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Herbivore influence on soil microbial biomass and nitrogen mineralization in a northern grassland ecosystem: Yellowstone National Park

Abstract Microorganisms are largely responsible for soil nutrient cycling and energy flow in terrestrial ecosystems. Although soil microorganisms are affected by topography and grazing, little is known about how these two variables may interact to influence microbial processes. Even less is known about how these variables influence microorganisms in systems that contain large populations of free-roaming ungulates. In this study, we compared microbial biomass size and activity, as measured by in situ net N mineralization, inside and outside 35- to 40-year exclosures across a topographic gradient in northern Yellowstone National Park. The objective was to determine the relative effect of topography and large grazers on microbial biomass and nitrogen mineralization. Microbial C and N varied by almost an order of magnitude across sites. Topographic depressions that contained high plant biomass and fine-textured soils supported the greatest microbial biomass. We found that plant biomass accurately predicted microbial biomass across our sites suggesting that carbon inputs from plants constrained microbial biomass. Chronic grazing neither depleted soil C nor reduced microbial biomass. We hypothesize that microbial populations in grazed grasslands are sustained mainly by inputs of labile C from dung deposition and increased root turnover or root exudation beneath grazed plants. Mineral N fluxes were affected more by grazing than topography. Net N mineralization rates were highest in grazed grassland and increased from dry, unproductive to mesic, highly productive communities. Overall, our results indicate that topography mainly influences microbial biomass size, while mineral N fluxes (microbial activity) are affected more by grazing in this grassland ecosystem.

Key words Microorganisms · Topography · Grazing · Nitrogen mineralization · Yellowstone

Introduction

Microorganisms are largely responsible for soil nutrient cycling and energy flow in terrestrial ecosystems. Decomposition of organic matter by microorganisms releases mineral nutrients for uptake by plants and other soil microorganisms. Microorganisms also serve as a reservoir for labile nutrients and play an important role in conserving mineral nutrients in soils (Paul 1984; Schimel 1986;Wardle 1992). Microorganisms thus serve as both a source and sink for plant-available nutrients, and the balance between these two functions may have important implications for the response of grassland ecosystems to disturbance (Bolton et al. 1993; Garcia and Rice 1994), climate change (Hobbie 1997), and grazing (Kieft 1994; Wilsey 1996).

Growth of heterotrophic microorganisms is typically limited by either carbon or nitrogen in terrestrial systems. Most organic C used by microbes is derived from above- and belowground plant material. Smith and Paul (1990) estimated that annual C inputs from plant litter are sufficient only to meet maintenance requirements of microbes and leave little C for additional growth. As a result, plant production should constrain microbial growth and be well correlated with microbial biomass standing crop. This relationship has been well documented across a variety of ecosystems (Myrold et al. 1989; Zak et al. 1994). However, other variables may also play a role in constraining microbial biomass (Merckx et al. 1985; Groffman et al. 1996). For example, fine-textured grassland soils typically contain greater quantities of microbial biomass relative to coarser-textured soils (Schimel 1986; Burke et al. 1989; Ruess and Seagle 1994). Because plant production, soil organic

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matter accumulation, and soil texture tend to be well correlated in grasslands (Schimel et al. 1985) we would expect soil microbial biomass to vary predictably with topography.

Herbivory is a major pathway by which carbon inputs from plant litter can be redirected away from soils in grasslands. To recoup aboveground tissues lost to herbivory, plants typically reduce carbon allocation to belowground growth (Bokhari and Singh 1974; Detling et al. 1979; Ingham and Detling 1984; Holland and Detling 1990; Holland et al. 1992). Less belowground allocation of carbon may reduce microbial growth and lower the capacity for N immobilization (Holland and Detling 1990). Redirection of organic carbon from belowground pools, then, should affect the size and activity of microorganisms and influence mineral nutrient availability for plants.

Grasslands on the northern range of Yellowstone National Park are topographically diverse and support some of the largest concentrations of native ungulates in North America (Houston 1982). Although some research has addressed how topography (Burke et al. 1989; Zak et al. 1994) and grazing (Kieft 1994; Ruess and Seagle 1994) can affect soil microorganisms, little work has evaluated both variables in one study. Even less is known about how these variables influence microorganisms in a system like Yellowstone National Park, which contains large populations of free-roaming ungulates. In this study, we compared microbial biomass and net N mineralization, inside and outside 35- to 40-year exclosures across a wide topographic gradient in northern Yellowstone National Park. The objective of this study was to determine the relative effect of topography and grazers on microbial biomass and activity across the northern range of Yellowstone.

