, stratified manner that ensured equal sampling among altitudinal levels and habitat types (see Austrheim et al., 2005, 2008b for details; Fig. 1). The abundance of all vascular plants was recorded as presence/absence in 16 sub-plots (each 0.0156 m^2) per plot. A total of 104 vascular plant species was recorded in 2001. Vegetation plots were re-analysed every second year (2003-2005-2007).

All studies in this thesis focused on herbs. In 2001, 55 different species of herbs were recorded (i.e. 53% of all recorded species; Austrheim et al., 2005). In order to study grazing frequency and variations in flowering frequency and plant height among sheep grazing treatments (Paper I), 17 of the most common herbs were included, all being perennial and determined to the species level. Although I initially defined "common" as being present in at least 10% of the permanent plots in 2001, I still included two less abundant species that were considered to be important constituents of sheep diet (*Leontodon autumnalis* and *Potentilla erecta*; Table 1). One species (*Veronica alpina*) was excluded due to problems of identification of small plants in the field.

When studying plant responses to enhancement and cessation of grazing in relation to plant traits (Paper II), I expanded the dataset to include also two annuals (*Euphrasia wettsteinii* and *Melampyrum sylvaticum*), two species determined at the genus level (*Alchemilla* sp. and *Taraxacum* sp.), and *V. alpina*, thus my dataset consisted of 22 herb species (Table 1). Intentions early in the study period were to include data on all abundant vascular plants in these analyses. Plant traits were collected also for graminoids (8 species) and dwarf shrubs (5 species). However, trait variation was predominantly structured by growth form (Fig. 2). I found in preliminary analyses that results of plant responses to cessation and enhancement of grazing mainly were structured by herb responses, partly because there was little variation in responses within the group of dwarf shrubs, and little variation in plant traits within the group of graminoids. As I had too small sample sizes of these groups to perform separate analyses, I

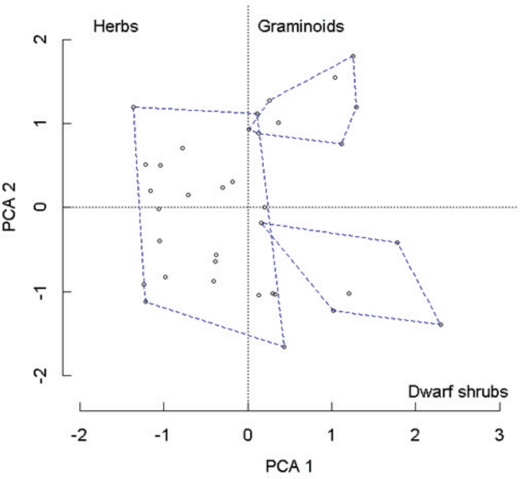

Figure 2. Results of a principal component analysis (PCA) of a species-traits matrix containing data on 28 plant traits for 35 species. Plant species are thus distributed among the axes based on similarities in traits. The three main growth form groups are marked.

chose to exclude the data and concentrate on understanding patterns of responses among herbs.

For the plant population dynamics studies, I focused on two herb species that I predicted would respond oppositely to the different levels of sheep densities; one tall, perennial species, supposedly herbivore selected, with means for clonal reproduction (*Geranium sylvaticum*; Paper III) and one low stature, non-selected perennial (*Viola biflora*; Paper IV; Table 1).

Table 1. Species included in the different parts of the study. Frequency refers to the proportion of permanent plots (*n* = 180) in which the species was present in 2001.

Species	**Frequency (%)**	**Paper I**	**Paper II**	**Papers III and IV**
Alchemilla alpina	16.1	X	X	
Alchemilla sp.	4.4		X	
Bistorta vivipara	30.6	X	X	
Euphrasia wettsteinii	11.7		X	
Geranium sylvaticum	26.1	X	X	X
Hieracium alpinum	25.0	X	X	
Leontodon autumnalis	7.2	X	X	
Melampyrum sylvaticum	12.2		X	
Omalotheca norvegica	18.3	X	X	
Omalotheca supina	11.1	X	X	
Potentilla erecta	8.9	X	X	
Pyrola minor	13.9	X	X	
Ranunculus acris	17.8	X	X	
Rumex acetosa	35.0	X	X	
Saussurea alpina	12.8	X	X	
Sibbaldia procumbens	13.9	X	X	
Solidago virgaurea	22.8	X	X	
Taraxacum sp.	12.2		X	
Trientalis europaea	47.8	X	X	
Veronica alpina	10.6		X	
Viola biflora	26.7	X	X	X
Viola palustris	11.1	X	X	

Field methods and statistical analyses

In order to monitor grazing pressure, plant height, presence/absence of reproductive structures (buds, flowers and/or fruits) and grazing status (grazed/ungrazed) was recorded in 2003 and 2004 for the 17 species included in Paper I. A minimum of 10 individual ramets in each of three randomly chosen plots per sub-enclosure was intended to be sampled. We calculated average values of plant height, flowering frequency and grazing frequency for each species each year, and estimated bootstrap standard errors. Model-based inference (Johnson and Omland, 2004) was used to evaluate the effect of sheep grazing treatment and other environmental covariates (vegetation type, altitude, exposure and slope) or soil variables on the focal traits. We measured total grazing pressure (extent of utilisation of the most important forage plants; Holechek et al., 1999) for high and low sheep densities using different subsets of the species, based on a sheep selectivity rank (data from Kausrud et al., 2006), and compared estimates of grazing pressure among treatments and years.

Species-specific plant traits (see Paper II: Table 2) were collected in the field for the 22 species included in August 2004. Ten individuals of each species were collected, using a protocol that ensured unbiased sampling of individuals, and the average trait value calculated. I used the handbook of Cornelissen et al. (2003) to assure that traits were measured in a standardised way. Fifteen plant traits, covering morphology, physiology and phenology, were included, all measured on a continuous scale.

For each species, three indices were calculated: a selectivity index (*SI*), a response to enhanced grazing pressure (*GR*) and a response to cessation of grazing (*CR*). To calculate *SI*, I used observational data of sheep foraging in the study area (Kausrud et al., 2006). *GR* was calculated as the relative abundance change of a species in the high sheep density treatment compared to the low sheep density treatment from 2001 to 2007, and *CR* correspondingly as the relative abundance change in the no sheep vs. the low sheep density. A negative *GR* would thereby imply that the species declined more in abundance in the high than in the low sheep density treatment, and *vice versa*. Linear regression with forward selection of variables was used in order to establish relationships between *SI*, *GR* and *CR* and plant traits.

The population dynamics studies were based upon annual demographic censuses in the permanent plots from 2002 through 2007 of *Geranium sylvaticum* and *Viola biflora* (Fig. 3). At the first census, all individuals of the two species were mapped and tagged, and at all later censuses, plants were relocated and new plants were recorded. I measured at each census several morphological variables that were related with plant size, and counted the number of flowers and/or capsules. Non-overlapping life stage classes were defined for both species, based on analyses of size-dependency of mortality and fecundity. Grazing marks on the individuals were noted at each census. For *V. biflora*, I noted whether the grazing was carried out by invertebrate or invertebrate herbivores. I could not distinguish grazing marks by sheep and rodents in the populations in which sheep was present.

Figure 3. Vegetation plots for annual census of *Geranium sylvaticum* and *Viola biflora*.

Transition matrix modelling is treated in detail in Caswell (2001). Most recent publications refer to this book in their methodology chapter, including my Papers III and IV. A description of methods is included here, however, in order to prepare readers that are unfamiliar with these methods for the results.

The life cycle graph of a species describes all the transitions an individual plant can make during a given time step (the projection interval). Stage based transition probability matrices link individual plant fate from year t to year $t + 1$. The probability matrices are on the form $n(t + 1) = \mathbf{A}n(t)$ where $n(t + 1)$ and $n(t)$ are vectors giving the number of individuals in each stage i at time t and $t + 1$, and $\mathbf{A}$ is the transition matrix where each matrix element a_{ij} represents the transition probability or contribution of an individual in stage j at time t to stage i at time $t + 1$. The dominant eigenvalue of the matrix is the projected population growth rate (λ). Sensitivity analyses measure how sensitive λ is to an absolute change in matrix element a_{ij} ($s_{ij} = \delta\lambda/\delta a_{ij}$). The elasticity of λ to a change in a matrix element a_{ij} is calculated as $e_{ij} = \delta\lambda/\delta a_{ij} \times a_{ij}/\lambda$. It quantifies the proportional change in λ resulting from a proportional change in a_{ij}, thereby measuring the relative importance of transitions in the life cycle to the population growth rate (de Kroon et al., 1986).

Life-table response experiment (LTRE) analyses represent another approach to investigating the importance of transitions in the life cycle to observed differences between populations. LTRE allows quantification of the contribution of different matrix elements to the difference in λ between two or more transition matrices (Caswell, 2001). Using sheep grazing treatment and year as fixed effects, a two-way model for population growth in treatment m and year n is written as:

$$\lambda^{(mn)} = \lambda^{(\cdot\cdot)} + \alpha_m + \beta_n + (\alpha\beta)_{mn}$$

where $\lambda^{(\cdot\cdot)}$ is the growth rate calculated from $\mathbf{A}^{(\cdot\cdot)}$, the grand mean of all the matrices, and α_m, β_n and $(\alpha\beta)_{mn}$ are the treatment, year and interaction effects, respectively. These effects are calculated as:

$$\alpha_m = \lambda^{(m\cdot)} - \lambda^{(\cdot\cdot)}$$

$$\beta_n = \lambda^{(\cdot n)} - \lambda^{(\cdot\cdot)}$$

$$(\alpha\beta)_{mn} = \lambda^{(mn)} - \alpha_m - \beta_n - \lambda^{(\cdot\cdot)}$$

where the growth rates $\lambda^{(m\cdot)}$and $\lambda^{(\cdot n)}$ are calculated from the mean over years of the matrices for treatment m and from the mean over treatments for year n, respectively. Decomposing these effects into contributions from vital rates we get:

$$\alpha_m \approx \sum_{ij}(a_{ij}^{(m\cdot)} - a_{ij}^{(\cdot\cdot)})s_{ij}|_{1/2(\mathbf{A}^{(m\cdot)} + \mathbf{A}^{(\cdot\cdot)})}$$

$$\beta_n \approx \sum_{ij}(a_{ij}^{(\cdot n)} - a_{ij}^{(\cdot\cdot)})s_{ij}|_{1/2(\mathbf{A}^{(\cdot n)} + \mathbf{A}^{(\cdot\cdot)})}$$

$$(\alpha\beta)_{mn} \approx \sum_{ij}(a_{ij}^{(mn)} - a_{ij}^{(\cdot\cdot)})s_{ij}|_{1/2(\mathbf{A}^{(mn)} + \mathbf{A}^{(\cdot\cdot)})} - \alpha_m - \beta_n$$

Calculating main effects is thus done by multiplying differences between each matrix element and the corresponding matrix element of the overall mean matrix with the sensitivity values of the matrix halfway between the matrix of interest and the overall mean matrix. In other words, both the change in transition probability and the sensitivity of λ to such a change are included. With the interaction term we get a quantification of the difference between the actual contribution of a_{ij} to $\lambda^{(mn)}$ and the difference predicted on the basis of an additive model (Caswell, 2001), and thus small interaction terms indicate that the main factors influenced λ independently.

To investigate causes behind observed variations in λ, local climatic variables (Papers III and IV) and biotic variables such as rodent density and proportion of populations grazed by invertebrate and vertebrate herbivores, were used (Paper IV).

RESULTS

Monitoring of grazing pressure – Paper I

Differences between years contributed more to variations in plant height than sheep grazing treatment for 12 of the 17 herbs, the plants being lower in 2004 than in 2003. For *Solidago virgaurea* and *Omalotheca norvegica*, however, the between-year variation in plant height was smaller in the high sheep density treatment (Paper I: Fig. 1). Flowering frequency was related to sheep grazing in only three species, *O. norvegica*, *Ranunculus acris* and *Leontodon autumnalis*. Treatment-by-year interactions (*L. autumnalis*) and variations in flowering frequency with habitat type (*O. norvegica*) did, however, complicate the usefulness of this variable for monitoring. For *R. acris*, flowering frequency was reduced even at low density, implying that recording of flowering would only be useful for separating grazed vs. ungrazed areas. Grazing frequency on *Pyrola minor*, *Rumex acetosa* and *Saussurea alpina* increased markedly as the density of sheep increased from low to high. The estimate of total grazing pressure depended on the number of species included in the estimate. It was lower in 2004 than in 2003, but it was always higher in the high sheep density treatment (Paper I: Fig. 2).

Plant traits and grazing response – Paper II

Sheep selectivity was linked to the plant traits aboveground biomass, C/N ratio in leaves and first flowering day, reflecting a preference for large herbs of high digestibility (C/N content negatively related to digestibility) in a phenologically young stage. Selected species did not respond negatively to enhancement of grazing pressure. Responses to enhanced grazing pressure (*GR*) were relatively modest; four species more than doubled their abundance and two species had their abundances reduced to less than one half (Paper II: Table 1). A combination of resistance and tolerance was found to be the best predictor of *GR* (Paper II: Fig. 2); low stature species were favoured by increased grazing pressure (avoidance), in combination with capacity for regrowth (root/shoot ratio). Responses to cessation of grazing (*CR*) were generally smaller than responses to enhanced grazing. *CR* was not related to selectivity *per se*, but to several traits that were linked to selectivity (early flowering species with low C/N content in leaves responded positively), indicating that release from sheep grazing had a positive effect on selected plants.

