PLANT ANIMAL INTERACTIONS

Contrasting effects of rabbit exclusion on nutrient availability and primary production in grasslands at different time scales

Johan Olofsson · C. de Mazancourt · M. J. Crawley

Abstract Herbivores influence nutrient cycling and primary production in terrestrial plant communities. However, both empirical and theoretical studies have indicated that the mechanisms by which herbivores influence nutrient availability, and thus their net effects on primary production, might differ between time scales. For a grassland in southeast England, we show that the effects of rabbits on primary production change over time in a set of grazed plots paired with exclosures ranging from 0 to 14 years in age. Herbivore exclusion decreased net aboveground primary production (APP) in the short term, but increased APP in the long term. APP was closely correlated with N mineralization rates in both grazed and ungrazed treatments, and accumulation of litter within the grazing exclosures led to higher N mineralization rates in exclosures in the long run. Rabbit grazing did not influence litter quality. The low contrast in palatability between species and the presence of grazing-tolerant plants might prevent rabbits from favoring unpalatable plant species that decompose slowly, in contrast to results from other ecosystems. Our results indicate that it is essential to understand the effects on N cycling in order to predict the effect of rabbit grazing on APP. Rabbits might decrease N mineralization and APP in the long term by increasing losses of N from grasslands.

Keywords Rabbit · Grazing · Nitrogen mineralization · Primary production · Litter decomposition

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Introduction

Herbivores can affect plant production through a range of mechanisms (Crawley 1983; Wardle 2002; Bardgett and Wardle 2003). However, as plant growth is limited by nitrogen in most ecosystems (Vitousek and Howarth 1991; Aerts and Chapin 2000), the effect of herbivores on primary production through altering the N cycle has received particular attention. Herbivores increase nutrient availability in some ecosystems (Frank and Evans 1997; McNaughton et al. 1997; Belovsky and Slade 2000; Olofsson et al. 2004; van der Wal et al. 2004), but they decrease nutrient availability in other ecosystems (Pastor et al. 1993; Ritchie et al. 1998; Stark and Grellmann 2002). Herbivores might be responsible for changes in various processes such as the litter decomposition rate (Pastor et al. 1993; Olofsson and Oksanen 2002), nutrient mineralization rate (Ritchie et al. 1998; Sirotnak and Huntly 2000), nutrient leaching (Ruess and McNaughton 1987; Frank et al. 2000), nitrogen fixation (Bazely and Jefferies 1989) and volatilization (Schimel et al. 1986; Frank et al. 2004). The importance of these processes may

differ between ecosystems, with the result that the net effect of herbivores on nutrient dynamics may also vary from system to system.

Although herbivores have been found to increase nutrient availability and primary production over several decades in many ecosystems (Frank and McNaughton 1993; Frank and Evans 1997; McNaughton et al. 1997; Olofsson et al. 2004), the effects of herbivory can vary at different time scales in the same ecosystem. Herbivore effects have been found to change from positive in the short term to negative in the long term in boreal forests (Pastor et al. 1993) and in riparian meadows (Sirotnak and Huntly 2000). In these cases, herbivores increased the nutrient turnover rate in the short term as they released easily available nutrients from urine and feces. In the long term, however, this positive effect was reversed by a stronger negative effect resulting from changes in plant species composition. By selectively foraging on plants with a low C/N ratio and low concentrations of secondary compounds, herbivores favored less palatable plant species with a high C/N ratio and high concentrations of secondary compounds. Such plants produced litter of lower quality and decreased the N turnover rate (Pastor et al. 1993; Ritchie et al. 1998). Theoretical models indicate that decomposition rates affect primary production only in the short term, and that it is the effect on nutrient inputs and outputs that determines primary production in the long term (de Mazancourt et al. 1998, 1999; de Mazancourt and Loreau 2000). This modeling work predicts that the effects of herbivores on losses and gains of N should be a more important determinant of primary production in the long-term than their transient effects on turnover rates. The effects of herbivores on nutrient retention have been much less intensively studied than have the effects on turnover rates (Ruess and McNaughton 1987; Frank et al. 2000).