Materials and methods

Study sites

The study was conducted on the Yellowstone northern winter range (Houston 1982). Four exclosures (2 ha each) established between 1958–1962 were used in this study. The exclosures were located at Stevens Creek (S), Mammoth (M), Blacktail (B), and Lamar Valley (L). Specific locations for these study sites can be found in Frank and Evans (1997). Stevens Creek, Mammoth and Lamar Valley exclosures had two sites each (S1 and S2, M1 and M2, L1 and L2, respectively), while the Blacktail exclosure had one (B). Sampling at each site was confined to paired plots (10 m × 10 m) located inside (ungrazed) and outside (grazed) the respective exclosures.

The seven sites encompassed different topographic positions. The B site was a dry grassland located on a hilltop dominated by *Festuca idahoensis* and *Psuedoroegneria spicata*. The S2, M2, and L2 sites were positioned on dry, midslope areas. Vegetation on the S2 and L2 sites was grassland dominated by *P. spicata* and *Koeleria cristata*. The M2 site was a shrub-grassland dominated by *Artemesia tridentata* (sagebrush), *F. idahoensis*, and *P. spicata*. The M1 and L1 sites were more mesic and located at the base of slopes. The S1 site was much drier and located on an alluvial outwash plain. Sites L1 and M1 were dominated by *Poa pratensis*, while the S1 site was dominated by *Stipa comata*.

The climate of the northern range is characterized by long, cold winters and short, dry summers. Thirty-year mean precipitation and temperature values for Mammoth Hot Springs on the northern range were 379 mm and 4.6°C (NOAA 1990). Soils on the northern range are derived from glacial till deposited during the Pleistocene. The till is mainly a mixture of andesite and sedimentary rocks (Keefer 1987). These soils characterize the Mammoth, Blacktail, and Lamar Valley sites, but soils at the Stevens Creek site are different. They are rich in bentonite deposited from Pleistocene landslides (Keefer 1987). Details of site soil characteristics are given in Table 1. Elevations across the study sites ranged from 1600 m to 1900 m.

The northern range is grazed primarily by large numbers of elk (*Cervus elaphus*) and bison (*Bison bison*) from fall to early spring (Houston 1982). Pronghorn antelope (*Antilocarpa americana*) commonly graze the Stevens Creek site. Grazing intensities vary greatly across the northern winter range (Frank and McNaughton 1992).

Methods

We evaluated microbial biomass C and N and net N mineralization. Microbial biomass was measured in May, June, July, and August 1996. At each sampling date, three soil cores were removed from random locations on each plot. Cores were 2.5 cm in diameter and taken to a depth of 10 cm. Soil cores were sieved (>2.0 mm) to remove rocks and large roots, and dry soils were moistened with distilled water to approach the field capacity of the respective sites. Shrubs are known to affect the distribution of microorganisms in semi-arid systems (Burke et al. 1989; Bolton et al. 1993; Kieft 1994). Only one site (M2) contained shrubs inside and outside exclosures, so we sampled between shrubs at this site to facilitate comparison with other sites.

Microbial biomass C was measured using the chloroform fumigation-incubation method (Jenkinson and Powlson 1976). A 10-g soil sample was removed from each core and fumigated with ethanol-free chloroform for 24 h. Following fumigation, each sample was incorporated with 0.2 g of soil inoculum and sealed in a Mason jar containing a 20-ml scintillation vial filled with 1 ml of 2 M NaOH. The jars were then incubated for 10 days at 20°C. At the end of the incubation, NaOH was titrated with 1 M HCl for C determination (Snyder and Trofymow 1984). Microbial biomass C was calculated as the flush of CO_2-C (minus an unfumigated control) divided by 0.41 (Voroney and Paul 1984).

Fumigated soil samples were extracted with 50 ml of 1 N KCl at the end of the 10-day incubations. Samples were shaken vigorously with KCl, left for 24 h and then filtered into 20-ml scintillation vials. Ammonium and nitrate were quantified with a Lachat Quikchem Autoanalyzer (Milwaukee, Wisc). Microbial biomass N was calculated from the flush of N (fumigated−unfumigated) divided by a correction factor (kn), where kn = −0.014(Cf/Nf) + 0.39 and Cf and Nf are flushes of C and N from fumigated samples, respectively (Voroney and Paul 1984).

