

Browsing by red deer negatively impacts on soil nitrogen availability in regenerating native forest

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Abstract

Herbivores can have important indirect effects on belowground properties and processes that govern ecosystem form and productivity. A major way that herbivores affect ecosystem productivity is by modifying feedbacks that occur between dominant plants and belowground properties, and especially by changing the rates of nutrient mineralisation. In this study, we examine the effects of browsing by red deer, relative to landscape factors such as variations in microclimate and topography, on soil biological properties and N cycling in regenerating forest in an upland region of the Scottish Highlands. The site at Creag Meagaidh in the Scottish Highlands was sampled three times over the growing season of 2001 and soil cores were taken from four exclosures. Measures of soil biological properties and nitrogen availability were made. The results presented here suggest that although spatial and temporal variation were the dominant factors affecting soil biological properties and nitrogen dynamics in this ecosystem, herbivory also had consistent and significant effects on these measures. Browsing significantly reduced measures of DOC (27%), NO_3^- (48%), NH_4^+ (49%) and N-mineralisation (53%). The microbial C:N ratio was also significantly greater (89%) in browsed than un-browsed areas, suggesting that the removal of deer reduced the extent that the microbial community was N-limited. These significant negative effects of browsing on soil nitrogen cycling have the potential to reduce ecosystem productivity. We conclude that removal of browsing over 14 years has accelerated native woodland regeneration, leading to subsequent increases in soil C- and N-mineralisation, further increasing plant N supply and tree growth in this ecosystem.

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1. Introduction

Herbivores can have important direct effects on ecosystems, including the removal and consumption of herbage, trampling of soil and vegetation, and the return of excreta (Floate, 1981). However, ecologists are becoming increasingly aware that there are also important indirect effects of herbivores on belowground properties and processes which can govern the net effect of herbivores on ecosystem form and productivity (Bardgett et al., 1998; Wardle et al., 2002). Whilst the effects of herbivory on plant community structure and function have been widely studied (McNaughton, 1984; Haukioja et al., 1990; Dyer et al., 1993; Lehtilä et al., 2000), the indirect effects of herbivory on soil biological properties and nutrient dynamics have often been overlooked, and, until recently, have not been integrated into a wider

understanding of how herbivores affect ecosystems (Bardgett et al., 1998).

A major way that herbivores affect ecosystem productivity is by modifying feedbacks that occur between dominant plants and belowground properties, especially through altering nutrient availability in soil. Several mechanisms have been proposed to explain how large herbivores can affect soil biological properties and soil nutrient cycling (Bardgett et al., 1998) and studies of herbivore impacts on ecosystems suggest that they mediate feedbacks between plants and soil organisms that are either positive or negative (Ritchie et al., 1998). Positive effects of herbivory on soil biota and nutrient cycling occur when dominant plant species benefit from grazing, exhibiting compensatory growth (Augustine and McNaughton, 1998). This mechanism is most common in grasslands of high soil fertility, where herbivory positively affects the decomposer subsystem through preventing colonisation of later successional plants which produce poorer litter quality, as well as

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through returning carbon and nutrients to the soil in labile forms as dung and urine, and as enhanced rhizodeposition (Holland and Detling, 1990; Holland et al., 1996; Bardgett et al., 1997; Frank and Groffman, 1998; Hamilton and Frank, 2001). In contrast, negative effects of herbivory on soil properties and ecosystem productivity occur in unproductive ecosystems with low consumption rates by herbivores, where selective foraging on nutrient rich plants can lead to the dominance of defended plants that produce recalcitrant litter (Ritchie et al., 1998). Since most nutrients will be returned to the soil as recalcitrant plant litter, the net effect of herbivory in these low productivity ecosystems is often to reduce soil biotic activity, nutrient mineralisation, and supply rates of nutrients from soil, despite inputs of dung and urine (Pastor et al., 1993).

Most studies on the impacts of grazers on soil biological properties have been carried out in grassland ecosystems, where positive responses to grazing are commonly detected (Chaneton et al., 1996; Bardgett et al., 1997, 2001; Tracy and Frank, 1998; Hamilton and Frank, 2001). Effects of browsing in woodland ecosystems, however, appear to be more idiosyncratic and hence difficult to predict. For example, studies of boreal forests show that selective grazing of palatable tree species by moose leads to a dominance of unpalatable tree species that produce low quality leaf litter, which ultimately slows down rates of N-mineralisation in soil (Pastor et al., 1993; Stark et al., 2000). However, in a study of a range of native forests in New Zealand, Wardle et al. (2001) showed that the effects of deer browsing on soil biota and nutrient cycling were highly idiosyncratic, with an equal number of positive and negative effects being detected across thirty locations. Browsing has also been shown to alter fine root growth in Boreal forest (Ruess et al., 1998) and mycorrhizal colonisation of trees (Rossow et al., 1997), both of which having the potential to alter carbon flux to soil and hence the activity of free-living soil microbes that govern the processes of nutrient mineralisation.

In this study, we examined the effects of browsing by red deer on soil biological properties and N cycling in regenerating forest in an upland region of the Scottish Highlands, in northern Britain. Historically, sheep and red deer have heavily grazed upland areas of Britain, and consequently the vegetation below the natural tree line is dominated by grassland and heath (Rodwell, 1994), with little regeneration of native woodland (Mitchell et al., 1995). In recent years, however, land management has been altered by conservation bodies with the aim of encouraging forest regeneration, either through fencing, to eliminate large grazers, or by intensive culling to reduce population densities of red deer (Ramsey, 1996). There is a dearth of information on the effects of large herbivores, such as red deer, on soil biological properties and processes in upland woodland ecosystems; however, these effects have the potential to feedback on tree growth as a result of alterations in soil nutrient availability. The objective of this study,

therefore, was to address this lack of information by comparing soil biological properties and measures of soil N availability inside and outside fenced exclosures at four topographically different locations below the historic tree line at Creag Meagaidh National Nature Reserve (NNR) in the Scottish Highlands. The use of fenced exclosures at different locations enabled us to determine the importance of browsing animals relative to landscape factors, such as variations in microclimate and topography, as determinants of soil biological properties and nutrient availability in this ecosystem. It is generally thought that the main factors that regulate soil biological properties at the ecosystem scale are abiotic (Frank and Groffman, 1998; Wardle, 1998; Verchot et al., 2002); variations in topography and microclimate between sites influences soil temperature and moisture regimes, which together act as strong determinants of soil biological activity (Zeller et al., 2001). In accordance with previous studies on sheep grazing in upland areas of Britain (Bardgett et al., 1997, 1998, 2001) we predict that browsing by red deer increases soil biological activity, nutrient mineralisation, and plant N supply in this regenerating forest ecosystem, and that these effects of browsing will outweigh the influence of landscape factors on these measures.

2. Study site and methods

2.1. Study site and soil sampling

Creag Meagaidh NNR covers an area of 3940 ha and lies in the central Scottish Highlands (56°57'N, 4°35'W) (Fig. 1). Mean annual temperature in this region is 6.7 °C and mean annual precipitation is around 1252 mm. Soils in this area are predominantly humic podzols. A key management objective of the reserve is to encourage regeneration and extension of native forests and boreal scrub vegetation on the lower slopes of the mountain. To achieve this aim, an active culling regime of the main grazer, red deer, was introduced in 1986. This programme has reduced red deer population densities from 19 to below 5 km⁻², resulting in active growth of downy birch (*Betula pubescens*) saplings and other tree species such as sessile oak (*Quercus petraea*) and rowan (*Sorbus aucuparia*) on the lower slopes of the mountain (NCC, 1989; Ramsey, 1996). In addition to the culling programme, four fenced exclosures measuring 10 m × 10 m were erected in 1987 to observe the effects of complete elimination of red deer browsing on tree regeneration. The presence of these exclosures made it possible to directly compare lightly browsed and un-browsed areas of regenerating native forest in four geographically distinct areas of the reserve (Fig. 1).