Plant population dynamics and sheep grazing – Papers III and IV

Geranium sylvaticum **(Paper III)**

Grazing frequencies on *Geranium sylvaticum* were relatively moderate; between 6−14% and 2−6% of the population exposed to high and low sheep densities, respectively, was grazed each year. Grazed *G. sylvaticum* plants showed higher clonal reproduction rates than ungrazed plants (Paper III: Fig. 4), but also reduced growth compared to ungrazed plants (Paper III. Fig. 5). Overall, there were no clear effects of sheep grazing treatment on population growth rate (λ). There was a small negative effect of high sheep density on λ in the LTRE analysis (Paper III: Fig. 8A), brought about mainly by negative contributions from growth (i.e. survival to a larger life stage class) and stasis (survival in the same life stage class). Increased clonal reproduction as well as retrogression (survival to a smaller life stage class) almost compensated for this. There was no positive effect of excluding sheep on λ, and both clonal reproduction and growth contributed negatively to the effect of the no sheep treatment on λ, i.e. rates of growth were lower than average in this population (Paper III: Fig. 8A). Transition probabilities of stasis were, however, largest in the population in the no sheep treatment.

Between-year variations in λ were large (Fig. 4A). Growing populations were characterised by high elasticities for fecundity and growth, and partly by low elasticities for retrogression. The best environmental predictor of among-year variation in λ was mean July temperature in the previous year (t – 1). Floral differentiation in *G. sylvaticum* takes place the autumn before outgrowth (Salomonson et al., 1994). As there was a strong functional link between λ and fecundity and growth, a favourable summer in t – 1 was likely to provide plants with more resources for growth and reproduction.

Viola biflora (Paper IV)

Although not selected by sheep, populations of *Viola bilora* exposed to both high sheep density, low sheep density and no sheep were indeed grazed (Paper IV; Fig. 4). Vertebrate grazing (sheep and rodents) was highest in the population in the high sheep density treatment. Two incidents of high grazing frequency in the population protected from sheep showed, however, that effects of rodent grazing could be substantial (Paper IV: Fig. 4A). Invertebrate grazing was more frequent in the population in the no sheep treatment, affecting almost 20% of the plants in some years (Paper IV: Fig. 4B).

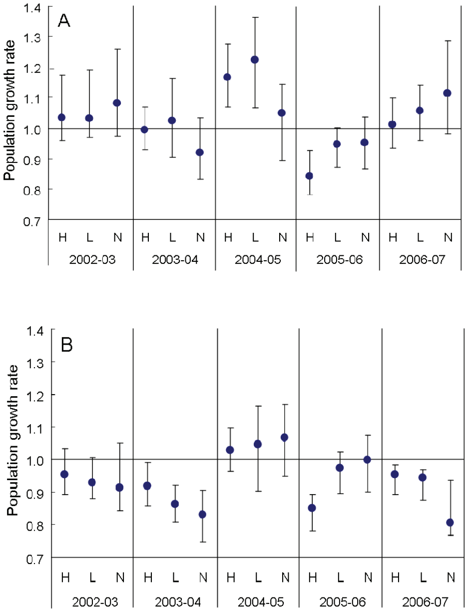

Figure 4. Projected population growth rates of *Geranium sylvaticum* (A) and *Viola biflora* (B) in the high sheep density (H), low sheep density (L) and no sheep (N) treatments from 2002−07. The error bars are 95% CI bootstrap intervals.

λ was generally lower for *V. biflora* than for *G. sylvaticum*, but the pattern of variation between years was remarkably similar (Fig. 4). Growing *V. biflora* populations were characterised by high elasticities for growth and low elasticities for retrogression and dormancy. LTRE analyses also demonstrated that growth contributed positively and retrogression negatively in years with λ above average.

Total LTRE treatment effects on λ were small. Nevertheless, growth was much lower and stasis was higher in the population in the no sheep treatment as compared to the populations with sheep (Paper IV: Fig. 6A). Furthermore, the treatment-by-year interaction effect in the LTRE analysis was negatively correlated with the proportion of the population that was grazed by sheep and rodents in $t + 1$, i.e. λ was lower than expected in the populations in years with high vertebrate grazing frequency.

GENERAL DISCUSSION AND CONCLUSION

Grazing effects

Large herbivores can change the state of ecosystems to lasting levels of higher (van der Wal, 2006) or lower (e.g. Bråthen et al., 2007) productivity. Direct grazing affects plant species differently; some are selected and other avoided by the herbivores. As there is a link between palatability and decomposability (Grime et al., 1996), how herbivore change the relative abundance of selected and avoided species will determine whether herbivores have promoting or retarding effects on nutrient cycling.

After six years of experimental grazing, net effects of sheep grazing were found to be moderate. No consistent decrease in abundance was found for the selected herbs under enhancement of grazing, suggesting that there is a link between selectivity and plant tolerance (Bullock et al., 2001), or that grazing pressure was too low to suppress growth of these species at the given time scales. For herbs, resistance through low stature, not low digestibility, was found as the main mechanism behind a positive response to enhanced grazing pressure. Combined with the modest changes in abundance found for other functional groups (shrubs and graminoids; Austrheim et al., 2008b), this indicates that the current levels of sheep density do not have a negative effect on ecosystem productivity.

Life history buffering of grazing effects

Grazing also affects stages in the life cycle of a given species differently; grazing can at the same time reduce the growth of large plants and increase recruitment from seeds (Lennartsson and Oostermeijer, 2001). Grazing probability on *Geranium sylvaticum* increased slightly with plant size (Paper III), and grazed plants showed reduced growth compared to ungrazed plants. Sheep did not graze on seedlings, and seedling survival was highest when sheep were stocked at low densities.

There was no effect of sheep grazing treatment on population growth rate (λ) of neither *G. sylvaticum* nor *Viola biflora*, contrary to our prediction of opposite effects of high sheep density and no sheep on these two species. However, identification of demographic processes and life history stages that are affected by given environmental factors, such as grazing, opens for the construction of predictions of long-term population trends (Carlsson and Callaghan, 1994). In the high sheep density treatment, clonal reproduction contributed to buffer negative effects on λ of high sheep density that arose due to reduced rates of growth and stasis. In *V. biflora*, the positive contribution from growth in the populations exposed to sheep suggests that sheep grazing did have the predicted positive effect of increasing light availability for this low stature species (see also Bullock et al., 1994). However, this effect was not manifested as higher λ.

In both *G. sylvaticum* and *V. biflora* there was a negative contribution from growth on λ in the populations protected from sheep. The predicted positive effect of excluding sheep on a tall, competitive herb was therefore not found. However, *G. sylvaticum* is tall and competitive only in parts of its life cycle (the largest stage classes), and growth is positively related to light conditions (Salomonson et al., 1994). It thus seems probable that shading affected both species in the no sheep treatment.

Geranium sylvaticum and *V. biflora* are both long-lived species, which could contribute to lack of effects of the sheep grazing treatments. Average conditional lifespan of the largest life stage class was 11 years for *G. sylvaticum* and 8 years for *V. biflora*. Conditional lifespan denotes the average time to death for an individual that survive to the given life cycle stage (cf. Ehrlén and Lehtilä, 2002), so total lifespan is considerably longer. Long lifespan of individual plants, as well as life history traits such as clonal reproduction, tend to increase population persistence (Eriksson, 1996, Eriksson and Jakobsson, 1998). Long-lived species show generally more stable population dynamics than short-lived (García et al., 2008), having lower dependency of λ on fecundity and showing lower temporal variability in fecundity than short-lived species. Negative effects of sub-optimal environmental conditions could thus be expected to be delayed (Morris et al., 2008).

Temporal variability

The short growing season in alpine areas make vegetation development strongly dependent on weather conditions, which influence both abundance and quality of forage plants (Lenart et al., 2002). Grazing pressure is therefore likely to vary between years, even if herbivore densities are kept constant (Jefferies et al., 1994). Grazing pressure on the most common herbs was indeed different between 2003 and 2004, and between-year variation in plant height was substantial.

Temporal variability was much more important than sheep grazing treatment for population dynamics of both *G. sylvaticum* and *V. biflora*, explaining about 60% of variation in λ for both species. Abiotic factors such as summer temperature and precipitation has been found to contribute strongly to seasonal fluctuations in growth of plants in alpine and arctic habitats (Callaghan et al., 1989, Callaghan et al., 1997). For both *G. sylvaticum* and *V. biflora*, the highest λ coincided with the lowest July temperatures during the study period (2004), which seems contra intuitive for alpine plants. However, responses of vascular plants to changes in weather conditions include a high noise-to-signal ratio (Semenov, 1995). Furthermore, it is the combined effect of all abiotic and biotic factors that affects birth and death rates in a population (Jonzén et al., 2002), thus trying to single out the one main determinant behind variations in population growth may be a search in vain (e.g. Ranta et al., 2000, Ranta et al., 2007). In alpine plants, preformation of flowers is common (Körner, 2003). Flowers are formed the autumn before outgrowth in *G. sylvaticum* (Salomonson et al., 1994), this is probably also the case for *V. biflora*. Consequently, a complex of current and historical factors are likely to contribute to observed demographic processes (e.g. Geber et al., 1997) and no causal relationship is necessarily involved in the link between low summer temperature and high population growth rates.

The importance of scale for grazing pressure

The current study documented low to moderate grazing pressure resulting from low (25 sheep per km^2 and high (80 sheep per km^2) sheep densities in a productive alpine habitat. A low grazing pressure, as defined by grazing ecologists, allows palatable species to increase their biomass, whereas a moderate grazing pressure allows palatable species to maintain, but not increase, their biomass (cf. Holechek et al., 1999). In alpine ecosystems with lower productivity, however, comparable, or even lower, densities of sheep will be expected to have stronger impacts on vegetation (e.g. Austrheim et al., 2007).

The study was carried out within a landscape-scale experiment, each sheep grazing treatment covering on average 0.9 km^2 (see *Study area*), thus allowing sheep to select among different habitat types for foraging. Non-random habitat use by sheep, with a strong selection for high productive habitats (Mobæk et al., 2008) implies that grazing pressure at the landscape scale is heterogeneous (Olofsson et al., 2008).

This is evident from recording of grazing pressure vs. recording of sheep selectivity: The sheep selectivity index used in Paper II was based on observational studies of sheep foraging. In sites in which the sheep were grazing, grazing marks on plants were recorded (Kausrud et al., 2006). In his study, K. Kausrud found that *G. sylvaticum* was grazed in 43% of the sites in which it was present. On the other hand, I recorded grazing on *G. sylvaticum* in all permanent vegetation plots. These plots were distributed to be representative of the variation in habitat types and altitudes in the study area (see *Study area*). I found maximum grazing frequency on the population in the high sheep density treatment to be 14% (Paper III). *Geranium sylvaticum* thereby persisted in many patches that the sheep did not use. Consequently, reported effects of grazing on small spatial scales are often larger than those on large spatial scales (Jefferies et al., 1994, Olff and Ritchie, 1998, Stohlgren et al., 1999) although examples of large-scale effects do exist (Bråthen et al., 2007).

Short- vs. long-term grazing effects

This thesis reports effects of grazing on short- to intermediate-term scales. Transplant experiments in a tundra heath have shown that short- and long-term effects of enhanced grazing pressure were largely similar (Olofsson, 2006), due to a rapid response of graminoids when grazing pressure increased. This may imply that the small effects observed in this study to enhancement of grazing may last over longer time scales. However, for *G. sylvaticum* plants, reduced growth of grazed plants resulted in high rates of retrogression. With time this may lead to a shift in stage distribution towards smaller plants, which on the long-term could be predicted reduce λ, as survival, fecundity and clonal reproduction rates all increase with size (e.g. Ehrlén, 1995a, Knight, 2004). This will, however, depend on future grazing pressure, i.e. how large proportion of the population is grazed. If sheep utilisation of habitats of lower quality increase over time at high densities, of which a weak tendency has been found (Mobæk et al., 2008), grazing pressure on selected herbs could be expected to increase at the landscape scale. Bullock et al. (2001) found that effects of grazing were indeed different after 4 and 12 years after establishment of the experiment, both in terms of appearance of new effects and strengthening of effects that were already present after 4 years.

Short-term effects of cessation of grazing have, however, been found be poor indicators of long-term effects in terms of plant species richness and biomass (Olofsson, 2006), and Eskelinen (2008) found that exclusion of herbivores did not reinforce competition in an alpine habitat on a short-term scale. Reduced rates of growth of *V. biflora* in the no sheep treatment compared to the populations exposed to sheep suggest, however, that such effects may be intensified at longer time-scales.

Long-term effects of the sheep grazing treatments on plants will also depend on the effects of treatments on other components of the ecosystem. Grazing by invertebrate herbivores on *V. biflora* was consistently highest in the population protected from sheep, suggesting a negative effect of sheep on invertebrates. On a short-term scale this was only found for two herbivore beetle species (Mysterud and Austrheim, 2005, Mysterud et al., 2005).