We need to know much more about the effects of herbivores on nutrient availability and aboveground primary production (APP) at different time scales. The mesic grasslands in Silwood Park, UK, provide a unique opportunity to study the effects of herbivores on the nutrient dynamic and primary production because the effects of different herbivores on plant community structure have been intensively studied for more than 25 years and provide valuable background information (Crawley 1990, 2005). Rabbits, *Oryctolagus cuniculus*, are keystone species in grasslands in Silwood Park, capable of preventing succession to *Quercus robur* woodland (Crawley 2005). Silwood Park contains a large number of rabbit exclosures of various ages. Instead of measuring the nutrient availability and nutrient cycling annually in a set of exclosures over many years (a longitudinal study), we conducted a cross-sectional study by comparing a range of different-aged rabbit exclosures in a single year. To reduce the effect of spatial heterogeneity, paired grazed and un-grazed plots were used at every site. We measured above- and belowground primary production, species composition of vascular plants and the depth of the moss layer inside and outside each fence to quantify the effects of rabbit grazing on the plant community. In addition, we determined the amount of litter, litter decomposition rate and nitrogen mineralization rate. These are considered to be key processes in understanding the net effect of herbivory on nitrogen availability for plants and in determining primary production (Bardgett and Wardle 2003).

Methods

The effects of rabbit exclusion were studied in acid grasslands at Silwood Park, Berkshire, UK (National Grid Reference 41/94469), an estate of 110 ha with a mosaic of vegetation types including managed parklands, grasslands, wetlands and oak woodland. Within this area, numerous rabbit exclosures have been built since 1975. In the autumn 2002, 13 of the exclosures were selected on the criteria that they should be located in dry acidic grassland (a variant of UK National Vegetation Classification MG5 described by Crawley 2005) and the exclosures should differ in age as much as possible. We avoided using exclosures of similar age situated close to each other, to minimise problems of spatial autocorrelation. New exclosures (0 years old) were constructed close to three of the oldest exclosures. The exclosures varied in size from 25 to 750 m^2 and were constructed of wire netting with a mesh sized of 3 cm, bent out at the base for 20 cm towards the rabbits (Crawley 1990). For some of the exclosures, a randomized grazed area had been marked out when the exclosure was constructed, but in cases where no original grazed area had been marked out, four suitable areas were chosen, and one of them was selected at random to be the grazed area for this study.

An index of rabbit population density at each location was obtained by measuring the rate of pellet deposition, a method known to provide a reliable estimate of rabbit density (Dias 1998). A quadrat measuring 1 m^2 was marked out at each site and cleared of droppings on 2 March 2003. Deposited feces were collected, dried and weighed every 6 weeks, until 28 September 2003.

Aboveground net primary production was measured in paired grazed areas and exclosures, using the

movable-cage method (McNaughton et al. 1996) and two calculation methods were adopted (one providing an underestimate and one an overestimate of APP; Sala and Austin 2000). Representative 0.25 m×0.25 m quadrats were marked in grazed and ungrazed areas. Cages were put out at the beginning of the growing season (28 February 2003) and moved every 4–6 weeks in a randomized sequence until the end of the growing season (6 October 2003). At the start of the study, and each time the cages were moved, the vegetation was harvested at ground level in grazed plots, movable exclosures and permanently ungrazed exclosures. Herbivore consumption was calculated as the sum of the differences in biomass between the temporary exclosures and the open plots (McNaughton et al. 1996; Oesterheld and McNaughton 2000). An underestimate of APP was calculated from the ungrazed plots inside the rabbit exclosures as the difference between the biomass at the end of the growing season (maximum biomass) and the biomass at the beginning of the growing season (minimum biomass). The comparable estimate for the grazed area is the difference in biomass between the end and the start of the growing season plus estimated total herbivore consumption (offtake). When the increase in biomass is not monotonic, this method can severely underestimate actual APP (Sala and Austin 2000). In many types of grassland, including the one we studied, plant biomass increases during spring, but decreases during a summer drought period then increases again in autumn. An overestimate of APP was calculated as the sum of all positive changes in biomass (i.e., ignoring the negative ones) in the ungrazed vegetation and temporary exclosures. This method overestimates APP if the measurement error and/or spatial heterogeneity in plant biomass is large compared to APP (Sala and Austin 2000). The analyses presented in the results section use the latter method, overestimating APP, but the results were qualitatively similar with the underestimate of APP.

We measured the depth of the moss layer at ten random points before each harvest. At one sampling occasion (in the middle of July 2003), plant community composition was studied by sorting the harvested vegetation to species prior to drying. The dissimilarity in botanical composition between the grazed and ungrazed quadrats was calculated using the Bray-Curtis dissimilarity measure, B:

$$B = \frac{\sum |Xij - Xik|}{\sum (Xij + Xik)}$$

where X_{ij}= abundance of species i in ungrazed plot and X_{ik}= abundance of species i in the paired grazed plot.

The Bray-Curtis dissimilarity measure is strongly influenced by abundant species, and rare species have small effects (Krebs 1989).