The site was sampled three times over the growing season of 2001, in May, late June and September. At each of the four locations, five individual soil cores (35 mm diameter × 100 mm depth) were taken from four randomly located 1 m² plots

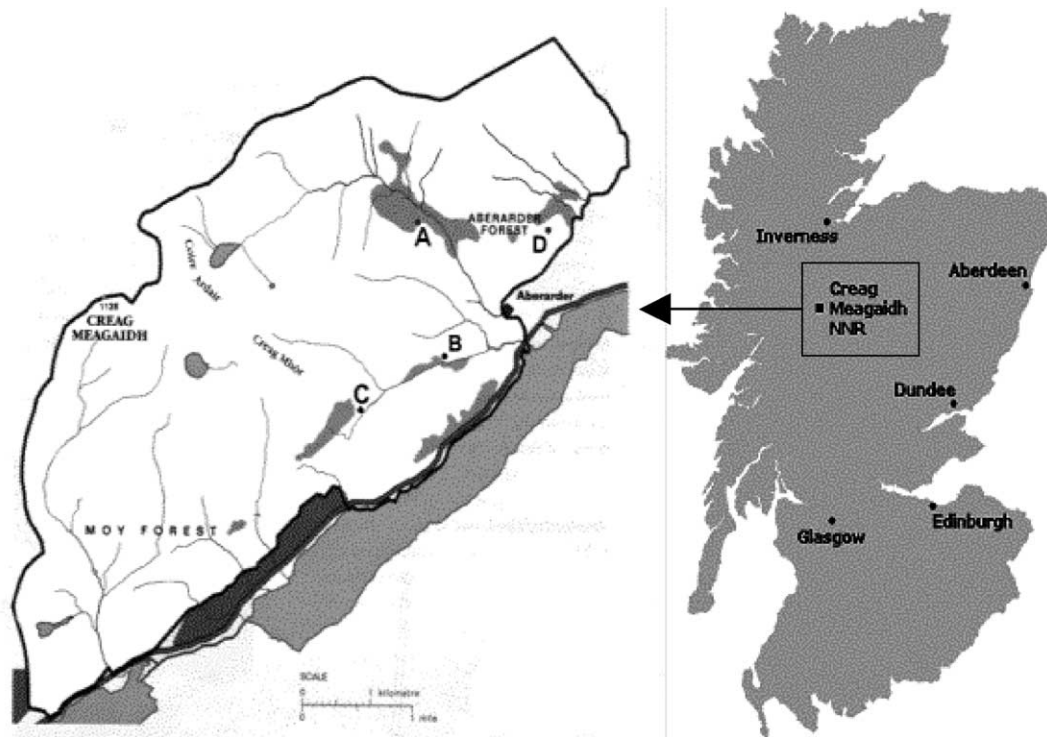


Fig. 1. Study site locations (adapted from Ramsey (1996)). National grid references for the sites are as follows: Site A (NN 466888); site B (NN 464868); site C (NN 455859); and site D (NN 48444887).

within the enclosure. Similarly, five soil samples were taken from four independent plots in a 10 m × 10 m area positioned outside the enclosure. Cores from each sub-plot were bulked, and then passed through a 5 mm sieve prior to analysis. This sampling yielded four independent replicate samples from inside and outside of the enclosure, at each location. Prior to analysis soil was stored at 4 °C. Abiotic properties of soil, such as pH, moisture content, and loss on ignition (LOI) were measured using standard protocol (Allen et al., 1989). Additionally, soil temperature was continuously measured inside and outside all enclosures using Tiny Talk Temperature Sensors (Preservation Equipment Ltd) inserted just below ground level. Data on birch tree numbers and trunk diameters of all trees (at 20 cm height) inside enclosures, and in the adjacent 10 m × 10 m browsed plot were collected in September 2001, together with litter samples. Where possible, senescent leaves were removed directly from the trees or from directly beneath the trees. Four independent litter samples were collected from inside each enclosure, and four from outside each enclosure. Total C and N were measured on ground, oven-dried material using an automated Dumas procedure on a Carbo Erba NA 1500 analyser (Erba Science, UK). Rarely were any other tree species recorded inside the enclosures.

2.2. Soil biological properties

Microbial biomass carbon (C) and nitrogen (N) were measured using the fumigation–extraction technique of

Vance et al. (1987). Briefly, soil samples (5 g fresh weight) were fumigated with CHCl_3 for 24 h at 25 °C. After removal of the CHCl_3 , soluble C was extracted from fumigated and un-fumigated samples with 0.5 M K_2SO_4 for 30 min on an orbital shaker (soil: solution 1:4 w/v). Total organic C (TOC) in filtered extracts (Whatman No. 1) was determined using a Shimadzu 5000A TOC analyser. Microbial C flush (difference between extractable C from fumigated and un-fumigated samples) was converted to microbial biomass C using a K_{EC} factor of 0.35 (Sparling et al., 1990). Extractable N in the above extracts was determined by oxidation with $\text{K}_2\text{S}_2\text{O}_8$, using the methodology of Ross (1992), and measurement of the resultant NO_3^- -N and NH_4^+ -N by autoanalyser procedures. The microbial N flush was converted to microbial biomass N using a K_{EN} factor of 0.18 (Voroney et al., 1993). Microbial activity was measured as basal respiration under laboratory conditions. 1 g of moist soil was placed in a 28 ml McCartney bottle at 25 °C. After 30 min equilibration, the bottle was sealed with a subaseal and incubated for 24 h. One millilitre headspace gas was then removed and CO_2 concentration was measured against a 1% standard gas on an infra-red gas analyser and expressed as $\mu\text{l CO}_2 \text{ g}^{-1} \text{ dry soil h}^{-1}$ (Bardgett et al., 1997).

2.3. Soil nitrogen availability

Effects of browsing on soil N availability was measured using three techniques. First, the soil concentration of mineral N was determined by shaking 5 g fresh soil with

25 ml 1 M KCl for 30 min on an orbital shaker. The resulting suspension was filtered through Whatman No. 1 paper. The concentration of NH_4^+ -N and NO_3^- -N in the extracts was determined by autoanalyser procedures. Second, net N-mineralisation potential was measured as the release of mineral N (NH_4^+ -N and NO_3^- -N) after incubation of soil samples in the laboratory (5 g) for 14 days at 25 °C (Ross, 1992). After incubation, soil samples were extracted with KCl as described above and the concentration of NH_4^+ and NO_3^- determined. Third, dissolved organic N (DON) and C (DOC) were measured by adding 70 ml distilled water to 10 g soil samples, which were shaken on an orbital shaker for 10 min prior to being filtered through Whatman No. 1 paper. TOC was then determined on the water extract using a Shimadzu 5000A TOC analyser, whereas total N was determined by oxidation with potassium persulphate ($\text{K}_2\text{S}_2\text{O}_8$), and measurement of the resultant NO_3^- -N and NH_4^+ -N by autoanalyser procedures. Total C and N in soil were also measured on ground sub-samples of soil using an automated Dumas procedure on a Carlo Erba NA 1500 analyser (Erba Science UK).

2.4. Statistical analyses

The effects of browsing, sampling site and date on soil microbial and nutrient properties were analysed using a three way ANOVA with the SAS statistical package (SAS 8.2, 1999). Dependent variables were normalised, if required, prior to analysis using \log_{10} transformations for data on microbial respiration, microbial biomass C, microbial biomass C:N, N-mineralisation, nitrate,

ammonium, DON, metabolic quotient, moisture content, litter C:N and total C:N. A square root transformation was used microbial biomass N and an arcsine transformation was carried out on data for LOI. Data on pH and DOC did not require transformation. The independent variables were date, which had three values (May, June and September), site, which had four values (A, B, C and D) and browsing, which had two values (browsed and un-browsed). Second order interactions consisted of date \times browsing, site \times browsing and date \times site and there was one third order interaction; date \times site \times browsing. Pearson correlations were then carried out on data to establish relationship between tree growth and soil nutrient properties. Only correlations significant at the $P \leq 0.05$ level are presented.

