COMMUNITY ECOLOGY 8(1): 111-117, 2007
1585-8553/$20.00 © Akadémiai Kiadó, Budapest
DOI: 10.1556/ComEc.8.2007.1.13

Response of a subalpine grassland to simulated grazing: aboveground productivity along soil phosphorus gradients

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Keywords: *Cervus elaphus*, Grazing history, Grazing pattern, High elevation, Primary production, Swiss National Park.

Abstract: Interactions between grassland ecosystems and vertebrate herbivores are critical for a better understanding of ecosystem processes, but diverge widely in different ecosystems. In this study, we examined plant responses to simulated red deer (*Cervus elaphus* L.) grazing using clip-plot experiments in a subalpine grassland ecosystem of the Central European Alps. We measured aboveground net primary production (ANPP) and phosphorus (P) concentration of leaf tissue from plants of two vegetation types with different grazing history. The experimental plots were placed on a soil-P gradient and subject to two different clipping treatments, which simulated moderate and heavy grazing, respectively. We found distinct differences in the response of both ANPP and P concentration in leaf tissues in the two vegetation types. Compared to moderate, heavy grazing simulation did not affect ANPP in the vegetation type adapted to grazing, but decreased ANPP in the non-grazing adapted vegetation type. High soil-P levels also had different effects on the response of the vegetation to clipping in the two vegetation types with different grazing history. ANPP correlated positively with soil-P in non-grazing adapted tall-grass vegetation, while in grazing adapted short-grass vegetation a positive relationship between soil-P and the P concentration in leaf tissues was found. Our experiments provide data for a better understanding of ecosystem processes in high-elevation grasslands of the Alps with possible implications for both nature conservation purposes in protected areas and the management of agriculturally used grasslands.

Abbreviations: ANPP – aboveground net primary production; SNP – Swiss National Park; Leaf-P – phosphorus concentration of leaf tissue; soil-P – phosphorus concentration in the top 10 cm of the mineral soil.

Nomenclature: Aeschimann and Heitz (1996) for higher plants.

Introduction

Grassland ecosystems and herbivores can interact in many ways. Grazers have been reported to increase or decrease above- and belowground primary production, change species composition, species richness and plant canopy architecture (Collins et al. 1998, Gough and Grace 1998, Knapp et al. 1999, Frank et al. 2002, Virtanen et al. 2002), and influence carbon and nutrient cycling in soils and vegetation (Detling 1988, McNaughton et al. 1997, Frank and Evans 1997, Knapp et al. 1999, Risch and Frank 2006, Schütz et al. 2006).

The response of grassland productivity to grazing can, however, be highly variable between ecosystems. In boreal and arctic ecosystems, the response of the vegetation to grazing has been reported to be negative (Moss et al. 1981, Post and Klein 1996) and neutral (Beaulieu et al. 1996, Post and Klein 1996, Fox et al. 1998, Raillard and Svoboda 1999). In contrast, research conducted in tropical African and Indian savannas and temperate North-American prairies, showed that grazing by large herbivores enhanced aboveground net primary production (ANPP; e.g., McNaughton 1976, Pandey and Singh 1992, Frank and McNaughton 1993). These examples suggest that it is not possible to predict the potential effect of grazers on grassland processes in ecosystems where these interactions have not yet been studied.

Consequently, the goal of this study was to acquire information on how grazing affects ANPP in subalpine grasslands in the Central European Alps, ecosystems that, to our knowledge, have not yet been included when studying the effect of grazers on grassland productivity. More specifically, our objectives were to investigate how simulated heavy and moderate grazing (clipping) affect ANPP and vegetation nutrient concentrations in such grassland ecosystems. We chose to investigate this along a soil-P gradient in two different vegetation types – short-grass and tall-grass – with different grazing histories. We focused on soil-P, since i) P is the limiting nutrient in subalpine and alpine grassland ecosystems (Dietl 1994); and ii) soil-P is immobile, and therefore leaching losses are low (Hilal et al. 1973). The short-grass type with predominance of red fescue (*Festuca rubra* L.) has been heavily grazed by red deer (*Cervus elaphus* L.) for an approximately 80-year period, while the tall-grass type with predominant *Carex sempervirens* Vill., is rarely grazed (e.g., Haller 2002, Schütz et al. 2003, 2006). Red fescue grasslands are preferred grazing sites of female red deer and are well adapted to grazing (Charles et al. 1977, Clutton-Brock et al. 1982, 1987, Osborne 1984, Gordon 1989, Suter et al. 2004), contrasting grasslands dominated by Cyperaceae, which generally seem to be avoided by these animals (Petrak 1982).