We measured belowground net primary production using ingrowth cores (Lauenroth 2000) in which three mesh bags (mesh size 1 mm) with a diameter of 32 mm were filled with sieved soil from the same location and buried in 10-cm deep holes at the beginning of the growing season (7–9 March 2003) and left until the end of the growing season (3–5 October 2003). Even though ingrowth cores have a number of methodological problems, they are still regarded as one of the most reliable ways to measure belowground production (Laurenroth 2000). As soon as they were collected from the field, all samples were processed by sieving and flotation, after which the resulting organic material was dried (70°C, >48 h) and weighed.

Aboveground standing dead biomass was clipped, dried and weighed in one 0.25 m×0.25-m plot in each exclosure and the grazed area at the end of November 2002. The litter decomposition rate was measured in litterbags with a mesh size of 1 mm. Litter quality was measured by decomposing litter from all grazed areas and exclosures at a common site. Litter decomposition conditions were assessed by leaving a standard litter of oak leaves (*Quercus robur*) to decompose in all exclosures and grazed controls at each of the 16 sites. The actual litter decomposition rate at each site was measured by decomposing site-specific litter at its original location. Sub-samples from the standing dead biomass samples were used as litter. Five litter bags were placed on top of the soil surface in each treatment and the average of these bags was used in statistical analyses. The litterbags were placed out on 4 December 2002 and collected on 10 September 2003, by which time they had been decomposing for about 9 months. The C and N contents of litter before and after decomposing in litterbags were analyzed on oven-dried milled material using an Elemental analyzer (Perkin Elmer mod. 2400 CHN Norwalk, CT, USA).

Soil moisture content in the top 5 cm was measured on six occasions in June, July and August by using a surface capacitance insertion probe (Delta T). At each occasion, measurements were performed within each treatment. This instrument measures the soil dielectric constant, which is closely related to soil moisture content (Robinson and Dean 1993). The nitrogen mineralization rate was measured in situ using undisturbed soil columns in PVC tubes with a diameter of 32 mm (Raison et al. 1987). The tubes were inserted into the soil to a depth of 10 cm, closed at top and bottom with PVC plastic, placed back in their original site and incubated in the field for

2 months from 26 June to 27 August 2003. The extractable ammonium and nitrate were measured at both treatments at all 16 sites in field soil samples at the time that the mineralization tubes were incubated, and from field soil samples and soils from the mineralization tubes when the tubes were collected. Three mineralization tubes were used in each treatment and the average of the three values were used in all statistical analyses. Available ammonium and nitrate were extracted from sieved soil by shaking 25 g soil in 100 ml 1 M KCl for 1 h. The resulting suspension was filtered through Whatman no. 1 paper and analyzed with a SKALAR continuous flow analyzer (SKALAR, Breda, The Netherlands). Mineralization was estimated as the increase of extractable ammonium and nitrate in the PVC tubes.

All analyses were performed with the R statistical package (R Development Core Team 2005). The effects of herbivory on APP and mineralization rates were tested by analysis of covariance with grazing treatment as a two-level factor, and age of the exclosure as a continuous variable. Litter decomposition rates were also tested by ANCOVA with the litter origin and litter decomposition rate as categorical variables and age of exclosure as a continuous variable. The correlation between APP and mineralized nitrogen was assessed by linear regression. The relationships between consumption and fecal droppings and the dissimilarity in the vegetation and age of exclosures were assessed using both linear and non-linear regression models.

Results

Both the dropping deposition rate and the biomass consumption rate showed that both grazing pressure and rabbit abundance were high. Biomass consumption varied between 88 and 381 g m^{-2} year^{-1} (n=16; mean±SE; 216±20 g m^{-2} year^{-1}) corresponding to between 38.0 and 97.7% of APP (mean±SE 70.0±6.6% per year). There was a positive linear relationship between the deposition of droppings and the level of consumption (r^2=0.41, df=14, t=3.1, P=0.007). Neither the amount of droppings nor consumption in the grazed area was significantly correlated with age of the exclosures, showing there was no confounding between exclosure age and grazing pressure.

As expected, dissimilarity in plant community composition between grazed and ungrazed vegetation was strongly correlated with the age of exclosure (Fig. 1). Dissimilarity increased linearly with age of the exclosures (r^2=0.55, df=14, t=4.1, P=0.001). The

composition of the vegetation in grazed and ungrazed plots was already significantly different in the 1st year of the study (Fig. 1, df=14, t=8.9, P<0.001). In the medium term, exclusion of rabbits involved replacement of short, grazing-tolerant or unpalatable graminoids like *Luzula campestris* and *Carex muricata* by taller, more palatable, often tussock-forming grasses like *Dactylis glomerata* and *Arrhenatherum elatius* (Crawley 1990, 2005). In some sites, these grasses continued to dominate in the exclosures even in the long term, while other exclosures were invaded by shrubs (e.g., *Rubus fructicosus*).