3. Results

3.1. Soil physicochemical properties and tree growth

Soil moisture content varied significantly across sampling dates ($F = 93.95$, $P < 0.0001$; 45% variance), being greatest in September and lowest in June (Tables 1 and 2). There was also a significant date \times browsing interaction ($F = 4.16$, $P = 0.0195$), however, this accounted for only 2% of the variance in this measure (Table 2). Soil pH varied between individual sites ($F = 115.32$, $P < 0.0001$; 72% variance), ranging from 4.1 in site A to 5.6 in site C (Tables 2 and 3). Browsing was also responsible for a significant amount of variance in this

Table 1
Effects of sampling date on soil microbial properties and nutrients in regenerating native woodland in Creag Meagaidh, Scotland

Property	Date		
	May	June	September
<i>Physical properties</i>			
Moisture content (%)	177.84 \pm 25.04 ^a	89.77 \pm 9.80 ^b	209.14 \pm 29.40 ^c
pH	5.07 \pm 0.10 ^a	4.97 \pm 0.11 ^{ab}	4.67 \pm 0.12 ^b
LOI (%)	ND	ND	ND
Total C:N	ND	ND	ND
<i>Microbial properties</i>			
Microbial respiration (ml CO_2 m^{-2} h^{-1} evolved)	221.11 \pm 13.50 ^a	2558.59 \pm 367.20 ^b	303.39 \pm 17.35 ^c
Microbial biomass N (g N m^{-2})	28.91 \pm 4.67 ^b	42.80 \pm 5.54 ^a	45.41 \pm 3.86 ^a
Microbial biomass C (g C m^{-2})	113.79 \pm 7.09 ^a	117.15 \pm 11.83 ^b	118.77 \pm 6.87 ^a
Microbial biomass C:N	7.31 \pm 1.25 ^a	3.50 \pm 0.28 ^b	2.56 \pm 0.17 ^c
Metabolic quotient (%)	201.95 \pm 8.29 ^a	2263.42 \pm 225.92 ^b	279.86 \pm 21.29 ^c
<i>Nutrient availability</i>			
DON (mg N m^{-2})	2838.01 \pm 494.48 ^a	1625.20 \pm 303.21 ^b	719.88 \pm 148.95 ^c
DOC (g C m^{-2})	14.38 \pm 1.08 ^a	5.83 \pm 0.96 ^b	8.27 \pm 0.61 ^c
N-mineralization (mg N m^{-2} day^{-1})	72.57 \pm 11.49 ^a	103.28 \pm 21.10 ^a	64.92 \pm 12.78 ^a
Nitrate (mg NO_3^- m^{-2})	415.34 \pm 124.37 ^a	349.01 \pm 62.92 ^a	473.43 \pm 40.73 ^b
Ammonia (mg NH_4^+ m^{-2})	1556.60 \pm 240.09 ^a	965.97 \pm 226.81 ^b	702.54 \pm 116.12 ^b
Litter C:N	ND	ND	ND

Values are means \pm se. Values with the same letters are not significantly different at the $P < 0.05$ level as determined using a Fisher LSD post-hoc test.

Table 2
Summary statistics of a three-way ANOVA looking at the effects of browsing, sampling site and sampling date on moisture content and pH

	d.f.	Moisture content		pH	
		F	P	F	P
Main effects					
Browsing	1	0.22	0.6438	19.02	<0.0001
Date	2	93.95	<0.0001	17.89	<0.0001
Site	3	16.78	<0.0001	115.32	<0.0001
Two-way interactions					
Date × browsing	2	4.16	0.0195	0.61	0.5467
Site × browsing	3	0.12	0.9461	5.44	0.0020
Date × site	6	87.70	<0.0001	0.98	0.4457
Three-way interactions					
Date × site × browsing	6	5.35	0.0001	0.31	0.9294
Residual	72			72	

Values for moisture content were normalised using \log_{10} transformations prior to analysis.

measure ($F = 19.02$, $P = < 0.0001$, 12% variance), with soil pH being consistently greater in browsed than un-browsed areas (Tables 2 and 3). Similarly, soil organic matter content, measured as LOI, varied significantly and greatly across sites ($F = 107.48$, $P = < 0.0001$; 97% variance), ranging from 18% at site B to 86% at site A (Tables 3 and 4). Soil organic matter quality measured as total C:N also differed greatly between sites ($F = 133.56$, $P = < 0.0001$; 91% variance), being highest, indicative of poor quality organic matter at site A, and lowest at site B, which had the lowest total organic matter content (Tables 3 and 4). There was also a significant site × browsing interaction ($F = 10.68$, $P = 0.0001$; 7% variance) in the soil C:N ratio (Table 4), being higher in browsed than un-browsed areas at site C, but higher in un-browsed than browsed areas at site D (Fig. 2a). At three of the individual sites, the removal of browsing significantly decreased soil temperature ($P = < 0.0001$ for all) (Fig. 2b).

3.2. Soil microbial properties

Microbial respiration varied greatly between sampling dates ($F = 308.87$, $P = < 0.0001$, 84% variance), ranging from 2559 ml CO₂-C m⁻² h⁻¹ in June to 221 ml CO₂-C m⁻² h⁻¹ in May (Tables 1 and 5). There was also considerable variation in microbial respiration between individual sites ($F = 30.16$, $P = < 0.0001$, 8% variance) (Tables 3 and 5), being greatest at site B, which had the lowest organic matter content, and lowest at site A, which had the greatest organic matter content in soil. Browsing significantly decreased microbial respiration at site A only, but the site × browsing interaction ($F = 5.64$, $P = 0.0016$) that explained this difference only accounted for 2% of the variance in this measure (Table 5) suggesting that effects of

browsing on microbial respiration were relatively unimportant.

Site differences accounted for most of the variance (45%) in microbial biomass N ($F = 35.93$, $P = < 0.0001$), being greatest in samples from site B and lowest in samples collected from site A (Tables 3 and 5). There was also a significant date × browsing interaction for this measure ($F = 13.76$, $P = < 0.0001$, 17% variance) (Table 5), with greater microbial biomass N being detected in un-browsed than browsed areas in May (Fig. 3a). Microbial biomass C varied greatly between the individual sites ($F = 59.62$, $P = < 0.0001$, accounting for 59% of the variability) (Tables 3 and 5) and there was also a significant site × browsing interaction ($F = 4.58$, $P = 0.0054$, 4% variance) (Table 5): microbial biomass C was greater in un-browsed areas at site B, whereas it did not differ in browsed and un-browsed areas at the other sites (Fig. 3b). The effects of browsing on microbial biomass C also varied with sampling date ($F = 3.71$, $P = 0.0293$) for the date × browsing interaction, accounting for 4% of the variance) (Table 5), being greater in un-browsed than browsed areas in May only (Fig. 3c). Sampling date accounted for 32% of the variance in microbial C:N ($F = 19.67$, $P = < 0.0001$). Microbial C:N was significantly greater in May than in June or September (Tables 1 and 5). The removal of browsing also significantly affected microbial C:N ($F = 12.87$, $P = 0.0007$, 21% variance), being greater in browsed than un-browsed areas (Tables 3 and 5). The metabolic quotient was most significantly affected by date of sampling ($F = 447.85$, $P = < 0.0001$, 94% variance), being highest in June and lowest in May (Tables 1 and 5). The removal of browsing did not significantly affect this measure.

