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Experimental effects of herbivore density on above-ground plant biomass in an alpine grassland ecosystem

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Abstract

Herbivores may increase or decrease aboveground plant productivity depending on factors such as herbivore density and habitat productivity. The grazing optimization hypothesis predicts a peak in plant production at intermediate herbivore densities, but has rarely been tested experimentally in an alpine field setting. In an experimental design with three densities of sheep (high, low, and no sheep), we harvested aboveground plant biomass in alpine grasslands prior to treatment and after five years of grazing. Biomass of vascular plants decreased at high sheep density, and marginally increased at low sheep density. The ungrazed treatment was found to be intermediate. Companion studies conducted at the same site suggest, (1) that changes in soil N-mineralization and plant community patterns are contributing to the herbivore-induced effects on plant productivity in alpine grasslands, (2) that herbivore-driven changes in plant productivity feed into the future performance for the herbivore as the marginal increase in productivity at low density corresponds with a temporal increase in lamb growth. Our study provides experimental evidence for a nonlinear effect of increased grazing on plant productivity as predicted by the grazing optimization hypothesis. This has important repercussions for ecosystem function and management, as it demonstrates how herbivore density can either increase or decrease ecosystem productivity over time.

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Introduction

Plant biomass (quantity) and nutrient content (quality) are of key importance for ecosystem functioning, with effects on trophic interactions such as decomposition and nutrient cycling as well as herbivore growth (Hobbs, 1996). However, herbivores may in return strongly affect available plant biomass because the processes of foraging, trampling, and deposition of feces and urine impact aboveground plant productivity (e.g., Milchunas and Lauenroth, 1993; Frank et al., 1994; Augustine and McNaughton, 1998). According to the grazing optimization hypothesis, increased grazing should affect plant productivity in a nonlinear way by increasing both biomass and nutrient content to a certain level (McNaughton, 1979; Hilbert et al., 1981; McNaughton, 1983; Dyer et al., 1986). At high densities, productivity is predicted to decrease. The optimal herbivore density for plant productivity is especially dependent on habitat productivity (McNaughton, 1979; Wardle et al., 2004). Positive effects of herbivory on plant productivity are most often found in productive systems with high soil fertility and moisture, such as subtropical grasslands grazed by large ungulates (McNaughton, 1979), but also in fertile tundra vegetation grazed by geese (Hik and Jefferies, 1990) and reindeer (Olofsson, 2001). However, since appropriate testing of the grazing optimization hypothesis requires at least three herbivore levels, this has rarely been done in fully experimental field studies.

Several mechanisms have been suggested to explain the positive effect of herbivory on plant productivity, including grazing effects on nutrient cycling, physiological processes in plants, as well as effects on plant species composition. First, herbivores may increase the rate of nutrient cycling (Mulder and Ruess, 1998; Wardle et al., 2004). Threshold levels or a

decline in productivity would thus imply a shortage in mineralized nitrogen or other important nutrients. However, a general assumption states that the fraction of nutrients removed by the herbivore should be smaller than the input for grazing optimization to occur (De Mazancourt et al., 1998). Second, accumulation of litter in the vegetation of nongrazed ecosystems may decrease light availability and plant growth, whereas herbivory is predicted to promote younger and photosynthetic-active plants, which would increase the productivity (Milchunas and Lauenroth, 1993). Third, herbivores may also induce a shift in the plant community composition toward dominance of less productive species at high as compared to low density (Augustine and McNaughton, 1998; Bråthen et al., 2007). Species-specific responses tend to depend on growth-form group. Tolerant graminoids are expected to increase at high herbivore densities in alpine grassland ecosystems, while selected herbs generally decrease (Austrheim et al., 2008). Woody species, which generally are less favored by grazing herbivores, are still browsed at the sapling stage. Even low herbivore densities are found to prevent recruitment of birch in the tree-line ecotone (Speed et al., 2010). Bryophytes and lichens, both important in alpine habitats, might show an increase at high herbivore densities due to reduced competition from vascular plants if they are not damaged by trampling (Van Der Wal and Brooker, 2004).

