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Ungulate stimulation of nitrogen cycling and retention in Yellowstone Park grasslands

Abstract We studied how ungulates and a large variation in site conditions influenced grassland nitrogen (N) dynamics in Yellowstone National Park. In contrast to most grassland N studies that have examined one or two soil N processes, we investigated four rates, net N mineralization, nitrification, denitrification, and inorganic N leaching, at seven paired sites inside and outside long-term (33+ year) exclosures. Our focus was how N fluxes were related to one another among highly variable grasslands and how grazers influenced those relationships. In addition, we examined variation in soil $\delta^{15}N$ among grasslands and the relationships between soil ^{15}N abundance and N processes. Previously, ungulates were reported to facilitate net N mineralization across variable Yellowstone grasslands and denitrification at mesic sites. In this study, we found that herbivores also promoted nitrification among diverse grasslands. Furthermore, net N mineralization, nitrification, and denitrification (kg N ha^{-1} year^{-1}, each variable) were postively and linearly related to one another among all grasslands (grazed and fenced), and grazers reduced the nitrification/net N mineralization and denitrification/net N mineralization ratios, indicating that ungulates inhibited the proportion of available NH_4^+ that was nitrified and denitrified. There was no relationship between net N mineralization or nitrification with leaching (indexed by inorganic N adsorbed to resin buried at the bottom of rooting zones) and leaching was unaffected by grazers. Soil $\delta^{15}N$ was positively and linearly related to in situ net N mineralization and nitrification in ungrazed grasslands; however, there was no relationship between isotopic composition of N and those rates among grazed grasslands. The results suggested that grazers simultaneously increased N availability (stimulated net N mineralization and nitrification per unit area) and N conservation (reduced N loss from the soil per unit net N mineralization) in Yellowstone grasslands. Grazers promoted N retention by stimulating microbial productivity, probably caused by herbivores promoting labile soil C. Process-level evidence for N retention by grazers was supported by soil $\delta^{15}N$ data. Grazed grassland with high rates of N cycling had substantially lower soil $\delta^{15}N$ relative to values expected for ungrazed grassland with comparable net N mineralization and nitrification rates. These soil ^{15}N results suggest that ungulates inhibited N loss at those sites. Such documented evidence for consumer control of N availability to plants, microbial productivity, and N retention in Yellowstone Park is further testimony for the widespread regulation of grassland processes by large herbivores.

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Introduction

Topography and large herbivores have important effects on grassland nitrogen (N) dynamics. Topoedaphic gradients of soil texture, moisture, redox values, and carbon (C) and N content play important roles in determining N cycling in grassland landscapes (Jenny 1941; Schimel et al. 1985; Burke 1989; Burke et al. 1989; Frank et al. 1994). Furthermore, ungulate trampling and excretory products increase labile soil C and N pools that often accelerate soil N processes (Floate 1981; McNaughton et al. 1988, 1997; Day and Detling 1990; Holland et al.

1992; Jaramillo and Detling 1992; Shariff et al. 1994; Frank and Groffman 1998a).

Most studies of grassland N dynamics have determined variation in one or sometimes two processes, i.e., net N mineralization and net nitrification, at the same time. Consequently, these investigations have provided information on only a narrow slice of the N cycle. Such studies have not resolved if the measured rate(s) characterizes other portions of the N cycle, how different soil N processes are associated with one another along edaphic gradients, and if grazers influence these relationships. In other words, most studies of N cycling in grasslands have not investigated whether diverse soil characteristics occurring along topographic gradients, and/or grazers variably affect different soil N transformations. Such information would be of value to accurately construct N budgets of grazed grasslands that are typically spatially heterogeneous.