Net APP was affected by grazing, and the direction of the effect changed with the age of exclosure (Fig. 2). APP was lower in the ungrazed plots than in the grazed plots during the 1st year of rabbit exclosure (Fig. 2, df=28, t=2.5, P<0.020), but APP increased over time in the exclosures and was higher in the older exclosures than in the grazed plots (Fig. 2, as a significant interaction term; df=28, t=2.2, P=0.003). There was no effect of excluding rabbits on the depth of mosses, or on the biomass or production of roots (Table 1).

Litter accumulated with time in the exclosures, but not on the grazed plots (Fig. 3a, Table 1). There was no effect of grazing on litter decomposition, measured as either litter quality (litter decomposition rate in standardized conditions, Fig. 3b, Table 1), or as the in-situ decomposition rate of standard litter (Fig. 3c, Table 1), or actual litter decomposition at each site (Table 1). There was no effect of grazing on C and N content in litter (grazing, df=28, t=0.7, P=0.477; df=28, t=1.6, P=0.116; grazing × age, df=28, t=0.7, P=0.477; df=28, t=–0.8, P=0.439) nor on the rate of N release from litter (grazing, t=–0.3, P=0.803; grazing × age, t=–0.4, P=0.726). The total N released from litter is therefore estimated to depend directly on the amount of litter, as litter quality did not change with the age of the exclosure.

The concentration of extractable nitrate in the soil was 1.0±0.2 μg/g in June 2003 and 2.2±0.3 μg/g in August 2003, and the concentrations of ammonium were 4.0±0.4 μg/g in June 2003 and 4.2±0.5 μg/g in August 2003; there were no significant effects of grazing on ammonium or nitrate concentrations. However, there was a significant interaction between mineralization of N and the age of exclosures (Fig. 2, df=28, t=2.6, P=0.014), and the mineralization rate was found to increase with the age of exclosures, but there was no such trend in the grazed plots. Net APP was correlated with nitrogen mineralization (Fig. 4, r^2=0.50, df=28, t=32.0, P<0.001), but there was no difference in this relationship between the two grazing treatments (df=28, t=0.4, P=0.710).
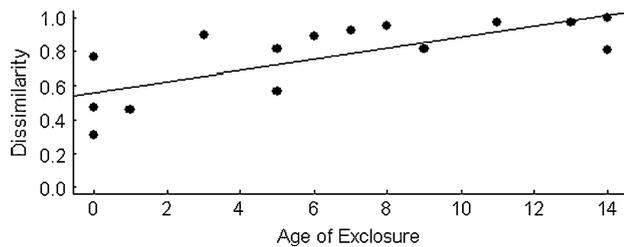
Fig 1 The influence of the duration of protection from rabbit grazing (age of exclosure) on the dissimilarity between the vegetation in grazed and ungrazed exclosures of various ages. The dissimilarity is calculated as Bray-Curtis dissimilarity measure. Each site is represented by a *solid symbol*. The model describing the statistically significantly positive relationship (r^2=0.55, P=0.001) is shown as a *solid line*. There was no statistical support for non-linearity
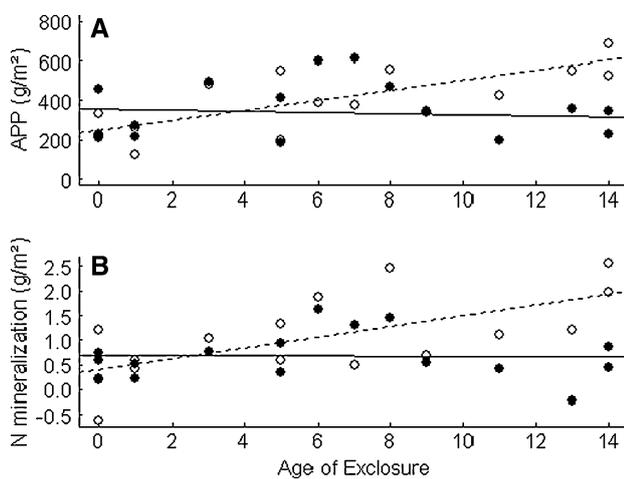
Fig. 2 a Net aboveground primary production (APP) and **b** nitrogen (N) mineralization, as a function of age of the exclosures. Exclosures are plotted as *open symbols* and grazed plots as *solid symbols*. The slopes are significantly different between grazed and ungrazed treatments (r^2=0.33, P=0.0103; r^2=0.38, P=0.014); the *dashed line* shows the exclosures and the *solid line* shows the grazed plots