Knowledge of the relative importance of these processes for plant productivity responses to grazing is still limited. Theoretical ecosystem models (Leriche et al., 2001) suggest that grazing optimization emerges as a complex result of several processes with positive and negative, direct and indirect effects on plant productivity. However, different relevant processes are often difficult to include within a common experimental design.

In this study, we examine the effect of three levels of grazing on plant productivity by calculating change in aboveground plant biomass (APB) after five years using an experimental design with high, low, and zero sheep replicated three times in an alpine ecosystem. Alpine ecosystems are heterogeneous with large variations in both plant quantity and quality (Körner, 2003). As an experimental habitat we used grasslands, which are highly selected by sheep (Mobæk et al., 2009) and dominated by herbaceous biomass with a more rapidly responding growth-form compared to woody plants (Skarpe and Hester, 2008). Aboveground plant biomass (APB) was harvested in 2002 (at the start of the grazing treatment) from caged plots protected from grazing during that year, and compared with biomass harvested after five years of grazing (2008) for all main growth-form groups (graminoids, herbs, shrub species, cryptogams) as well as total biomass and total vascular plant biomass. We addressed the following questions: (1) Will APB peak at intermediate grazing levels as predicted by the grazing optimization hypothesis? (2) To what extent are herbivore-induced changes in APB related to plant growth-form group? To assess potential mechanisms, grazing effects on APB are discussed in an ecosystem perspective by linking the results to previously published data from the same experimental design on how sheep density affects N-mineralization and content in plants, plant demography, and plant community composition as well as the performance of sheep, rodents, and herbivorous insects.

Methods

STUDY AREA

The study was conducted in an alpine ecosystem in Hol municipality, southern Norway (between 60°40′–60°45′N and 7°55′–8°00′E). Dwarf-shrub heathland dominates the vegetation cover (51%) with lichen heaths (17%) as well as more productive lee-side grasslands (9%) and snowbed vegetation (12%) also common (see Austrheim et al., 2008, for more details). Mean annual temperature as interpolated from nearby weather stations is –1.6 °C, mean temperature from June to August is 7.9 °C, while mean annual precipitation amounts to 1000 mm (data provided by Norwegian Meteorological Institute for the period 1957–2009).

EXPERIMENTAL DESIGN

We used an experimental enclosure (2.7 km²), split into nine parallel subenclosures (~0.3 km² each) with three different densities of sheep in a randomized block design in the low alpine zone from 1050 m to ~1320 m a.s.l. (Fig. 1). Each treatment was thus replicated three times in a blockwise manner. The fences were erected in 2001, and experimental grazing started in summer 2002. Grazing lasted from late June to late August/early September, and 80, 25, and 0 sheep per km² were chosen for high sheep density, low sheep density, and ungrazed treatments. Densities of sheep were set based on grazeable area quantified by a vegetation survey and represent density levels typical for alpine pastures in southern Norway (Rekdal, 2001). All sheep were of the Dala breed, which is the most common breed used in Norway. The sheep were found to select high productivity grasslands (Mobæk et al., 2009). Sheep diet varied within a season and among years, and both sheep age class (adult vs. lamb) and density affected the quantity of different plant taxa in the diet (Mobæk et al., 2012b).

We sampled plant biomass from six grassland plots (circumference between 2 and 5 m) in each subenclosure, giving a total of

54 plots. The grassland plots used for this study were moderately base-rich (mean soil base saturation of 41.9% and 27.5% in lee sides and snowbeds, respectively [Martinsen et al., 2011] and exchangeable Ca ~110 mg 100 g soil⁻¹ as a mean for both grassland habitats [Martinsen, 2010]). Mean soil pH was 4.8 and 4.5 in lee-side and snow-bed soil, respectively. Potential N-mineralization rates were low (0.1–1.6 µg N g soil organic matter⁻¹ day⁻¹) and amounts of available N in situ were decreasing during the growing season (Martinsen et al., 2012). Estimated atmospheric N-deposition was 0.42 g N m⁻² yr⁻¹, which compensated the estimated N removal by sheep at high densities (Martinsen et al., 2012). All soil studies were conducted in summers 2006–2008.