Rates of in situ net N mineralization were evaluated in the field using the buried-bag technique (Eno 1960). Three soil cores (2.5 cm diameter, 10 cm depth) were taken from random locations in each plot. Each core was sealed in a plastic bag and buried at a depth of 10 cm. Another soil core (initial) was taken adjacent to each buried bag and immediately extracted for ammonium and nitrate as described above. After 30 days the buried bags were removed from the ground and soils extracted. We measured net N mineralization rates each month during the growing season (May–August). Measures of soil pH, field capacity, texture and total soil N and C were taken from a composite sample of five randomly located soil cores (10 cm diameter, 10 cm depth). Soil pH, field capacity, and texture analysis were conducted using standard methods and total N and C were measured using a Carlo Erba CNS Autoanalyzer.

Herbaceous plants were collected at peak biomass (May/June). Plants were clipped within five randomly located quadrats (20 cm × 50 cm) on each plot. Clippings were dried at 65°C for at

Table 1 Soil characteristics of the respective sites. *M1* and *M2* are Mammoth exclosure sites, *L1* and *L2* are sites at the Lamar Valley exclosure, *S1* and *S2* are Stevens Creek exclosure sites, and *B* is a site at the Blacktail exclosure. The letters *i* and *o* refer to paired plots inside (ungrazed) and outside (grazed) each exclosure site, respectively. Table modified from D.A. Frank and P.K. Groffman (submitted)

Site	pH	Field capacity (% H$_2$O)	Bulk density (g/cm^3)	Sand (%)	Silt (%)	Clay (%)	Soil N (%)	Soil C (%)
S1 i	7.0	24.5	1.2	47	28.1	24.9	0.13 ± 0.01	1.5 ± 0.10
S1 o	7.1	22.1	1.2	43.8	27	29.2	0.13 ± 0.01	1.3 ± 0.2
S2 i	7.3	22.6	1.3	50	21.1	28.9	0.09 ± 0.01	1.0 ± 0.1
S2 o	7.2	21	1.3	55.8	17.6	26.6	0.09 ± 0.01	1.0 ± 0.1
M1 i	7.9	44.4	0.75	35.1	34.1	30.8	0.86 ± 0.03	16.2 ± 0.7
M1 o	7.8	45.3	0.77	32.1	37.8	30.1	0.79 ± 0.04	15 ± 0.7
M2 i	6.5	23.4	1.1	46.5	35.9	17.6	0.34 ± 0.01	3.8 ± 0.2
M2 o	6.3	25.3	1.1	44.6	36.8	18.6	0.38 ± 0.02	4.3 ± 0.3
L1 i	6.6	36.1	0.9	35	41.7	23.3	0.95 ± 0.03	10.7 ± 0.4
L1 o	6.8	34.6	0.9	33.5	42.3	24.2	0.82 ± 0.04	9.4 ± 0.5
L2 i	7.6	19.8	1.3	45.5	34.8	19.7	0.25 ± 0.02	3.3 ± 0.2
L2 o	7.7	18	1.4	48.5	28.2	23.3	0.17 ± 0.08	3.0 ± 0.2
B1 i	6.7	34.3	1.2	45.5	38.4	16.1	0.27 ± 0.01	3.0 ± 0.1
B1 o	6.7	19.5	1.2	44.7	39.2	16.1	0.29 ± 0.01	3.3 ± 0.2

Table 2 Main plot effects from split-plot ANOVAs for the respective soil variables from laboratory incubations

|	Fence		Site	
	$F_{1,6}$	P	$F_{6,6}$	P
Microbial N	0.94	0.3687	12.76	0.0034
Microbial C	0.75	0.4185	91.82	0.0001
In situ net N mineralization	3.83	0.0980	1.29	0.2284
In situ net N turnover	6.474	0.0438	5.422	0.0295
In situ net N Mineralization/microbial N	3.081	0.1297	2.885	0.1115

least 48 h, then weighed, ground, and analyzed for C and N using a Carlo Erba CNS Autoanalyzer. Roots were collected simultaneously with aboveground biomass. Soil cores (10 cm diameter) were taken inside each quadrat down to maximum rooting depth, which was less than 30 cm at most sites due to rocky soil. Roots were then picked from cores, washed, dried, weighed and then ground for C and N analysis.