Discussion

In the short term, excluding rabbits from a mesic grassland in southern England significantly decreased net APP, but had no significant effect on the nitrogen (N) mineralization. In the longer term, however, excluding rabbits led to increased N mineralization rates and increased APP. These contrasting short-term and longer-term effects of rabbit grazing on APP suggest that different processes might be important at different time scales. A 15-year fertilization experiment (Crawley 2005) showed that plant growth was primarily N-limited in this grassland. APP was indeed closely correlated with N mineralization, both in grazed and ungrazed plots. We therefore assume that

N availability is a main determinant of APP at the community level and that the effects of rabbits on N availability determine their effect on APP. Although rabbits had significant effects on N mineralization and APP, there was still a wide scatter within treatments, indicating that many other factors such as land use history or topography are important determinants of APP.

Our results are consistent with the positive short-term effects and negative long-term effects of herbivores reported in previous studies (Pastor et al. 1993; Sirotnak and Huntly 2000), but the mechanism might be different in our case. In published studies the short-term increase in nutrient availability and APP is attributed to excretion of fecal pellets and urine (Sirotnak and Huntly 2000; Ruess and McNaughton 1987; Ruess et al. 1989; Frank and Groffman 1998). Herbivore excreta provide highly decomposable substrates that are rich in labile nutrients capable of stimulating N mineralization (Molvar et al. 1993; McNaughton et al. 1997; Frank and Groffman 1998). In previously published work, this positive short-term effect has been overshadowed by a stronger negative effect of grazing on decreased litter quality, resulting from the fact that herbivores selectively consume nutrient-rich plants and favor nutrient-poor plants that produce litter of low quality (Pastor and Naiman 1992; Pastor et al. 1993; Sirotnak and Huntly 2000). In other cases, selective grazing by herbivores might reduce N inputs by reducing the abundance of N-fixing legumes (Sirotnak and Huntly 2000; Ritchie et al. 1998).

In our study, grazing did not reduce the rates of decomposition or nitrogen release from litter, so a different mechanism must be responsible for the switch from positive to negative effects of grazing on APP over time. Grazing can reduce nitrogen mineralization rates by preventing the accumulation of litter (van Wijnen et al. 1999). Litter quantity was indeed accumulating with time inside the grazing exclosures, and more litter mass should lead to a higher total release of nitrogen because the litter qualities were similar inside and outside the fences. Herbivores are commonly found to reduce litter biomass (Bazely and Jefferies 1989; Sirotnak and Huntly 2000), and in this grassland, herbivores short-circuit the litter-decomposition pathway by consuming more than 70% of APP. Most nutrients therefore return to the soil via dung and urine, rather than from decomposing plant litter. The mineralization estimates are likely to underestimate the nutrient availability in the grazed areas because incubation temporarily excludes the herbivore excreta pathway. Although our soil incubations recorded similar N mineralization rates in young exclosures and

Table 1 The effects of rabbit grazing and age of rabbit exclosure fences on 11 response variables (left-hand column)
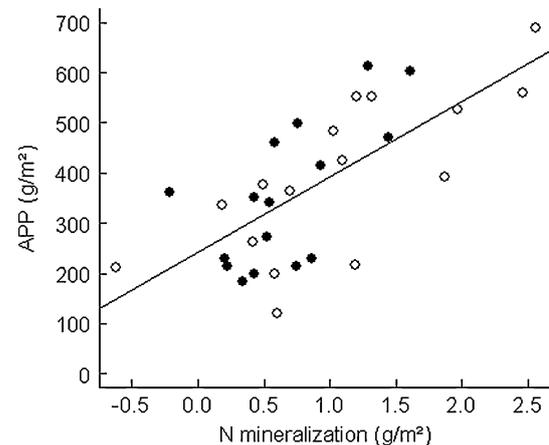
	Grazing		Age		Grazing × age	
	$F_{1,28}$	P	$F_{1,28}$	P	$F_{1,28}$	P
Moss depth	0.5	0.589	0.3	0.90	0.1	0.899
Root						
Production	0.1	0.909	0.6	0.574	0.1	0.959
Biomass spring	0.6	0.550	0.2	0.800	0.8	0.431
Biomass autumn	0.1	0.921	0.2	0.864	0.6	0.563
Litter						
Biomass	0.0	0.975	2.5	0.017	2.2	0.035
Quality	0.4	0.662	0.4	0.701	0.3	0.771
Decomposition conditions	0.6	0.429	0.1	0.887	0.1	0.934
Actual decomposition rate	0.1	0.737	0.3	0.614	0.7	0.423
C content	0.7	0.477	0.1	0.901	0.7	0.477
N content	1.6	0.116	0.1	0.941	0.8	0.439
Soil water content	0.0	0.977	0.1	0.937	0.0	0.975