The impact of rodents on plants may be large on small spatial scales in alpine habitats (e.g. Olofsson et al., 2004). Rodent grazing on *V. biflora* was indeed substantial in two years (see also Moen and Oksanen, 1998), and high levels of grazing did have the potential for suppressing population growth rate of *V. biflora*. On the other hand, rodent winter grazing in snowbeds may indirectly benefit small dicotyledon species such as *V. biflora* through a reduction in the cover of bryophytes (Virtanen, 2000, Ims et al., 2007). Future population dynamics of rodents could thus have strong impacts on *V. biflora* (Rydgren et al., 2007), and the effect of sheep on long-term population dynamics should be evaluated. On a short term, sheep affected rodent populations negatively in the high sheep density treatment, but not in the low sheep density treatment (Steen et al., 2005). Positive associations between reindeer and rodents were found on large spatial scales in Finnmark, Norway (Ims et al., 2007), suggesting facilitation between large and small herbivores.

Furthermore, ongoing studies aim to explore the relative importance of sheep grazing and altitude on C/N ratios of soil and plants in the study area. Preliminary results indicate that C/N ratios in two herb species are lower in the high sheep density compared with the no sheep treatment, but with no consistent pattern in C/N ratios of the soil O-horizon (Martinsen et al., 2008, V. Martinsen, pers. comm.). Further studies of biogeochemical processes related to sheep grazing will contribute to our understanding of long-term ecosystem effects of sheep grazing.

Conclusion

The ecosystem’s evolutionary history of grazing and productivity are the main predictors of vegetation response to grazing (Milchunas et al., 1988, Proulx and Mazumder, 1998, Cingolani et al., 2005a). Considering the long-term perspective of grazing in Scandinavian alpine ecosystems, the regional species pool is likely to include mainly species that are adapted to cope with a certain level of grazing (Austrheim and Eriksson, 2001). Furthermore, the majority of plant species in are long-lived. This, combined with the moderate grazing pressures that the present densities of sheep exert, can explain the relatively modest impacts of sheep on plants in this study.

Our results suggest that the current levels of sheep densities not substantially changed plant community or population dynamics, at least on the time-scale included here. Between-year variation in weather patterns was important both for vegetation development (plant height) and biomass removal by sheep (grazing pressure), and between-year variation in population growth rate of two herbs was much larger than variation related to sheep grazing. The similar pattern of variation in *Geranium sylvaticum* and *Viola biflora* was unexpected, given that one is tall and grazed and the other is small and not grazed, and thus they were predicted to respond in different directions to changes in grazing regime. This strongly indicates the existence of external factors controlling the between-year variation in vegetation that does not discriminate between species with different life history strategies. Furthermore, effects of sheep on other herbivores in the ecosystem (rodents, invertebrates) may contribute to the lack of consistent results.

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Selecting herb species and traits as indicators of sheep grazing pressure in a Norwegian alpine habitat[1]

Marianne EVJU, Department of Botany, Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway.
Atle MYSTERUD[2], Centre for Ecological and Evolutionary Synthesis, Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway, e-mail: atle.mysterud@bio.uio.no
Gunnar AUSTRHEIM, Museum of Natural History and Archeology, Section of Natural History, Norwegian University of Science and Technology, N-7491 Trondheim, Norway.
Rune H. ØKLAND, Department of Botany, Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway.

Abstract: A common management aim is to keep large herbivore densities at sustainable levels. However, measuring grazing pressure is difficult. We seek combinations of herb species and morphological traits that serve as indicators of grazing pressure in alpine areas of Scandinavia. In a fully replicated, landscape-scale experiment with three replicates of each of three levels of sheep density (zero, low, and high), we measured grazing frequency (numbers of plants eaten, as a proportion), flowering frequency, and plant height for 17 common herb species for two consecutive grazing seasons. For eight species, grazing frequency varied significantly between treatments, and for four of these species there was additional strong between-year variation. The estimate for total grazing frequency of herbs decreased when more species of decreasing preference were included, and it was significantly lower in the second grazing season. There were large between-year differences in plant height probably related to weather patterns. A grazing treatment effect on plant height was found only for two species. Flowering frequency in selected species changed even at low sheep densities and was thus not considered suitable except for indicating ungrazed areas. Grazing frequency of three herbs, *Saussurea virgaurea, Rumex acetosa*, and *Pyrola minor*, provided a useful indicator of total grazing pressure, as these species were grazed only at high sheep density. Our study area is likely to be representative of alpine areas in southern Norway, but we advise careful calibration using monitoring procedures before similar management decisions on stocking rates can be fully implemented in other ecosystems.
Keywords: flowering frequency, grazing frequency, herbivory, monitoring, selectivity.

Résumé : Un objectif d'aménagement courant est de maintenir les densités de grands herbivores à des niveaux durables. Cependant, il est difficile de mesurer la pression de broutement. Nous recherchons des combinaisons d'espèces d'herbes et de traits morphologiques pouvant servir d'indicateurs de la pression de broutement dans les zones alpines de la Scandinavie. Dans une expérience à l'échelle du paysage comprenant trois réplicats pour chacun des trois niveaux de densité de moutons (nulle, faible, élevée), nous avons mesuré la fréquence de broutement (le nombre de plantes consommées, en proportion), la fréquence de floraison et la hauteur des plantes pour 17 espèces d'herbes communes durant deux saisons de broutement consécutives. Pour huit espèces, la fréquence de broutement variait de façon significative entre les traitements mais pour quatre d'entre elles, il y avait en plus de fortes variations entre les années. La fréquence totale de broutement estimée était moins élevée lorsque plus d'espèces peu préférées étaient présentes et était aussi significativement plus basse lors de la deuxième saison de broutement. Il y avait de grandes différences dans la hauteur des plantes entre les années probablement en lien avec les patrons météorologiques. Un effet du traitement de broutement sur la hauteur des plantes a été détecté pour deux espèces seulement. La fréquence de floraison des espèces choisies changeait même à faible densité de moutons et n'était donc pas considérée comme un indicateur adéquat sauf pour indiquer les zones non broutées. La fréquence de broutement de trois herbes, *Saussurea virgaurea*, *Rumex acetosa* et *Pyrola minor*, procurait un indicateur utile de la pression totale de broutement puisque ces espèces n'étaient broutées que lorsque la densité de moutons était élevée. Notre aire étude est probablement représentative des zones alpines de Norvège mais nous recommandons de faire une calibration prudente à l'aide de mesures de suivi avant de prendre des décisions de gestion similaires dans l'application de taux chargement pour d'autres écosystèmes.
Mots-clés : fréquence de broutement, fréquence de floraison, herbivorisme, suivi, sélectivité.

Nomenclature: Lid & Lid, 1994.

Introduction

Large herbivores affect the composition of plant communities by grazing, browsing, trampling, urinating, and defecating (Jefferies, Klein & Shaver, 1994; Hobbs, 1996; Augustine & McNaughton, 1998; Austrheim & Eriksson, 2001; Vesk & Westoby, 2001). Plants can respond to herbivory in two different ways: by showing resistance to herbivory or by compensating for loss of tissue (tolerance to herbivory; McNaughton, 1983; Strauss & Agrawal, 1999).

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[2] Author for correspondence.

At low animal population densities, grazing frequency on resistant plants may be low due to avoidance, but as population densities increase (and biomass of tolerant species is reduced), grazers may expand their diet breadth to include plants with limited ability to tolerate grazing (Choquenot, 1991). Therefore, herbivore density and grazing pressure are likely to be important predictors of ecosystem responses to grazing.

Grazing pressure in the livestock literature is defined as "animal demand per unit weight of forage at any instant" (Scarnecchia & Kothmann, 1982; Scarnecchia, 1985). In order to monitor grazing impact, we need a suite of plant species and/or morphological traits of plants that respond differently at different levels of grazing pressure (Bühler & Schmid, 2001; Mysterud, 2006). Relevant monitoring techniques include recording of grass height (Hall & Bryant, 1995; Clary & Leininger, 2000), height of individual forb species (Anderson, 1994), and the proportion of herbs flowering (Anderson, 1994). However, monitoring is complicated by stochastic weather patterns that may lead to substantial differences in plant abundances between years and thus to differences in the frequency with which a plant species is grazed even in the absence of any change in animal density. A suitable indicator of grazing pressure should display consistent responses over relevant temporal and spatial scales. Additionally, there should be either (1) a gradual increase/decrease of an indicator from areas not grazed to areas heavily grazed or (2) threshold value(s) in the frequency of indicator species that can be related to specific levels of grazing pressure.

The use of unamended pastures by domestic herbivores is controversial (Oesterheld, Sala & McNaughton, 1992; Simpson *et al.,* 1998) as the animals are often held at much higher densities than wild herbivores (Oesterheld, Sala & McNaughton, 1992). Domestic sheep (*Ovis aries*) that forage in unamended upland pastures are economically important in some regions (Warren & Mysterud, 1993). Norwegian mountains have been used as summer pasture for sheep since the Bronze Age (Kvamme, 1988). Some 2.2 million sheep currently graze in unamended Norwegian pastures in summer (Drabløs, 1997), mostly in the alpine zone. The sustainability of current grazing levels in these pastures is controversial, partly because empirical studies of the grazing impact are lacking (Mysterud & Austrheim, 2005). Sheep are highly selective grazers, and their preferred forage is herbs (Bowns & Bagley, 1986; Hæggström, 1990), followed by graminoids, dwarf shrubs, and shrubs (Nedkvitne, Garmo & Staaland, 1995). Many of the preferred herbaceous forage plants have a limited ability to tolerate grazing compared to graminoids (Bowns & Bagley, 1986). As herbs are fairly distinctive in appearance, they are good candidates as biomonitors of grazing pressure in montane habitats of Scandinavia.

Data from a fully replicated, landscape-scale experiment with three replicates and three densities of sheep (Austrheim, Evju & Mysterud, 2005; Mysterud *et al.,* 2005; Steen, Mysterud & Austrheim, 2005) were analyzed for this study. We measured grazing frequency (proportion of individual plants eaten over a given time period) and the height and frequency of flowering of 17 common herb species that differ in fodder value to sheep (Kausrud *et al.,* 2006) during two years (2003 and 2004) in order to assess which combinations of herb species and easily recordable morphological traits could serve as indicators of the grazing impact of sheep.

Methods

STUDY AREA

The study area is located in Hol municipality, Buskerud county, south Norway (60° 40' to 60° 45' N, 7° 55' to 8° 00' E). The climate is sub-continental and alpine, with low to moderate precipitation (700–800 mm annually; Førland, 1993). The bedrock consists of meta-arkose (Sigmond, 1998), and the soil is moderately base-rich, especially in landscape depressions in which seepage water collects (Austrheim, Evju & Mysterud, 2005). The vegetation predominantly consists of low shrubs interspersed with grass-dominated meadows, with scattered birches (*Betula* spp.) in the low-lying areas (Rekdal, 2001). Prior to fencing, the study area had a history of very low sheep density (< 10 sheep·km^{-2}). The area is occasionally visited by single individuals or small herds of wild reindeer (*Rangifer tarandus*) in spring and by moose (*Alces alces*) during summer nights.

EXPERIMENTAL DESIGN

During the summer of 2001, a large enclosure covering 2.7 km^2 (*ca* 3 × 0.9 km) with a total of 17.3 km of standard sheep fencing (110 cm high), was established in an alpine habitat (1050–1300 m a.s.l.) on a mainly south-facing hillside (Mysterud *et al.,* 2005). The large enclosure was divided into nine parallel sub-enclosures, each running from low to high elevation and having an average size of 0.3 km^2. A vegetation survey that included the fodder value for sheep based on an assessment of the distribution of vegetation types was carried out in 2001 by a skilled range ecologist (Rekdal, 2001). The distribution of main vegetation types used by sheep was similar among sub-enclosures (Rekdal, 2001).

We used a block-wise randomized design. For each group of three adjacent sub-enclosures, we randomly assigned the following treatments: control (no sheep), low density of sheep (25 sheep·km^{-2}), and high density of sheep (80 sheep·km^{-2}). These densities, which are within the range of sheep stocking in similar alpine habitats of Norway (Mysterud & Mysterud, 1999), were chosen on the basis of the results of the vegetation survey (Rekdal, 2001; for further details see Mysterud *et al.,* 2005; Steen, Mysterud & Austrheim, 2005). 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; the same time period as used in most mountain regions in southern Norway. All sheep were of the common breed "norsk Kvit sau" (formerly called the "Dala breed"). Individual animals are relatively large; ewes averaged 83 kg in live weight in spring (A. Mysterud, unpubl. data).

FIELD METHODS

In 2001, 180 permanent plots were sampled for vegetation using a random, stratified design that ensured a balanced distribution of plots between altitudinal levels (Austrheim, Evju & Mysterud, 2005) and an even representation of main vegetation types (graminoid-dominated snow-beds [30% of all plots]; dwarf-shrub vegetation type dominated by *Vaccinium* spp. [29%]; willow [*Salix* spp.] scrub meadows [21%]; and lichen-dominated ridges [20%]). In each sub-enclosure (area 0.3 km^2), twenty 0.5 × 0.5 m plots were positioned using a stratified design and divided into 16 sub-plots (each 0.125 × 0.125 m).