Statistical analysis

For laboratory incubation and net N mineralization data, the subsamples from each plot (n = 3) were averaged for each month sampled. We then analyzed soil variables from laboratory and field incubations using a split-plot design ANOVA with fencing (inside and outside) and site as main plot effects, and month (May, June, July, August) as a subplot effect. Plant and root data were analyzed with a two-factor ANOVA using site and fencing as main effects. In part because of the few degrees of freedom used in these analyses, we considered α = 0.10 as statistical significance throughout this paper.

Results

Microbial C and N were strongly affected by site variables, i.e., topography, but not by grazing (Table 2). Across the sites, microbial biomass C was positively correlated with total soil C (r = 0.86, P < 0.001) as was microbial N with total soil N (r = 0.88, P < 0.001). Figure 1 shows that microbial C tended to increase with total plant biomass (above- + belowground biomass)
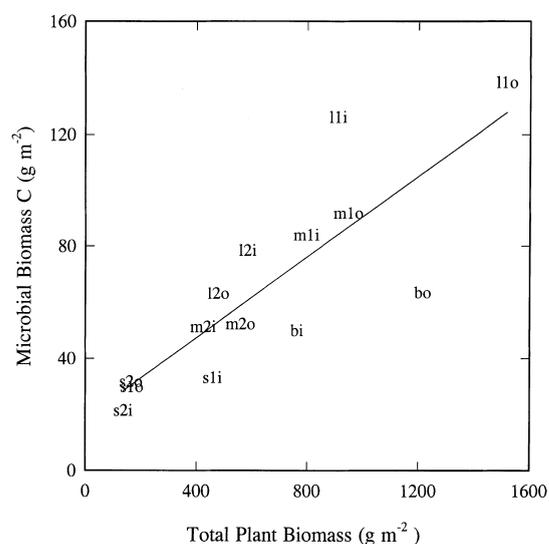

Fig. 1 Linear regression of microbial biomass C and total plant biomass (above- + belowground) across the study sites. Equation for the regression: microbial biomass C = 18.569 + 0.072(total plant biomass) (r^2 = 0.68, P < 0.001, df = 12). *Plot symbols are given in Table 1*

across sites. Productive, mesic sites located in topographic depressions (e.g., L1, M1) contained more plant biomass and microbial biomass compared with drier, less productive sites (e.g. S1, S2). A similar relationship was noted

for microbial N and total plant N ($r = 0.79$, $P < 0.001$) with maximal values occurring at productive, mesic sites (Fig. 2). Peak shoot and root biomass were unaffected by grazing, but shoot tissue from grazed grassland possessed a narrower C:N ratio and more N compared with shoots from ungrazed grassland (Table 3).

Unlike microbial biomass variation, rates of in situ net N mineralization were better explained by grazing effects rather than site effects (Table 2). Figure 3 shows that net N mineralization rates increased with microbial
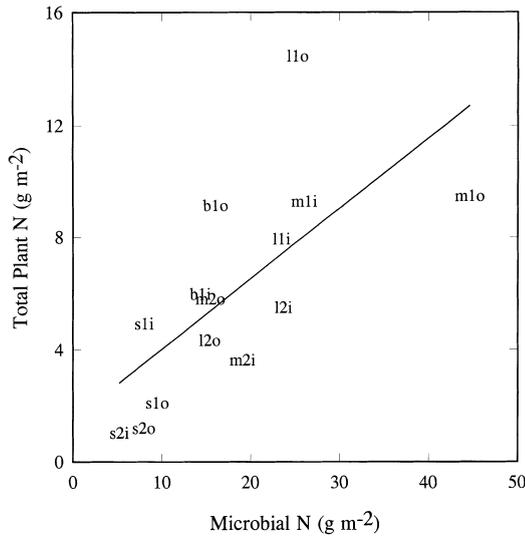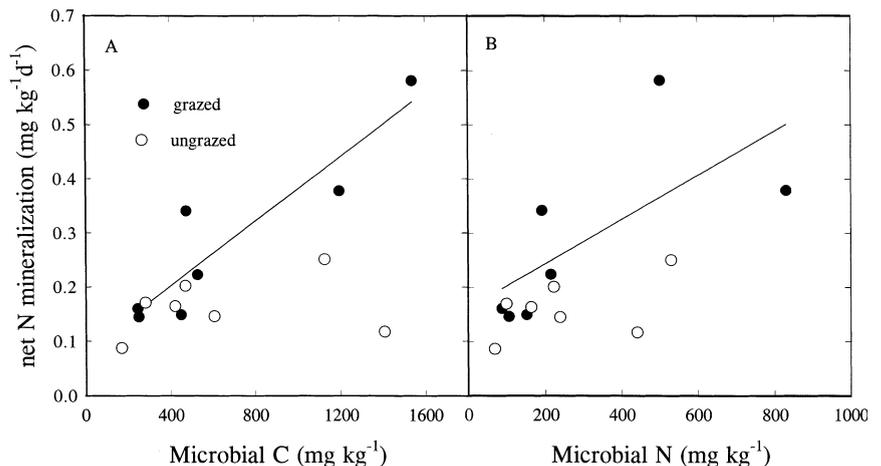