Grazing is a two-level factor (grazed and ungrazed) that influences the intercept in the analysis of covariance, age is a continuous variable (in years), and the grazing-by-age interaction reflects a difference between slopes attributable to grazing. Significance values (F and P) on 28 degrees of freedom from the analysis of covariance
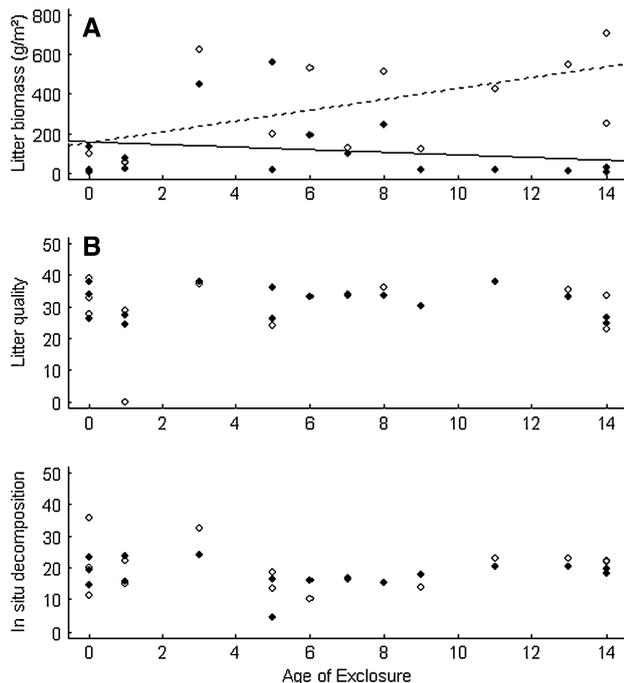
Fig. 3 The effects of age of exclosure on: **a** litter biomass, **b** litter quality and **c** decomposition of standardized litter during 10-month period from November until September. Exclosures are plotted as *open symbols* and grazed plots as *solid symbols*. The relationship between age and litter biomass is shown as a *dashed line* for exclosures and a *solid line* for grazed plots. The slopes of the *two lines* are statistically significantly different ($r^2=0.34$, $P=0.035$). No significant relationships were found between litter quality and litter decomposition conditions and age of exclosure

Fig. 4 Aboveground primary production as a function of net nitrogen mineralization in all exclosures and grazed areas ($r^2=0.50$, $P<0.001$). Exclosures are plotted as *open symbols* and grazed plots as *solid symbols*. There were no significant differences between the grazing treatments (analysis of covariance, $P>0.05$)

grazed plots, N availability is likely to be higher in grazed areas. This could be one explanation for the higher APP in grazed areas than in the 1st-year exclosures.

Higher nutrient losses in the herbivore-waste pathway than in the plant-decomposition pathway could also explain these results. The elevated turnover rate of N in herbivore waste can be expected to enhance N loss from the ecosystem through volatilization, leaching and denitrification (Schimel et al. 1986; Ruess and McNaughton 1987; Frank et al. 2000; Bardgett and Wardle 2003; Frank et al. 2004). As with many other herbivores (Schlesinger et al. 1996; Augustine and Frank 2001), rabbits also change the spatial distribution of nutrients. Although rabbits deposit dung throughout their range, the dung deposition is higher in places where the animals congregate and a large proportion of the dung is deposited in a small number of

latrines (Willot et al. 2000). Soils in latrines are extremely nutrient rich and plants grow better in that soil (Willot et al. 2000). However, nutrient losses from volatilization, leaching and denitrification should be expected to be extremely high in latrines where the nutrients are highly concentrated. Moreover, rabbits can move nutrients from where they forage in grasslands to their harborage in adjacent woodlands (Willot et al. 2000).

The results from this field study support the conclusions of de Mazancourt et al. (1998) and Loreau (2000) that an acceleration of nutrient cycling will only increase APP in the short term. These authors suggest that in the long run APP should be determined by the efficiency of nutrient recycling and by the ability of plants to deplete soil mineral nutrients. Rabbits are likely to decrease both these parameters: N recycling efficiency should be low in grazed areas because N losses are high, and grazing should reduce the ability of plants to deplete soil nutrients because plant biomass is reduced (Tilman 1988).

