Plant quality, seasonality and sheep grazing in an alpine ecosystem

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Abstract

Large herbivores are affecting a suite of plant traits in many ecosystems, including plant quality. At northern latitudes, the phenological development of plants over the growing season is also regarded crucial for plant quality. The relative role of grazing and seasonality for quality of different plant functional groups has not been quantified in northern, alpine ecosystems, but are assumed to form a key role in the ecosystems due to the feedback on herbivore behaviour and performance. In an experimental setting (3 sheep density treatments replicated 3 times) and based on 1518 samples from 6 species of plants belonging to 3 functional groups collected over the entire growing season, we tested the relative role of grazing and seasonality for plant quality as indexed by N- and P-content and C:N and C:P ratios. We examined sheep diet composition and quality in faeces. There was a marked seasonal decline in specific N- and P-content for all plant species. N-content was higher for grass tissue collected at high sheep density late in the season relative to those from controls without sheep, but not for forb and dwarf shrub tissue. P-content in tissue peaked at low sheep density for *Avenella flexuosa* (late season), forbs and *Vaccinium myrtillus*. C:N and C:P ratios mainly followed the patterns for N- and P-content, respectively. The grass *A. flexuosa* increased while forbs and *Salix* sp. declined in proportion in the diet over the growing season. *A. flexuosa* were more consumed at high sheep density, while forbs were more consumed at low density. N- and P-content in sheep faeces declined markedly over the grazing season, but was not related to treatment. We conclude that the endogenous seasonal changes in plant quality over the growing season are stronger than grazing effects, but that grazing extends the season of access to high quality grasses suggesting potential for grazing facilitation.

Zusammenfassung

In vielen Ökosystemen beeinflussen große Pflanzenfresser eine Reihe von Pflanzenmerkmalen, einschließlich der Pflanzenqualität.

In nördlichen Breiten wird auch die phänologische Entwicklung der Pflanzen während der Vegetationsperiode als entscheidend für die Pflanzenqualität angesehen.

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Die relative Rolle von Beweidung und Saisonalität für die Qualität unterschiedlicher funktioneller Pflanzengruppen ist in nördlichen alpinen Ökosystemen nicht quantifiziert worden, man nimmt aber an, dass diese Faktoren wegen der Rückkopplung auf Verhalten und Performanz der Herbivoren eine Schlüsselrolle in Ökosystemen spielen.

In einer experimentellen Anlage (drei Schafbesatzdichten, drei Replikate) und basierend auf 1518 Proben von sechs Pflanzenarten aus drei funktionellen Gruppen, die über die gesamte Vegetationsperiode gesammelt wurden, testeten wir die relative Bedeutung von Beweidung und Saisonalität für die Pflanzenqualität, die als N- und P-Gehalt und C/N- und C:P-Verhältnisse gemessen wurde.

Wir untersuchten die Nahrungszusammensetzung der Schafe und die Qualität der Faezes.

Wir fanden einen deutlichen saisonalen Abfall im spezifischen N- und P-Gehalt bei allen Pflanzenarten. Der N-Gehalt war bei Grassmaterial, das spät im Jahr bei hoher Schafdichte gesammelt worden war, höher verglichen mit Proben aus der Kontrolle ohne Schafe. Für Proben von Krautpflanzen und Zwergsträuchern ergaben sich keine Unterschiede. Der P-Gehalt war am höchsten bei geringer Schafdichte für *A. flexuosa* (späte Saison), Krautpflanzen und *V. myrtillus*. Die C:N- und C:P-Verhältnisse folgten im wesentlichen den N- und P-Gehalten.

Das Gras *A. flexuosa* nahm im Saisonverlauf in der Schafnahrung zu, während Krautpflanzen und *Salix* sp. abnahmen. *A. flexuosa* wurde stärker bei hoher Schafdichte gefressen, während Krautpflanzen eher bei geringen Dichten gefressen wurden.

N- und P-Gehalte im Schafkot gingen im Laufe der Weidesaison unabhängig von der Beweidungsvariante deutlich zurück. Wir schließen, dass endogene saisonale Änderungen der Pflanzenqualität während der Vegetationsperiode stärker sind als Beweidungseffekte. Aber Beweidung verlängert die Saison mit Zugang zu hochwertigem Gras, wodurch die Möglichkeit für eine Förderung durch Beweidung nahelegt wird.

Introduction

Large herbivores have a marked impact on many ecosystem processes (Hobbs 1996). It is well documented that herbivory induces changes to plant community composition. Typically, the responses of plant communities to grazing are affected by the interaction of multiple factors (Milchunas, Sala, & Lauenroth 1988; Milchunas, Lauenroth, & Burke 1998), but can be fairly well predicted depending on plant functional traits (Lavorel, McIntyre, Landsberg, & Forbes 1997), herbivore traits (Augustine & McNaughton 1998), and ecosystem characteristics (Proulx & Mazumder 1998). Grazing can also have a substantial effect on plant biomass production and plant quality (Arsenault & Owen-Smith 2002). Plant–herbivore interactions are indeed highly dynamic and may frequently involve feedback processes (Frank 1998, 2005; Frank, Groffman, Evans, & Tracy 2000; Augustine, McNaughton, & Frank 2003). Herbivory may over longer time spans lead to a decrease or an increase in habitat productivity. For grazers one may expect a trade-off between quantitative and qualitative measures of plants, since accumulation of high biomass may deplete the specific nutrient content causing nutrient deficient food, while high grazing pressure and high nutrient recycling will facilitate a low standing biomass with high nutrient content (Sterner & Elser 2002). Overbrowsing may, however, also reduce diet quality and impact population performance in the long term as shown for white-tailed deer (*Odocoileus virginianus*) (Simard, Côté, Weladji, & Huot 2008).