In this investigation we provide a more complete picture of the N cycle in grasslands of Yellowstone National Park. Rates of net mineralization, nitrification, denitrification, and leaching are reported for paired fenced and grazed grasslands at sites that vary dramatically in topographic position and edaphic properties. Furthermore, we examined variation in soil natural ^{15}N abundance (δ^{15}N) which is a function of N input, soil transformations, and N output from the soil system (Nadelhoffer and Fry 1994; Högberg 1997). Soils become enriched in ^{15}N when ^{15}N-depleted products (i.e., NH_3, NO_3^-, N_2O, N_2), resulting from fractionation occurring during soil N transformations, are lost from the soil system (Evans and Ehleringer 1993; Högberg and Johannisson 1993; Nadelhoffer and Fry 1994; Högberg 1997). Because it is assumed that higher N cycling will yield greater N loss, soil δ^{15}N is presumed to be an index of N cycling (Nadelhoffer and Fry 1994). In this study, we examined how soil δ^{15}N was related to in situ rates of several N transformations. In addition, we determined if grazers affected these relationships, to explore if herbivores changed rates of soil N loss. Consequently, the objectives of this study were twofold: (1) to determine the effects of edaphic variation and ungulates on relationships between several important soil N processes and (2) to use soil isotope measurements to examine N loss and retention in grazed grassland.

Material and methods

The study area was the northern winter range of Yellowstone National Park, comprising 100,000 ha of primarily grassland and shrub-grassland habitat in the Yellowstone and Lamar River valleys (Houston 1982; Frank and McNaughton 1992; Frank and Evans 1997; Frank and Groffman 1998a). Elk (21,000), bison (300–700), and pronghorn(600) graze the winter range November–April each year (Frank and McNaughton 1992; Singer and Mack 1993; Frank et al. 1998).

The climate of the northern winter range is cool and dry. Mean annual temperature and precipitation vary 2–7°C and 28–32 cm, respectively, on the range (Houston 1982). Soils throughout the winter range were formed from glacial till deposited in the Pleisto-

cene, except at Stevens Creek, where soil was derived from bentonite-rich landslide deposits (Keefer 1987).

We measured N dynamics at seven sites. Each site had paired plots (8×8 m or 10×10 m) with the same slope and aspect located inside and outside 2-ha exclosures established by Yellowstone Park in 1958 and 1962. Sites were scattered 45 km up an elevation gradient from Stevens Creek (1620 m) to the Lamar Valley (2000 m) and were located on hilltops, slopes, and slope bottoms (Frank and Evans 1997). Site properties, presented in detail elsewhere (Frank and Evans 1997; Frank and Groffman 1998a; Tracy and Frank 1998), ranged widely as a primary function of variable topographic position and a secondary consequence of a climatic gradient up the winter range. Briefly, monthly soil moisture during the growing season ranged 11–45%, and soil N and C content varied 0.09–0.9% and 1–16%, respectively, among the sites.

We examined the relationships between several N pools and flows. Net N mineralization, denitrification, and soil δ^{15}N were previously reported within the context of their independent responses to grazing and topography. Net nitrification and inorganic leaching are reported here for the first time, as are relationships among processes. Net N mineralization was determined over a 12-month period (May 1995–April 1996) with the buried-bag technique (Frank and Groffman 1998a) and was calculated as the difference between the sum of NH_4^+ and NO_3^- extracted from soil at the beginning and end of 1-month incubations during the growing season and a winter-long incubation. Net nitrification was derived by subtracting initial from final amounts of NO_3^-. Denitrification rates were measured at four sites in 1995 using the Tiedje et al. (1989) C_2H_2-based soil core technique (Frank and Groffman 1998b). Soil δ^{15}N was determined at six sites in 1995 (Frank and Evans 1997).

Nitrogen leached from soils at four sites was indexed with inorganic N absorbed to mixed-bed resin (Dowex MR-3, a 1:1 mixture of HCRS[H$^+$] and SBR[OH$^-$]). Five nylon-mesh bags with two level tablespoons of resin were buried at the bottom of rooting zones in September 1995 at each plot and collected in August 1996. Resin was washed with deionized water within 24 h after removal from the soil, air dried, and extracted with 1 M KCl (1 g resin/15 ml KCl). The NH_4^+ and NO_3^- content of the extract were determined with a Perstorp Flow Injection Analyzer. To examine if exchange sites had become saturated during the 12-month period that resin was buried in the field, limiting our ability to determine a fencing effect on leaching, we compared the inorganic N adsorbed to 1.5 g field-incubated resin (two resin bags per plot) rinsed with 15 ml 0.002 M NH_4NO_3 with that of resin rinsed with distilled water. Resin was air-dried and NH_4^+ and NO_3^- were extracted as above.