Soil samples were taken from the upper 5-cm layer at two fixed corners outside each plot in August 2001. Sub-samples were mixed to avoid spatial variation in soil environment data. Soil analyses included pH (measured electrometrically) (Krogstad, 1992), dry matter (DM; percent weight reduction after drying for 6 h at 105 °C) (Krogstad, 1992), loss on ignition (LOI; percent weight reduction after ignition for 3 h at 550 °C) (Krogstad, 1992), and total amounts of nitrogen (measured using the Kjeldahl-N method) (Smith, 1990). We also estimated exchangeable amounts of phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), and sodium (Na) as determined by Egnér's AL-method (Egnér, Riehm & Domingo, 1960). All soil analyses were performed at the Norwegian Centre for Soil and Environmental Research (Jordforsk) except for LOI and DM, which were performed at the Department of Biology, University of Oslo (*cf.* Austrheim, Evju & Mysterud, 2005).

For this study, we included data for all perennial herb species that occurred in 10% or more of the permanent plots in 2001 (when the first vegetation analysis was performed; Austrheim, Evju & Mysterud, 2005), with the following exceptions: *Veronica alpina*, which was found to be difficult to separate from the less common species *Epilobium anagallidifolium* when small, and species of two genera that were only determined to genus level (*Alchemilla* and *Taraxacum*). Two less common but potentially important constituents of the diet of herbivores, *Potentilla erecta* and *Leontodon autumnalis* (present in 8.9% and 7.2% of all plots, respectively) were included. In total, 17 species were studied.

We intended to sample 10 individuals of each species in each of three randomly chosen permanent vegetation plots in each sub-enclosure, giving for each treatment a total of 90 (30 × 3) individuals per species. However, two factors restricted the sampling. First, we did not want to choose subjectively which individuals were sampled within a plot. Therefore, a fixed route of sampling through the 16 sub-plots was followed by numbering the sub-plots from 1 (in the southeast corner of the plot) through 16 (in the northwest corner of the plot). All individuals in a sub-plot were measured, with a minimum of 10 individuals (ramets for clonal species) per species per plot. If needed, additional 0.5- × 0.5-m plots were placed 1 m to the N, E, S, and W of the permanent plot (in that order) to ensure sampling of a minimum of 10 individuals. Second, as species were unevenly distributed on sub-enclosures, not all species were found in the required minimum number of plots. The number of sub-enclosures with successful sampling for each species varied from 5 to 9, while the number of plots in each treatment varied from 3 to 15.

For each individual plant, grazing status (grazed/ungrazed, *i.e.,* presence/absence of bite marks on leaves, stem, etc.) and reproductive status (presence/absence of buds, flowers, and/or fruits) were noted, and plant height (stretched, in cm) was recorded.

Sampling was performed in late July/August for two consecutive grazing seasons, 2003 and 2004, and the same permanent vegetation plots were used both years. The summer of 2004 was cooler and drier than that of 2003. Mean daily temperature at Geilo (the weather station closest to the study area) for June and July was 10.0 °C and 12.3 °C in 2004 and 2003, respectively, while total rainfall amounts for the same periods were 129.1 mm and 164.0 mm (Norwegian Meteorological Institute, 2005).

STATISTICAL ANALYSES

Our data contained some imbalances: not all species were present in all locations (see above). The assumptions inherent in "design-based inference" (Buckland, Goudie & Borchers, 2000) were not fully met by the data. Statistical analysis of a properly replicated experiment assumes that the effect of other factors is distributed randomly among treatments and thus can be ignored when treatments are compared. We calculated average values of grazing frequency, plant height, and flowering frequency for each combination of species, year (2003 and 2004), and treatment (control, low sheep density, and high sheep density). However, instead of statistical analyses by standard parametric statistical methods, we used bootstrap techniques (*cf.* Efron & Tibshirani, 1993) to calculate bootstrap standard errors (1000 iterations) for all observed means. Bootstrap techniques are very robust when there are imbalances in the data, and bootstrap analyses are not influenced by single outlying values. They are also very robust to the effects of variations in the statistical distribution of the data (*i.e.,* no assumption of normality or other specified distributional property is required as data themselves are used to generate distributions). Our focus, therefore, shifted from ordinary significance testing to assessment of 95% confidence intervals of the estimated parameters (mean ± 2 SE). Considering whether the confidence interval includes zero or not is roughly equivalent to significance testing at $P = 0.05$. Based on the results, we identified species and traits that could potentially serve as indicators for further detailed evaluation.

Models were developed to explore the effect of treatment and year on traits, as well as interactions effects between them. We used an exact test based upon the binomial distribution (Sokal & Rohlf, 1995) to test whether plant height varied between years for more species than expected by chance. This test estimates the probability of obtaining at least n "positive" outcomes of a total of N trials when the probability for "positive outcome" is 0.05 in each trial and the trials are independent. This is thus a global test that decreases the likelihood of type I error at the $P = 0.05$ level brought about by the inclusion of a large data set.

We used more "explorative methods" (or "model-based inference"; Johnson & Omland, 2004) to evaluate if other environmental covariates (vegetation type, altitude, exposure, and slope) or soil variables (pH, N, P, K, Ca, Mg, Na, dry matter content, and loss of ignition) affected the focal traits (grazing frequency, flowering frequency, and plant height). We were able to identify if, and how much, these other covariates affected the measured traits. We used the Akaike Information Criterion (AIC; Burnham & Anderson, 1998; Johnson & Omland, 2004) to select an appropriate model for parameter estimation. The AIC is defined as

$$-2*\ln([\theta|y]) + 2p \qquad [1]$$

where y is data, p is a count of free parameters, and θ is the likelihood of the model parameters. The model with the lowest AIC value is considered to be the most parsimonious model, *i.e.,* the best compromise between explaining as much of the variation as possible and using as few parameters as possible. Accordingly, we used the model with the lowest AIC for subsequent parameter estimation. Model selection was performed using linear models (LM; McCullagh & Nelder, 1989; Venables & Ripley, 2002).

We used linear mixed models (LME; McCulloch & Searle, 2002; Venables & Ripley, 2002) as implemented in S-Plus version 6.2 (Crawley, 2003) for improved parameter estimation. LME is an extension of linear modeling that allows observations to be grouped, and explicitly estimates the covariance at the different levels of a hierarchical structure. LME thus provides estimates both for random and fixed effects.

Two random-effect predictors were included to account for the fact that our data were nested in two different ways: (1) dependency of observations derived from repeated sampling of the same plot (temporal autocorrelation) and (2) dependency of observations (plots) derived from use of the same sub-enclosures (spatial autocorrelation). We used treatment (grazing levels) and year as fixed explanatory variables, with "plot" nested within "sub-enclosure" as random effects. This ensured that an appropriate number of degrees of freedom (df) was used in parameter estimation. Our models took into account both that observations from the same plot were dependent and that all plots within a sub-enclosure were dependent when it comes to the treatment effect (*i.e.,* we have three replicates, and the number of plots within sub-enclosures cannot change this). The reason LME was not used for model selection with AIC (see above) is that LME uses restricted maximum likelihood estimation, for which the AIC criterion is not meaningful (Crawley, 2003).

When explanatory variables other than treatment and year significantly affected the trait/variable in question, we tested for each explanatory variable that varied between grazing treatments, using linear regression for continuous variables and Fisher's exact test for categorical variables.

All continuous variables were log-transformed prior to analysis. Plant height was log-transformed and a constant added in order to obtain zero skewness of the transformed variable, and the data were subsequently translated onto a 0–1 scale (Økland, Økland & Rydgren, 2001). The frequency data were arcsine-transformed to avoid heteroscedasticity.

Total grazing frequency, measured as degree of utilization of the most important forage plants (*cf.* Holechek *et al.,* 1999), was estimated for high and low sheep densities. The 17 herb species were ranked according to degree of selection by the sheep, based on an independent field study of the area in the summer of 2002 (Kausrud *et al.,* 2006). Selection is usually defined as use divided by availability and multiplied by 100 (Thomas & Taylor, 1990), but a number of methods exist to estimate selection. Selection ranks (Table I) were estimated from data on diet selection

TABLE I. Observed values of (a) grazing frequency (proportion of number of individuals eaten), (b) plant height (cm), and (c) flowering frequency for each combination of species, treatment, and year (± bootstrap SE), for species for which the parameter estimates do not overlap zero, *i.e.*, corresponding to significant differences between treatments ($P < 0.05$)[1]. Selection rank is averaged over different estimates of selection scores (details in Kausrud *et al.*, 2006).

a)

Species	Selection rank	Treatment	Grazing frequency (%) 2003	2004
Saussurea alpina	2	Control	0.0 ± 0.0	0.0 ± 0.0
		Low-density	2.4 ± 1.4	10.7 ± 6.4
		High-density	45.0 ± 5.5	17.5 ± 10.2
Solidago virgaurea	3	Control	4.8 ± 2.4	0.0 ± 0.0
		Low-density	25.2 ± 6.7	42.7 ± 14.3
		High-density	73.9 ± 7.2	46.3 ± 8.5
Omalotheca norvegica	4	Control	0.0 ± 0.0	0.0 ± 0.0
		Low-density	39.3 ± 10.1	12.7 ± 4.7
		High-density	60.7 ± 10.7	17.6 ± 6.3
Rumex acetosa	5	Control	3.3 ± 2.3	0.0 ± 0.0
		Low-density	8.9 ± 2.7	3.3 ± 3.3
		High-density	22.9 ± 7.2	21.6 ± 7.5
Ranunculus acris	6	Control	1.5 ± 1.4	0.0 ± 0.0
		Low-density	10.6 ± 2.9	12.5 ± 5.1
		High-density	12.8 ± 3.4	24.7 ± 6.5
Leontodon autumnalis	7	Control	1.1 ± 1.0	0.0 ± 0.0
		Low-density	6.0 ± 3.6	0.0 ± 0.0
		High-density	30.4 ± 5.6	10.0 ± 7.5
Pyrola minor	9	Control	0.0 ± 0.0	0.0 ± 0.0
		Low-density	2.0 ± 1.8	0.0 ± 0.0
		High-density	13.6 ± 2.5	6.3 ± 4.5
Geranium sylvaticum	10	Control	0.0 ± 0.0	0.0 ± 0.0
		Low-density	5.4 ± 2.8	2.8 ± 2.0
		High-density	19.3 ± 5.4	3.9 ± 2.1

b)

Species	Selection rank	Treatment	Plant height (cm) 2003	2004
Solidago virgaurea	3	Control	12.1 ± 0.47	11.3 ± 0.51
		Low-density	12.9 ± 0.71	9.8 ± 0.50
		High-density	7.4 ± 0.45	6.7 ± 0.35
Omalotheca norvegica	4	Control	11.9 ± 0.49	8.7 ± 0.31
		Low-density	7.2 ± 0.33	6.3 ± 0.33
		High-density	4.5 ± 0.28	4.1 ± 0.21
Leontodon autumnalis	7	Control	9.4 ± 0.62	6.5 ± 0.31
		Low-density	7.2 ± 0.55	6.0 ± 0.37
		High-density	6.8 ± 0.59	6.3 ± 0.56

c)

Species	Selection rank	Treatment	Flowering frequency (%) 2003	2004
Solidago virgaurea	3	Control	17.4 ± 6.3	16.9 ± 4.0
		Low-density	0.0 ± 0.0	2.5 ± 1.5
		High-density	0.0 ± 0.0	0.0 ± 0.0
Ranunculus acris	6	Control	9.6 ± 4.1	15.8 ± 6.1
		Low-density	0.0 ± 0.0	3.0 ± 2.9
		High-density	0.0 ± 0.0	0.0 ± 0.0
Leontodon autumnalis	7	Control	23.8 ± 5.3	8.4 ± 3.2
		Low-density	5.8 ± 2.0	10.2 ± 2.9
		High-density	1.7 ± 1.5	5.0 ± 3.2

[1] Species included in the study but but that did not show significant treatment effects for any of the variables, with selection rank in brackets: *Hieracium alpinum* (1), *Potentilla erecta* (8), *Sibbaldia procumbens* (11), *Omalotheca supina* (12), *Viola palustris* (13), *Bistorta vivipara* (14), *Alchemilla alpina* (15), *Trientalis europaea* (16), and *Viola biflora* (17).

and species abundance (Kausrud *et al.,* 2006). Grazing frequency estimates were made both by determining decreasing selection rank and by including the species found in this study to be the most utilized. We used paired-samples *t*-tests to test differences in grazing frequency estimates between treatments and years.

Only models with significant treatment effects are presented.

Results

GRAZING FREQUENCY OF INDIVIDUAL SPECIES

For eight species, the estimates of grazing frequency varied significantly between treatments. However, four of these had a significant treatment:year interaction, *i.e.,* grazing was lower in high-density sites in 2004 than in 2003 (Table IIa).

For the remaining four species no between-year effect was found on grazing frequency (Table IIa). The most parsimonious models for S*aussurea alpina, Rumex acetosa,* and *Ranunculus acris* included treatment as the only explanatory variable, revealing no difference in grazing frequency between control and low-density treatments, but significant differences between control and high-density treatments. Both *S. alpina* and *R. acetosa* showed significantly higher grazing frequencies in high-density compared to low-density treatments (l.s. [least-squares] estimate = 0.258, $T = 3.644$, $P = 0.015$, and l.s. estimate = 0.171, $T = 2.736$, $P = 0.041$, respectively). For *R. acris*, no difference was found between low- and high-density treatments (l.s. estimate = 0.086, $T = 1.657$, $P = 0.149$).