Ruminants are selective herbivores (Shipley, Forbey, & Moore 2009). High plant quality gives per definition higher return of energy as well as essential nutrients for each bite. Importantly, high quality forage also lowers rumination time, which are known to limit the energy-time budgets of ruminants (Belovsky & Jordan 1978), giving more time left to forage. This "multiplier effect" principle (White 1983) put a key focus on plant quality for herbivore performance. It is here important to consider that not only energy, but also the specific content of key elements like N (White 1993), P (Grasman & Hellgren 1993; Sterner & Elser 2002) as well as calcium (Ca) and sodium (Na) may be in short supply relative to demands by grazers (WallisDeVries 1996) and successfully predict their distribution (Anderson et al. 2010). While N is crucial for protein synthesis and thus growth, P is needed for bony structures, phospholipids and nucleic acids. A further focus on N and P in terrestrial grazing ecosystems is important (Frank 2008).

There is a strong seasonal component in the plant quantity–quality dualism (Christianson & Creel 2009). Young, newly emergent plants have a much higher quality than older senescent plants. This is at least partly the reason for migration of large herbivores in several regions of the world (McNaughton 1985; Fryxell & Sinclair 1988). In the seasonal environments at northern latitudes, the phenological development of plants over the growing season is therefore regarded crucial for herbivore behaviour (Albon & Langvatn 1992; Hebblewhite, Merrill, & McDermid 2008) and, consequently, performance (Mysterud, Langvatn, Yoccoz, & Stenseth 2001). The seasonal pattern of plant quality in alpine ecosystems is well described and related both to soil available nitrogen and biomass increase (Körner 2003). The relative role of seasonality and how herbivores themselves affect plant quality over time has not been quantified for northern alpine ecosystems in an experimental setting. Also, the

grazing levels required to obtain given effects on plant quality are less clear, as studies typically compare ungrazed with heavily grazed areas, while a study comparing multiple density levels found evidence of grazing optimization (Stewart, Bowyer, Ruess, Dick, & Kie 2006).

We here test predictions and quantify the effects of three density levels of a large herbivore, domestic sheep (*Ovis aries*), on plant quality over the growing season in an alpine ecosystem after 7 years of grazing. As proxies for plant quality, we use N- and P-content and C:N and C:P ratios, the benefits and limitations of such a choice is discussed. We further quantify how plant quality development affects seasonal dietary choices of sheep by aid of microhistological analysis. We present analyses of new data based on 1518 plant tissue samples collected in the early, mid and late growing season from six species of plants belonging to three plant functional groups; grasses, forbs and dwarf shrubs. We follow in parallell sheep diet composition and quality at high and low population density. We test the hypotheses that (H_{1a}) seasonal effects are stronger on plant quality than grazing effects, or (H_{1b}) vice versa. We predict (H_{2a}) positive effects of grazing on quality of grasses tolerant to grazing, and (H_{2b}) potentially negative effects for herbs and woody species, because the latter groups of species are less tolerant on average (Austrheim et al. 2008). Such main effects would be indicative of longer-term grazing effects (since it was 7 years since grazing was initiated). We argue that if grazing mainly operated by keeping grasses in a young phenological stage during the grazing season, one might expect the effect of grazing to be stronger towards the end of the grazing season when grasses have completed their life cycle and normally senesce. We therefore predict (H_3) any positive effect of grazing to be stronger towards the end of the grazing season, indicating a grazing induced phenology effect on quality. We generally predict (H_4) sheep diet composition and quality to reflect seasonal changes in plant quality of different functional groups.

Materials and methods

Study area

The study area was conducted in Hol municipality, Buskerud county in the southern part of Norway (7°55′–8°00′E; 60°40′–60°45′N). The habitat is alpine with a sub-continental alpine climate with moderate to low annual precipitation (1000 mm). The experimental enclosure extends from 1050 m to 1320 m a.s.l. The areas with lowest elevation have scattered birch (*Betula pubescens*) trees, but the main areas are within the lower alpine zone (Speed, Austrheim, Hester, & Mysterud 2010). Vegetation is dominated by low shrubs interspersed with grass-dominated meadows selected for by sheep (Mobæk, Mysterud, Loe, Holand, & Austrheim 2009). A total of 104 vascular plant species were recorded in the study area and forbs dominated

(53%). Before the study was initiated, there was a very low grazing pressure by domestic sheep (<10 sheep per km^2) in the area. Moose (*Alces alces*) have been observed to occasionally enter the area, but likely have very limited impact on the system.

Experimental design

In 2001, a large enclosure covering 2.7 km^2 and surrounded with standard sheep fencing (110 cm high; total length: 17.3 km) was established enabling research on a broad range of ecosystem impact of domestic sheep grazing (e.g. Austrheim et al. 2008; Mysterud et al. 2010; Speed et al. 2010). The large enclosure was split into 9 compartments referred to as sub-enclosures with an average size of 0.3 km^2. We used a block-wise randomization design with 3 blocks (i.e., 3 replicates) consisting of three adjacent sub-enclosures. Within blocks, we randomly assigned the treatments "control" (no sheep), low and high density of sheep. Treatments were similar for all years. Our "low density" treatment was 25 sheep per km^2 and "high density" was 80 sheep per km^2, all of the same breed ("Norsk kvit sau"). These density levels span the most typical current densities of sheep on alpine pastures in Norway, and were chosen after a grazing ecologist had mapped the vegetation of the area and assessed its grazing value for sheep (Mobæk et al. 2009). Based on frequency of forbs eaten, the low density and high density corresponds to low and moderate grazing pressures (Evju, Mysterud, Austrheim, & Økland 2006) when compared to studies in productive habitats in North America (Holechek, Gomez, Molinar, & Galt 1999). The experiment was run from 2002, with a grazing season lasting from the last week of June through the last week of August or first week of September and similar to the season for free ranging sheep in mountain regions in southern Norway. The study was conducted in 2008, i.e., in the 7th year of grazing.