Fig. 2 Linear regression of total plant N on microbial N. The regression equation: total plant $N = 1.010 + 0.188$(microbial N) ($r^2 = 0.62$, $P < 0.001$, $df = 12$). *Plot symbols are given in Table 1*

biomass C and N, but only on grazed sites (linear regressions, $P < 0.05$). Rates of net N mineralization (mg/kg per day) were approximately 40% higher in grazed grassland (0.282 ± 0.05, $n = 28$) compared with ungrazed grassland (0.162 ± 0.01, $n = 28$). The percentage of total soil N mineralized over the 1996 growing season (net N turnover) was also significantly greater in grazed than in ungrazed areas (Table 2, Fig. 4). Both net N turnover and net N mineralized per unit microbial N decreased with increasing microbial C, but these trends were significant only for ungrazed grassland (Fig. 4). Lastly, microbial biomass and net N mineralization were generally higher in early spring compared with late summer (split-plot ANOVAs, month effect $P < 0.10$). Interactions of month × grazing effects and grazing × topographic effects were not statistically significant for net N mineralization and microbial biomass.

Discussion

Microbial C and N varied by almost an order of magnitude across the Yellowstone sites ranging from 166–1539 mg C/kg ($\bar{x} = 652$) and 50–463 mg N/kg ($\bar{x} = 183$). Microbial biomass values measured across a topographic gradient in a Wyoming sagebrush grassland were generally lower and encompassed a narrower range than those measured in Yellowstone (500–1200 mg C/kg and 80–200 mg N/kg) (Burke et al. 1989). The wider range of values reported in our Yellowstone study may reflect the greater diversity of plant communities and edaphic gradients that were sampled. Mean microbial

Table 3 Nitrogen and carbon contents for shoots and roots collected at peak biomass. Each grazed and ungrazed number is a mean of seven samples with 1 SE. Also given are the respective *F*-ratios and *P*-values from two-factor ANOVAs

	Grazed	Ungrazed	$F_{1,6}$	P-value
Shoot biomass(g/m^2)	100 ± 34	114 ± 39	0.82	0.4012
Shoot N(g/m^2)	1.76 ± 0.49	1.30 ± 0.39	5.53	0.0569
Shoot C:N	26 ± 2.4	31 ± 1.7	21.89	0.0034
Root biomass(g/m^2)	606 ± 174	480 ± 82	1.31	0.2965
Root N(g/m^2)	4.89 ± 1.4	4.17 ± 0.72	0.47	0.5183
Root C:N	42 ± 3.9	41 ± 3.1	0.10	0.7574

Fig. 3 Relationships between in situ net N mineralization and microbial C (**A**) and N (**B**). *Solid circles* are grazed grassland and *open circles* are ungrazed grassland. Regressions were significant for grazed grassland only: net N mineralization = 0.083 + 0.00029 (microbial C), ($r^2 = 0.85$, $P = 0.003$) and net N mineralization = 0.162 + 0.00041 (microbial N) ($r^2 = 0.47$, $P = 0.087$)