Aboveground plant biomass was harvested twice in 54 grassland plots (44 cm × 80 cm). Plots were selected with a balanced stratification among vegetation types (lee side and snowbeds) and altitudinal levels. The harvest was done by the same person between 6 and 10 August 2002 and 2008 by clipping with cutters as close to the ground as possible without including the roots of vascular plants. All plots were protected by a wire cage (mesh size 1.5 cm) during the summer seasons of 2002 and 2008 to prevent grazing by sheep, rodents, and other vertebrate herbivores in the year of harvest. The plots were grazed as normal during summers 2003–2007; thus the grazing treatment lasted five years. Rodent population growth rate varied among years (Steen et al., 2005), but rodent grazing was not found to be affected by sheep grazing in the grassland habitats (Austrheim et al., 2008). Each sample was sorted into four main growth-forms; herbs, graminoids, shrub species (dwarf and erect shrubs), and cryptogams (bryophytes and lichens), dried at 60 °C for 24 hours, and weighed.

STATISTICAL ANALYSES

We examined how grazing affected change in relative aboveground plant biomass (APB) from year 2002 and 2008 by modeling the difference in biomass between years ($\text{biomass}_{2008} - \text{biomass}_{2002}$) offset against the baseline biomass in 2002 for each growth-form group (graminoids, shrub species, herbs, cryptogams), as well as for all vascular plant groups and total plant biomass. Gaussian family linear mixed models were used with grazing treatment (three levels: high, low, and zero sheep densities) as a fixed factor and plot nested within subenclosure included as a random effect. Contrasts between low and high density, and low and ungrazed are presented as the low sheep density represents a continuum of previous management (Austrheim et al., 2008). The effects of block and elevation were examined but did not improve the models as evaluated by Akaike's information criterion (AIC). Analyses were conducted using the program R ver. 2.15.0 (R Development Core Team, 2012) and the nlme package (Pinheiro et al., 2012).

Results

Mean aboveground plant biomass (APB) in 2002 (prior to grazing treatment) was 160.2 g m⁻². Graminoids formed the largest constituent of the aboveground biomass (75.6 g m⁻², 47%), over shrubs (50.1 g m⁻², 31%), herbs (19.4 g m⁻², 12%), and cryptogams (15.1 g m⁻², 9%) (Table 1).

Aboveground vascular plant biomass decreased from 2002 to 2008 at high sheep densities (Fig. 2, part a). The resulting change in aboveground biomass at high density differed significantly from the low density treatment (–42.85 g m⁻², s.e. = 15.57, df = 6, p = 0.033), which marginally increased (20.47 g m⁻², s.e. = 11.01, df = 6, p = 0.070). Change in total APB in plots with low sheep density