We were surprised to find that there were no effects of excluding rabbits on litter quality. Over long time scales, herbivory often favors unpalatable species by foraging selectively on palatable species (Crawley 1983; Pastor and Naiman 1992; Wardle 2002; Bargett and Wardle 2003). As palatability of foliage and decomposability of plant litter are governed by similar traits, palatable plant species typically produce litter of higher quality for decomposers (Grime et al. 1996; Cornelissen 1996) and herbivory should be expected to reduce litter quality in the long run. Although rabbit grazing changed the species composition in this grassland (Crawley 1990), grazing had no effect on litter C or N contents or the decomposition rate. One explanation for the lack of a grazing effect on litter quality could be that grazing favors tolerant as well as unpalatable plants in these grasslands (Del-Val and Crawley 2005). Grazing tolerant species should differ from unpalatable species in producing high quality litter (Olofsson and Oksanen 2002; Cingolani et al. 2005). An alternative explanation is that a lack of strong contrasts in litter quality between grazed and ungrazed plant species might limit the ability of selective herbivory to reduce litter quality. Strong negative effects of herbivory on litter quality have been found in grasslands when herbivores reduce the abundance of legumes with high nitrogen contents (Ritchie et al. 1998; Sirotnak and Huntly 2000). In Silwood Park, legumes increased inside the exclosures, but they made up only 1.7% of the biomass compared to about 14% (Ritchie et al. 1998) and 10% (Sirotnak and Huntly 2000) in those grasslands where herbivore exclusion led to increased litter quality.

Excluding rabbits had no effect on root biomass or root production measured with ingrowth cores. This lack of response is in agreement with conclusions from Milchunas and Laurenroth's meta-analysis (1993) where there were as many positive as negative responses of belowground biomass to grazing. This might be surprising, as most studies on the effects of herbivory on individual plants have found that damage to the shoots results in reduced root biomass or lower root production (Crawley 1983). However, on a plant community level, change in root biomass depends on altered plant community composition as well as on altered allocation patterns (Frank et al. 2002).

In this study, we used exclosures of different ages to demonstrate that the effect of herbivores on nutrient availability and APP depends on the duration of the study. Excluding rabbits reduced APP in the short term, but increased APP in the long run. Accumulation of litter increased N mineralization rates inside the exclosures to a greater extent than enhanced N supply from rabbit excreta in grazed plots could match in the long run. The Silwood Park rabbit-grazed grasslands are characterized by high consumption rates that lead to high nutrient losses. The grazing regime favors both unpalatable and grazing-tolerant plant species, and does not lead to the reduction in decomposition rate that has been observed in other ecosystems.

References

Aerts R, Chapin FS (2000) The mineral nutrition of wild plants revisited: a re-evaluation of processes and patterns. Adv Ecol Res 30:1–67

Augustine DJ, Frank DA (2001) Effects of migratory ungulates on spatial heterogeneity of soil nitrogen properties on a grassland ecosystem. Ecology 82:3149–3162

Bardgett RD, Wardle DA (2003) Herbivore-mediated linkages between aboveground and belowground communities. Ecology 84:2258–2268

Bazely DR, Jefferies RL (1989) Lesser snow geese and the nitrogen economy of a grazed salt marsh. J Ecol 77:24–34

Belovsky GE, Slade JB (2000) Insect herbivores accelerate nutrient cycling and increases plant production. Proc Natl Acad Sci USA 97:14412–14417

Cingolani AN, Posse G, Collantes MB (2005) Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. J Appl Ecol 42:50–59

Cornelissen JHC (1996) An experimental comparison of leaf decomposition rates in a wide range of temperate plant species and types. J Ecol 84:589–598

Crawley MJ (1983) Herbivory: the dynamics of plant herbivore interactions. Blackwell Scientific, Oxford

Crawley MJ (1990) Rabbit grazing, plant competition and seedling recruitment in acid grasslands. J Appl Ecol 27:803–820

Crawley MJ (2005) The flora of Berkshire. Brambleby Books, Harpenden

Del-Val E, Crawley MJ (2005) Are grazing increaser species better tolerators than decreasers? An experimental assessment of defoliation tolerance in eight British grassland species. J Ecol 93:1005–1016

Dias A (1998) Comparison of methods for measuring rabbit incidence on grasslands. Mammalia 62:205–212

de Mazancourt C, Loreau M, Abbadie L (1998) Grazing optimization and nutrient cycling: when do herbivores enhance plant production? Ecology 79:2242–2252

de Mazancourt C, Loreau M, Abbadie L (1999) Grazing optimization and nutrient cycling: potential impact of large herbivores in a savanna ecosystem. Ecol Appl 9:784–797

de Mazancourt C, Loreau M (2000) Effect of herbivory and plant species replacement on primary production. Am Nat 155:735–754