Plant sampling

The vegetation composition in the study area was examined in 180 permanent plots from 2001 and every 2nd year (Austrheim et al. 2008), and we used these plots as a basis for sampling plant material in 2008. The basis for choosing plants was based on them being common plants (Austrheim et al. 2008) with some grazing value to sheep (Kausrud, Mysterud, Rekdal, Holand, & Austrheim 2006) in our ecosystem. The frequency of occurrence of the plant species included in this study changed over time (see Appendix A: Fig. 1). We only sampled green vegetation and not dead plant material, and we sampled either whole plants or plant parts depending on our observations of what sheep mainly ingested. We sampled plant tissue ($n = 1518$) from two grass species (whole plant: *Anthoxantum odoratum*; *A. flexuosa*), two forb species (leaves: *Alchemilla alpina*; *Rumex acetosa*) and two woody species (leaves: *Salix lapponum*; leaves including the outer-

Table 1. Parameter estimates from analyses of (ln) N-content (as % of dry weight) with linear mixed-effects models. "Sub-enclosure" was always entered as a random factor. Lower = lower 95% confidence limit; upper = upper 95% confidence limit. Density = sheep density. Bolded values indicate that the 95% confidence interval does not overlap 0.

Parameter	Estimate	Lower	Upper	Estimate	Lower	Upper
Grasses	A. *Avenella flexuosa*			B. *Anthoxantum odoratum*		
Intercept	**0.558**	**0.448**	**0.668**	**0.489**	**0.300**	**0.677**
Season (mid vs. early)	**−0.365**	**−0.512**	**−0.218**	**−0.747**	**−1.013**	**−0.481**
Season (late vs. early)	**−0.767**	**−0.914**	**−0.620**	**−1.177**	**−1.443**	**−0.911**
Density (high vs. control)	−0.066	−0.218	0.085	−0.198	−0.456	0.059
Density (low vs. control)	−0.127	−0.284	0.031	−0.110	−0.381	0.162
S (m vs. e): D (H vs. C)	0.006	−0.196	0.208	0.067	−0.295	0.428
S (l vs. e): D (H vs. C)	**0.352**	**0.149**	**0.554**	**0.460**	**0.098**	**0.821**
S (m vs. e): D (L vs. C)	**0.230**	**0.019**	**0.442**	0.359	−0.025	0.743
S (l vs. e): D (L vs. C)	**0.293**	**0.082**	**0.505**	−0.020	−0.401	0.362

Parameter	Estimate	Lower	Upper	Estimate	Lower	Upper
Forbs	C. *Alchemilla alpina*			D. *Rumex acetosa*		
Intercept	**0.711**	**0.629**	**0.794**	**1.066**	**0.959**	**1.172**
Season (mid vs. early)	**−0.237**	**−0.306**	**−0.169**	−0.031	−0.106	0.045
Season (late vs. early)	**−0.432**	**−0.500**	**−0.365**	**−0.194**	**−0.270**	**−0.118**
Density (high vs. control)	0.056	−0.046	0.157	−0.054	−0.191	0.082
Density (low vs. control)	0.057	−0.047	0.161	0.014	−0.125	0.153

Parameter	Estimate	Lower	Upper	Estimate	Lower	Upper
Woody species	E. *Vaccinium myrtillus*			F. *Salix lapponum*		
Intercept	**0.601**	**0.517**	**0.685**	**1.061**	**0.999**	**1.123**
Season (mid vs. early)	**−0.160**	**−0.244**	**−0.076**	**−0.337**	**−0.405**	**−0.268**
Season (late vs. early)	**−0.388**	**−0.472**	**−0.304**	**−0.477**	**−0.546**	**−0.409**
Density (high vs. control)	0.020	−0.075	0.115	−0.048	−0.115	0.019
Density (low vs. control)	0.048	−0.050	0.147	−0.033	−0.104	0.037

most branches: *V. myrtillus*). Data from all species and plots at which they had been registered as present was gathered during early (June 30–July 9), mid (July 29–August 7) and late growing season (August 25–August 30) in 2008 (see Appendix A: Table 1 for an overview of sample sizes per plant species and treatment).

Sheep diet composition and quality

Sheep faeces were sampled from marked individuals during observation of sheep habitat selection (see detailed descriptions in Mysterud, Iversen, & Austrheim 2007; Mobæk et al. 2009). We followed a stratified sampling procedure ensuring representation of high and low density of sheep, ewes and lambs and from early, mid and late growing season. All faeces samples ($n = 110$) were put in plastic bags and frozen. Sheep had access to a salt lick at mid elevation in each sub-enclosure. Salt licks were of type "KNZ" containing NaCl, Na and Mg and trace elements Zn, Mn, Fe, I, Co and Se (www.knzsalt.com). None of these contents are focus

of our article and thus access to salt licks is unlikely to affect our results.

Sheep diet composition was determined based on micro-histological analysis (Holechek, Vavra, & Pieper 1982; Henley, Smith, & Raats 2001). We boiled 1 ml of faeces in 4 ml of nitric acid. Plant fragments were identified to species whenever possible, otherwise family names were determined. Forb species were only recognized at plant group level. We here only analyze target species. A detailed analysis of diet selection from the period 2002–2007 can be found elsewhere (Mobæk, Mysterud, Holand, & Austrheim 2011), while the data presented here are new (2008). We also assessed N- and P-content in faeces using the same procedure as for plants.