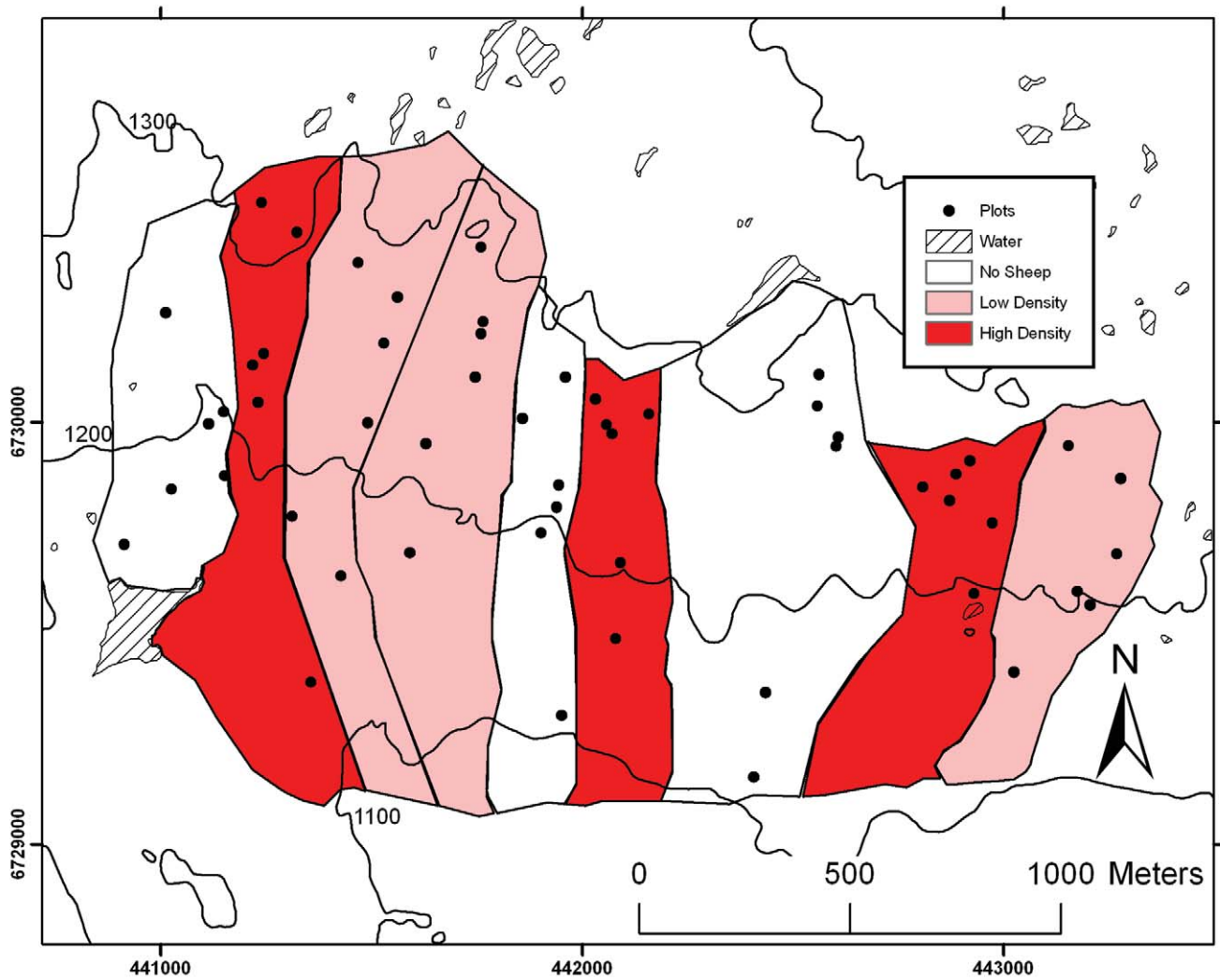


FIGURE 1. Study area and experimental design of the sheep grazing study in Hol, Norway. Black dots represent experimental plots used for biomass harvest in 2002 and 2008. Contour lines (100 m) are included to show elevation. UTM grid zone 32V.

TABLE 1

Aboveground plant biomass (g m^{-2}) given for different growth form groups as a mean value for plots at each grazing treatment in 2002 and 2008. TVPB = total vascular plant biomass; TPB = total plant biomass. Number of biomass plots = 6 for each enclosure (total = 54). SE given in parentheses.

Grazing treatment and year	Graminoids	Shrubs	Herbs	TVPB	Cryptogams	TPB
No sheep						
2002	74 (11.9)	63.6 (10.8)	17.9 (6.2)	155.5 (15.1)	17 (3.4)	172.5 (14)
2008	72.6 (7.2)	72.8 (12.9)	16.6 (4.2)	161.9 (15.8)	8.9 (3.3)	170.8 (16.1)
Low sheep density						
2002	88.2 (12.4)	42 (9.5)	18.6 (4.4)	148.8 (10.1)	16.2 (4.3)	165 (10.5)
2008	88 (15.8)	59.7 (11.7)	21.6 (6.1)	169.3 (13.5)	6.9 (2.8)	176.2 (12.9)
High sheep density						
2002	64.5 (10.7)	44.6 (12.7)	21.6 (4.6)	130.8 (12.6)	12.3 (2.7)	143.1 (13.1)
2008	56.4 (13.1)	34.7 (7.6)	17.2 (3.3)	108.4 (13.7)	14.5 (4.5)	122.9 (12.8)

