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EFFECTS OF NATIVE GRAZERS ON GRASSLAND N CYCLING IN YELLOWSTONE NATIONAL PARK

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Abstract. We investigated the effects of native ungulates on grassland N cycling in Yellowstone National Park by examining natural ^{15}N abundance ($\delta^{15}N$) of soils and plants inside and outside long-term (32–36 yr) exclosures. Across six topographically diverse sites, grazers increased $\delta^{15}N$ of soil (0–20 cm) by 0.7‰, which was substantial considering that values for ungrazed soil ranged 2.4‰ (2.4–4.8‰). The magnitude of grazer ^{15}N enrichment was positively related ($r^2 = 0.70$) to the intensity of herbivore activity during the study, indexed by the amount of dung (g/m^2) deposited at the sites. We also found that soil $\delta^{15}N$ of ungulate urine and dung patches was significantly higher than that of control areas. Grazers probably increased soil $\delta^{15}N$ by promoting N loss from the soil via leaching, ammonia volatilization, and/or denitrification. Each of these processes results in the removal of ^{15}N depleted products from the soil and, consequently, ^{15}N enrichment of the remaining soil. In contrast to soil results, grazers reduced plant ^{15}N by an average of 0.7‰, probably due to isotopically light, soil NO_3^- (compared to soil NH_4^+) constituting a more important N source for plants in grazed grassland relative to those in ungrazed grassland.

These findings indicate that native grazers increased N loss from this north-temperate grassland as a result of accelerated losses on urine- and dung-affected microsites and, potentially, from elevated N loss throughout the grazed landscape due to grazers promoting N cycling. Furthermore, these results suggest that herbivores increase plant NO_3^- assimilation, which may positively affect primary productivity in this grazed ecosystem.

Key words: bison; elk; grassland; grazing; herbivore; ^{15}N; nitrogen; stable isotopes; ungulate; Yellowstone National Park.

INTRODUCTION

Large herbivores are a major and integral component of nitrogen (N) cycling in grazed grassland. Grazers directly remove plant N and spatially redistribute it within ecosystems. Indirectly, large herbivores can accelerate N cycling by: (1) increasing litter turnover during trampling (Ruess 1987), (2) recycling N in forms more available to plants and soil microbes than those found in the original forage (Floate 1981, McNaughton et al. 1988), and (3) reducing litter and soil C:N ratios (Davidson and Milthorpe 1966, Evans 1973, Hodgkinson and Baas Becking 1977, Shariff et al. 1994) and, consequently, lowering microbial immobilization (Holland and Detling 1990, Holland et al. 1992).

Large herbivores also promote N loss from grasslands via ammonia volatilization from urine patches. Rates of urea-N hydrolysis and subsequent ammonia volatilization are a function of vegetation and soil urease activity, pH, moisture, cation exchange capacity, and texture (e.g., Woodmansee et al. 1978, Schimel et al. 1986, Ruess and McNaughton 1988, Frank and Zhang 1997). Measured ammonia-N losses from grassland soils range 1–90% of urea-N applied, with most values falling between 10 and 40% (Musa 1968, Stewart 1970, Denmead et al. 1974, Vallis et al. 1982, Bouwmeester et al. 1985, Schimel et al. 1986, Ruess and McNaughton 1988, Frank and Zhang 1997).

In recent years, variation in the natural abundance of ^{15}N ($\delta^{15}N$) in soil and plant material has emerged as a useful tool to study N cycling. Soil $\delta^{15}N$ is a function of the rate and isotopic composition of soil N inputs and outputs, and how the isotopic composition of N is altered during soil N transformations (Nadelhoffer and Fry 1994). Because discrimination against ^{15}N occurs during each soil N transfer, i.e., mineralization (ammonification), nitrification, ammonia volatilization, and denitrification, the product of each of these reactions is depleted in ^{15}N relative to the substrate, except when the conversion of the substrate is complete (Shearer and Kohl 1986, Handley and Raven 1992, Nadelhoffer and Fry 1994). Consequently, N lost from the soil system during ammonia volatilization, denitrification, and leaching leads to ^{15}N enrichment of the remaining soil (Nadelhoffer and Fry 1994). The gradual increase in ^{15}N of organic material due to the losses during decomposition, coupled with the downward movement of that decomposing material over time, likely yields the often observed positive relationship between soil ^{15}N abundance and depth (Shearer et al. 1978, Mariotti et al. 1980, Steele et al. 1981 Ledgard et al. 1984, Tiessen et al. 1984, Shearer and Kohl 1986,