Plant chemical analysis

All plant tissue were grounded and homogenized (1 mm sieve size) by a plant mill (Culatti, type DFH48). This yielded a uniform powder of plant mass that was dried (60 °C) for 48 h before subsamples were added to pre-weighed Zn capsules
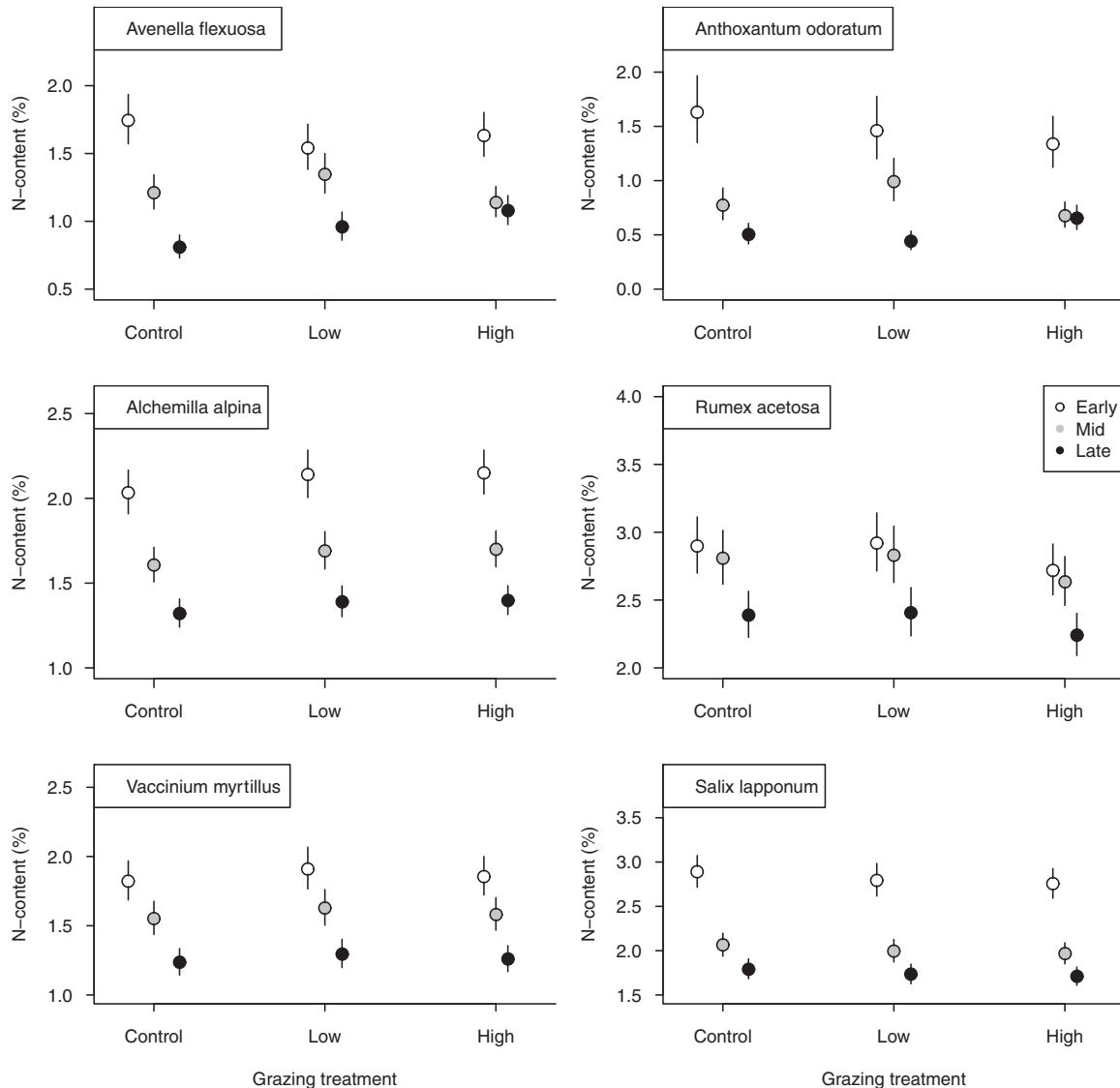
Fig. 1. N-content (as % of dry weight) in grasses, forbs and woody species as a function of treatments control (no sheep), low density (25 sheep per km^2) and high density (80 sheep per km^2) of sheep in alpine habitats in Norway after 7 years of grazing.

for C and N analysis by combustion in Flash EA^{TM} 1112 automatic elemental analyzer (Thermo Finnegan, Milan, Italy). Total P content was measured on the same homogenate by persulfate digestion followed by a molybdate-blue assay (Menxel & Corwin 1965).

Statistical analyses

We used linear-mixed models for analyses using library "lme4" (Bates & Maechler 2009) in the statistical package R vs. 2.9.2 (R Development Core Team 2008). When analysing variation in plant quality, we started with species specific models with a basic structure including "period" (3 levels) and "grazing treatment" (3 levels) as fixed effects and with "sub-enclosure" as a random term. We then used AIC to determine whether an interaction term between period

and grazing treatment improved the model fit (Burnham & Anderson 2002). Only best models are presented, while results from the model selection can be found in Appendix A: Table 2. We initially also tried models with "block" or "plot" as random terms, but ended up with less parsimonious models. We plotted the data using histograms to assess potential outliers. Distribution was substantially improved by ln-transformation. Using other transformations such as arcsine–sqrt yielded comparable results. During plotting of the data, one strong outlying value for N-content for *A. flexuosa* and *A. alpina* and two for *R. acetosa* were removed (all very small values). For C:N ratios, one outlier was removed for *A. alpina* and *V. myrtillus* and two for *R. acetosa*. For C:P ratios, one outlier was removed for *V. myrtillus*. Though removal of these outliers did not change the qualitative conclusions, they were removed to provide more reliable quantitative estimates.

Table 2. Parameter estimates from analyses of (ln) P-content (as % of dry weight) with linear mixed-effects models. "Sub-enclosure" was always entered as a random factor. Lower = lower 95% confidence limit; upper = upper 95% confidence limit. Density = sheep density. Bolded values indicate that the 95% confidence interval does not overlap 0.