Fig. 4 Net N mineralized per unit microbial N (**A**) and (**B**) net N turnover (percent of total soil N mineralized/10 days) as related to microbial C. *Solid circles* are grazed grassland and *open circles* are ungrazed grassland. Regressions were significant only for ungrazed grassland. Net N mineralized/microbial N $= 0.015 - 0.0000093$ (microbial C) ($r^2 = 0.74$, $P = 0.013$, $df = 6$) and net N turnover $= 0.112 - 0.000075$ (microbial C) ($r^2 = 0.74$, $P = 0.012$, $df = 6$)
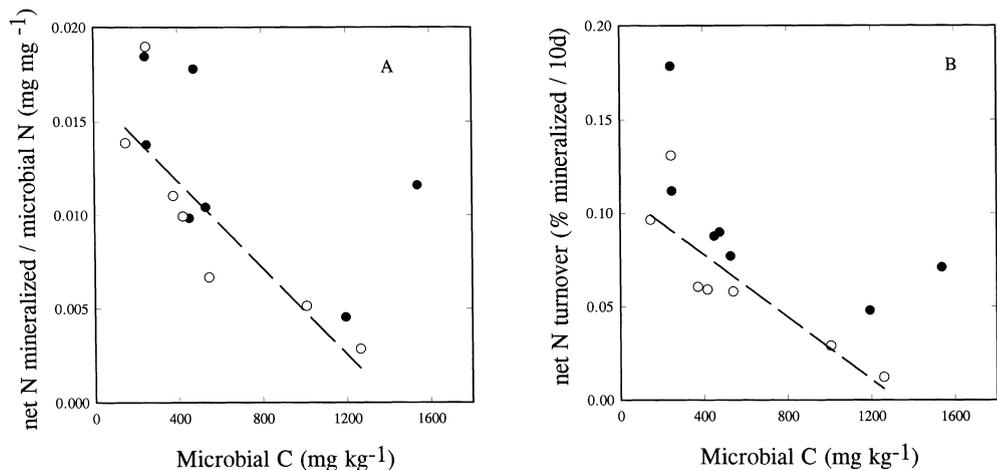
biomass values measured in Kansas tallgrass prairie (Garcia and Rice 1994) were also lower than those measured in Yellowstone (average 529 mg C/kg and 116 mg N/kg). On the other hand, microbial C biomass values measured across the Serengeti (Reuss and Seagle 1994), another large ecosystem dominated by large grazers, were greater than Yellowstone values (552–3971 mg C/kg, average = 1450). The Serengeti differs from Yellowstone in that it possesses a larger herbivore biomass, higher rates of primary production, and a warmer, equatorial climate (McNaughton 1985).

Topographic depressions that contained high plant biomass and fine-textured soils generally supported the greatest amounts of microbial biomass (e.g., L1, M1). These results are not surprising since microbial processes are often tightly coupled to topographic variation in semi-arid grasslands (Schimel et al. 1985; Burke 1989; Burke et al. 1989; Frank et al. 1994). The topographic variation in microbial biomass was most likely controlled by plant inputs to soil. As in other studies (Myrold et al. 1989; Zak et al 1994), we found that plant biomass accurately predicted microbial biomass across our sites, suggesting that carbon inputs from plants constrained microbial biomass (Smith and Paul 1990). Variation in soil texture, however, also affects microorganisms, with fine-textured soils generally supporting more microbial biomass than coarser-textured soils (Merckx et al. 1985). Thus the high microbial biomass in topographic depressions (e.g., L1, M1) may also reflect fine-textured soils that characterize these sites. If this was completely true, however, we might have expected our S1 site to support relatively high amounts of microbial biomass since this site contained a higher percentage of clay compared to upslope sites like L2 and B (Table 1). The Stevens Creek sites (S1 and S2), however, were approximately 300 m lower in elevation and considerably hotter and drier than other sites. This fact may be evidence suggesting that climatic constraints on primary production are more important than soil texture in controlling microbial biomass variation at this landscape scale.

Winter grazing by large mammals may strongly influence microorganisms because grazing can reduce the flow of plant litter to decomposers. Aboveground litter biomass on the plots was measured at the beginning and end of winter (1995–1996), which is the period that includes the most intense seasonal grazing on these plots. From these measurements we estimated that an average of 27 g/m^2 of plant biomass entered decomposer food webs outside exclosures compared with 147 g/m^2 inside exclosures. Despite the difference in C input to soils, microbial biomass levels inside and outside exclosures were virtually identical (Table 2). The same trend was noted for total soil C and root biomass (Tables 1, 3). In a New Mexico grassland, Kieft (1994) also found no difference in microbial C between grazed grassland and one protected from grazing for 16 years. Our results suggest that chronic grazing neither depletes soil C nor reduces microbial biomass levels on the northern winter range. We hypothesize that microbial populations in grazed grasslands are sustained mainly by inputs of labile C from dung deposition (Ruess and McNaughton 1987), and increased root turnover or root exudation beneath grazed plants (Dyer and Bokahri 1976; Holland et al 1996; D.A. Frank and P.M. Groffman, submitted).