Recently, Bardgett and Wardle (2003) showed in a review that, in general, grazing related stimulation of ANPP occured when i) intensity of grazing was moderate (McNaughton 1979, Dyer et al. 1986, Holland et al. 1992), ii) grazing was coupled with high soil fertility (e.g., Hik and Jefferies 1990, Loreau 1995) or iii) extended periods passed between grazing events (Georgiadis et al. 1989, Hamilton et al., 1998). Based on these general processes of grazer-grassland interactions, we formulated the following hypotheses, which we tested in our experiment:

> i) ANPP is higher on grassland adapted to grazing compared to grassland not adapted.
> ii) ANPP is positively correlated with soil-P in both vegetation types and under both grazing treatments.
> iii) Simulated moderate grazing leads to increased ANPP in the grazing-adapted short-grass vegetation type when associated with high soil-P levels.
> iv) The P concentration of leaf-tissue (leaf-P) is positively correlated with soil-P and is enhanced under simulated heavy grazing.

Methods

Study site

The study was conducted in a subalpine grassland ecosystem of the Swiss National Park. The Park was founded in 1914, and is located in the south-eastern part of Switzerland in the Central European Alps (46°40’N, 10°15’E). The study site, Alp Stabelchod (10.7 ha), is located at 1950 m and has a uniform slope of six degrees in southerly direction. The underlying parent material consists of calcareous sediments dominated by dolomites (Trümpy et al. 1997). Average annual temperature and precipitation are 0.2 °C ± 0.76 and 925 mm ± 162, respectively (means ± standard deviation; recorded at the Parks weather station: Buffalora 1977 m). The growing season starts in early June and ends in late September.

Alp Stabelchod has been created many centuries ago after clear-cutting – first records date back to the year 1421 – and was thereafter used as summer pasture for domestic livestock (cattle/sheep) until the Parks foundation in 1914 (Schorta 1988, Parolini 1995). This former agricultural land use resulted in the development of a distinct soil nutrient pattern: today, the most nutrient-rich areas are found around former huts and stables, the most nutrient-poor areas along the forest edge (Schütz et al. 2003, 2006). After the Parks foundation, grazing pressure was negligible for several years (Braun-Blanquet et al. 1931), since wild ungulates became virtually extinct in this particular area in the early 19th century. During the late 1920’s, red deer (*Cervus elaphus* L.) gradually re-invaded the Park and the population subsequently increased exponentially until the mid 1970’s. Today, roughly 2000 animals inhabit the Park during the summer months (Haller 2002). The winter range of this population is in the surrounding lower elevation valleys outside the Park. In spring, red deer gradually follow snowmelt from the lowlands to higher altitudes, and start grazing the Parks subalpine grasslands, such as Alp Stabelchod, in early June (Blankenhorn et al. 1979). Thereafter, most animals migrate to alpine grasslands located above timberline, while hinds with calves remain at lower elevations and regularly visit the subalpine grasslands during the entire growing season. Red deer created distinct patterns on Alp Stabelchod with permanently grazed short-grass patches (plant height approximately 2 cm) and rarely grazed tall-grass patches (plant height exceeding 20 cm; Schütz et al. 2003, 2006).

Experimental design

We stratified Alp Stabelchod into grid cells of 20 m × 20 m dominated by short- and tall-grass based on a vegetation survey conducted in summer 1998 (Achermann

2000). The short-grass vegetation type is characterized by graminoids such as *Festuca rubra* L., *Briza media* L., *Poa alpina* L., and herbs such as *Trifolium repens* L., *Galium pumilum* M., *Crepis aurea* L, whereas the tall-grass community is dominated by *Carex sempervirens* Vill.