Parameter	Estimate	Lower	Upper	Estimate	Lower	Upper
Grasses	A. *Avenella flexuosa*			B. *Anthoxantum odoratum*		
Intercept	**−1.433**	**−1.635**	**−1.232**	**−1.449**	**−1.678**	**−1.221**
Season (mid vs. early)	**−0.361**	**−0.555**	**−0.168**	**−0.551**	**−0.722**	**−0.380**
Season (late vs. early)	**−0.544**	**−0.737**	**−0.350**	**−1.099**	**−1.269**	**−0.928**
Density (high vs. control)	−0.046	−0.328	0.236	−0.013	−0.301	0.274
Density (low vs. control)	0.004	−0.284	0.292	0.209	−0.085	0.503
S (m vs. e): D (H vs. C)	0.143	−0.124	0.409			
S (l vs. e): D (H vs. C)	**0.297**	**0.030**	**0.563**			
S (m vs. e): D (L vs. C)	**0.498**	**0.219**	**0.776**			
S (l vs. e): D (L vs. C)	**0.385**	**0.106**	**0.664**			

Parameter	Estimate	Lower	Upper	Estimate	Lower	Upper
Forbs	C. *Alchemilla alpina*			D. *Rumex acetosa*		
Intercept	**−1.498**	**−1.659**	**−1.338**	**0.447**	**0.375**	**0.519**
Season (mid vs. early)	**−0.157**	**−0.267**	**−0.046**	**−0.094**	**−0.163**	**−0.024**
Season (late vs. early)	**−0.258**	**−0.367**	**−0.150**	**−0.143**	**−0.213**	**−0.074**
Density (high vs. control)	0.145	−0.061	0.352	0.018	−0.082	0.118
Density (low vs. control)	**0.257**	**0.047**	**0.468**	0.052	−0.051	0.154

Parameter	Estimate	Lower	Upper	Estimate	Lower	Upper
Woody species	E. *Vaccinium myrtillus*			F. *Salix lapponum*		
Intercept	**−1.647**	**−1.784**	**−1.511**	**−0.966**	**−1.149**	**−0.782**
Season (mid vs. early)	**−0.311**	**−0.403**	**−0.220**	**−0.689**	**−0.803**	**−0.574**
Season (late vs. early)	**−0.356**	**−0.448**	**−0.265**	**−0.856**	**−0.970**	**−0.741**
Density (high vs. control)	0.030	−0.147	0.207	0.033	−0.208	0.274
Density (low vs. control)	**0.205**	**0.026**	**0.384**	0.167	−0.077	0.411

Analyses of dietary proportion and quality in faeces followed a similar procedure. We ln-transformed all values. One outlier was removed for diet composition of *V. myrtillus*. We started with a basic model including "Julian date" (continuous), "grazing treatment" and "sheep age" (lambs vs. ewe) as fixed effects and with "sub-enclosure" as a random term. We then tried adding interactions.

Results

N-content (as % of dry weight) varied between plant species, but peaked in early summer and decreased substantially over the grazing season for all species (Table 1 and Fig. 1). Specific N concentrations in late summer (controls: *A. flexuosa*: 0.8%; *A. odoratum*: 0.5%; *A. alpina*: 1.3%; *R. acetosa*: 2.4%; *V. myrtillus*: 1.2%; *S. lapponum*: 1.8%) were generally reduced by some 50% compared with early summer (controls: *A. flexuosa*: 1.7%; *A. odoratum*: 1.6%; *A. alpina*: 2.0%; *R. acetosa*: 2.9%; *V. myrtillus*: 1.8%; *S. lapponum*: 2.9%). The temporal development in N-content over the growing season interacted with the density effect only

for the two grasses (Table 1; Appendix A: Table 2), most strongly for *A. flexuosa*. N-content of *A. flexuosa* during the beginning of the growing season was similar between treatments (control: 1.7%; low density: 1.5%; high density: 1.6%), but N-content was higher towards the mid and end of the season at low and high density of sheep compared to controls without grazing (control: 0.8%; low density: 1.0%; high density: 1.1%). N-content in the forb and dwarf-shrub species did not differ depending on sheep density (Table 1 and Fig. 1). The C:N ratio largely followed the same pattern as N-content (Appendix A: Tables 2 and 3), reflecting the low variability in specific C-content across season or treatment.