Finally, we examined the influence of grazers on soil microbial production by comparing the respiration:microbial biomass ratio, often used as an index of microbial productivity (Ingham et al. 1985; Mikola and Setälä 1998). Soils were collected in May, June, and July (the most microbially active period of the growing season) 1996, from the same seven exclosure sites where mineralization and nitrification rates were determined. Soil microbial C and respiration were measured using the methods of Tracy and Frank (1998).

We used least-squares regression analysis to examine relationships among N fluxes and between N fluxes and soil δ^{15}N. The effect of grazers on a relationship was examined with analysis of covariance (ANCOVA). Throughout, we employ $\alpha=0.10$ to reflect statistical significance.

Results

Net nitrification was linearly and positively related to net N mineralization across all samples (Fig. 1). Grazers increased net N mineralization by 100% (signed rank test, $P=0.02$; Frank and Groffman 1998a) and nitrification by 68% (signed rank test, $P=0.035$). Furthermore, the linear
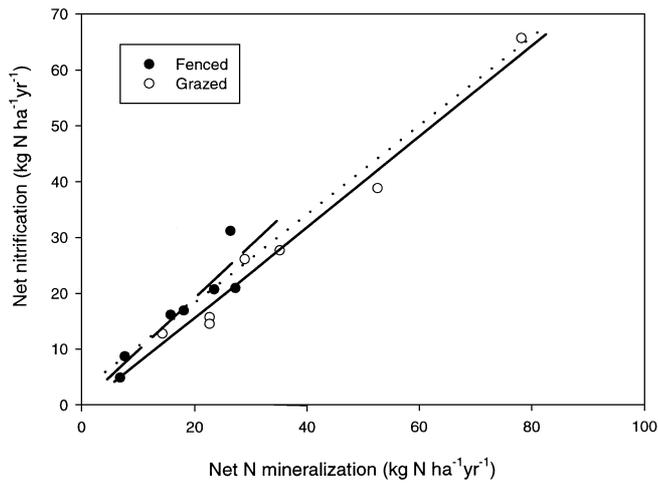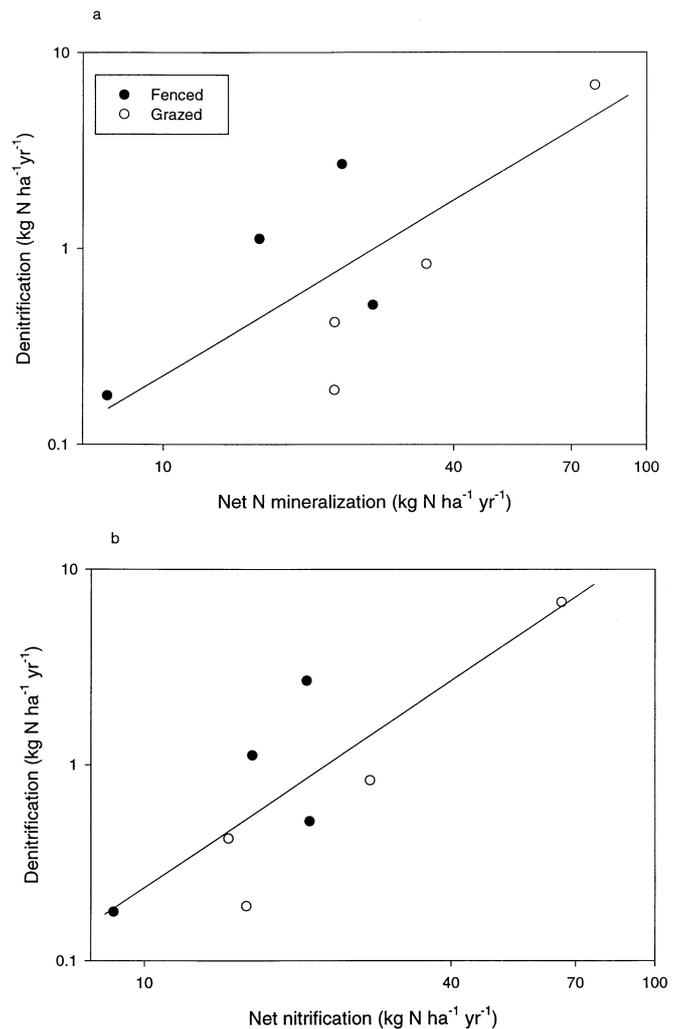
Fig. 1 Relationships between net nitrification (nit) and net mineralization (min) among grassland sites in Yellowstone National Park. *Dashed line* for fenced grasslands: nit=0.11+0.95min, r^2=0.84, *P*=0.0035. *Solid line* for grazed grasslands: nit=0.83min–1.6, r^2=0.98, *P*<0.0001. *Dotted line* for all grasslands: nit=1.45+0.79min, r^2=0.95, *P*<0.0001