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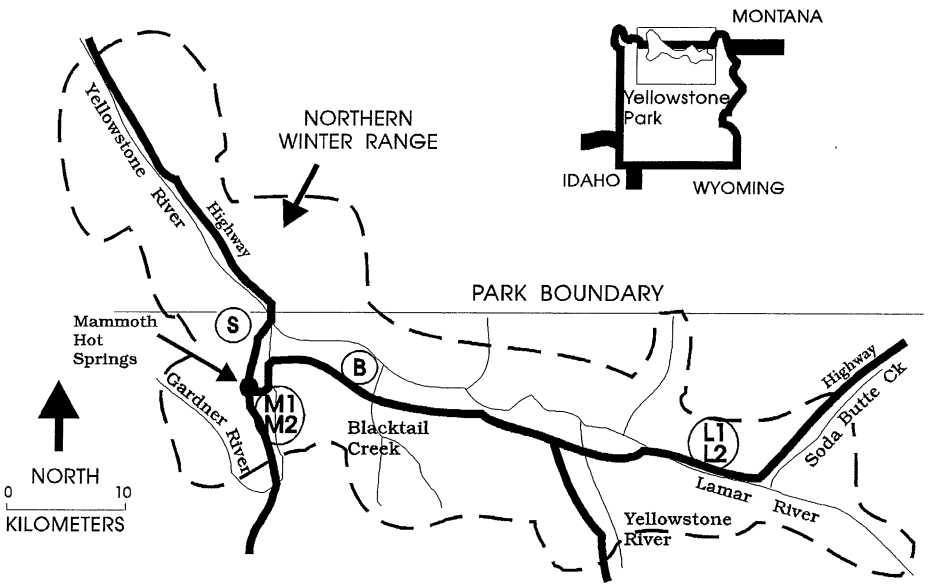

FIG. 1. Location of study sites at Stevens Creek (S), Mammoth (M1, M2), Blacktail Plateau (B), and Lamar Valley (L1, L2) in Yellowstone Park's northern winter range.

Nadelhoffer and Fry 1988, Evans and Ehleringer 1993, Nadelhoffer and Fry 1994).

Some recent studies illustrate how natural ^{15}N abundance has been used to examine soil N dynamics. In a desert ecosystem, removal of the N_2-fixing cryptogamic crust by disturbance increased soil ^{15}N abundance, a direct consequence of the elimination of the primary source of N to this ecosystem (Evans and Ehleringer 1993). Variation in soil ^{15}N among topographically diverse sites has been linked to differences in denitrification rates in grassland (Sutherland et al. 1993) and arctic (Chapin 1996) ecosystems. Finally, comparisons of the isotopic composition of N inputs vs. outputs of "declining" European forests exposed to high atmospheric N deposition indicated that almost no atmospheric N was retained by those ecosystems, which was in stark contrast to healthy, low N-input forests that processed up to 84% of the atmospheric N deposited (Durka et al. 1994).

Plant natural ^{15}N abundance provides information about the relative importance of N sources for plants. For example, ^{15}N abundance is used to determine the proportion of plant N coming from N_2 fixation vs. inorganic soil pools in N_2-fixing plants (Virginia and Delwiche 1982, Shearer and Kohl 1986, 1989, Virginia et al. 1989). For nonfixing species, ^{15}N reflects the relative importance of N deposited from the atmosphere vs. soil N sources (Heaton 1987, Vitousek et al. 1989, Abbadie et al. 1992, Garten 1993, Evans and Ehleringer 1994*a*, Michelsen et al. 1996). In addition, differences in plant ^{15}N abundance among sympatric species can reflect the relative rooting depths of species in the field (Schulze et al. 1994, Evans and Ehleringer 1994*b*), since soil ^{15}N abundance usually increases with depth.