3.3. Soil nutrient availability

DON varied significantly between sampling dates ($F = 14.63$, $P = < 0.0001$, 59% variance), being greatest in May and lowest in September (Tables 1 and 6). Sampling date also accounted for 60% of the variance in DOC ($F = 29.60$, $P = < 0.0001$), being maximal in May (Tables 1 and 6). DOC was also significantly affected by the removal of browsing ($F = 9.40$, $P = 0.0031$, 19% variance), being 27% lower in browsed than un-browsed areas across all sites (Tables 3 and 6).

A large proportion of the variance (59%) in potential N-mineralisation was attributed to differences between individual sites ($F = 40.73$, $P = < 0.0001$) (Table 6). However, this measure was also significantly affected by the removal of browsing ($F = 11.78$, $P = < 0.0012$, 17% variance), with rates of N-mineralisation being significantly greater in un-browsed areas (Tables 3 and 6). When integrated across sites, potential N-mineralisation was 53% lower in browsed than un-browsed areas. Soil concentrations of both nitrate ($F = 74.24$, $P = < 0.0001$; 47% variance) and ammonium ($F = 42.50$, $P = < 0.0001$; 47% variance) similarly varied greatly across sites (Tables 3 and 6), and

Table 3
Effects of browsing and sampling site on soil microbial properties and nutrients in regenerating native woodland in Creag Meagaidh, Scotland

Property	Browsing		Site			
	Browsed	Un-browsed	A	B	C	D
<i>Physical properties</i>						
Moisture content (%)	151.49 ± 17.43 ^a	166.34 ± 22.37 ^a	300.06 ± 43.77 ^a	103.58 ± 6.30 ^b	110.60 ± 7.67 ^b	121.42 ± 10.98 ^b
PH	5.03 ± 0.10 ^a	4.78 ± 0.09 ^b	4.12 ± 0.06 ^a	5.15 ± 0.07 ^b	5.57 ± 0.06 ^c	4.76 ± 0.10 ^d
LOI (%)	39.68 ± 7.21 ^a	41.47 ± 7.58 ^a	86.12 ± 3.06 ^a	18.03 ± 2.22 ^c	19.85 ± 0.98 ^c	38.30 ± 4.83 ^b
Total C:N	17.07 ± 1.61 ^a	17.81 ± 1.65 ^a	26.88 ± 0.99 ^a	12.25 ± 0.32 ^c	12.65 ± 0.37 ^c	17.98 ± 1.33 ^b
<i>Microbial properties</i>						
Microbial respiration (ml CO ₂ m ⁻² h ⁻¹ evolved)	987.96 ± 209.14 ^a	1067.43 ± 256.14 ^a	301.83 ± 33.24 ^b	1730.09 ± 492.83 ^a	1303.29 ± 340.37 ^a	775.58 ± 192.09 ^c
Microbial biomass N (g N m ⁻²)	33.86 ± 4.30 ^a	42.70 ± 4.05 ^a	15.69 ± 2.18 ^a	56.99 ± 5.30 ^{bc}	47.84 ± 5.78 ^{cc}	32.63 ± 5.44 ^d
Microbial biomass C (g C m ⁻²)	115.35 ± 6.58 ^a	117.79 ± 7.82 ^a	64.94 ± 7.98 ^a	141.22 ± 9.37 ^b	127.77 ± 8.00 ^b	132.36 ± 7.29 ^b
Microbial biomass C:N	6.08 ± 0.96 ^a	3.21 ± 0.24 ^b	4.30 ± 0.43 ^{ab}	3.59 ± 0.73 ^{cc}	5.66 ± 1.74 ^{ac}	5.30 ± 0.73 ^{ad}
Metabolic quotient (%)	767.97 ± 129.92 ^a	1062.19 ± 208.80 ^a	1091.67 ± 321.75 ^a	1125.41 ± 288.22 ^a	872.14 ± 204.66 ^a	571.09 ± 118.09 ^b
<i>Nutrient availability</i>						
DON (mg N m ⁻²)	1715.04 ± 296.31 ^a	1825.67 ± 336.35 ^a	1141.02 ± 207.88 ^a	2501.27 ± 400.59 ^a	1800.52 ± 422.98 ^a	1817.40 ± 838.56 ^a
DOC (g C m ⁻²)	8.07 ± 0.69 ^a	10.98 ± 1.06 ^b	10.21 ± 1.63 ^{ab}	11.04 ± 1.47 ^{ac}	9.28 ± 0.83 ^a	7.54 ± 1.03 ^d
N-mineralization (mg N m ⁻² day ⁻¹)	49.85 ± 7.56 ^a	106.35 ± 14.39 ^b	20.14 ± 6.49 ^b	115.25 ± 17.67 ^{ac}	122.64 ± 15.49 ^{ad}	25.78 ± 4.91 ^c
Nitrate (mg NO ₃ ⁻ m ⁻²)	282.54 ± 22.90 ^a	542.65 ± 90.21 ^b	213.42 ± 36.50 ^a	373.30 ± 41.52 ^b	845.03 ± 152.75 ^c	218.63 ± 19.89 ^d
Ammonia (mg NH ₄ ⁺ m ⁻²)	730.13 ± 110.74 ^a	1419.94 ± 204.93 ^b	493.95 ± 130.06 ^a	1430.91 ± 290.01 ^b	1979.27 ± 231.50 ^{c,0}	396.01 ± 109.77 ^a
Litter C:N	50.54 ± 4.54 ^a	58.50 ± 4.78 ^a	67.67 ± 6.39 ^a	43.38 ± 2.40 ^b	52.88 ± 4.12 ^{ab}	54.16 ± 9.43 ^{ab}

Values are means ± se. Values with the same letters are not significantly different at the $P < 0.05$ level as determined using a Fisher LSD post-hoc test.

Table 4

Summary statistics of a two-way ANOVA looking at the effect of browsing and sampling site on leaf litter C:N, total soil C:N and LOI

	d.f.	LOI		Soil total C:N		Leaf litter C:N	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Main effects							
Browsing	1	0.17	0.6813	1.07	0.3115	3.68	0.0669
Site	3	107.48	<0.0001	133.56	<0.0001	4.22	0.0156
Two-way interaction							
Site × browsing	3	2.58	0.0774	10.68	0.0001	8.53	0.0005
Residual		24		24		24	

Values for leaf litter C:N and total soil C:N were normalised using \log_{10} transformations, whereas values for LOI were normalised using an arcsine square root transformation prior to analysis.

sampling dates (Tables 1 and 6) (Ammonium, $F = 10.43$, $P = 0.0001$; 12% variance, nitrate, $F = 33.73$, $P = < 0.0001$; 21% variance). Browsing also significantly decreased soil concentrations of nitrate

($F = 24.48$, $P = < 0.0001$, 15% variance) and ammonium ($F = 9.34$, $P = 0.0031$, 10% variance) (Tables 3 and 6).

3.4. Leaf litter properties

Leaf litter C:N of birch was most significantly affected by the site × browsing interaction ($F = 8.53$, $P = 0.0005$), which accounted for 49% of the variance in this measure (Table 4). At site C, leaf litter C:N was greater in browsed areas, whereas, at site D this ratio was greater in un-browsed areas (Fig. 4).

3.5. Relationships between soil properties and tree growth

No significant relationships were detected between birch tree number and any soil nutrient property; however, four significant correlations were identified for birch tree diameter. These included positive relationships between birch tree diameter and N-mineralisation ($r = 0.75$, $P = 0.0312$) (Fig. 5a), dissolved inorganic N (nitrate plus ammonium) ($r = 0.72$, $P = 0.0459$) (Fig. 5b) and microbial biomass N ($r = 0.79$, $P = 0.02$) (Fig. 5c). A negative relationship was identified between birch tree diameter and microbial biomass C:N ($r = -0.75$, $P = 0.03$) (Fig. 5d).