relationships for fenced and grazed samples differed (ANCOVA, $F_{1,11}$=3.79, *P*=0.078). The calculated slope for fenced samples (0.95, SE=0.18) was indistinguishable from 1 (*P*=0.78) and that for grazed samples was less than 1 (0.83, SE=0.055, *P*=0.042). y-Intercepts of lines derived for both treatments were not different than zero (grazed *P*=0.53, fenced, *P*=0.98). Thus, all available NH_4^+ was nitrified among fenced grasslands, while an average of only 83% of available NH_4^+ was nitrified in grazed grassland.

Denitrification was positively related to both net N mineralization and net nitrification (Fig. 2). y-Intercepts were significantly less than zero in both cases (mineralization *P*=0.04, nitrification *P*=0.009). Consequently, the percentage of available NH_4^+ and NO_3^- that was denitrified increased with greater rates of net mineralization and nitrification, respectively. For example, denitrification was 2% of net mineralization when the rate of mineralization was 10 kg N ha^{-1} year^{-1} and 5% when mineralization was 70 kg N ha^{-1} year^{-1}. Likewise, percent denitrified increased from 2% to 10% as net nitrification increased from 10 to 70 kg N ha^{-1} year^{-1}. The percentage of net mineralized N that was denitrified was inhibited in grazed grassland (ANCOVA, $F_{1,5}$=3.84, *P*=0.10; average fenced=6%; average grazed=3%). Grazers had no effect on the denitrification/nitrification ratio (ANCOVA, $F_{1,5}$=3.13, *P*=0.13; average fenced=6%, average grazed=4%).

The relationships of soil $\delta^{15}N$ with (1) net mineralization and (2) nitrification were qualitatively the same (Fig. 3). There was a positive logarithmic association among all samples for each relationship. In each case, the logarithmic function was a result of a linear association between variables for ungrazed grassland and the absence of any relationship among grazed samples,
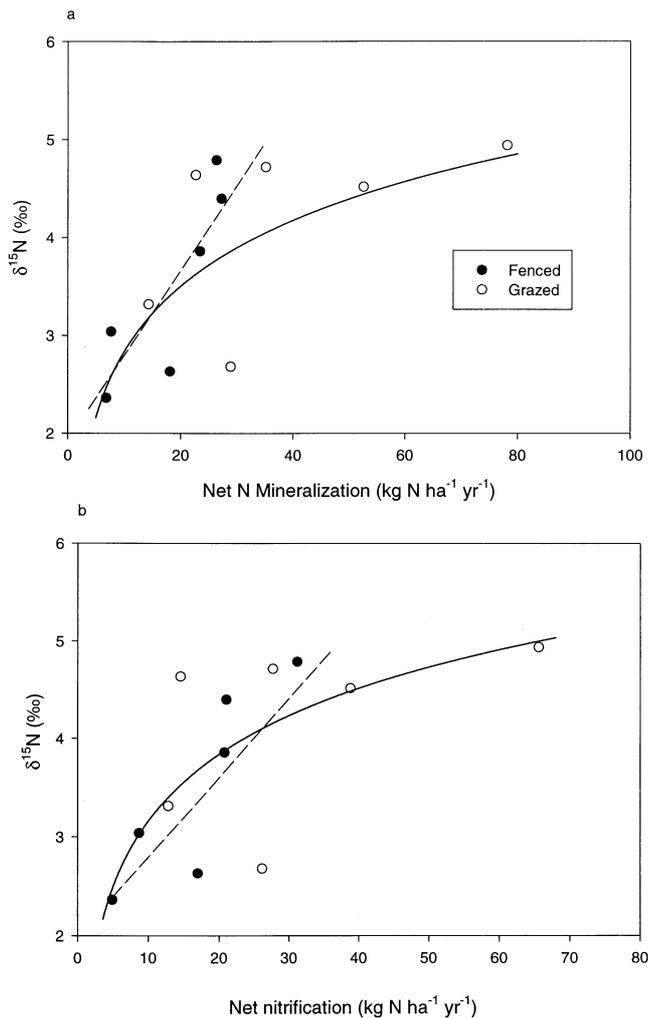