Plants and microbes may compete for mineral N in soils (Schimel et al. 1989; Kaye and Hart 1997), and the relationship between plant N and microbial N may indicate a potential competitive interaction for mineral N (Hungate et al. 1996). In this study, total plant N varied with topography and increased with microbial N in both grazed and ungrazed grassland (Fig. 2). The positive relationship between microbial N and plant N suggests that the competitive balance between plants and microbes remained unchanged over this topographic gradient and that increasing microbial N immobilization may not necessarily result in reduced plant N uptake (Hungate et al. 1996).

Mineral N fluxes were affected more by grazing than topography. Net N mineralization rates were significantly higher in grazed grassland compared with ungrazed grassland during the 1996 growing season (Table 2). The higher N mineralization rates may have been partially responsible for the higher N content of

plants on grazed grassland. The narrower C:N ratios of aboveground plant tissue in grazed grassland similarly may have helped reduce N immobilization in grazed grassland soils (Table 3).

Mineralization rates in grazed grassland increased with the topographic gradient of increasing microbial biomass (Fig. 3). In ungrazed grassland, mineralization rates remained constant over this topographic gradient. Grazer stimulation of N mineralization thus increased from dry, unproductive to mesic, highly productive communities. Grazing also influenced net N turnover and net N mineralized per unit microbial N. In ungrazed grassland, both variables decreased with increasing microbial biomass across sites (Fig. 4). The trends suggest that as site productivity increased, proportionally less of the total N and microbial N pools were turned over to plants. Grazers appear to nullify this negative trend and equalize N fluxes to plants among these widely divergent topographic positions.

In summary, we found that variation in microbial biomass across the northern range was strongly linked to topography. This topographic effect is closely associated with variation in plant production across the northern range. Microbial biomass, however, was largely unaffected by grazing. Chronically grazed grassland contained the same amount of microbial biomass as grassland protected from grazers for > 35 years. We hypothesize that microbial populations in grazed grassland are sustained by inputs of labile C that may arise from dung deposition and increased root turnover and root exudation beneath grazed plants. Although grazers had little effect on microbial biomass, they increased mineral N fluxes, particularly in mesic, topographic depressions containing high plant biomass. Overall, our results suggest that the size of microbial biomass was determined mainly by topographic variables, while large grazers played a more dominant role in influencing microbial activity (i.e., mineral N fluxes) in this grassland ecosystem.

References

Bokhari UG, Singh JS (1974) Effects of temperature and clipping on growth, carbohydrate reserves and root exudation of western wheatgrass in hydroponic culture. Crop Sci 14: 790–794

Bolton H, Smith JL, Link SO (1993) Soil microbial biomass and activity of a disturbed and undisturbed shrub-steppe ecosystem. Soil Biol Biochem 25: 545–552

Burke IC (1989) Control of nitrogen mineralization in a sagebrush steppe landscape. Ecology 70: 1115–1126

Burke IC, Reiners WA, Schimel DS (1989) Organic matter turnover in a sagebrush steppe landscape. Biogeochemistry 7: 11–31

Detling JK, Dyer MI, Winn DT (1979) Net photosynthesis, root respiration and regrowth of *Bouteloua gracilis* following simulated grazing. Oecologia 41: 127–134

Dyer MI, Bokari UG (1976) Plant-animal interactions: studies of the effects of grasshopper grazing on blue grama grass, Ecology 57: 762–772

Eno CF (1960) Nitrate production in the field by incubating the soil in polyethylene bags. Soil Sci Soc Am Proc 24: 277–279

Frank DA, McNaughton SJ (1992) The ecology of plants, large mammalian herbivores and drought in yellowstone National Park. Ecology 73: 2043–2058

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

Frank DA, Inouye RS, Huntly N, Minshall GW, Anderson JE (1994) The biogeochemistry of a north-temperate grassland with native ungulates: nitrogen dynamics in Yellowstone National Park. Biogeochemistry 26: 163–188