4. Discussion

Variation in landscape factors, such as topographic position and climate, are generally considered the pre-dominant variables affecting soil C and N dynamics in grassland ecosystems (Frank et al., 1994; Frank and Groffman, 1998; Zeller et al., 2001; Verchot et al., 2002), and the same appears to be true in the regenerating woodland ecosystem studied here. Although spatial and temporal variation was the dominant factor affecting soil biological properties and nutrient dynamics in this ecosystem, browsing was still identified as an important and significant determinant of these properties. That grazer effects were detectable in this ecosystem against spatial and

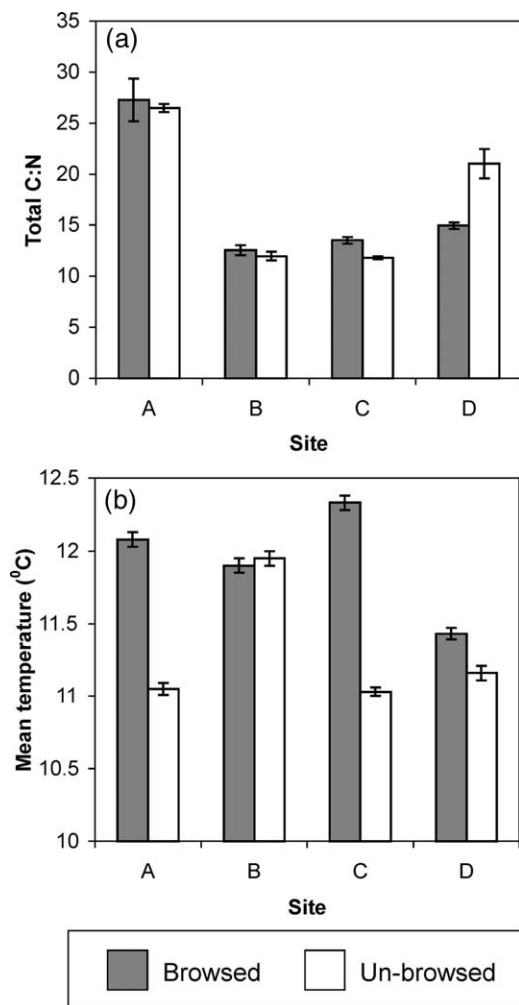


Fig. 2. Soil physicochemical properties. The effect of browsing on (a) total C:N at four sampling sites and (b) soil temperature at four sampling sites at Creag Meagaidh, Scotland. Values are means \pm se. All interactions are significant at the $P < 0.05$ level or above.

Table 5

Summary statistics of a three-way ANOVA looking at the effects of browsing, sampling site and sampling date on soil microbial properties

	d.f.	Microbial respiration		Microbial biomass N		Microbial biomass C		Microbial biomass C:N		Metabolic quotient	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Main effects											
Browsing	1	0.81	0.3702	3.86	0.054	0.89	0.3482	12.87	0.0007	3.2	0.0777
Date	2	308.87	<0.0001	10.15	0.0002	7.5	0.0011	19.67	<0.0001	447.85	<0.0001
Site	3	30.16	<0.0001	35.93	<0.0001	59.62	<0.0001	4.13	0.0099	6.37	0.0007
Two-way interactions											
Date × browsing	2	0.01	0.9906	13.76	<0.0001	3.71	0.0293	15.52	<0.0001	2.57	0.0837
Site × browsing	3	5.64	0.0016	7.62	0.0002	4.58	0.0054	3.87	0.0135	8.13	<0.0001
Date × site	6	19.70	<0.0001	5.61	0.0003	23.36	<0.0001	1.04	0.4013	2.71	0.0199
Three-way interactions											
Date × site × browsing	6	1.01	0.4257	2.84	0.0229	1.09	0.3752	2.94	0.0194	2.14	0.0595
Residual		72		61		72		60		72	

Values for microbial respiration, microbial biomass C, microbial biomass C:N and metabolic quotient were normalised using \log_{10} transformations. Values for microbial biomass N were normalised using a square root transformation prior to analysis.

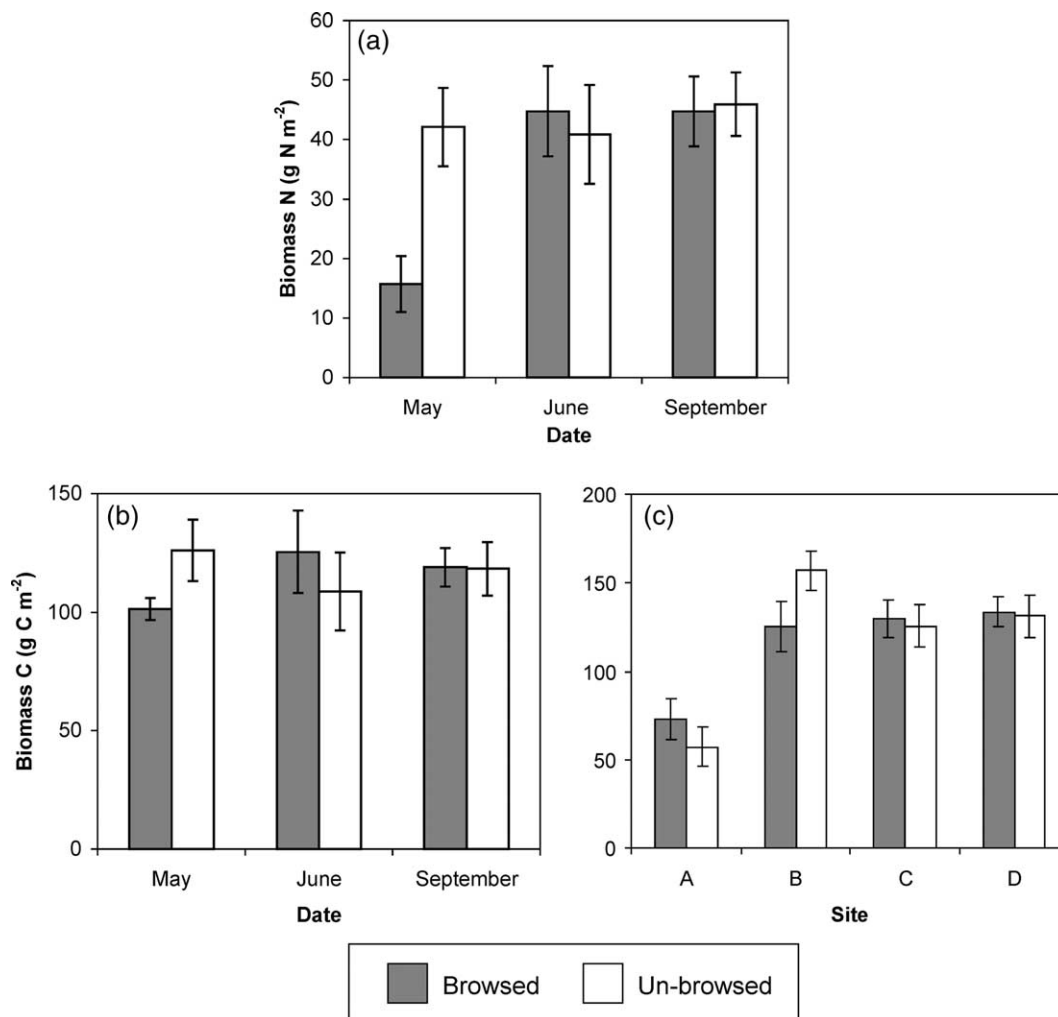


Fig. 3. Soil microbial properties. The effect of browsing on (a) microbial biomass N on three sampling dates; (b) microbial biomass C at three sampling sites and (c) microbial biomass C on four sampling sites at Creag Meagaidh, Scotland. Values are means \pm se. All interactions are significant at the $P < 0.05$ level or above.