Fig. 2 The relationships between denitrification (denit) and net N mineralization (min) (log denit=1.37log min–2.00, r^2=0.51, *P*=0.046) (**a**) and denitrification and net nitrification (nit) among Yellowstone grasslands (log denit=1.78log nit–2.43, r^2=0.69, *P*=0.011) (**b**)

which supported higher levels of mineralization and nitrification and were relatively enriched in $\delta^{15}N$ compared to fenced plots (paired *t*-test: t_5=2.52, *P*=0.05; Frank and Evans 1997).

In situ incubated resin that was rinsed with a dilute NH_4NO_3 solution in the laboratory after retrieval from the field had more NH_4^+ (*P*<0.0001) and NO_3^- (*P*=0.0001) adsorbed to it than controls rinsed with distilled water. This result indicated that our ability to determine a fencing effect on N leaching was not limited by the saturation of resin exchange sites during field incubation.

The amount of NH_4^+, NO_3^-, and their sum were unaffected by fencing [NH_4^+, average fenced=4.5±1.1 (SE) µg N/g resin, average grazed =6.3±2.7 µg N/g resin, paired *t*-test *P*=0.17; NO_3^-, average fenced=9.5±7.7 µg N/g resin, average grazed =16.5±9.1 µg N/g resin, paired *t*-test *P*=0.42; total inorganic N, average fenced

Fig. 3 Relationships between $\delta^{15}N$ and net N mineralization (min) [all grasslands (*solid line*): $\delta^{15}N=0.68+2.31\log$ min, $r^2=0.49$, $P=0.0069$; fenced grasslands (*dashed line*): $\delta^{15}N=1.82+0.09$min, $r^2=0.73$, $P=0.031$] (**a**) and $\delta^{15}N$ and net nitrification (nit) [all grasslands (*solid line*): $\delta^{15}N=0.91+2.25\log$ nit, $r^2=0.49$, $P=0.0114$; fenced grasslands (*dashed line*): $\delta^{15}N=1.93+0.09$nit, $r^2=0.77$, $P=0.022$] (**b**)

ern winter range grasslands. Topography and climate are important determinants of grassland soil characteristic (Jenny 1941; Schimel et al. 1985; Burke 1989; Burke et al. 1989; Frank et al. 1994; Frank and Groffman 1998a). Among our seven topographically and climatically variable grassland sites, growing season soil moisture ranged by 4-fold, soil C by 10-fold, and soil N by 16-fold (Frank and Groffman 1998a).

Large herbivores also have important effects on grassland nutrient cycling. Ungulates can increase grassland N cycling by promoting the quality of decomposing material. Nitrogen availability to plants and microbes is greater in patches of ungulate waste compared to control patches and grazers narrow C/N ratios of plant litter and roots and soil organic material (Floate 1981; McNaughton et al. 1988, 1997; Day and Detling 1990; Holland and Detling 1990; Holland et al. 1992; Jaramillo and Detling 1992; Shariff et al. 1994). However, understanding the influence of grazers on grassland ecosystem processes requires that their effects be placed within a context of a spatially heterogeneous system, which is a common characteristic of grassland habitats.