Based on soil-P concentration data of the top 10 cm of the mineral soil, which was also collected in summer 1998, we selected 22 pairs of short- and tall-grass grid cells on a soil-P gradient from 144 to 275 mg P per kg soil. The difference in soil-P concentration between cell pairs did not exceed 3 mg P kg^{-1}. Five additional grid cells with soil-P concentrations between 93 and 135 mg P kg^{-1} were selected for the tall-grass vegetation only, since no grid cells existed in the short-grass community with concentrations lower than 144 mg P kg^{-1} (Schütz et al. 2006).

Immediately after snowmelt in June 2001 we protected two subplots within each grid cell from large herbivores using grazing-proof wire baskets of 28 × 48 × 20 cm and a mesh-size of 1.5 cm. We simulated moderate grazing pressure (early season grazing by red deer) by clipping vegetation in one of the two baskets immediately after snowmelt (early June 2001) to the height of 2 cm above soil surface. Heavy grazing pressure was simulated by clipping re-growth to a height of 2 cm at monthly intervals (mid-July, mid August, mid-September) in the other basket. The clipped biomass was collected in paper-bags, oven-dried to constant weight at 60°C, and weighed. Yearly aboveground net primary production (ANPP) was calculated as the sum of all clippings of a treatment and grid cell. 2001 summer temperature and precipitation were within the 30-year average (based on weather data recorded between 1975 and 2005 at Parks weather station: Buffalora 1977 m).

Phosphorus concentration of leaf tissue

We analyzed leaf-P concentrations of all the harvests separately by digesting dried plant tissue with nitric acid and analyzing the digest with inductively coupled plasma optical emission spectrometry (Zarcinas et al 1987). We compared average leaf-P concentration from the monthly clipped plots (heavy grazing) with leaf-P concentrations of the plots with moderate grazing in September.

Statistical analysis

All data were analyzed with the software package SPSS V11.0 (SPSS, Inc, Chicago, IL, USA). A two-way ANCOVA for each vegetation type was performed to compare seasonal production with grazing treatment and soil-P concentration. Grazing treatment was considered as fixed factor and soil-P as covariate. To compare monthly trends in productivity, a repeated measures ANCOVA model was applied. Within-subject factor was month and between-subject factors were vegetation type and soil-P. Differences in leaf-P concentrations related to grazing treatment and soil-P were analyzed using ANCOVA, with grazing treatment as fixed factor and soil-P as covariate.

All data on biomass were transformed using the natural log to meet criteria of normality and homogeneity. Data on leaf-P concentrations were not transformed, since they already met criteria of normality and homogeneity. The September harvest of the tall-grass sites, which was clipped monthly, did not show homogeneity of variances since the total amount of material harvested was close to zero for most of the samples. Interactions were only incorporated in a model if they showed significance.

Results

Aboveground net primary production (ANPP) and soil-P

We found distinct differences in the response of ANPP to simulated grazing along the soil-P gradients in the two vegetation types with different grazing histories: Grazing treatment ($p = 0.96$) and soil-P ($p = 0.14$) did not affect ANPP in short-grass, which averaged 93 g dry biomass m^{-2} $year^{-1}$ in both grazing treatments (Figure 1). In contrast, tall-grass vegetation ANPP was strongly correlated to soil-P (Figure 1), and was significantly higher under simulated moderate compared to heavy grazing ($p = 0.03$).

The two vegetation types showed significantly different responses in monthly ANPP over the course of the growing season under simulated heavy grazing ($p = 0.003$, Table 1, Figure 2). ANPP decreased from July through August to September in both vegetation types ($p < 0.001$, Table 1, Figure 2), however, late season ANPP in the short-grass vegetation (mid-August until mid-September) was still about one third of what was measured in mid-June/mid-July (13 vs. 40 g dry biomass m^{-2}), whereas ANPP ceased during the last clipping interval in the tall-grass type (Figure 2). In contrast to the significant interaction between ANPP and soil-P, no significance was detected between time of clipping and soil-P ($p = 0.14$, Table 1).