Table 6

Summary statistics of a three-way ANOVA looking at the effects of browsing, sampling site and sampling date on soil nutrient properties

	d.f.	DON		DOC		N-mineralisation		Nitrate		Ammonium	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Main effects											
Browsing	1	2.94	0.0920	9.40	0.0031	11.78	0.0012	24.48	<0.0001	9.34	0.0031
Date	2	14.63	<0.0001	29.60	<0.0001	0.71	0.4967	33.73	<0.0001	10.43	0.0001
Site	3	0.97	0.4139	2.58	0.0606	40.73	<0.0001	74.24	<0.0001	42.50	<0.0001
Two-way interactions											
Date × browsing	2	2.22	0.1175	0.25	0.7804	5.14	0.0091	1.35	0.2657	0.77	0.4649
Site × browsing	3	0.84	0.4797	3.86	0.0129	5.95	0.0014	8.2	<0.0001	18.47	<0.0001
Date × site	6	1.52	0.1881	2.30	0.0438	1.39	0.2355	15.33	<0.0001	3.77	0.0025
Three-way interactions											
Date × site × browsing	6	0.67	0.6747	0.39	0.8829	1.92	0.1202	1.17	0.3318	3.61	0.0035
Residual		57		71		53		72		72	

Values for rates of N-mineralisation, nitrate, ammonium and DON were normalised using a log₁₀ transformation prior to analysis.

temporal variation contrasts to the study of Verchot et al. (2002) who showed that topography in a semi-arid grassland ecosystem at Yellowstone National Park was the dominant factor explaining variance in both N-mineralisation and immobilisation rates with grazing animals having no significant effects on these measures.

Our results show that that browsing by deer had consistent and significant effects on soil nitrogen availability in this ecosystem. Measures such as DIN, DOC and net N-mineralisation were all found to be significantly greater in un-browsed than browsed areas. The microbial C:N ratio was also significantly lower in un-browsed than browsed areas, suggesting that the removal of deer reduced the extent that the microbial community was N-limited. These findings are contrary to those of studies on the effects of herbivores on

nutrient cycling processes in productive grasslands, where herbivores increase nutrient cycling rates leading to increased plant productivity, or compensatory growth (Holland and Detling, 1990; Chaneton et al., 1996; Holland et al., 1996; Bardgett et al., 1997, 2001; Frank and Groffman, 1998; Tracy and Frank, 1998; Hamilton and Frank, 2001). Our findings are more in line with those of Pastor et al. (1993), Ritchie et al. (1998) and Stark et al. (2000) who all found that herbivores can decrease nutrient cycling rates and hence ecosystem productivity. Positive effects of herbivores on nutrient cycling that occur in grasslands with high consumption rates are largely attributed to the return of carbon and nutrients to the soil in labile forms as dung and urine, or as enhanced rhizodeposition (Bardgett et al., 1998; Hamilton and Frank, 2001). That browsing had negative effects on N-mineralisation in our study indicates that these mechanisms were of low significance, probably due to the low density of herbivory and consequent patchy, infrequent, return of animal wastes to soil.

There are a number of mechanisms that could explain the increased mineralisation and availability of N in un-browsed areas. The most likely is the increased growth and number of birch trees in un-browsed areas, which is likely to have significant effects on soil biological properties and N cycling. Strong support for this suggestion comes from the finding that soil concentrations of mineral N and net N-mineralisation were positively correlated with tree growth, measured as tree diameter, which was significantly greater in un-browsed sites. Further, it is well known that grazer-induced changes in vegetation composition in upland ecosystems cause corresponding changes in labile soil properties (Miles, 1985); it has been shown that colonisation of moorland soils with birch trees increases nutrient release (Miles and Young, 1980; Hester et al., 1991; Bradley and Fyles, 1995) and the reputation of birch as a soil

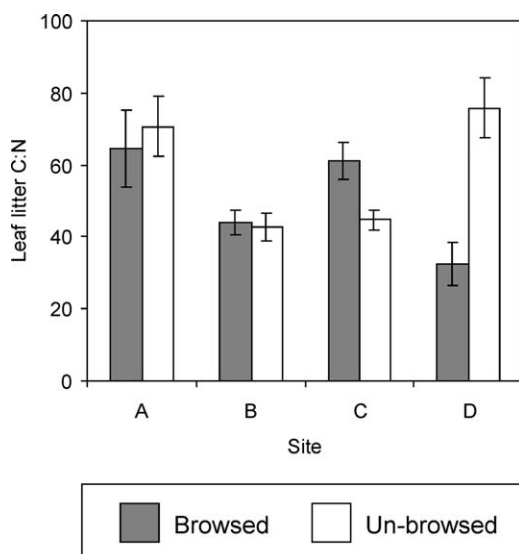


Fig. 4. The effect of browsing on birch litter C:N at four sampling sites at Creag Meagaidh, Scotland. Values are means \pm se.