Grazing on *Pyrola minor* occurred only at high sheep density and increased with increasing Ca levels in the soil (Table IIa). There was no difference in Ca levels between treatments ($F = 0.636$, df = 2 and 16, $P = 0.542$). However, within high-density treatments there was a significant correlation between Ca levels in soil and grazing frequency ($r^2 = 0.552$, df = 1 and 6, $P = 0.035$). The explanatory value of Ca was attached to one sample plot that had high Ca content (sample maximum = 247.0 mg Ca·100 g soil^{-1}) and was heavily grazed (F15; 20% and 40% in 2003 and 2004, respectively). This was the only plot in which more than 15% of the individuals showed signs of being grazed. Deleting this sample plot from the analysis made Ca insignificant, but the significant grazing effects in high-density sites were retained.

PLANT HEIGHT

With year as only explanatory variable in LME, 12 species had significantly lower heights in 2004 than in 2003. This is significantly more species than expected by chance (exact test based upon binomial distribution: $P < 0.0001$).

Plant height was significantly affected by treatment in two species only. For *Solidago virgaurea*, height was significantly lower in high-sheep-density treatments than in controls (Table IIb) and in low-density treatments (l.s. estimate = -0.216, $T = -3.251$, $P = 0.023$). There was a significant interaction between treatment and year, reflecting a lower plant height in low-density sites in 2004 (Figure 1b).

Height of *Omalotheca norvegica* was significantly lower in sites with a low grazer density than in control plots (Table IIb) and significantly lower in high- than in low-density treatments (l.s. estimate = -0.157, $T = -4.452$, $P = 0.011$). However, a significant effect of year (lower in 2004 than 2003) and an interaction between year and treatment (Figure 1a) were observed. In addition, significant effects of both altitude and pH were observed for both variables: plant height decreased with increasing values of these variables. There was no difference in altitude ($F = 0.294$, df = 2 and 21, $P = 0.748$) or pH ($F = 0.832$, df = 2 and 21, $P = 0.449$) between treatments, and no correlation was observed between these two variables ($r^2 = 0.003$, $P = 0.806$).

FLOWERING FREQUENCY

Only three species showed a treatment effect on flowering frequency. For *Omalotheca norvegica* there was no flowering at all in high-density plots and flowering was observed in only two out of eight low-density plots in 2004. Vegetation type had, however, a strong influence on flowering frequency (Table IIc), and flowering was more common in snow-beds and in willow-shrub vegetation than in dwarf-shrub vegetation. Vegetation types were evenly distributed within all treatments (Fisher's exact test, $P = 0.240$).

Treatment was the only explanatory variable that accounted for the difference in flowering frequency observed in *R. acris* (Table IIc). Flowering frequency was close to zero when sheep were present (close to significant for low-density treatment), regardless of sheep density (l.s. estimate high- *versus* low-density -0.016, df = 6, $T = –0.279$, $P = 0.789$).

Flowering frequency was lower in *Leontodon autumnalis* in high- and low-density than in control treatments. However, there was a strong treatment:year interaction: flowering was less common in 2004 than in 2003 in control plots, but more common in areas with sheep (Table IIc).

OVERALL FREQUENCY OF GRAZING ON HERBS

The ranking of herbs using detected signs of grazing partly corresponded to the species' selection rank by sheep. The species experiencing highest grazing frequency were *Solidago virgaurea* (selection rank 3; low density: 34.0%, high density: 60.1%), *Omalotheca norvegica* (selection rank 4; low density: 26.0%, high density: 39.1%), *Rumex acetosa* (selection rank 5; low density: 6.3%, high density: 22.2%), and *Saussurea alpina* (selection rank 2; low density: 6.5%, high density: 31.3%). Estimated total frequency of grazing on herbs varied depending on the number of species included in the estimates (Figure 2). Including the four most selected species according to the selection rank (*Hieracium alpinum, S. alpina, S. virgaurea,* and *O. norvegica*) gave an estimate of grazing frequency of 39.3% for high sheep density, but this estimate decreased to 15.1% when all 17 species studied were included. Using only the species in which a significant treatment effect on grazing frequency was observed gave higher estimates. The two most strongly selected species (*S. alpina* and *S. virgaurea*) gave an estimated grazing frequency of 49.6% for high density, whereas including all eight species gave an estimate of 25.0%. The comparable numbers for low-density sites were 18.6% and 7.1% for the set of 17 species and 16.7% and 10.6% for the set of eight species, respectively. Total grazing frequency

TABLE II. The most parsimonious models for species-trait combinations with significant grazing treatment effects on (a) grazing frequency (proportion eaten), (b) plant height (cm), and (c) flowering frequency (percentage of individuals that flowered).

		least-squares estimate	SE	df	*T*	*P*
a)						
Saussurea alpina	Intercept	0.000	0.058	16	0.000	1.000
	High-density *versus* control	0.326	0.082	5	3.983	0.011
	Low-density *versus* control	0.068	0.071	5	0.956	0.383
Solidago virgaurea	Intercept	-0.404	5.891	24	-0.067	0.946
	High-density *versus* control	32.900	9.004	5	3.654	0.015
	Low-density *versus* control	25.059	12.787	5	1.960	0.107
	Year	-0.048	0.092	24	-0.521	0.607
	Altitude	0.064	0.831	24	0.077	0.940
	High-density:Year	-0.359	0.135	24	-2.666	0.014
	Low-density:Year	0.258	0.159	24	1.621	0.118
	High-density:Altitude	-4.510	1.268	24	-3.556	0.002
	Low-density:Altitude	-3.515	1.808	24	-1.945	0.064
Omalotheca norvegica	Intercept	0.000	0.123	38	0.000	1.000
	High-density *versus* control	0.717	0.171	4	4.192	0.014
	Low-density *versus* control	0.448	0.176	4	2.541	0.064
	Year	0.000	0.104	38	0.000	1.000
	High-density:Year	-0.561	0.158	38	-3.556	0.001
	Low-density:Year	-0.295	0.152	38	-1.937	0.060
Rumex acetosa	Intercept	0.017	0.045	27	0.372	0.713
	High-density *versus* control	0.215	0.064	5	3.383	0.020
	Low-density *versus* control	0.045	0.062	5	0.716	0.506
Ranunculus acris	Intercept	0.008	0.043	23	0.180	0.859
	High-density *versus* control	0.196	0.057	6	3.435	0.014
	Low-density versus control	0.110	0.056	6	1.956	0.098
Leontodon autumnalis	Intercept	0.011	0.035	28	0.317	0.753
	High-density *versus* control	0.301	0.055	6	5.420	0.002
	Low-density *versus* control	0.049	0.059	6	0.838	0.434
	Year	-0.011	0.050	28	-0.224	0.824
	High-density:Year	-0.197	0.078	28	-2.507	0.018
	Low-density:Year	-0.049	0.083	28	-0.592	0.558
Pyrola minor	Intercept	-0.137	0.062	19	-2.213	0.039
	High-density *versus* control	0.115	0.033	5	3.533	0.017
	Low-density *versus* control	0.0027	0.036	5	0.075	0.943
	Ca	0.035	0.015	10	2.340	0.037
Geranium sylvaticum	Intercept	0.000	0.039	64	0.000	1.000
	High-density *versus* control	0.197	0.052	6	3.786	0.009
	Low-density *versus* control	0.055	0.053	6	1.040	0.338
	Year	0.000	0.046	64	0.000	1.000
	High-density:Year	-0.157	0.061	64	-2.549	0.013
	Low-density:Year	-0.026	0.063	64	-0.419	0.677
b)						
Solidago virgaurea	Intercept	0.539	0.0376	362	14.319	< 0.0001
	High-density *versus* control	-0.195	0.0552	5	-3.536	0.017
	Low-density *versus* control	0.021	0.0647	5	0.316	0.765
	Year	-0.321	0.0217	362	-1.478	0.140
	High-density:Year	-0.0093	0.0325	362	-0.287	0.775
	Low-density:Year	-0.108	0.0387	362	-2.784	0.006
Omalotheca norvegica	Intercept	505.155	170.372	469	2.965	0.003
	High-density *versus* control	-0.279	0.037	4	-7.627	0.002
	Low-density *versus* control	-0.122	0.035	4	-3.445	0.026
	Year	-0.107	0.018	469	-6.077	< 0.0001
	Altitude	-70.764	23.926	14	-2.958	0.010
	pH	-323.044	110.254	14	-2.930	0.011
	High-density:Year	0.088	0.027	469	3.230	0.001
	Low-density:Year	0.072	0.026	469	2.737	0.006
	pH:Altitude	45.309	15.483	14	2.926	0.011
c)						
Omalotheca norvegica	Intercept[1]	0.244	0.037	28	6.509	0.615
	High-density *versus* control	-0.234	0.045	4	-5.153	0.007
	Low-density *versus* control	-0.202	0.044	4	-4.617	0.010
	Willow-shrub habitat	0.147	0.068	14	2.153	0.049
	Snow-bed habitat	0.206	0.062	14	3.340	0.005
	Grass meadow habitat	0.175	0.101	14	1.736	0.105

TABLE II. Continued.

		l.s. estimate	SE	df	*T*	*P*
Ranunculus acris	Intercept	0.143	0.041	23	3.495	0.002
	High-density *versus* control	-0.143	0.057	6	-2.501	0.047
	Low-density *versus* control	-0.128	0.056	6	-2.265	0.064
Leontodon autumnalis	Intercept	0.244	0.037	28	6.509	< 0.0001
	High-density *versus* control	-0.227	0.059	6	-3.871	0.008
	Low-density *versus* control	-0.187	0.062	6	-3.008	0.024
	Year	-0.159	0.051	28	-3.143	0.004
	High-density:Year	0.193	0.080	28	2.406	0.023
	Low-density:Year	0.204	0.085	28	2.401	0.023

[1] Intercept for control areas and dwarf-shrub vegetation type.

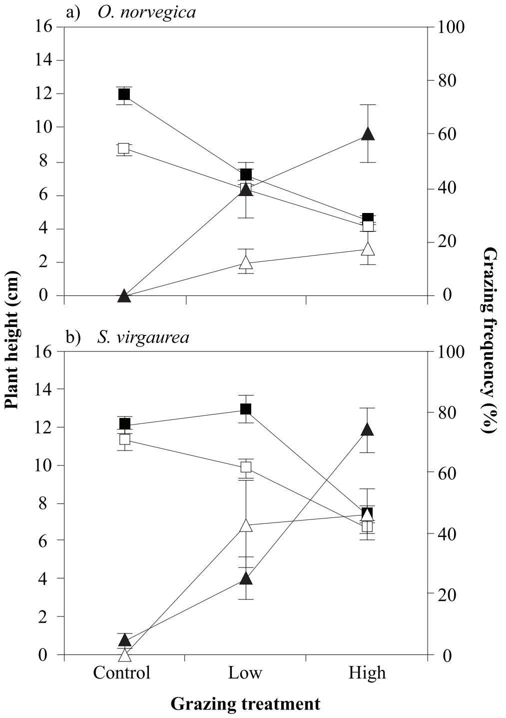

FIGURE 1. Plant height (squares) and grazing frequency (triangles) of a) *Omalotheca norvegica* and b) *Solidago virgaurea* in areas with no sheep, low density, and high density of sheep in the two years 2003 (filled symbols) and 2004 (open symbols). Vertical bars are bootstrap standard errors (1000 iterations).

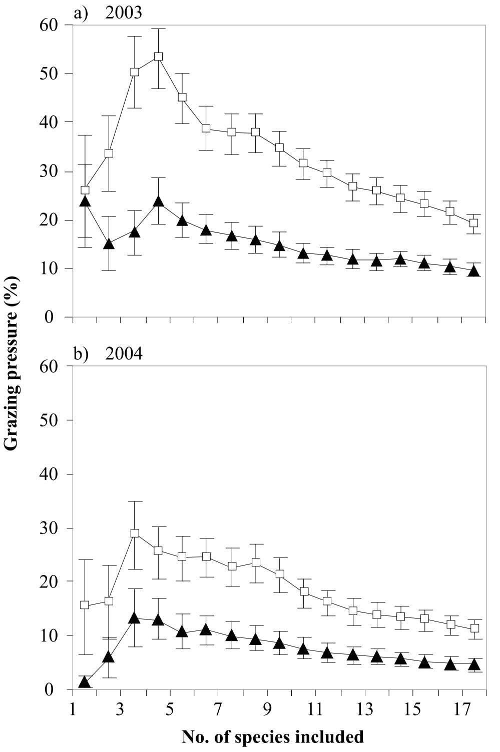

FIGURE 2. Grazing frequency (proportion of individuals grazed or partly grazed) with increasing number of species (ranked according to selection rank) included in low (triangles) and high (squares) sheep density areas in a) 2003 and b) 2004. Vertical bars are bootstrap standard errors (1000 iterations).

was significantly higher in high- compared to low-density treatments (paired-samples *t*-test, $P < 0.0001$ for both sets of 17 and eight species).