Leaf-P and soil-P

We found significantly higher leaf-P concentrations under simulated heavy compared to moderate grazing in both vegetation types (short-grass: $p < 0.001$, tall-grass: $p < 0.001$, Figure 3, Table 2). Average leaf-P concentration was 34% higher in the simulated heavy compared to the moderate grazing treatment in the short-grass vegetation (1.08 vs. 0.81 g P kg^{-1} dry biomass). Similar differences

Table 1. Repeated measures ANCOVA for the effects of vegetation type on monthly ANPP along soil-P gradients, and the interaction effects month × vegetation type and month × soil-P on monthly ANPP. Vegetation type short-grass = heavily grazed for approximately 80-years; vegetation type tall-grass = rarely grazed.

Source	Type III SS	df	MS	F	p
Between-subject effects					
Vegetation type	1.99	1	1.99	9.499	0.003
Soil-P	2.207	1	2.207	10.533	0.002
Error	9.638	46	0.21		
Within-subject effects					
Month	7.53	2	3.765	47.562	<0.001
Month x vegetation type	95.097	2	47.548	600.661	<0.001
Month x soil-P	0.313	2	0.156	1.977	0.144
Error (month)	7.283	92	0.0792		

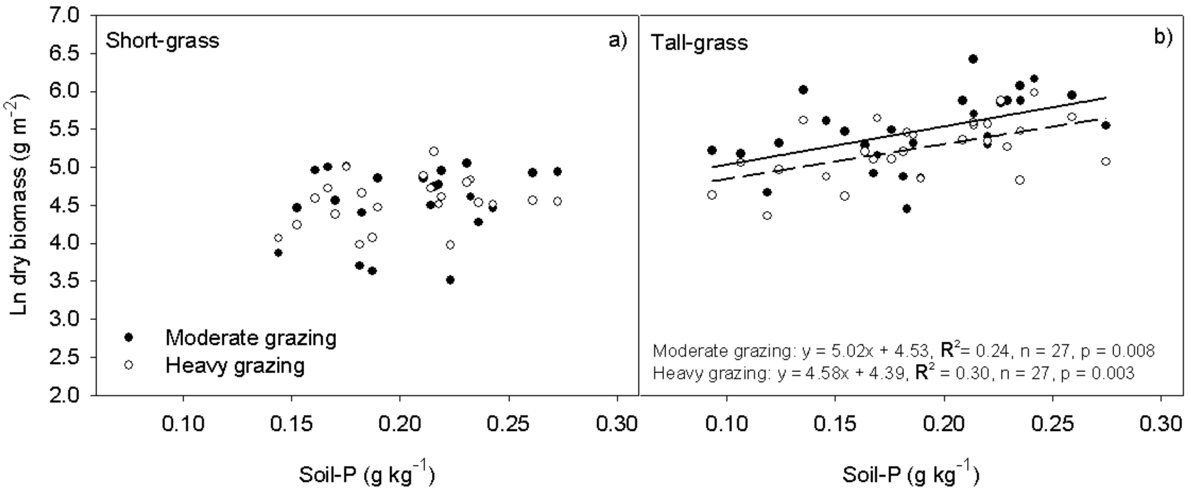

Figure 1. Response of ANPP to moderate and heavy grazing simulation along soil-P gradients in dependence of grazing history: a) short-grass (heavily grazed for approximately 80-years), b) tall-grass (rarely grazed).

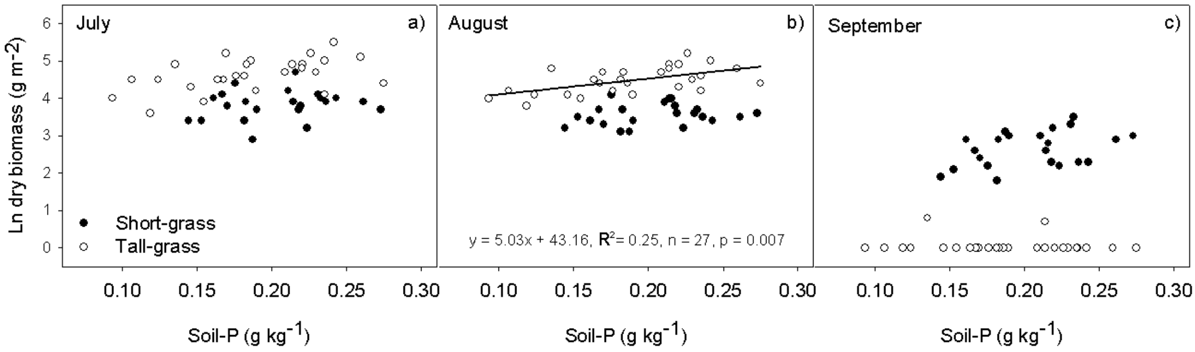

Figure 2. Monthly response of ANPP to heavy grazing simulation along soil-P gradients in dependence of grazing history: a) July, b) August, c) September: vegetation type short-grass = heavily grazed for approximately 80-years; vegetation type tall-grass = rarely grazed.