In this study we examined the effects of native ungulates on N cycling in Yellowstone National Park grassland using natural ^{15}N abundance, an approach that allowed us to investigate grazer impacts on soil and plant processes that are impossible to determine in intact, unmanipulated systems using conventional techniques. Long-term effects by herbivores on grassland isotopic composition were determined by comparing ^{15}N abundance of soil and vegetation inside and outside 32–36 yr old exclosures. Results clearly show that ungulates enriched grassland soil in ^{15}N, but depleted ^{15}N in vegetation. These findings bear on our current understanding of how herbivores interactively influence grasslands that they occupy.

MATERIAL AND METHODS

Study sites

This study was conducted on the northern winter range of Yellowstone National Park (Fig. 1), which has been described in detail elsewhere (Meagher 1973, Houston 1982, Despain 1990). Briefly, this range includes ~100 000 ha of relatively low elevation grassland and shrub–grassland habitat in the Yellowstone and Lamar River drainages that is grazed by large herds of elk (*Cervus elaphus*) and bison (*Bison bison*) during the winter. Pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*) also are seasonal or year-long inhabitants of the northern winter range. Elevations vary from 5300 m at the northern end of the range in Montana to 6300 m in the Lamar Valley within Yellowstone Park.

The climate of the northern winter range is cool and

dry. Mean annual temperature and precipitation at Mammoth Hot Springs (Fig. 1) are 4.6°C and 37.9 cm, respectively (NOAA 1990). Soils of the northern winter range are mostly derived from glacial till of andesitic and sedimentary origin laid down during the Pleistocene (Keefer 1987).

We studied four, 2-ha exclosures on the northern winter range established by Yellowstone Park in 1958 and 1962: Stevens Creek (S), Mammoth (M), Blacktail Plateau (B), and Lamar Valley (L) (Fig. 1). Stevens Creek and Lamar Valley exclosures were separated by ~45 km. Grazing intensities on the winter range have been shown to vary considerably as a function of herbivores concentrating at lower elevations on the northern range during the late winter (Houston 1982) and rolling topography leading to heterogeneous forage quality and availability across landscapes (Frank and McNaughton 1992, Wallace et al. 1995). Elk and bison were the predominant grazers on all four landscapes (S, M, B, L); pronghorn were also common at S.

We established six study sites at the exclosures, one at each of S and B, and two at each of M (M1, M2) and L (L1 and L2) (Fig. 1). Each site consisted of paired plots inside and outside the exclosures with the same aspect and slope. Plot size was either 8 × 8 m or 10 × 10 m to maximize within-plot homogeneity. The sites varied topographically. B was a dry grassland hilltop dominated by *Festuca idahoensis* and *Psuedoroegneria spicata* (formerly *Agropyron spicatum*). S, M2, and L2 were dry slopes. S and L2 were grasslands dominated by *P. spicata* and *Koeleria cristata,* and M2 was a shrub–grassland community with *Artemisia tridentata, F. idahoensis,* and *P. spicata* as codominants. M1 and L1 were mesic meadows at the base of slopes, dominated by *Poa pratensis.*

Sample collection

Natural ^{15}N abundance was determined for soil and plant material collected from five randomly located 1 × 1 m quadrats (reps) within each plot in June 1994. Each rep was a composited sample. For soil, five random, 4 cm diameter cores were drawn from each quadrat and pooled. We collected 0–5, 5–10, 10–20, and 20–30 cm soil at each site, except B, where soil was only sampled to 20 cm. At the mesic sites, M1 and L1, we also collected 40–50 cm soil. The depth to which soils were sampled varied according to rooting depth at the sites. Soil %N of reps also was measured. Bulk density of each soil interval was determined on a single composited sample per plot (Blake 1965), created by pooling subsamples of the five reps. For plants, one dominant grass species at each site was collected inside and outside exclosures from the same five quadrats used for soil sampling. We pooled the most recent, fully expanded leaf from 4 to 5 random plants in each quadrat (rep). Material was sampled while plants at each of the sites were growing. We collected *P. spicata* at S, M2, B, and L2, and *P. pratensis* at M1 and L1.