Estimated grazing frequency differed between the two years (see Figure 2): for the set of 17 species grazing frequency was lower in 2004 than in 2003 (paired-samples *t*-test, $P < 0.0001$ for both low- and high-density treatments). When only the eight species with significant treatment effect were included, grazing frequency was lower in 2004 in high-density sites only (paired-samples *t*-test, $P < 0.0001$ and $P = 0.574$ for high and low densities, respectively).

Discussion

In order to be suitable as biomonitors of grazing pressure, variables such as grazing frequency, plant height, and flowering frequency should be relatively unaffected by temporal and spatial variability. Of the 17 herb species studied, 12 had a significantly lower height in the cooler and drier year of 2004 compared to the warmer and wetter year of 2003, demonstrating the difficulty of using plant height as an indicator of sheep grazing pressure because of the strong effect of weather patterns on plant height. However, in the case of *Solidago virgaurea* and *Omalotheca norvegica*, for which a significant grazing treatment effect on plant height was observed, only small differences in height within sheep-grazing treatments were recorded between years, perhaps reflecting the tendency of herbivores to leave stubble of a certain height when grazing (Illius & Gordon, 1987). This effect is also seen in the herb *Trillium grandiflorum*, for which relatively small yearly variation in stem height is observed, compared with the effect of white-tailed deer (*Odocoileus virginianus*) browsing shrubs (Anderson, 1994). Therefore, the relative effect of the weather on plant height may be smaller on preferred grazing species, making the height of *O. norvegica* and *S. virgaurea* a suitable ecological indicator of sheep grazing pressure. Stubble height, a measure of the herbaceous vegetation remaining after grazing, is indeed widely used as an indicator of grazing impact in US riparian forests (Clary & Leininger, 2000). The natural variation in plant height caused by altitude and soil status does, however, complicate the use of this variable. Additionally, potential long-term effects of tissue removal, *e.g.,* depletion of below-ground resources, may alter the observed patterns.

As grazing pressure increases, the standing biomass of tolerant species is lowered; grazers are then expected to expand their diet breadth and graze plants intolerant of grazing (Choquenot, 1991). The crossing of such thresholds may be used to indicate when grazing pressure has increased to a level where grazing impacts on other functional groups that are less tolerant to increased grazing. Sheep utilization of *Saussurea virgaurea, Rumex acetosa*, and *Pyrola minor* was negligible at a low density of sheep but significant at a high density (*ca* 30%, 20%, and 10% for the three species, respectively). If the aim is to keep grazing impact below a certain threshold, the frequency of grazing of these species may be useful indicators. The significantly lower overall grazing frequency in 2004 may reflect differences in the phenological development of plants due to between-year weather variation. Herbs constituted a smaller proportion of the diet in 2004 compared to that in 2003 (Mysterud & Austrheim, 2005). Therefore, grazing impact on functional groups closer to the resistant end of the spectrum may be more strongly affected in years of poor vegetation development.

For the majority of species, grazing treatment has no significant impact on flowering frequency, as observed by Crawley *et al.* (2004), who showed that sheep grazing pressure is not the main determinant of flowering stem density in most species on St. Kilda, Scotland. However, for highly selected species, our results confirm the common view that flowering frequency is a trait very responsive to grazing, even at very low grazing pressures, because inflorescences are often preferentially consumed (Anderson, 1994; Mulder & Harmsen, 1995; Augustine & Frelich, 1998; Mulder & Ruess, 1998). These results are also consistent with data on the flowering frequencies of two annual species within our study area (*Melampyrum sylvaticum* and *Rhinanthus minor*; S. Lindgren & G. Austrheim, unpubl. data). We observed flowering frequencies of both *Omalotheca norvegica* and *Ranunculus acris* close to zero when grazed, regardless of whether sheep density was high or low. This suggests these indicators are only useful for detecting ungrazed areas. However, the strong effect of vegetation type on flowering frequency of *O. norvegica* requires further study if this species is to be used as an index of the absence of grazing. Data on densities of domestic herbivores are usually easy to obtain, at least on a broad scale. In the southern part of Norway, densities of sheep in alpine ranges are usually between 10–20 and 100 animals per km^2 (Mysterud *et al.,* 2002). Our study was designed to cover this range of densities in unamended pasture. A review of studies from North America found that low grazing pressure corresponds to an average utilization of the most important forage plants, based on individuals grazed, of 32%, moderate grazing corresponds to 43%, and heavy grazing corresponds to 57% (Holechek *et al.,* 1999). In this context, the high density used in this experiment is close to a moderate grazing pressure, whereas low density corresponds to a low grazing pressure. However, we demonstrate (see Figure 2) that estimation of grazing pressure based on grazing frequency is highly dependent on the definition of important forage plants. At the study sites, herbs made up 20–30% of the sheep diet, while graminoids made up 50–60% (Kausrud *et al.,* 2006). Excluding graminoids is likely to cause an underestimation of the overall grazing pressure, and the use of herb species alone to assess grazing pressure should take this into account. Herbs were chosen for this study because they are easy to identify in the field and because the recording of earlier grazing marks on graminoids can be difficult, especially on narrow-leaved species, as they are often removed in subsequent grazing (Kausrud *et al.,* 2006).

Short-term grazing effects may differ from long-term effects, which may lead to an alteration of competitive interactions between species and a possible decline of palatable species and increase in resistant species (Augustine & McNaughton, 1998; Crawley *et al.,* 2004). In their review of grazing studies in North America, Holechek *et al.* (1999) found that moderate grazing pressure corresponds to a degree of herbage utilization that allows the palatable species to maintain themselves but usually does not permit them to increase their contribution to herbage biomass. Under low grazing pressure, palatable species are allowed to maximize their herbage-producing ability. Although the grazing treatments in our study area correspond to moderate and low grazing pressures, long-term studies of changes in plant abundance will be necessary to evaluate the effects of the current grazing regimes. Graminoids, being more tolerant to grazing, may be expected to increase in abundance in high-density areas, whereas herbs may be expected to decrease. From 2001 to 2005, however, only small changes in the vascular plant communities have occurred in the study area (G. Austrheim, R. Økland, M. Evju & A. Mysterud, unpubl. data).

Conclusion

By recording grazing frequency on 17 abundant herb species, we demonstrated that the grazing in our landscape-scale experiment corresponds to low or moderate grazing pressure (Holechek *et al.,* 1999). We sought candidate species and traits/morphological variables suitable for assessing grazing pressure and impact. We defined two alternative characteristics of an indicator: (*i*) that it shows a gradual increase or decrease in abundance along a gradient in grazing pressure or (*ii*) that it shows an abrupt response beyond a certain threshold level of grazing. Plant height of two species, *Solidago virgaurea* and *Omalotheca norvegica*, did show a gradual decrease from control to low- to high-density sites that was relatively independent of weather conditions. Grazing frequency of three species could, in contrast, be used to separate areas with low grazing pressure from moderate to high grazing pressure by sheep in Scandinavian montane habitats. These species, *Pyrola minor, Rumex acetosa,* and *Saussurea alpina* are only lightly grazed (1.0%, 6.3%, and 6.5%, respectively) where sheep density is low, while grazing is substantial (9.9%, 22.2%, and 31.3%, respectively) where sheep density is high, giving a good indication of total grazing pressure.

Our study area is considered to be representative for large parts of the montane areas of southern Norway, and thus we expect our results to be reasonably representative for productive montane habitats rich in herb species. Herbivore selectivity will depend on local grazing history, productivity, and the available species pool. In a less productive habitat (Setesdal Vesthei, Norway) with much lower herb species richness than our study area, herbs constitute only 26% of the vascular plant species pool (*versus* 53% in our study area) and only two of the eight species reported here to display grazing effects are present (Austrheim, Evju & Mysterud, 2005). Interpretation of grazing data collected in regions with different species pools should therefore be made with caution. Such interpretation is further complicated by the tendency of single species to show inconsistent responses to grazing between areas (Vesk & Westoby, 2001).

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II

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

Marianne Evju*[1], Gunnar Austrheim[2], Rune Halvorsen[1] and Atle Mysterud[3]

[1] Department of Botany, Natural History Museum, University of Oslo, P.O. Box 1172
Blindern, N-0318 Oslo, Norway
[2] Museum of Natural History and Archaeology, Norwegian University of Science and
Technology, N-7491 Trondheim, Norway
[3] Centre for Ecological and Evolutionary Synthesis (CEES), Department of Biology,
University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway

*Corresponding author: marianne.evju@nhm.uio.no, fax no: +47 22 85 18 35

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 long history of grazing, plants are expected to respond to both enhanced and reduced grazing pressures, and the interaction between plant traits and species' abundance change are expected to differ between the two types of alteration of grazing regime. To understand the mechanisms behind species' responses, we investigated the relationship between sheep selectivity (measured *in situ*), plant traits and experimentally derived measures of species abundance change as response to 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 low C/N-ratio in leaves. Species that increased in abundance in response to enhanced grazing pressure were generally small and had high root/shoot-ratio, thus exhibiting traits reflecting both resistance (through avoidance) and tolerance (through regrowth capacity) strategies. The abundance of selected species remained stable during the study period, also in 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 removal of tall competitors, combined with a certain amount of regrowth capacity, seem to be the main mechanism behind a positive response to enhanced grazing pressure in this study. The plant trait perspective clearly improve our insight into mechanisms behind observed abundance changes of species when disturbance regime is altered.

Keywords: abundance change, cessation of grazing, enhancement of grazing, plant traits, sheep

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, that 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 type and density of herbivore as well as on plant community composition (Augustine and McNaughton 1998; Kausrud et al. 2006). Small herbivores (both in terms of species and life stage) are, for instance, more selective than large herbivores (with the same digestive system), and selectivity normally decrease with herbivore density (Demment and Van Soest 1985; Choquenot 1991; Mobæk et al. in press). If herbivore densities increase to such an extent that high-quality forage becomes scarce, also less-preferred species may be affected by grazing to an extent that their abundance decline (Augustine and McNaughton 1998; Westoby 1999).

Both 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 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 link for understanding the mechanisms behind species' responses to grazing (Lavorel et al. 1997; McIntyre et al. 1999; Weiher et al. 1999). The literature on effects of grazing on plant communities and the relationship between grazing frequency and plant traits is large and growing (see review in Díaz et al. 2007). Plants with positive response to grazing are frequently found to be short-statured (Díaz et al. 2001; Cingolani et al. 2005; Díaz et al. 2007), i.e. they most probably increase in abundance through avoiding grazing (resistance strategy), but also traits related to the tolerance strategy have been found to be positively related to grazing response [specific leaf area (SLA, positively correlated with growth rate); Díaz et al. 2001; Cingolani et al. 2005]. However, the relationship between grazing response and plant traits seem to depend upon grazing regime (Bullock et al. 2001), site productivity (Pakeman 2004), or and regional climatic conditions (Vesk and Westoby

2001; de Bello et al. 2005). Furthermore, the majority of grazing studies suffer from a lack of experimental approach (but see: Bullock et al. 2001), which complicates the use of species' abundance change 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 non-linear responses of species and plant traits to increasing 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; Billings 1987). Scandinavian alpine ecosystems have a long history of grazing (Austrheim and Eriksson 2001), and thus plants are expected to respond to both enhanced and reduced grazing pressures. The interaction between plant traits and species' abundance change can be expected to differ between the two types of altered grazing regimes. In a previous study, we have investigated the effect of sheep grazing on plant species abundance change on a short-term scale (four years; Austrheim et al. 2008). To understand the mechanisms behind species' responses, we here 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; (i) a selectivity index (*SI*), (ii) a grazing response index (*GR*), and (iii) 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 generally low selectivity for dwarf shrubs and generally low variation in plant traits for graminoids (M. Evju, unpublished data), we concentrated our study on the 22 most common herb species. Three related issues, in 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 sheep is expected to prefer tender leaves with high specific leaf area (SLA), high nutrient content, but low C/N and C/P content (Coley et al. 1985; Pérez-Harguindeguy et al. 2003). Secondly, we study the relation between species' responses to enhanced grazing pressure and plant traits that express grazing tolerance/resistance strategies (Fig. 1a). 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 creation of gaps and opening of the vegetation, we predict that enhanced grazing pressure will also favour small-seeded species (Bullock et al. 1995; Bullock 2000) and species with high capacity for vegetative reproduction (Oksanen and Ranta 1992; Vandvik 2004). Thirdly, we study the relationship between species' responses to cessation of grazing and plant traits (Fig. 1b). We predict that species which increase in response to cessation of grazing will have high competitive ability (tall, large-leaved species), as such plants benefit from reduced disturbance. Furthermore, reduced gap creation due to reduced herbivory activity is predicted to favour large-seeded species compared to 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 January temperature −10.8°C and July temperature 8.9°C, and mean annual precipitation is approximately 1000 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, with grass-dominated meadows interspersed (Rekdal 2001). A large enclosure covering *c.* 2.7 km^2 was set up in the low alpine zone (1050−1300 m a.s.l.) in 2001 on a mainly south-facing hillside. The enclosure was split into nine parallel sub-enclosures each covering *c.* 0.3 km^2 and spanning the altitudinal gradient.