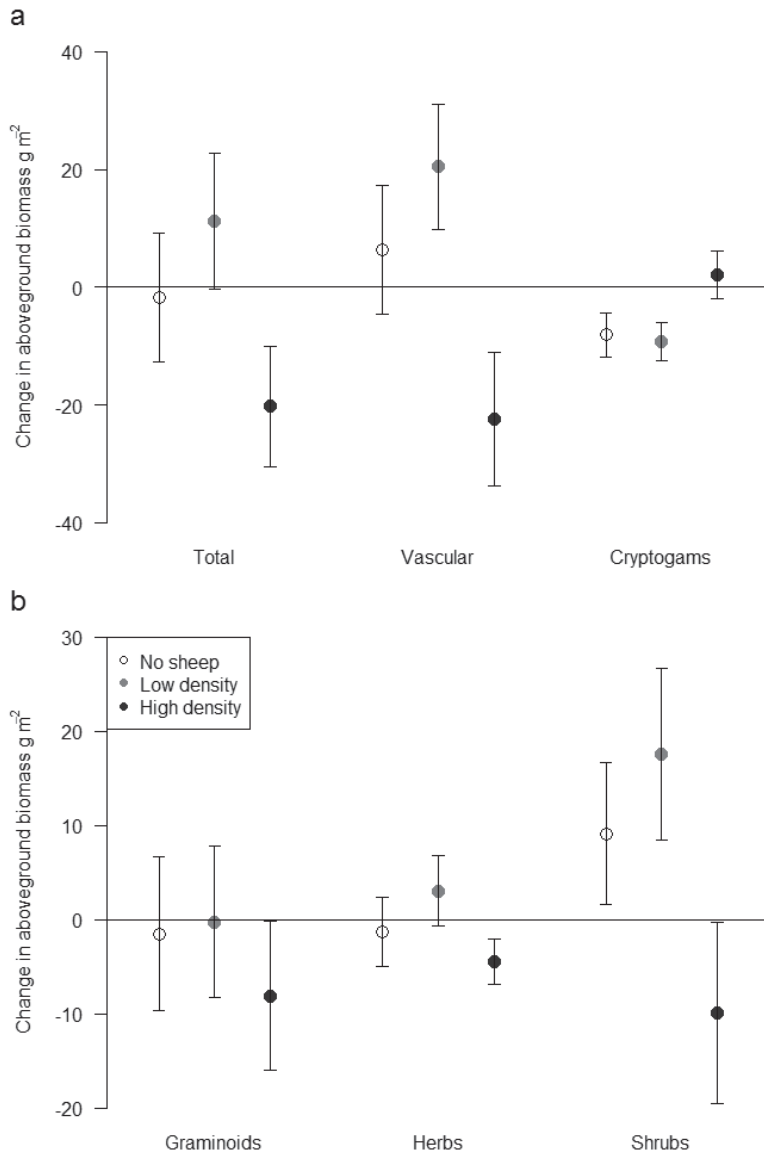


FIGURE 2. Change in aboveground plant biomass from 2002 to 2008 for different growth-form groups. Number of biomass plots = 6 for each enclosure (total = 54). Error bars denote standard errors estimated from the mixed model. (a) Change in total plant biomass, vascular plant biomass, and cryptogam biomass. (b) Change in biomass for graminoids, herbs, and shrubs.

did not differ from APB at high densities (l.s. = 0.2449, s.e.=0.12, df = 6, $p = 0.089$) due to a decrease in cryptogams at low densities (-9.26 g m^{-2} , s.e. = 4.20, df = 6, $p = 0.032$), while cryptogams marginally increased at high sheep densities (11.44 g m^{-2} , s.e. = 5.93, df = 6, $p = 0.102$, Fig. 2, part a). Graminoids showed no differences in change in APB between grazing treatments, but woody species (-27.50 g m^{-2} , s.e. = 14.83, df = 6, $p = 0.113$) and herbs (-7.50 g m^{-2} , s.e. = 4.71, df = 6, $p = 0.162$) tended to decrease at high versus low density (Fig. 2, part b).