In the controls, P-content peaked in early summer (*A. flexuosa*: 0.24%; *A. odoratum*: 0.24%; *A. alpina*: 0.22%; *R. acetosa*: 0.40%; *V. myrtillus*: 0.19%; *S. lapponum*: 0.39%), and (as for N) decreased substantially over the grazing season for all plant species (late season: *A. flexuosa*: 0.14%; *A. odoratum*: 0.08%; *A. alpina*: 0.17%; *R. acetosa*: 0.32%; *V. myrtillus*: 0.14%; *S. lapponum*: 0.16%) (Table 2 and Fig. 2). Levels of P in the forbs *A. alpina* (early season; control: 0.22%; low density: 0.28%; high density: 0.26%) and *R. acetosa* (control: 0.40%; low density: 0.50%; high density:
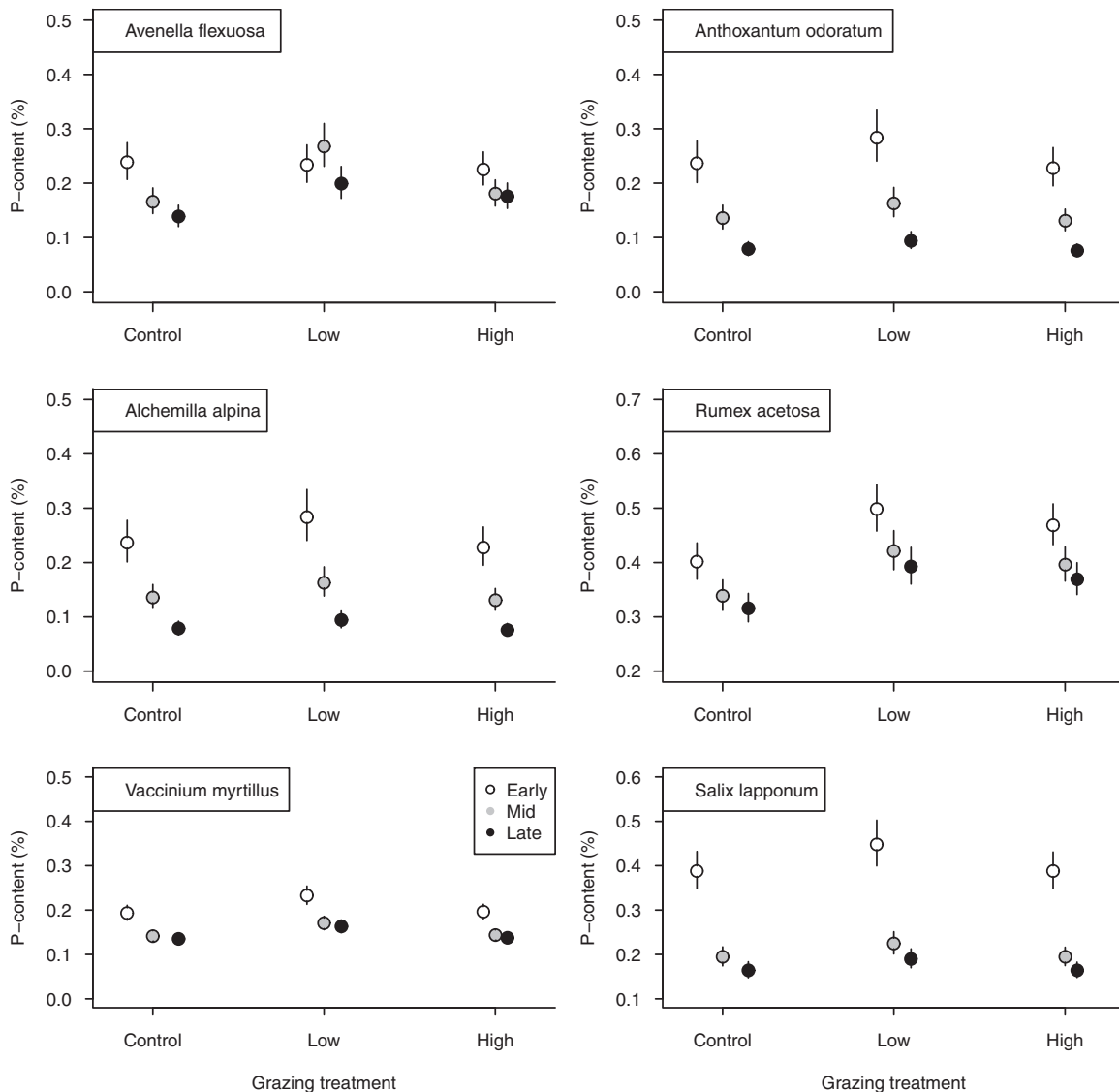
Fig. 2. P-content (as % of dry weight) in grasses, forbs and woody species as a function of treatments control (no sheep), low density (25 sheep per km^2) and high density (80 sheep per km^2) of sheep in alpine habitats in Norway after 7 years of grazing.

0.47%) and the dwarf-shrub *V. myrtillus* (control: 0.19%; low density: 0.23%; high density: 0.20%) peaked at low sheep density, while there was no grazing effect in the grass *A. odoratum* and the dwarf-shrub *S. lapponum*. For *A. flexuosa*, the model including the interaction term between period and grazing was competitive, and P-content decreased less as the season progressed in enclosures grazed by sheep, particularly in enclosures with low densities (Table 2 and Fig. 2). The C:P ratio largely followed the same pattern as P-content (Appendix A: Tables 2 and 4).

Diet of sheep was dominated by *A. flexuosa* (Fig. 3). The proportion of *A. flexuosa* increased markedly over the grazing season (from 17.2% on 1st of July to 42.5% on 1st of September for a ewe at low density), while proportion of forbs (from 31.3% to 20.6%) and *Salix* sp. (from 19.2% to 5.1%) declined over the same period. Proportion of *V. myrtillus* was low (∼2%) and fairly stable over the season. N-content and

P-content in faeces declined markedly over the season (N: from 2.68% to 1.74%; P from 0.75% to 0.37%;) and was higher in lambs (1st of July; $N = 3.0\%$; $P = 0.95\%$) than in ewes (Table 3). *A. flexuosa* were consumed more at high (23.5%) than low (17.2%) sheep density (at 1st of July), while forbs were consumed more at low (31.3%) than high (16.8%) density.