The sub-enclosures were grouped into three blocks, each with three sub-enclosures. The treatments no sheep, low sheep density (25 sheep per km^2) and high sheep density (80 sheep per km^2) were assigned to sub-enclosures in each block at random, in accordance with block-wise randomised 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 all years. Since the low sheep density treatment shows the smallest amount of vegetation change (Austrheim et al. 2008), we interpret this treatment as 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 sub-enclosure. 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; Austrheim et al. 2008). The abundance of all vascular plants was recorded in 2001 and 2007 using sub-plot frequency (presence-absence in 16 sub-plots of 0.125 × 0.125 m^2) as abundance measure. 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 field recording of vegetation, *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 slightly lower frequency than 10%, due to their potential importance as constituents of sheep diet. Two taxa were only determined to genus level (*Alchemilla* sp. and *Taraxacum* sp.). The final dataset consisted of 22 taxa (Table 1), which are hereafter referred to as species. Nomenclature follows Lid and Lid (2005).

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 healthy, typical, fully grown and with developed fruits, preferably located in well-lit environments, and not strongly affected by herbivores or pathogens. To ensure an unbiased sampling of individuals, the following sampling protocol was used: each sub-enclosure 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. The individual of each species fulfilling the criteria above that was located closest to the midpoint of the compartment was selected for sampling. For each species one compartment was randomly selected for sampling of two individuals, so that the total number of individuals sampled per species was 10. 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 values recorded for all sampled individuals were used (see Table S1 in 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 the species was recorded that it 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:

$$GR = \log_2\left(\frac{\overline{X}_{High07}}{\overline{X}_{High01}}\right) - \log_2\left(\frac{\overline{X}_{Low07}}{\overline{X}_{Low01}}\right)$$

where $\overline{X}_{High07}$ is the average abundance (over all 60 plots in that treatment) of species *X* in the high density treatment in year 2007, etc. Correspondingly, we calculated the response to cessation of grazing (*CR)* for each species as the relative abundance change from 2001 to 2007 in the no sheep treatment compared to the low sheep treatment:

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

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 of the grazing regime were small.

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 included only terms that significantly reduced deviance (at the $p < 0.05$ level). The resulting model is termed 'best model'.

The relationship between *GR* and *CR* was investigated by calculating correlation coefficients (a negative correlation was predicted, i.e. that species which 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.

In order to investigate if different traits were important for predicting responses of selected vs. unselected species, we divided the dataset into two subsets: 50% of the species ($n = 11$) were observed to be grazed in less than 25% of the plots in which they were observed ($SI < 0.25$; unselected species), whereas the remaining 50% ($n = 11$) were grazed in more than 25% of the plots in which they were observed ($SI > 0.25$; selected species).

Traits for which the observed values were strongly skewed to the left were log-transformed prior to the analyses. Phylogenies are not taken into account as analysis of herb abundance-trait relationships using phylogenetic independent contrasts (PIC) showed minor differences as compared to analyses without using PIC (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. Variation in selectivity was best explained by a combination of aboveground biomass, C/N content and first flowering day (Table 3A), *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 abundance change in 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.

The response to enhanced grazing pressure was best predicted by a combination of plant height and root/shoot ratio (Table 3B, Fig. 2). 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, thus species with large roots relative to shoot increased at high grazing, while species with small roots decreased. Separate analyses of subsets of selected and unselected species revealed that the best model for predicting grazing response in selected species included plant height only, whereas root/shoot ratio as well as plant height were significant predictors of grazing response of unselected herbs (Table 3B). As the models were strongly influenced by two annual species with low root/shoot ratio, we also ran the analyses without these species. The resulting model included plant height as the only significant predictor variable ($F_{1,18} = 12.51$, $R^2_{adj} = 0.377$, $p = 0.002$).

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

The relative abundance change in no sheep vs. 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.

Response to cessation of grazing was best predicted by first flowering day (positive relationship; late-flowering species thus increased in response to cessation of grazing), and C/N content in leaves (negative relationship; species with high C/N levels decreased; Table 3C). For the subset of selected herbs no traits could explain variation in *CR* at the $p < 0.05$ level, and for unselected herbs the best model included first flowering day only (Table 3C).

Discussion

Alterations of grazing regimes affect the abundance of plants (Mulder 1999; Hester et al. 2006), but the mechanisms for 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 for explaining 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-ratio 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. 2008). Small size and early flowering thus seem as viable avoidance strategies in this alpine environment.

The question of herbivore selectivity and response of palatable vs. unpalatable species to grazing is certainly a complex matter; reported patterns range from a decrease of selected species (Anderson and Briske 1995; Díaz 2000; Bråthen and Oksanen 2001; Pakeman, 2004), to no relationship (Cingolani et al. 2005), to increased abundance 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 persistence of selected species under high sheep densities is particularly important for long-term ecosystem productivity, as selected species are more easily decomposed, promoting positive feedback of nutrient cycling in the system (Frank and Groffman 1998; Frank et al. 2000).

The response to enhanced grazing pressure was best predicted by a combination of traits typical of resistance/avoidance (short plants increased in abundance when grazing pressure was enhanced while tall plants decreased) and tolerance (plants with high root/shoot ratio increased) strategies (Fig. 2), despite the fact that alpine plants in general are 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 traits that related to the response, but also 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 partly be explained by the relatively smaller difference in herbivore density between the no sheep and low sheep density treatment (0 vs. 25 sheep per km^2) compared to the low vs. high sheep density (25 vs. 80 sheep per km^2). However, the results also accord with findings of

Olofsson (2006), that immediate responses to reduced grazing pressure (indirect effects of competition) are much slower than the 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, through the generally more positive response 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 response of species with low C/N levels in leaves, both traits correlated with selectivity. We did not find evidence for an increase in tall competitive species on the expense of small, less competitive species, and no indication of decrease of 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 as 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 thus is expected to be adapted to grazing (Austrheim and Eriksson 2001), small changes in plant community structure is 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 abundances 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 non-linear 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 as functional groups are widely applied when studying grazing effects (e.g. Olofsson 2006; Bråthen et al. 2007), but inconsistent responses to grazing within growth forms are not uncommon (Grellman 2002; Austrheim et al. 2008). The plant trait perspective clearly improve our insight into mechanisms behind observed abundance changes of species when disturbance regime is altered. We found no evidence for a general decline in abundance of selected species when herbivore densities were enhanced. Instead we found that short-statured species were favoured by increased grazing pressure, probably through a combination of avoidance of herbivores and reduced competition for light, but additionally that capacity for regrowth (root/shoot ratio) was an important prerequisite for responding positively when grazing pressure was increased.

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TABLES

Table 1. Selectivity (*SI*), the proportion of sites in which the species was recorded that it was grazed, response to enhanced grazing pressure (*GR*), the relative abundance change of the species in the high sheep density treatment compared to the low sheep density treatment from 2001 to 2007, and response to cessation of grazing (*CR*), the relative abundance change of the species in the no sheep density treatment compared to the low sheep density treatment from 2001 to 2007. Selected species are defined as species with *SI* > 0.25, and unselected species as having *SI* < 0.25.

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

Table 2. Plant traits included in the study.

No	Code	Variable	Unit	Comments
1	SM	Seed mass	mg	Weight of individual seeds, estimated 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 Appendix 1).
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).
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, 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 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, Connecticut, USA) and Elemental Analyzer (PerkinElmer, Norwalk, Connecticut, USA). Between two and four samples of dried leaves were analysed 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		

Table 3. Stepwise linear regression results of (A) sheep selectivity (*SI*), (B) response to enhanced grazing pressure (*GR*), and (C) response to cessation of grazing (*CR*) as a function of plant traits, for the whole dataset ($n = 22$), and for the subsets of selected ($SI > 0.25$, $n = 11$) and unselected ($SI < 0.25$, $n = 11$) species. l.s. est. is least squares estimate, and SE is standard error. AGB = aboveground biomass, C/N = carbon/nitrogen ratio in leaves, FFD = first flowering day, PLH = plant height, RS = root/shoot ratio.

A

	SI		
	l.s. est.	SE	p
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

	GR, all			*GR*, selected			*GR*, unselected		
	l.s. est.	se	p	l.s. est.	se	p	l.s. est.	se	p
log(PLH)	−0.563	0.133	0.0007	−0.624	0.220	0.020	−0.560	0.127	0.002
log(RS)	0.418	0.150	0.0005				0.418	0.096	0.002
R^2_{adj}			0.531			0.413			0.816

C

	CR, all			*CR*, unselected		
	l.s. est.	se	p	l.s. est.	se	p
FFD	0.015	0.004	0.003	0.011	0.004	0.030
C/N	−0.029	0.012	0.024			
R^2_{adj}			0.372			0.360

FIGURES

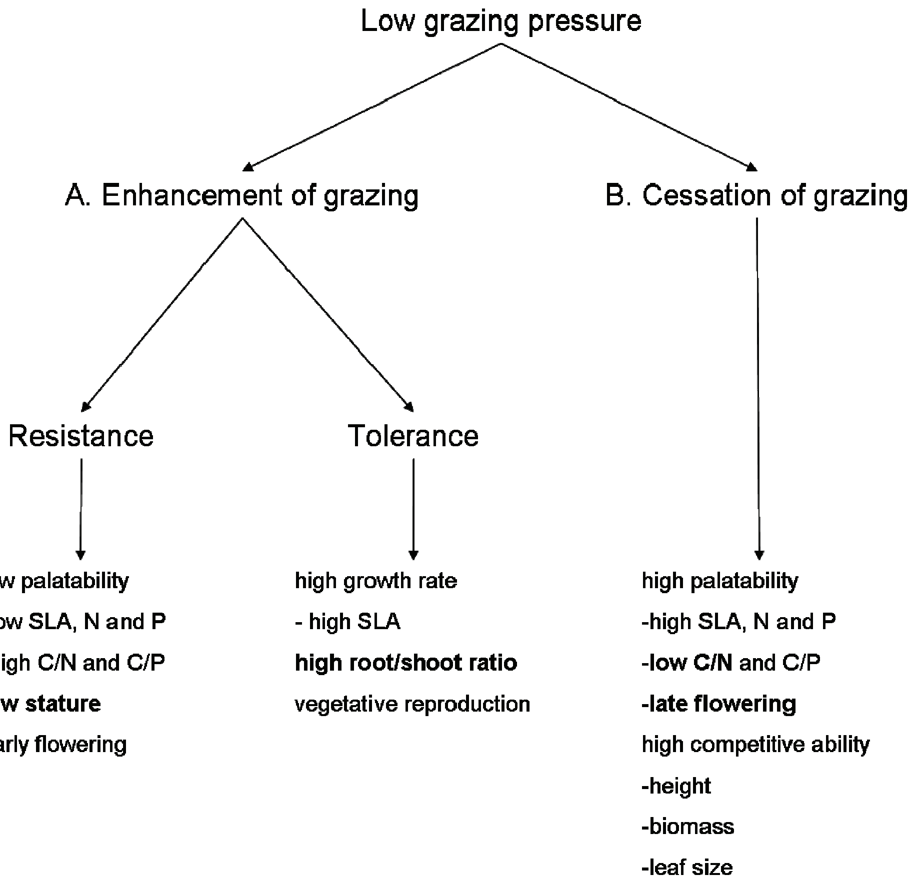

Figure 1. Plant traits associated with a positive response (in terms of abundance change of plants) in an experimental design with a. enhancement or b. cessation of grazing pressure, depending on the main strategy of species response to grazing; resistance or tolerance. Traits in bold are found as significant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

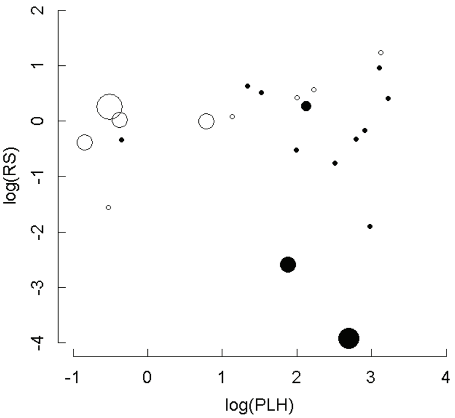

Figure 2. The relationship between response to enhanced grazing pressure, shown as circles, and plant height (PLH) and root/shoot ratio (RS). Black circles are negative responses (GR < 0), open circles are positive responses (GR > 0), and the size of the circles reflects the magnitude of response.

SUPPLEMENTARY MATERIAL

to Evju, Austrheim, Halvorsen and Mysterud:

Table S1. Average trait values (± standard deviation) for each species, based on sampling of 10 individuals for each trait, except plant height, which was sampled on 20 individuals for each species.