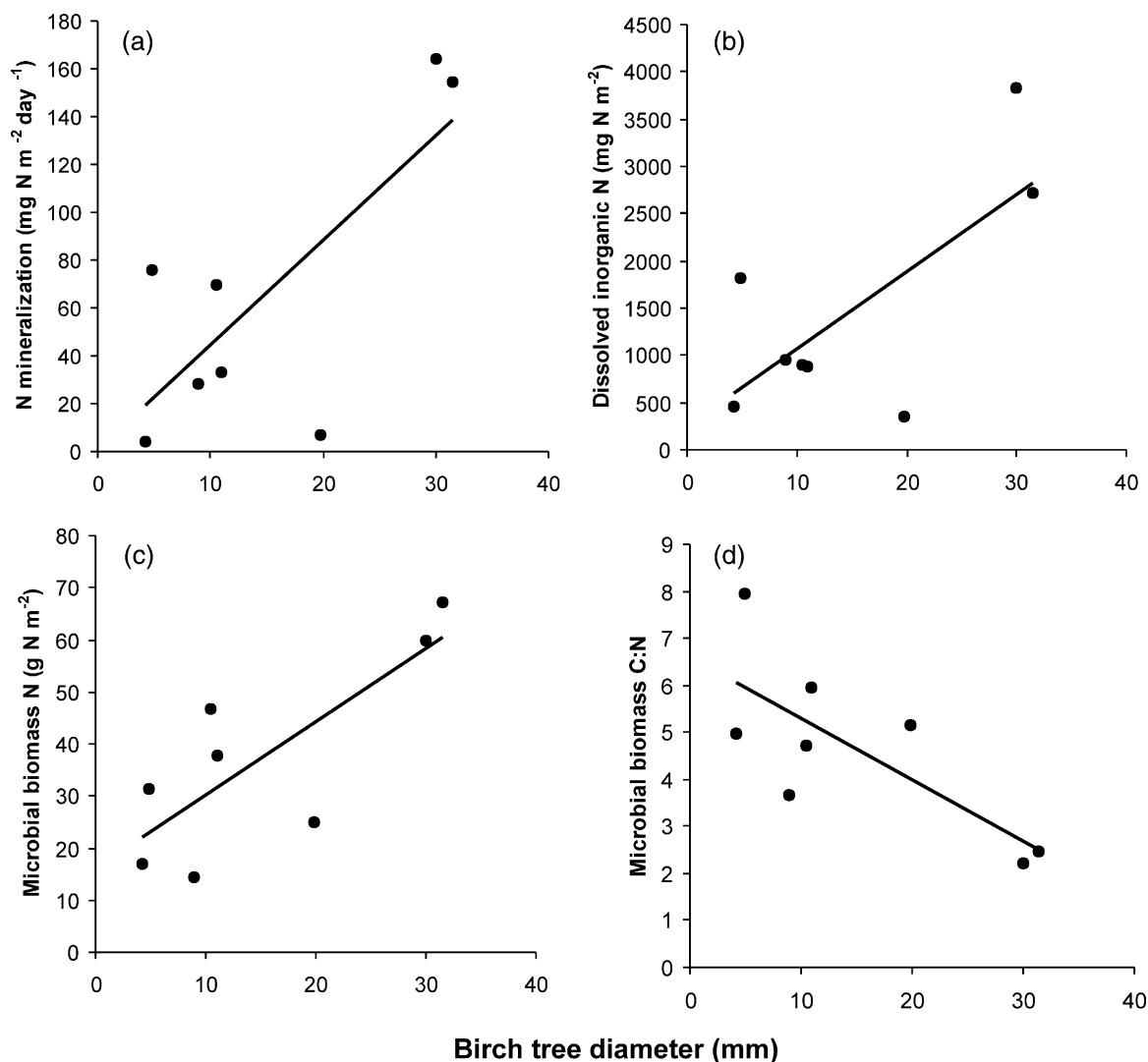


Fig. 5. Pearson correlation between (a) birch tree diameter and N-mineralisation; (b) dissolved inorganic N; (c) microbial biomass N and (d) microbial biomass C:N. Values are means for inside and outside each enclosure at four sites at Creag Meagaidh NNR. Means were calculated from data collected from three sampling dates except the birch tree diameter values, which are means calculated from one sampling time point. Dissolved inorganic N values were calculated by adding soil concentrations of nitrate and ammonium values together.

improving species is well established (Dimbleby, 1952; Gardiner, 1968).

This positive effect of birch tree growth on soil N availability may be due to the type of litter being returned to the ground (Lodhi, 1977) or the indirect effect of below-ground processes, such as fine root production and mycorrhizal colonisation. We did not examine root growth in this study, but it is highly likely that the significant increase in aboveground tree growth was associated with more profuse root development (Piggot, 1983), which in turn will have increased soil C supply to microbes in the rhizosphere. Support for this suggestion comes from previous studies, which show that paper birch seedlings (*Betula papyrifera*) increase the availability of soluble C in soil (Bradley and Fyles, 1995), and, consistent with this, we found that DOC was 37% greater in un-browsed than browsed areas. Since the microbial biomass was more

C-limited in the un-browsed than browsed areas (i.e. significantly lower microbial C:N ratio), the increased provision of soluble C to microbes will have stimulated mineralisation of N, thereby increasing soil N availability. Increases in tree growth will also have changed the quantity and quality of litter that is returned to soil. For example, it is plausible that increased litter quantity in un-browsed areas would have significant knock-on effects on litter decomposition and hence nutrient cycling in these ecosystems. Further, we might expect increased availability of N in soil in un-browsed areas to have led to increased litter N content, increasing decomposition rates and accelerating nutrient mineralisation. Conversely, lower nutrient mineralisation of N in unfenced areas may have been due, in part, to enhanced production of secondary metabolites in foliage of browsed trees, which in turn may have reduced decomposition of, and nutrient release from, decomposing litter (Findlay et al.,

1996; Cornelissen et al., 1999). We have little support for these suggestions since we found no consistent effect of browsing on leaf litter quality of birch, measured as litter N content, and we did not measure secondary metabolite concentrations in litter. Despite the uncertainty over mechanisms, our data indicate that the removal of browsing has set a significant and positive feedback mechanism in motion, whereby increased tree growth stimulates soil C supply and N-mineralisation, thereby further increasing plant N supply and tree growth in these ecosystems.

Although herbivory had consistent effects on nutrient dynamics in this study, the effects of deer browsing on the biomass and activity of soil microbes that drive these processes were more idiosyncratic. The lower microbial biomass C:N ratio observed in un-browsed areas was consistent with the increased DIN and N-mineralisation measured. However, herbivory did not significantly affect the microbial biomass C or N. This lack of coupling between measures of microbial biomass and nutrient mineralisation in grazed ecosystems has been reported elsewhere. For example, a study of native grasslands in northern Yellowstone National Park by Tracy and Frank (1998), showed that although rates of N-mineralisation were greater in grazed than un-grazed grassland areas, soil microbial biomass was not influenced by grazing, being affected more by topography, as was most likely the case in our study. Therefore, it may be the case, that soil microbial activities, for example soil enzyme activities (McNaughton et al., 1997), rather than the size of microbial biomass, are better related to nutrient mineralisation in these ecosystems.

The idiosyncratic nature of the effects of browsing on soil biological properties such as microbial biomass is also consistent with a study of deer browsing in New Zealand by Wardle et al. (2002). These authors found an equal number of positive and negative effects of browsing on soil biological properties across thirty locations, and it was argued that this reflected the range of mechanisms through which browsers can affect belowground biota (Wardle et al., 2002). It is also likely that effects of browsers on soil biota are multi-trophic, with different trophic levels responding to browsing. In our study, idiosyncratic responses of the microbial biomass to browsing may reflect changes in the abundance of higher level trophic groups such as nematodes and microarthropods that feed on microbes. It is well known that interactions between fauna and microbes are influenced by aboveground herbivory (Bardgett et al., 1998), and that these interactions, which show large temporal dynamics, lead to changes in nutrient mineralisation in soil (Clarholm, 1985a,b). Further analysis of the response of different trophic groups of soil biota to browsing are required to understand the role of these interactions in these regenerating ecosystems.

In conclusion, although spatial and temporal variations were the dominant factors affecting soil biological properties and nutrient dynamics in this ecosystem, our data show that low densities of deer browsing have significant negative

effects on these properties in regenerating woodland ecosystems. In particular, our data indicate that the removal of deer browsing sets a significant and positive feedback mechanism in motion, whereby increased tree growth stimulates soil C- and N-mineralisation, further increasing plant N supply and tree growth in these ecosystems. This impact of browsing, which contrasts with the positive effects of grazers in productive grasslands, appears to be related to the prevention of the growth of trees that have substantial positive effects on soil N cycling.

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References

- Allen, M.F., Richards, J.H., Busso, C.A., 1989. Influence of clipping and soil water status on vesicular–arbuscular mycorrhizae of two semi-arid tussock grasses. *Biology and Fertility of Soils* 8, 285–289.
- Augustine, D.J., McNaughton, S.J., 1998. Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. *Journal of Wildlife Management* 52, 1165–1183.
- Bardgett, R.D., Leemans, D.K., Cook, R., Hobbs, P., 1997. Seasonality of the soil biota of grazed and ungrazed hill grasslands. *Soil Biology & Biochemistry* 29, 1285–1294.
- Bardgett, R.D., Wardle, D.A., Yeates, G.W., 1998. Linking above-ground and below-ground interactions: how plant responses to foliar herbivory influence soil organisms. *Soil Biology & Biochemistry* 30, 1867–1878.
- Bardgett, R.D., Jones, A.C., Jones, D.L., Kemmitt, S.J., Cook, R., Hobbs, P., 2001. Soil microbial community patterns related to the history and intensity of grazing in sub-montane ecosystems. *Soil Biology & Biochemistry* 33, 1653–1664.
- Bradley, R.L., Fyles, J.W., 1995. Growth of paper birch (*Betula papyrifera*) seedlings increases soil available C and microbial acquisition of soil nutrients. *Soil Biology & Biochemistry* 27, 1565–1571.
- Chaneton, E.J., Lemcoff, J.H., Lavado, R.S., 1996. Nitrogen and phosphorus cycling in grazed and ungrazed plots in a temperate subhumid grassland in Argentina. *Journal of Applied Ecology* 33, 291–302.
- Clarholm, M., 1985a. Interactions of bacteria, protozoa and plants leading to mineralisation of soil nitrogen. *Soil Biology & Biochemistry* 17, 181–187.
- Clarholm, M., 1985b. Possible roles for roots, bacteria, protozoa and fungi in supplying nitrogen to plants. In: Fitter, A.H., Atkinson, D., Read, D.J., Usher, M.B. (Eds.), *Ecological Interactions in Soil: Plants, Microbes and Animals*, Blackwell, Oxford, pp. 355–365.