Discussion

Plant quality is a crucial factor for herbivore performance (White 1983). The potential effect of herbivores on the forage quality creates feedback processes important for understanding of ecosystem processes (Frank 1998), yet quantitative estimates of the relative role of season and grazing effects on plant quality from alpine ecosystems are lacking. We found
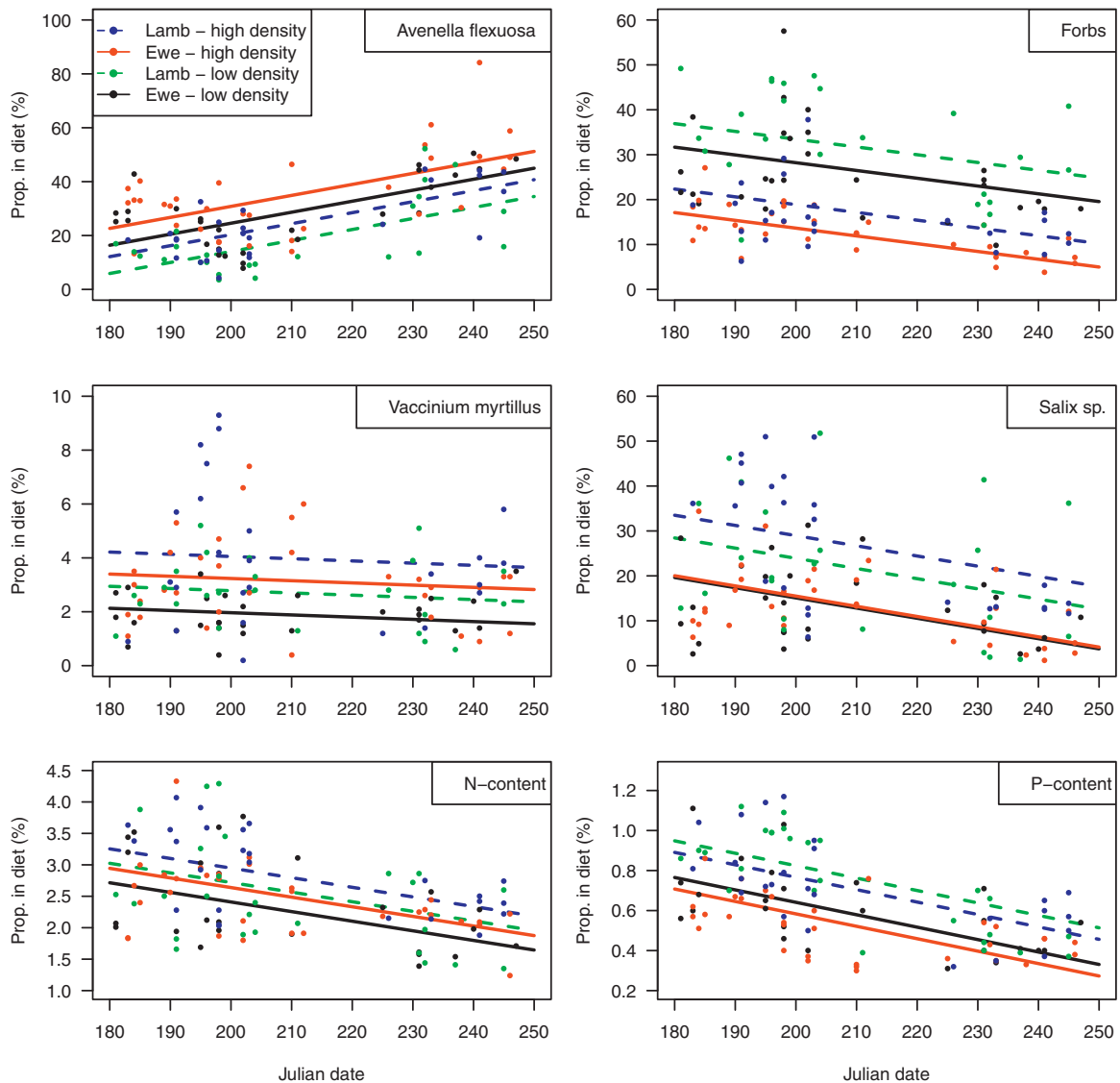
Fig. 3. Dietary proportions of *A. flexuosa*, forbs, *V. myrtillus* and *Salix* sp. (pooled) based on microhistological analyses of faeces and N- and P-content (as % of dry weight) of faeces based on chemical analyses over the grazing season as a function of treatments low (25 per km^2) and high density (80 per km^2) of lambs and ewes in alpine habitats in Norway after 7 years of grazing.

clear evidence that (H_{1a}) seasonal effects are stronger than grazing effects on plant quality as measured by N- and P-content or C:N and C:P ratios. There was, however, also clear evidence that grazing positively affected plant quality in grasses, so that grazing can partly buffer the seasonal decline in plant quality. This was only evident for N in the mid or late part of the growing season (supporting H_3 and not H_{2a}). This suggests that grazing can affect plant quality within a season by keeping grasses in young phenological stages, as has frequently been suggested (Albon & Langvatn 1992; Mysterud et al. 2001; Hebblewhite et al. 2008). However, we cannot exclude that these patterns indicate a longer-term effect of grazing, if graminoids are able to exploit a surplus of available nitrogen at high sheep densities only at a late developmental stage. Indeed for P, there was a main positive effect of low grazing levels, supporting H_{2a}. As also

predicted, the marked seasonal shift in plant quality leads to reduced diet quality of the grazing sheep over the growing season (H_4). Since we measured quality of plants not yet eaten by the sheep, we might have underestimated the plant quality differences among treatments if the sheep had already removed the best quality forage. Since higher quality was nevertheless found at high sheep density for some parameters, this result seems robust and likely conservative, but it might overestimate the relative role of seasonal effects vs. grazing effects.

Alpine ecosystems provide rather extreme climatic conditions for plants (Körner 2003). It is therefore important to quantify the relative strength of grazing effects versus climate effects – on both seasonal and annual scales. At broad scales, climate may be a more important driver for vegetation dynamics than large herbivore grazing (Stohlgren, Schell, &

Table 3. Parameter estimates from analyses of (ln) (A–D) dietary composition and (E–F) quality with linear mixed-effects models. "Sub-enclosure" was always entered as a random factor. Lower = lower 95% confidence limit; upper = upper 95% confidence limit. Density = sheep density. Bolded values indicate that the 95% confidence interval does not overlap 0.