Species	**Seed mass (mg)**	**Seed number**	**Allocation to reproduction**	**First flowering day (Julian day)^a**	**Plant height (cm)**	**Leaf size (mm^2)**	**Above-ground biomass (mg)**	**Below-ground biomass (mg)**
Alchemilla alpina	0.36^a	25.0^a	0.17 ± 0.05	193.0	7.4 ± 2.2	396.7 ± 206.9	0.26 ± 0.16	0.35 ± 0.22
Alchemilla sp.	0.21 ± 0.07	59.8 ± 44.7	0.13 ± 0.09	169.3	8.4 ± 5.9	1954.2 ± 1371.0	0.82 ± 0.54	1.03 ± 0.89
Bistorta vivipara	1.44^f ± 0.78	22.1^f ± 8.2	0.42 ± 0.11	174.7	9.3 ± 4.0	215.9 ± 122.9	0.11 ± 0.06	0.17 ± 0.09
Euphrasia wettsteinii	0.18^a	44.0^a	0.32 ± 0.07	193.1	6.6 ± 2.5	8.3 ± 3.7	0.012 ± 0.007	0.0009 ± 0.0006
Geranium sylvaticum	3.7 ± 1.2	20.7 ± 11.9	0.26 ± 0.11	193.1	25.1 ± 9.6	1501.5 ± 833.1	0.90 ± 0.36	1.40 ± 0.72
Hieracium alpinum	0.38 ± 0.09	64.1 ± 21.2	0.29 ± 0.12	202.1	0.67 ± 0.32	345.1 ± 159.8	0.23 ± 0.11	0.15 ± 0.08
Leontodon autumnalis	0.56 ± 0.03	39.7 ± 14.1	0.25 ± 0.14	198.9	0.55 ± 0.23	184.6 ± 100.9	0.11 ± 0.06	0.098 ± 0.045
Melampyrum sylvaticum	5.6 ± 0.4	10.2 ± 5.1	0.39 ± 0.10	187.1	14.8 ± 3.2	119.0 ± 88.8	0.26 ± 0.22	0.0057 ± 0.0051
Omalotheca norvegica	0.061 ± 0.006	983.9 ± 477.5	0.48 ± 0.08	203.1	12.3 ± 3.3	287.0 ± 86.4	0.32 ± 0.12	0.15 ± 0.06
Omalotheca supina	0.075 ± 0.022	33.0 ± 21.3	0.36 ± 0.11	194.2	0.43 ± 0.21	21.6 ± 8.7	0.025 ± 0.010	0.017 ± 0.009
Potentilla erecta	0.21 ± 0.03	22.9 ± 22.8	0.075 ± 0.068	187.1	22.4 ± 10.1	265.3 ± 107.0	0.55 ± 0.41	1.09 ± 0.97

Pyrola minor	0.0007[a]	5000[a]	0.27 ± 0.05	200.4	0.59 ± 0.21	465.8 ± 203.5	0.29 ± 0.10	0.058 ± 0.018
Ranunculus acris	0.80 ± 0.04	34.6 ± 22.5	0.25 ± 0.08	171.6	18.3 ± 6.6	343.8 ± 230.6	0.23 ± 0.20	0.18 ± 0.12
Rumex acetosa	0.79 ± 0.27	76.6 ± 131.7	0.31 ± 0.09	172.3	22.7 ± 9.9	374.9 ± 283.3	0.44 ± 0.38	1.23 ± 1.01
Saussurea alpina	2.1[a]	5.5[a]	0.38 ± 0.11	209.7	19.7 ± 7.7	756.7 ± 320.2	1.03 ± 0.55	0.16 ± 0.13
Sibbaldia procumbens	0.45 ± 0.02	52.9 ± 44.7	0.39 ± 0.13	168.6	3.1 ± 0.9	189.0 ± 83.8	0.15 ± 0.08	0.14 ± 0.15
Solidago virgaurea	0.46[a]	17.3[a]	0.31 ± 0.10	200.7	16.3 ± 7.1	471.1 ± 117.1	0.66 ± 0.42	0.45 ± 0.33
Taraxacum sp.	0.82 ± 0.08	67.5 ± 42.6	0.24 ± 0.08	180.6	0.69 ± 0.35	696.4 ± 214.7	0.33 ± 0.15	0.33 ± 0.19
Trientalis europaea	0.68[e]	9.6[e]	0.16 ± 0.08	188.3	4.6 ± 3.4	124.6 ± 83.2	0.030 ± 0.024	0.027 ± 0.025
Veronica alpina	0.054[a]	282[a]	0.32 ± 0.13	183.3	7.3 ± 1.5	62.2 ± 23.4	0.071 ± 0.032	0.042 ± 0.022
Viola biflora	0.77 ± 0.09	10.1 ± 7.4	0.35 ± 0.14	161.5	3.8 ± 1.6	182.1 ± 87.8	0.046 ± 0.022	0.058 ± 0.033
Viola palustris	0.58 ± 0.08	18.4 ± 6.9	0.36 ± 0.14	169.4	2.2 ± 1.2	311.3 ± 141.2	0.045 ± 0.016	0.045 ± 0.027

Table S1 continued

Species	**Root/shoot ratio**	**Vegetative reproduction (% of sampled plants)**	**Specific leaf area (mm^2/mg)**	**N content in leaves (%)**	**P content in leaves (%)**	**C/N in leaves**	**C/P in leaves**
Alchemilla alpina	1.53 ± 0.80	30	9.9 ± 1.0	1.75 ± 0.24	0.25 ± 0.02	27.6 ± 3.6	190.4 ± 12.1
Alchemilla sp.	1.30 ± 0.49	20	14.9 ± 2.6	1.66 ± 0.34	0.18 ± 0.03	28.3 ± 5.6	253.8 ± 44.9
Bistorta vivipara	1.75 ± 0.81	0	15.3 ± 2.6	3.11 ± 0.09	0.56 ± 0.004	15.3 ± 0.1	85.1 ± 1.3
Euphrasia wettsteinii	0.075 ± 0.028	0	31.0 ± 14.3	2.93*	0.47*	15.6*	98.2*
Geranium sylvaticum	1.51 ± 0.60	10	14.7 ± 2.3	2.12 ± 0.19	0.22 ± 0.03	22.5 ± 1.8	219.5 ± 28.9
Hieracium alpinum	0.71 ± 0.30	0	20.5 ± 4.9	2.59 ± 0.22	0.45 ± 0.03	17.4 ± 1.5	100.7 ± 6.8
Leontodon autumnalis	1.29 ± 0.58	30	19.5 ± 3.1	2.54 ± 0.35	0.25 ± 0.13	17.8 ± 2.7	210.4 ± 84.7
Melampyrum sylvaticum	0.02 ± 0.008	0	15.4 ± 3.0	1.49 ± 0.07	0.24 ± 0.01	29.9 ± 1.3	182.3 ± 6.1
Omalotheca norvegica	0.47 ± 0.17	0	18.2 ± 2.1	2.13 ± 0.49	0.33 ± 0.16	21.4 ± 4.5	150.5 ± 68.5
Omalotheca supina	0.68 ± 0.26	50	29.6 ± 7.8	2.44 ± 0.19	0.37 ± 0.07	18.8 ± 1.6	125.7 ± 23.0
Potentilla erecta	2.61 ± 1.77	80	18.4 ± 3.7	2.53 ± 0.22	0.23 ± 0.04	18.5 ± 1.6	210.8 ± 38.3
Pyrola minor	0.21 ± 0.07	20	14.9 ± 1.8	1.73 ± 0.30	0.23 ± 0.07	29.7 ± 5.2	230.1 ± 63.4
Ranunculus acris	0.85 ± 0.25	0	17.6 ± 3.1	2.66 ± 0.06	0.24 ± 0.01	17.1 ± 0.9	192.6 ± 11.7
Rumex acetosa	3.44 ± 2.48	0	21.6 ± 3.8	3.87 ± 0.23	0.44 ± 0.03	11.9 ± 0.7	103.6 ± 6.1
Saussurea alpina	0.15 ± 0.06	30	16.7 ± 2.5	2.14 ± 0.35	0.16 ± 0.03	20.8 ± 2.8	280.4 ± 38.2
Sibbaldia procumbens	1.08 ± 1.09	60	15.1 ± 2.4	2.17 ± 0.25	0.26 ± 0.08	22.2 ± 2.5	195.2 ± 53.5

Solidago virgaurea	0.72 ± 0.34	20	17.8 ± 1.6	2.51 ± 0.39	0.33 ± 0.09	18.7 ± 2.6	148.4 ± 33.6
Taraxacum sp.	1.01 ± 0.44	20	27.8 ± 4.7	2.88 ± 0.10	0.31 ± 0.02	15.5 ± 0.5	143.7 ± 8.2
Trientalis europaea	1.67 ± 2.55	100	34.5 ± 5.9	1.92 ± 0.29	0.22 ± 0.04	25.0 ± 3.9	217.3 ± 46.9
Veronica alpina	0.59 ± 0.19	40	25.8 ± 7.4	2.64 ± 0.13	0.23 ± 0.02	17.6 ± 0.8	200.7 ± 15.3
Viola biflora	1.89 ± 1.85	0	31.4 ± 6.1	2.84 ± 0.02	0.37 ± 0.02	15.6 ± 0.1	118.5 ± 7.6
Viola palustris	0.99 ± 0.46	20	23.0 ± 3.1	2.67 ± 0.45	0.25 ± 0.01	16.7 ± 2.9	178.4 ± 6.0

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[f] bulbil number and mass.

Table S2. Single trait correlations (Pearson's correlation coefficient) with sheep selectivity (*SI*), response to enhanced grazing (*GR*), and response to cessation of grazing (*CR*) for the whole dataset ($n = 22$), selected species ($SI > 0.25$, $n = 11$) and unselected species ($SI < 0.25$, $n = 11$).

Trait	***SI***	***GR***	***GR*, selected**	***GR*, unselected**	***CR***	***CR*, selected**	***CR*, unselected**
log(seed mass)	0.196 ns	−0.130 ns	0.087 ns	−0.367 ns	−0.101 ns	0.217 ns	−0.541 *
log(seed number)	0.045 ns	0.081 ns	0.008 ns	0.162 ns	0.139 ns	−0.010 ns	0.406 ns
Allocation to reproduction	0.030 ns	−0.079 ns	−0.021 ns	−0.095 ns	0.283 ns	0.479 ns	−0.067 ns
First flowering day	0.416 *	0.085 ns	0.168 ns	−0.125 ns	0.503 **	0.456 ns	0.651 **
log(plant height)	0.235 ns	−0.633 ***	−0.687 **	−0.708 **	−0.216 ns	−0.192 ns	−0.437 ns
log(leaf size)	0.583 ***	0.019 ns	−0.481 ns	0.246 ns	−0.218 ns	−0.463 ns	−0.359 ns
log(aboveground biomass)	0.771 ***	−0.189 ns	−0.714 **	−0.183 ns	−0.093 ns	−0.374 ns	−0.149 ns
log(belowground biomass)	0.590 ***	0.123 ns	−0.481 ns	0.493 ns	−0.198 ns	−0.497 ns	−0.344 ns
log(root/shoot)	0.044 ns	0.420 *	0.111 ns	0.703 **	−0.226 ns	−0.296 ns	−0.339 ns
Vegetative reproduction	−0.265 ns	0.185 ns	0.120 ns	0.331 ns	−0.210 ns	−0.174 ns	−0.292 ns
log(specific leaf area)	−0.295 ns	0.147 ns	0.423 ns	0.074 ns	0.188 ns	0.408 ns	0.165 ns
Nitrogen	0.050 ns	0.251 ns	0.222 ns	0.258 ns	0.188 ns	0.263 ns	0.016 ns
C/N	−0.107 ns	−0.316 ns	−0.336 ns	−0.288 ns	−0.285 ns	−0.528 *	0.023 ns
Phosphorus	−0.083 ns	−0.011 ns	0.027 ns	−0.013 ns	0.163 ns	0.230 ns	0.139 ns
C/P	0.112 ns	0.021 ns	−0.023 ns	0.033 ns	−0.271 ns	−0.360 ns	−0.166 ns

ns: $p > 0.10$, *: $0.05 < p < 0.10$, **: $0.01 < p < 0.05$, ***: $p < 0.01$

Evju, M., Halvorsen, R., Rydgren, K., Austrheim, G. and Mysterud, A. 2008. Effects of sheep grazing and temporal variability on population dynamics of the clonal herb Geranium sylvaticum in an alpine habitat. Manuscript.

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Effects of sheep grazing and temporal variability on population dynamics of the clonal herb *Geranium sylvaticum* in an alpine habitat

Marianne Evju[1*], Rune Halvorsen[1], Knut Rydgren[2], Gunnar Austrheim[3] and Atle Mysterud[4]

[1] Department of Botany, Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway
[2] Faculty of Science, Sogn og Fjordane University College, P.O. Box 133, N-6851 Sogndal, Norway
[3] Museum of Natural History and Archaeology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway
[4] Centre for Evolutionary and Ecological Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway
*Corresponding author; marianne.evju@nhm.uio.no, fax: +47 22 85 18 35

Running headline: Population dynamics of a grazed perennial

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Population dynamics of *Viola biflora*, a small, non-selected herb in a sheep grazing experiment

Marianne Evju[1*], Rune Halvorsen[1], Knut Rydgren[2], Gunnar Austrheim[3] and Atle Mysterud[4]

[1] Department of Botany, Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

[2] Faculty of Science, Sogn og Fjordane University College, P.O. Box 133, N-6851 Sogndal, Norway

[3] Museum of Natural History and Archaeology, Norwegian University of Science and Technology, N-7491 Trondheim, Norway

[4] Centre for Evolutionary and Ecological Synthesis (CEES), Department of Biology, University of Oslo, P.O. Box 1066 Blindern, N-0316 Oslo, Norway

*Corresponding author; marianne.evju@nhm.uio.no, fax: +47 22 85 18 35

Running headline: Population dynamics of a non-grazed herb