Net N mineralization, nitrification, and denitrification were positively associated with one another among Yellowstone grasslands with radically different soils. The rate of denitrification as a proportion of net N mineralization increased as net N mineralization increased. A similar relationship was found between nitrification and the proportion of NO_3^- denitrified. Thus, among Yellowstone grasslands, soils became leakier, with respect to N_2O and N_2 loss, as net mineralization and nitrification rates increased. In contrast, leaching was unrelated to mineralization, suggesting that grasslands were relatively effective at immobilizing inorganic N in the soil profile, even when NO_3^- production was high. Because denitrification was low relative to mineralization and nitrification, denitrification probably did not prevent leaching.

Soil N transformations are controlled by multiple factors, including soil temperature, soil moisture, carbon, and the availability of the inorganic N reagent (e.g., NH_4^+ for nitrification and NO_3^- for denitrification). The positive relationships among transformations in Yellowstone may simply be due to the product of an N transformation limiting the subsequent reaction in the N cycle. This would occur if, for instance, the availability of NH_4^+ or NO_3^- limited nitrification or denitrification, respectively. Alternatively, positive relationships may stem from more than one transformation being limited by the same factor. For example, net mineralization and nitrification are influenced by soil temperature and moisture in similar ways (Paul and Clark 1996). In addition, previous studies in Yellowstone (Frank and Groffman 1998b) have indicated that denitrification in saturated soils is not limited by NO_3^- and is strongly regulated by carbon availability. Control of mineralization (Paul and Clark 1996) and denitrification by the amount of available C supports the notion that common requirements are involved in the positive relationships among transformations in Yellowstone.

$=14.0\pm8.8$ µg N/g resin, average grazed$=22.8\pm9.1$ µg N/g resin, paired *t*-test $P=0.28$]. In addition, leaching was unrelated to mineralization or nitrification ($P>0.10$).

The microbial respiration:microbial C ratio was higher (signed rank test; $P=0.052$) in grazed soil (average$=1.60\pm0.61$) compared to ungrazed soil (average $=0.79\pm0.12$). Such an increase in microbial respiration per unit microbial C suggests that grazers stimulated microbial turnover and production.

Discussion

We examined the effects of two factors (1) variable site conditions, due to differences in topography and climate, and (2) herbivory, on N dynamics of Yellowstone north-

Large herbivores had two effects on N processes. First, ungulates increased rates, promoting net N mineralization by 100% (Frank and Groffman 1998a), nitrification by 68%, and denitrification at mesic grassland sites by as much as 150% (Frank and Groffman 1998b). In addition, grazers reduced the nitrification/net N mineralization and denitrification/net N mineralization ratios. In other words, grazers in Yellowstone decreased the proportion of plant-available NH_4^+ that was nitrified and denitrified. Because the methods used in this study measured soil processes in the absence of plant uptake, ungulates must have inhibited the relative rates of nitrification and denitrification (per unit N mineralized) by increasing microbial immobilization, and thus reducing the amount of soil NH_4^+ that was nitrified. Previously (Tracy and Frank 1998), microbial biomass was shown to be unaffected by grazers in Yellowstone. However, despite herbivores having no influence on the size of the microbial population, results of this study indicate that grazers facilitate microbial productivity, probably by stimulating microbial turnover rates. A grazer-induced increase in microbial production would result in higher microbial immobilization in grazed compared to ungrazed grassland.

How could herbivores stimulate microbial productivity? Ungulates in Yellowstone increase the labile C fraction of soil (Frank and Groffman 1998a). Thus, grazers increase the energy available to microbial populations. However, greater available C does not explain how ungulates could increase microbial production while not affecting microbial biomass. One possible explanation for higher microbial productivity in the face of static microbial biomass is that grazers stimulated belowground microbial grazing. Higher rates of grazing on soil microbes has been shown to increase microbial production in a microcosm study examining the response of belowground processes to increased trophic complexity (Mikola and Setälä 1998). In Yellowstone, Merrill et al. (1994) found that microbial-feeding nematodes were more abundant in grazed grassland than in a paired fenced grassland on the northern winter range. Consequently, large herbivores may facilitate microbial production by altering the structure of the decomposer food web and increasing grazing rates on microbes in Yellowstone grasslands.