Parameter	Estimate	Lower	Upper	Estimate	Lower	Upper
	A. *A. flexuosa*			B. Forbs		
Intercept	0.464	−0.440	1.368	**4.491**	**3.787**	**5.194**
Julian date	**0.014**	**0.010**	**0.019**	**−0.010**	**−0.013**	**−0.006**
Density (low vs. high)	**−0.291**	**−0.469**	**−0.114**	**0.715**	**0.577**	**0.853**
Age (lamb vs. ewe)	**−0.481**	**−0.659**	**−0.303**	**0.244**	**0.106**	**0.383**
Parameter	Estimate	Lower	Upper	Estimate	Lower	Upper
	C. *V. myrtillus*			D. *Salix* sp.		
Intercept	**1.324**	**0.135**	**2.513**	**5.821**	**4.524**	**7.117**
Julian date	−0.002	−0.007	0.003	**−0.017**	**−0.022**	**−0.011**
Density (low vs. high)	−0.334	−0.913	0.244	0.021	−0.688	0.729
Age (lamb vs. ewe)	**0.232**	**0.009**	**0.454**	**0.797**	**0.467**	**1.128**
Density*Age				−0.448	−0.927	0.031
Parameter	Estimate	Lower	Upper	Estimate	Lower	Upper
	E. N-content			F. P-content		
Intercept	**2.135**	**1.696**	**2.574**	**1.425**	**0.927**	**1.923**
Julian date	**−0.006**	**−0.008**	**−0.004**	**−0.010**	**−0.012**	**−0.008**
Density (low vs. high)	−0.101	−0.389	0.187	0.088	−0.028	0.205
Age (lamb vs. ewe)	**0.117**	**0.039**	**0.194**	**0.279**	**0.181**	**0.377**

Heudel 1999). Annual variation was a more important driver of population dynamics of the forb *Viola biflora* than the grazing effect in our study system (Evju, Halvorsen, Rydgren, Austrheim, & Mysterud 2010). The seasonal effect with peak quality in early season may partly rely on the pool of available soil nutrients and high plant growth rates at the onset of the growing season before this is built into plant biomass (Rehder 1976; Jaeger, Monson, Fisk, & Schmidt 1999). Also solar intensity (causing high C-fixation) later in summer may reduce the specific nutrient content and lead to elevation of C:P and C:N-ratios (Orians & Milewski 2007). In this study, plant quality was mainly driven by seasonal changes, while grazing played a more marginal, yet measurable role. Part of this seasonal pattern was also found in a study of reindeer forage plants, and was partly related to snowmelt patterns (Mårell, Hofgaard, & Danell 2006).

Grazing facilitation is the process by which herbivores create positive feedback on the forage-based carrying capacity (Arsenault & Owen-Smith 2002). We found in our study system higher abundance of field voles (*Microtus agrestis*) at low sheep density compared to high density, with abundance in controls at levels intermediate between high and low density (Steen, Mysterud, & Austrheim 2005). This is indicative of facilitation at low density only, and that increased plant quality is not sufficient to compensate for reduced standing biomass at high sheep density. Similarly, there was density dependent growth of sheep in our experiment (Mysterud &

Austrheim 2005), suggesting clearly that increased quality of grasses towards the end of the season cannot compensate for lower standing biomass. The rather similar estimates for N at the beginning of the season suggest no strong long-term effects at the beginning of the 7th year of grazing, but for P, low grazing had given increased levels. Diet selection of sheep was strongly seasonal, age and density dependent, as we have earlier reported (Kausrud et al. 2006; Mobæk et al. 2011). We here add to this by showing how diet quality assessed by N and P output in faeces similarly declined markedly over the grazing season, was higher for lambs than for ewes, while there was no clear density effect (Fig. 3). Clearly, information regarding plant quality alone is not sufficient to predict responses of the herbivore community. Changes in plant composition and biomass production are also important factors for grazing facilitation (Arsenault & Owen-Smith 2002) as well as for patterns of seasonal diet selection (Hanley 1997).

Plant quality can be extremely difficult to quantify satisfactorily, as it depends on both nutrient content (our focus), chemical defenses and how these interact with the digestive system of the herbivore (Provenza 1995, 1996). For large herbivores, it was documented that tannins reduce digestibility of forage (Hanley, Robbins, Hagerman, & McArthur 1992), and secondary compounds have a major impact on dietary choices of ruminants (Freeland & Janzen 1974; Burritt & Provenza 2000). However, in grasses, secondary compounds

are generally lacking. Silicates are functionally important in a few species (Massey, Smith, Lambin, & Hartley 2008). However, such species were not included here, and N-contents are likely a very good proxy for protein content and plant quality (Langvatn & Hanley 1993; Wilmshurst & Fryxell 1995). N was indeed an important focus in ecosystem dynamics (Frank & Groffman 1998; Frank et al. 2000). The strong decline in specific nitrogen content over the season is strongly indicative of a quality deterioration and an increased risk of mineral nutrient deficiency in late season. The sheep also foraged as predicted from changes in N-content in the plants, increasing the proportion of grasses in the diet over the season as these retained higher quality when grazed. Owing to the strong stoichiometric mismatch between plants and herbivore requirements also for P (Sterner & Hessen 1994; Sterner & Elser 2002), it is also likely that P-deficiency could play a role for mammalian grazers like sheep. Interestingly, while specific N-content in grasses increased with grazing pressure, the P-content (of all plants) gave the strongest response at intermediate sheep density.

Our study provides a quantitative assessment of the relative role of seasonality and grazing for plant quality in a northern, alpine ecosystem. Though seasonal effects were clearly stronger than grazing effects on plant quality, we found clear evidence that grazing can partly buffer the qualitative deterioration of plant biomass (in terms of elevated C:N and C:P ratio) over the season. The effect of providing an extended period of access to high quality grasses may have marked impacts on herbivore performance (Mysterud et al. 2001; Hebblewhite et al. 2008).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.baae.2011.03.002.

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