Garcia FO, Rice CW (1994) Microbial biomass dynamics in tallgrass prairie. Soil Sci Soc Am J 58: 816–823

Groffman PM, Eagan P, Sullivan WM, Lemunyon JL (1996) Grass species and soil type effects on microbial biomass and activity. Plant Soil 183: 61–67

Hobbie SE (1997) Temperature and plant species control over litter decomposition in Alaskan tundra. Ecol Monogr 66: 503–522

Holland EA, Detling JK (1990) Plant response to herbivory and belowground nitrogen cycling. Ecology 71: 1040–1049

Holland EA, Parton WJ, Detling JK, Coppock DL (1992) Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. Am Nat 140: 685–706

Holland JN, Cheng W, Crossley DA (1996) Herbivore-induced changes in plant carbon allocation: assessment of below ground C Fluxes using carbon H. Oecologia 107: 87–94

Houston DB (1982) The northern Yellowstone elk: ecology and management. Macmillan, New York

Hungate BA, Canadell J, Chapin FS (1996) Plant species mediate changes in soil microbial N in response to elevated CO_2. Ecology 77: 2505–2515

Ingham RE, Detling JK (1984) Plant-herbivore interactions in a North American mixed-grass prairie. III. Soil nematode populations and root biomass on *Cynomys ludovicianus* colonies and adjacent uncolonized areas. Oecologia 63: 307–313

Jenkinson DS, Powlson DS (1976) The effects of biocide treatments on metabolism in soil. I. Fumigation with chloroform. Soil Biol Biochem 8: 167–177

Kaye JP, Hart SC (1997) Competition for nitrogen between plants and soil microorganisms. Trees 12: 139–143

Keefer WR (1987) The geological story of Yellowstone Park. Yellowstone Library and Museum Association, Mammoth, Wyo

Kieft TL (1994) Grazing and plant canopy effects on semi-arid soil microbial biomass and respiration. Biol. Fert. Soils 18: 155–182

McNaughton SJ (1985) Ecology of a grazing ecosystem. Ecol Monogr 55: 259–294

Merckx R, Hartog AD, Veen JAV (1985) Turnover of root-derived material and related microbial biomass formation in soils of different texture. Soil Biol Biochem 17: 565–569

Myrold DD, Matson PA, Peterson DL (1989) Relationships between soil microbial properties and aboveground stand characteristics of conifer forests in Oregon. Biogeochemistry 8: 265–281

NOAA (1990) Climatological data for Wyoming. US Department of Commerce, Washington, DC

Paul EA (1984) Dynamics of organic matter in soils. Plant Soil 76: 275–285

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

Ruess RW, Seagle SW (1994) Landscape patterns in soil microbial processes in the Serengeti National Park, Tanzania. Ecology 75: 892–904

Schimel DS (1986) Carbon and nitrogen turnover in adjacent grassland and cropland ecosystems. Biogeochemistry 2: 345–357

Schimel D, Stillwell MA, Woodmansee RG (1985) Biogeochemistry of C, N, and P in a soil catena of the short-grass steppe. Ecology 66: 276–282

Schimel JP, Jackson LE, Firestone MK (1989) Spatial and temporal effects on plant-microbial competition for inorganic nitrogen in a California annual grassland. Soil Biol Biochem 21: 1059–1066

Smith JL, Paul EA (1990) The significance of soil microbial biomass estimations. In: Bollag J, Stotsky G (eds) Soil biochemistry Dekker, New York, pp 357–393

Snyder JD, Trofymow JA (1984) A rapid accurate wet oxidation diffusion procedure for determining organic and inorganic carbon in plant and soil samples. Commun Soil Sci Plant Anal 15: 587–597

Voroney RP, Paul EA (1984) Determination of kc and kn in situ for calibration of the chloroform fumigation incubation method. Soil Biol Biochem 16: 9–14

Wardle DA (1992) A comparative assessment of factors which influence microbial biomass carbon and nitrogen levels in soil. Biol Rev 67: 321–358

Wilsey B (1996) Urea additions and defoliation affect plant responses to elevated CO_2 in a C_3 grass from Yellowstone National Park. Oecologia 108: 321–327

Zak DR, Tilman D, Parmenter RR, Rice CW, Fisher FM, Vose J, Milchunas D, Martin CW (1994) Plant production and soil microorganisms in late-successional ecosystems: a continental-scale study. Ecology 75: 2333–2347