Table 2. ANCOVA for the effects of moderate and heavy grazing simulation along soil-P gradients on leaf-P concentration in two vegetation types with different grazing histories (vegetation type short-grass = heavily grazed for approximately 80-years; vegetation type tall-grass = rarely grazed).

Short-grass (n = 44)	Type III SS	df	MS	F	p	Tall-grass (n = 54)	Type III SS	df	MS	F	p
Soil-P	0.311	1	0.311	23.934	<0.001	Soil-P	0.113	1	0.113	3.410	0.077
Block	0.659	20	0.033			Block	0.971	25	0.039		
Grazing	0.811	1	0.811	62.324	<0.001	Grazing	1.367	1	1.367	116.508	<0.001
Soil-P x Grazing	0.120	1	0.120	9.251	0.006	Soil-P x Grazing	0.004	1	0.004	0.357	0.556
Error	0.260	20	0.013			Error	0.293	25	0.011		

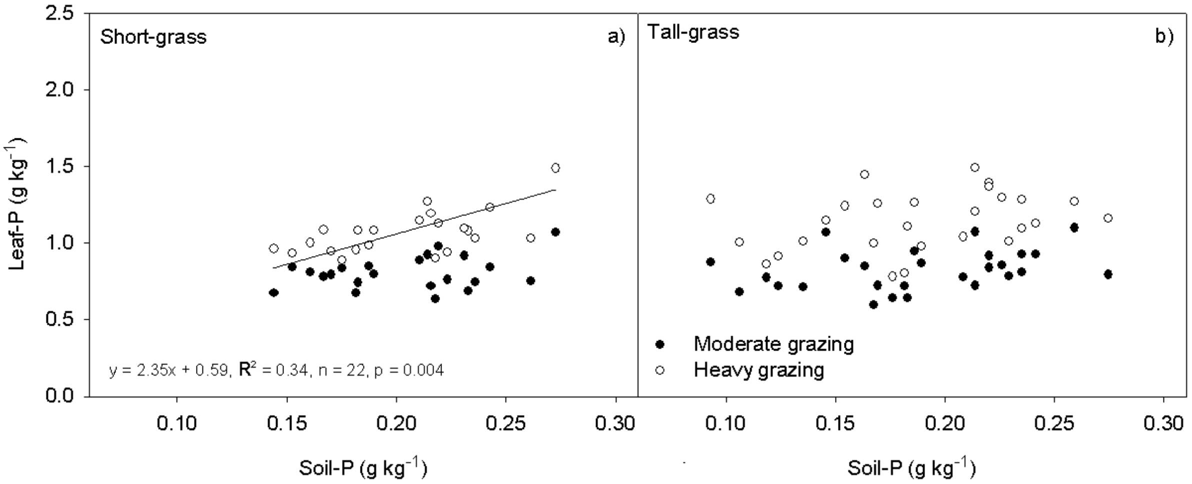

Figure 3. Response of leaf-P concentration to moderate and heavy grazing simulation along soil-P gradients in dependence of grazing history a) short-grass (heavily grazed for approximately 80-years), b) tall-grass (rarely grazed).

were found for the tall-grass vegetation, where average leaf-P concentration was found to be 39% higher in plant material harvested from simulated heavy compared to moderate grazing treatment (1.14 vs. 0.82 g P kg^{-1} dry biomass, Fig. 3, Tab. 3). Soil-P, however, only had a significant effect on leaf-P concentrations in the short grass vegetation under heavy grazing (Figure 3, Table 2).