Frank DA, Evans RD (1997) Effects of native grazers on grassland N cycling in Yellowstone National Park. Ecology 78:2238–2248

Frank DA, Groffman PM (1998) Ungulate vs landscape control over C and N processes in grasslands of Yellowstone National Park. Ecology 79:2229–2241

Frank DA, McNaughton SJ (1993) Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. Oecologia 96:157–161

Frank DA, Groffman PM, Evans RD, Tracy BF (2000) Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands. Oecologica 123:116–121

Frank DA, Kuns MM, Guido DR (2002) Consumer control of grassland plant production. Ecology 83:602–606

Frank DA, Evans RD, Tracy BE (2004) The role of ammonia volatilization in controlling the natural N-15 abundance of a grazed grassland. Biogeochemistry 68:169–178

Grime JP (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. Oikos 77:489–494

Krebs CJ (1989) Ecological methodology. Harper Collins, New York

Lauenroth WK (2000) Methods of estimating belowground net primary production. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) Methods in ecosystem science. Springer, Berlin Heidelberg New York, pp 58–71

McNaughton SJ, Milchunas DG, Frank DG (1996) How can net primary productivity be measured in grazing ecosystems? Ecology 77:974–977

McNaughton SJ, Banyikwa FF, McNaughton MM (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. Science 278:1798–1800

Milchunas DG, Laurenroth WK (1993) Quantitative effects of grazing on vegetation and soils over a global range of environments. Ecol Monogr 63:327–366

Molvar EM, Bowyer RT, van Ballenberghe V (1993) Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94:472–479

Oesterheld M, McNaughton SJ (2000) Herbivory in terrestrial ecosystems. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) Methods in ecosystem science. Springer, Berlin Heidelberg New York, pp 151–158

Olofsson J, Oksanen L (2002) Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer, a litterbag experiment. Oikos 96:507–515

Olofsson J, Stark S, Oksanen L (2004) Herbivore influence on ecosystem processes in the tundra. Oikos 105:386–396

Pastor J, Naiman RJ (1992) Selective foraging and ecosystem processes in boreal forests. Am Nat 131:690–705

Pastor J, Dewey B, Naiman RJ, McInnes PF, Cohen Y (1993) Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. Ecology 74:467–480

R development Core Team (2005) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. ISBN 3–900051–07–0, http://www.R-project.org

Raison RJ, Connell MJ, Khanna PK (1987) Methodology for studying fluxes of soil mineral-N in situ. Soil Biol Biochem 19:521–530

Ritchie ME, Tilman DJ, Knops MH (1998) Herbivore effects on plant and nitrogen dynamics in oak savanna. Ecology 79:165–177

Robinson M, Dean TJ (1993) Measurement of near surface soil water content using a capacity probe. Hydrol Proc 7:77–86

Ruess RW, McNaughton SJ (1987) Grazing and the dynamics of nutrients and energy regulated microbial processes in the Serengeti grasslands. Oikos 49:101–110

Ruess HW, Hik DS, Jefferies RL (1989) The role of lesser snow geese as nitrogen processors in a sub-arctic marsh. Oecologia 79:23–29

Sala OE, Austin AT (2000) Methods of estimating aboveground net primary productivity. In: Sala OE, Jackson RB, Mooney HA, Howarth RW (eds) Methods in ecosystem science. Springer, Berlin Heidelberg New York, pp 33–41

Schimel DS, Parton WJ, Adamsen FJ, Woodmansee RG, Senft RI, Stillwell MA (1986) The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. Biogeochemistry 2:39–52

Sirotnak JM, Huntly NJ (2000) Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. Ecology 81:78–87

Schlesinger WH, Raikes JA, Hartley AE, Cross AF (1996) On the spatial distribution of soil nutrients in desert ecosystems. Ecology 77:364–374

Stark S, Grellmann D (2002) Soil microbial responses to herbivory in an arctic tundra heath at two levels of nutrient availability. Ecology 83:2736–2744

Tilman DA (1988) Plant strategies and the dynamics and structure of plant communities. Princeton University Press, Princeton

Van der Wal R, Bardgett RD, Harrison HA, Stien A (2004) Vertebrate herbivores and ecosystem control: cascading effects on tundra ecosystems. Ecography 27:242–252

Van Winjen HJ, Van der Wal R, Bakker JP (1999) The impact of herbivores on nitrogen mineralization rate: consequences for salt-mash succession. Oecologia 118:225–231

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13:87–115

Wardle DA (2002) Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton

Willot SJ, Miller AJ, Incoll LD, Compton SG (2000) The contribution of rabbits (Oryctolagus cuniculus L.) to soil fertility in semi-arid Spain. Biol Fertil Soils 31:379–38