Discussion

Large herbivores are an important driver in many ecosystems with strong effects on vital components such as plant productivity and plant nutrient quality. Both positive (Olofsson et al., 2001) and negative effects of herbivory on plant productivity (Bråthen et al., 2007) are reported from alpine ecosystems, and diverging effects are suggested to depend on factors such as herbivore density, habitat productivity, and spatiotemporal scale (Milchunas and Lauen-

roth, 1993). A former study reporting a peak in plant productivity at intermediate herbivore density levels relied on a mixture of naturally occurring spatial variation and grazing exclosures (Stewart et al., 2006). However, no fully experimental studies that we are aware of have examined the effect of different levels of herbivore density on plant productivity.

In this study conducted in alpine grasslands using an experimental design at a landscape scale, we found a decrease in APB of vascular plants at high sheep densities after five years of experimental grazing. The change in vascular APB differed significantly from the low sheep density treatment where APB marginally increased, while nongrazed enclosures showed no change in APB. Though marginally significant, our results indicate a facilitation process at low sheep density in accordance with the grazing optimization hypothesis. A temporal increase in lamb growth at low density at the same experimental enclosure (Møbæk et al., 2012a) is also indicative of a facilitation process at the low density treatment mediated by grazing effects on plants. A corresponding decrease in lamb growth (Møbæk et al., 2012a), rodent population growth

rates (Steen et al., 2005), and herbivorous-invertebrate abundance (Mysterud et al., 2010) at high versus low sheep densities shows that herbivore growth is limited (along with APB) at high grazing and highlights the importance of grazing-induced changes in plant productivity for trophic interactions.

Herbivore-mediated increases in plant productivity are usually explained by an accelerating mineralization of nitrogen (N) or other essential nutrients (Loreau, 1995; McNaughton et al., 1997; Frank and Groffman, 1998; De Mazancourt et al., 1998). Particularly in productive habitats, the N-mineralization rate has been shown to respond positively to high herbivore density (McNaughton, 1979; Wardle et al., 2004). Although the grassland plots used in this experiment are considered to be productive with easy decomposable plant biomass, the growing season is limited (~74 days at 1222 m a.s.l., >5 °C) with fairly low temperatures that likely slow down turnover rates of soil organic matter (Budge et al., 2011). However, grazing did increase the rates of potential N-mineralization in the order high density > low density > no grazing, although the effect was evaluated as minor (Martinsen et al., 2012). N-content was higher for the two most abundant grasses (*Avenella flexuosa* and *Anthoxanthum odoratum*) at high and low sheep density as compared to no sheep at the end of the growing season. N-content did not increase for herbs and woody species, indicating that graminoids were good competitors for bio-available N (Mysterud et al., 2011). However, bio-available soil N, which decreased in the course of the growing season, was also slightly higher at high and low density as compared to no grazing at the end of the growing season (Martinsen et al., 2012). Our results thus indicate that grazing causes an increase in N-mineralization even from low to high sheep densities. Moreover, the N budget for the total system indicates an accumulation of N at low sheep densities (Martinsen et al., 2012). Our study system thus fulfills the assumption of a positive nutrient budget at low herbivore density, which is needed for grazing optimization to occur (De Mazancourt et al., 1998).

According to physiological mechanisms, grazing is expected to increase plant growth in comparison to ungrazed plots where litter and old, less active photosynthetic plant tissue accumulate (Milchunas and Lauenroth, 1993; De Mazancourt et al., 1998; Knapp et al., 2012). Demographic studies on two herbs within the same experimental design show a grazing-induced transition toward younger plants (Evju et al., 2010, 2011). Although our results show a tendency for increased plant productivity at low sheep density as compared to no grazing, which partly may be caused by increased light availability, the reduced productivity at high sheep density where vegetation is subjected to high plant removal and thus high light availability is more striking.