Grazer promotion of microbial N immobilization could have important consequences on grassland N budgets by reducing the proportion of mineralized N that is lost from grazed ecosystems. Nitrogen isotope results lend some support to the notion that grazers inhibit N loss. Soil ^{15}N is determined by long-term rates of N inputs and losses. Nitrogen losses will increase soil $\delta^{15}N$ when N substrates are not limiting and ^{15}N-depleted products, such as NH_4^+, NO_3^-, N_2O, and N_2, are lost from the soil (Nadelhoffer and Fry 1994). In addition to atmospheric N inputs, which were probably similar between paired plots inside and outside fences, grazed grasslands also received N from ungulate urine and dung. Elsewhere (Frank and Evans 1997), it was shown that both urine and dung increased soil $\delta^{15}N$ in Yellowstone. But despite ungulate waste increasing soil ^{15}N,

grazed soils supporting high rates of net N mineralization (>40 kg N ha^{-1} year^{-1}) and nitrification (>35 kg N ha^{-1} year^{-1}) were still substantially depleted in ^{15}N relative to levels predicted by regression for ungrazed grassland (Fig. 3). Lower ^{15}N abundance of grazed soils at such sites suggests, particularly in light of ungulate urine and feces effects on soil ^{15}N, that herbivores reduced soil N loss and enhanced N conservation among grasslands that supported high rates of N cycling.

Soil $\delta^{15}N$ levels increased as a linear function of net N mineralization and nitrification in ungrazed grasslands (Fig. 3). Compared to the large number of studies describing variation in isotopic values of organic matter, relatively few investigations have examined the relationships between ^{15}N abundance and N processes to help understand factors controlling isotopic variation. Previous studies have related soil ^{15}N with decomposition (Nadelhoffer and Fry 1988) and potential net N mineralization (Evans and Ehleringer 1994) in laboratory experiments, and rates of N fixation and loss in deserts (Evans and Ehleringer 1993; Evans and Belnap 1999). In addition, plant $\delta^{15}N$ has been related to N fixation (see Shearer and Kohl 1986; Handley and Raven 1992; Högberg 1997), atmospheric N deposition (Vitousek et al. 1989; Garten 1993) and N leaching (Högberg and Johannisson 1993; Nohrstedt et al. 1996). To our knowledge, this study is the first to demonstrate that soil ^{15}N abundance is positively related to in situ net N mineralization or nitrification, as had been predicted by several studies (Nadelhoffer and Fry 1994).

In contrast to results for ungrazed grasslands, there was no relationship between soil $\delta^{15}N$ with either net mineralization or net nitrification among grazed grasslands. The different relationships among grazed versus ungrazed soils suggests that ^{15}N abundance may be under different controls in the two types of grasslands. For example, ammonia loss from ungulate urine and dung patches, a process that does not occur in ungrazed grassland, has been identified as a potentially important mechanism determining soil ^{15}N abundance in grazed soil in Yellowstone (Frank and Evans 1997). Different fractionation factors associated with important pathways of N loss from the two types of grasslands, in addition to contrasting degrees of substrate limitation in grazed versus ungrazed grasslands, also may have contributed to the different relationships between N processes and soil $\delta^{15}N$ that we observed in this study.

Herbivores and topoedaphic gradients can interact with grassland N cycling in complex ways. In this study we have shown that three important soil N transformations, net mineralization, nitrification, and denitrification, are positively and linearly related to one another, and rates of N loss via denitrification and leaching respond differently to gradients of N cycling in grassland landscapes. Grazers increased net N mineralization, nitrification, and denitrification; but also reduced the proportion of plant-available NH_4^+ that was nitrified and denitrified. This inhibitory effect of herbivores on processes downstream of mineralization was likely due to herbi-

vores promoting microbial production. Increased microbial production and immobilization could have important consequences on the N budget of Yellowstone grassland, if stimulated N immobilization by herbivores reduces N loss. Further evidence for ungulate promotion of N retention came from soil N isotope measurements that revealed soil of grazed grassland to be depleted in ^{15}N relative to levels predicted for ungrazed soils, although differences in fractionation factors associated with dominant pathways of N loss and dissimilar levels of substrate limitation may have also contributed to contrasting soil ^{15}N abundance in grazed versus ungrazed grassland. Herbivores, therefore, appear to increase N transformations and microbial production, which simultaneously lead to greater N cycling and N conservation.

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