Discussion

Grazing history

We were interested in how grazing adapted (short-grass) and non-grazing adapted (tall-grass) vegetation would respond to experimentally simulated grazing along a soil-P gradient. In contrast to our expectations, we found lower ANPP in the grazing adapted short-grass compared to the non-grazing adapted tall-grass vegetation. Our results are similar to findings from American tall-grass prairies, where grazing adapted plots produced less biomass than ungrazed plots (Turner et al. 1993, Knapp et al. 1999), but contrast research from the Serengeti (McNaughton 1985) and Yellowstone National Park (Frank and McNaughton 1993), where higher ANPP was found in grazed compared to ungrazed grassland. Since these latter grasslands are nutrient limited, large mammals are likely to accelerate nutrient cycling through dung and urine input. The production of our grazing adapted short-grass vegetation was, in contrast, not nutrient limited as ANPP was independent of the soil-P concentration and also of dung input by red deer (Schütz et al. 2006). Yet, in this vegetation type there was close to no dung input (Schütz et al. 2006) and ANPP therefore not stimulated.

Another possible reason for not finding a positive response to grazing in our grazing adapted short-grass vegetation could be that the time frame for coexistence between red deer and their forage was not sufficiently long, similarly to what Knapp et al. (1999) showed for the Konza prairie in Kansas, USA. In savanna grasslands of the Serengeti and the prairies of western North America

(Yellowtone National Park), plants and large herbivores coevolved for millions of years (Stebbins 1981, Holland et al. 1992, McNaughton 1993, Hobbs 1996), which leads to a high sustainability of the grasslands (Frank et al. 1998), and may account for the stimulation of plant productivity.

Grazing intensity and soil-P

Our results also showed significantly different responses of ANPP to simulated heavy grazing among the two vegetation types: ANPP completely ceased at the end of the season in the tall-grass vegetation, while only a slight drop was detected in the short-grass vegetation. Consequently, we found a neutral response of ANPP to heavy grazing in the short-grass vegetation, while the one in the tall-grass vegetation was negative. These findings contrast our hypotesis, but are similar to what has been reported from arctic and boreal ecosystems (e.g., Post and Klein 1996, Beaulieu et al. 1996, Raillard and Svoboda 1999).

We expected increasing plant growth with increasing soil-P concentration in the short-grass vegetation, however, to our surprise, we only found this effect in the tall-grass vegetation. The reasons for not finding any response of ANPP in the short-grass likely was related to the small amount of biomass produced, which likely is a result of overgrazing. Red deer removed on average 85% of ANPP and the grassland only produced 93 g m^{-2} $year^{-1}$ above-ground biomass in our study area (Schütz et al. 2006). Fescue dominated pastures generally would produce considerably more ANPP when less intensively grazed as shown by Dietl (1994) for other areas of Switzerland where ANPP was between 150 and 350 g m^{-2} $year^{-1}$.

As expected, we found significantly higher leaf-P concentrations under heavy compared to moderate grazing regardless of vegetation type. The reason for this can be twofold. First, the quality of young leaf-tissue is generally higher than the one of older leaves (McNaughton 1979). Second, as shown in grazing simulation models (Holland and Detling 1990, Seagle et al. 1992), grazing can lead to decreases in carbon allocation to roots, which results in decreased root- and microbial biomass. This in turn, results in increases in the ratio of nutrient mineralization/immobilization and facilitates plant nutrient uptake.

Our results showed distinct differences in the response of grazing adapted and non-adapted high-elevation grasslands to clipping. Since the response of grazing ecosystems can be highly variable across continents and climates, our experiment conducted in the Alps provides important information for a better understanding of grazer-grassland interactions. Further, the knowledge from the results gained might become important for implementing conservation strategies for protected areas as well as the management of agriculturally used grasslands.

Acknowledgments. We thank the authorities of the Swiss National Park for their permission to conduct this unusual and controversially discussed field work. The field assistance provided by V. and D. Egenter, D. Thiel and C. Elmiger and the laboratory work conducted by the USDA Forest Service, Rocky Mt. Research St., Forestry Science Laboratories, Moscow ID and Rocky Mt. Research Laboratory, Logan UT, at the Utah State University is very much appreciated. We are grateful for the statistical advice provided by W. Blanckenhorn and L. Gygax at the University of Zurich.

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Received 14 December, 2006
Revised May 2, 2007
Accepted May 27, 2007