An herbivore-mediated change in plant community composition is an alternative or additive mechanism for grazing-induced changes in plant productivity (Arsenault and Owen-Smith, 2002). These are more indirect effects caused by changes in competitive interactions that reflect direct responses to grazing and trampling as well as changing nutrient conditions. Although the low sheep density treatment caused minor changes in plant species abundances (Austrheim et al., 2008; Speed et al., 2012), facilitation could be identified as herbs, which are more nutrient rich compared to shrub species and graminoids (Mysterud et al., 2011), tended to increase their productivity at low sheep densities while decreasing at high sheep densities. This corresponds with a higher grazing frequency and lower herb height at high versus low sheep densities at the same site (Evju et al., 2006).

More surprisingly, shrubs also tended to increase at low sheep density, despite the fact that *Salix* spp. (which is the dominating

shrub taxa in grasslands; Austrheim et al., 2008) is used to some extent by sheep at the site (Møbæk et al., 2012b). A corresponding decrease in APB at high sheep density might indicate that *Salix* productivity is not sustained at high grazing in grassland, which is a habitat preferred by sheep (Møbæk et al., 2009). In contrast, radial growth of mountain birch (*Betula pubescens* ssp. *czerepanovii*) was constrained by both low and high sheep densities (Speed et al., 2011b), while shoot growth was only constrained at high sheep densities (Speed et al., 2011a). Interestingly, the more grazing-tolerant graminoids, which are found to be good competitors for nutrients in grazed systems in arctic/alpine ecosystems (Olofsson et al., 2002; Stark et al., 2002), showed no response in APB after five years of grazing treatment.

Bryophytes and lichens, which are not eaten by sheep, were found to increase at high sheep density compared to both low density and ungrazed enclosures. It is well known that the general increased importance of cryptogams (and in particular bryophytes) in Arctic and alpine systems relative to herbivore-selected vascular plants is mediated by grazing, especially in humid habitats (Van Der Wal and Brooker, 2004). At our study site, subjected to only summer grazing by sheep, bryophytes, which are able to photosynthesize at lower temperatures as compared to vascular plants (Longton, 1988), may have a competitive advantage in both early spring and autumn when both snow and sheep are absent. We suggest that bryophytes use the mineralized N to increase or maintain their growth in high sheep density enclosures at the end of the growing season when vascular plants in the preferred grassland habitat are low.

In addition to grazing-induced changes among main growth-form groups, grazing may also affect plant productivity through changing the composition of plant functional types (Skarpe and Hester, 2008). Grazing is in general expected to increase the root:shoot ratio among plants (Diaz S. et al., 2007) but Evju et al. (2009) also found a species-specific increase of herbs with a high root:shoot ratio from 2001 to 2007 at high densities in Hol, suggesting that grazing might induce a change in community composition favoring plants that are more grazing tolerant but also poorer in APB. Thus, it is important to keep in mind that total plant biomass (i.e., including the belowground biomass) will not necessarily decrease as a consequence of increased herbivore densities. However, APB is the most relevant parameter for the management of grazing in alpine ecosystems.

Conclusions

Plant productivity is an important factor for several aspects of sustainable management but could cause both positive and negative ecosystem effects. High productivity is a key for maintaining herbivore growth (Stewart et al., 2006), while an increase in APB in seminatural grassland ecosystems often leads to a decrease in vascular plant diversity due to competitive interactions (Skarpe and Hester, 2008). Our study shows a nonlinear relationship between vascular plant productivity and herbivore density, with an increased APB at low sheep density and a decreased APB at high density. Thus, we highlight that a herbivore density threshold for sustaining productivity in alpine grasslands exists. This insight has huge repercussions for management of large herbivores. Management practices may thus drive the ecosystem toward either lower or higher productivity in the long-term depending on herbivore density.

Companion studies conducted at the same experimental site suggest that changes in soil N-mineralization, plant demography,

plant N-content, and plant community patterns are all potential mechanisms for explaining these herbivore-induced changes in plant productivity. Although N-mineralization increased linearly with grazing, grazing induced contrasting effects in plant community patterns at low versus high sheep densities that most likely limited plant productivity at high densities. The increase in productivity at low density corresponds with a temporal increase in lamb growth, and shows that herbivore-driven changes in plant productivity feed into future performance for the herbivore.

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