- Cornelissen, J.H.C., Pérez-Harguindeguy, N., Diaz, S., Grime, J.P., Marzano, B., Cabido, M., Vendramini, F., Cerabolini, B., 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. *New Phytologist* 143, 191–200.
- Dimbleby, G.W., 1952. Soil regeneration on the North-East Yorkshire moors. *Journal of Ecology* 40, 331–341.
- Dyer, M.I., Turner, C.L., Seastedt, T.R., 1993. Herbivory and its consequences. *Ecological Applications* 3, 10–16.
- Findlay, S., Carreiro, M., Kriskich, V., Jones, C.G., 1996. Effects of damage to living plants on leaf litter quality. *Ecological Applications* 6, 269–275.
- Floate, M.J.S., 1981. Effects of grazing by large herbivores on N cycling in agricultural ecosystems. In: Clark, F.E., Rosswall, T. (Eds.), *Terrestrial Nitrogen Cycles—Processes, Ecosystem Strategies and Management Impacts*, Ecological Bulletins (Stockholm) Swedish Nature Science Research Council, pp. 585–597.
- Frank, D.A., Groffman, P.M., 1998. Ungulate vs. landscape control of soil carbon and nitrogen processes in grasslands of Yellowstone National Park. *Ecology* 79, 2229–2241.
- Frank, D.A., Inouye, R.S., Huntly, N., Minshall, G.W., Anderson, J.E., 1994. The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. *Biogeochemistry* 26, 163–188.
- Gardiner, A.S., 1968. The Reputation of Birch for Soil Improvement. A Literature Review, Research and Development paper, No. 67, Forestry Commission, London.
- Hamilton, E.W., Frank, D.A., 2001. Can plants stimulate soil microbes and their own nutrient supply? Evidence from a grazing tolerant grass. *Ecology* 82, 2397–2402.
- Haukioja, E., Ruohomäki, K., Senn, J., Suomela, J., Walls, M., 1990. Consequences of herbivory in the mountain birch (*Betula pubescens* spp. *tortuosa*): importance of the functional organisation of the tree. *Oecologia* 82, 238–247.
- Hester, A.J., Grimingham, C.H., Miles, J., 1991. Succession from heather moorland to birch woodland. III. Seed availability, germination and early growth. *Journal of Ecology* 79, 329–344.
- Holland, E.A., Detling, J.K., 1990. Plant response to herbivory and belowground nitrogen cycling. *Ecology* 71, 1040–1049.
- Holland, J.N., Cheng, Jr. W., Crossley, D.A., 1996. Herbivore-induced changes in plant carbon allocation: assessment of below-ground carbon fluxes using C-14. *Oecologia* 107, 87–94.
- Lehtilä, K., Haukioja, E., Kaitaniemi, P., Laine, R.A., 2000. Allocation of resources within mountain birch canopy after simulated winter browsing. *Oikos* 90, 160–170.
- Lodhi, M.A.K., 1977. The influence and comparison of individual forest trees on soil properties and possible inhibition of nitrification due to intact vegetation. *American Journal of Botany* 64, 260–264.
- McNaughton, S.J., 1984. Grazing lawns: animals in herds, plant form and co-evolution. *American Naturalist* 124, 863–886.
- McNaughton, S.J., Zuniga, G., McNaughton, M.M., Banyikwa, F.F., 1997. Ecosystem catalysis: soil urease activity and grazing in the Serengeti ecosystem. *Oikos* 80, 467–469.
- Miles, J., 1985. The pedogenic effects of different species and vegetation types and the implications of succession. *Journal of Soil Science* 36, 571–584.
- Miles, J., Young, W.F., 1980. The effects on heathland and moorland soils in Scotland and northern England following colonization by birch (*Betula* sp.). *Bulletin d'Ecologie* 11, 233–242.
- Mitchell, F.J.G., Hester, A.J., Kirb, K.J., 1995. Effects of season and intensity of sheep grazing on a British upland woodland: Browsing damage to planted saplings. *Botanical Journal of Scotland* 48, 199–207.
- NCC, 1989. Creag Meagaidh National Nature Reserve, First Management Plan 1989–1993. Conservancy Council Report. Aberdeen.
- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F., Cohen, Y., 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74, 467–480.
- Piggot, C.D., 1983. Regeneration of oak-birch woodland following exclusion of sheep. *Journal of Ecology* 71, 629–646.
- Ramsey, P., 1996. Revival of the land. Creag Meagaidh National Nature Reserve, Scottish Natural Heritage.
- Ritchie, M.E., Tilman, D., Knops, J.M.H., 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79, 165–177.
- Rodwell, J.S., 1994. *Creating New Native Woodlands*, HMSO, London.
- Ross, D.J., 1992. Influence of sieve mesh size on estimates of microbial C and N by fumigation–extraction procedures in soils under pasture. *Soil Biology & Biochemistry* 24, 343–350.
- Rossow, L.J., Bryant, J.P., Keilland, K., 1997. Effects of aboveground browsing by mammals on mycorrhizal infection in an early successional taiga ecosystem. *Oecologia* 110, 94–98.
- Ruess, R.W., Hendrick, R.L., Bryant, J.P., 1998. Regulation of fine root dynamics by mammalian browsers in early successional Alaskan taiga forests. *Ecology* 79, 2706–2720.
- Sparling, G.P., Feltham, C.W., Reynolds, J., West, A.W., Singleton, P., 1990. Estimation of soil microbial C by a fumigation extraction method: use on soils of high organic matter content, and a reassessment of the K_{ec} factor. *Soil Biology & Biochemistry* 22, 301–307.
- Stark, S., Wardle, D.A., Ohtonen, R., Helle, T., Yeates, G.W., 2000. The effect of reindeer grazing on decomposition, mineralisation and soil biota in a dry oligotrophic Scots Pine forest. *Oikos* 90, 301–310.
- Tracy, B.F., Frank, D.A., 1998. Herbivore influence on soil microbial biomass and N mineralisation in a northern grassland ecosystem: Yellowstone National Park. *Oecologia* 114, 556–562.
- Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. *Soil Biology & Biochemistry* 19, 703–707.
- Verchot, L.V., Groffman, P.M., Frank, D.A., 2002. Landscape versus ungulate control of gross mineralisation and gross nitrification in semi-arid grassland of Yellowstone National Park. *Soil Biology & Biochemistry* 34, 1691–1699.
- Voroney, R.P., Winter, J.P., Beyaert, R.P., 1993. Soil microbial biomass C and N. In: Carter, M.N., (Ed.), *Soil Sampling and Methods of Analysis*, Lewis Publications, Boca Raton, FL, pp. 277–286.
- Wardle, D.A., 1998. Controls of temporal variability in the soil microbial biomass. A global-scale synthesis. *Soil Biology & Biochemistry* 30, 1627–1637.
- Wardle, D.A., Barker, G.M., Yeates, G.W., Bonner, K.I., Ghani, A., 2001. Introduced browsing mammals in New Zealand natural forests: aboveground and belowground consequences. *Ecological Monographs* 71, 587–614.
- Wardle, D.A., Bonner, K.I., Barker, G.M., 2002. Linkages between plant litter decomposition litter quality and vegetation responses to herbivores. *Functional Ecology* 16, 585–595.
- Zeller, V., Bardgett, R.D., Tappeiner, U., 2001. Site and management effects on soil microbial properties of subalpine meadows: a study of land abandonment along a north-south gradient in the European Alps. *Soil Biology & Biochemistry* 33, 639–659.