We used the amount of ungulate dung deposited (grams per square meter) during the 1994/1995 winter as an index of the level of herbivore use at the sites. Previously (Frank and McNaughton 1992), ungulate dung was shown to be strongly correlated with grazing intensity on the northern range. Dung piles were counted along four, 8-m transects through grazed plots, then converted to dry mass using values for average dry mass of dung piles for each ungulate species that occurred at the sites (Frank and McNaughton 1992, Frank et al. 1994). Soil pH, field capacity, and texture for each plot were determined on 0–10 cm soil, composited from five random samples with a 10 cm diameter corer.

We examined the effects of ungulate urine and dung on soil N isotopic composition by determining ^{15}N abundance of 0–5, 5–10, and 10–20 cm soil collected on and off (control) three urine patches appearing dark green in color (similar to Day and Detling 1990) and three dung piles. Each sample was a composite of four randomized collections within or off each of the patches using a 4-cm corer. Control samples were collected >1 m from patches. Urine and dung soils were collected from two different *A. tridentata–P. spicata–F. idahoensis* communities near Mammoth Hot Springs in July 1994. Urine was produced by either bison or elk, according to species of grazers represented by dung at the site. It was unclear when urine was added to the plots; however, judging from the green pigmentation of plots where urea-N was experimentally added in April that year during a related study, ungulates probably urinated on plots sometime in the spring 1994. Dung was estimated as <11 mo old (since the previous fall), according to form and pigmentation of feces.

The isotopic composition of ungulate urine and dung was also examined. $\delta^{15}N$ was determined for elk and bison dung and elk urine (n = 5 each) collected on Yellowstone's northern winter range in March and April 1995 in freshly (<12 h) fallen snow. Samples were frozen within 2 h after collection until they were freeze-dried (<3 mo). Lyophilization does not result in N discrimination (R. D. Evans and C. Cook, *unpublished data*).

Laboratory analyses

^{15}N abundance of soil and plant samples was determined with a Finnigan MAT model delta S mass spectrometer following Evans and Ehleringer (1993, 1994*b*). N isotopic composition is reported as $\delta^{15}N$, the per mil (‰) ^{15}N excess above the atmospheric standard (Mariotti 1984):

$$\delta^{15}N = \frac{(^{15}N/^{14}N)_{sample} - (^{15}N/^{14}N)_{standard}}{(^{15}N/^{14}N)_{standard}} \times 1000‰. \quad (1)$$

Soil N content was determined with a Carlo Erba N Analyzer Model 1500 (Carlo Erba Instruments, Milan, Italy).

TABLE 1. Soil characteristics and dung deposited at the sites.

Site	pH	Bulk density (g/cm^3)	Water-holding capacity (% H_2O)	USDA texture categories (%)			Dung (g/m^2)
				Sand	Silt	Clay	
S							
Inside	7.3	1.3	22.6	50.0	21.1	28.9	
Outside	7.2	1.3	21.0	55.8	17.6	26.6	27.1
M1							
Inside	7.9	0.75	44.4	35.1	34.1	30.8	
Outside	7.8	0.77	45.3	32.1	37.8	30.1	73.6
M2							
Inside	6.5	1.1	23.4	46.5	35.9	17.6	
Outside	6.3	1.1	25.3	44.6	36.8	18.6	32.6
B							
Inside	6.7	1.2	34.3	45.5	38.4	16.1	
Outside	6.7	1.2	19.5	44.7	39.2	16.1	20.2
L1							
Inside	6.6	0.9	36.1	35.0	41.7	23.3	
Outside	6.8	0.9	34.6	33.5	42.3	24.2	28.0
L2							
Inside	7.6	1.3	19.8	45.5	34.8	19.7	
Outside	7.7	1.4	18.0	48.5	28.2	23.3	14.7

Data analysis

We performed a three-way analysis of variance (ANOVA), with grazing and soil depth blocked by site, on mean plot values for soil %N and $\delta^{15}N$. Because an inspection of the data indicated large site × grazing and site × depth interactions, we did not test site (blocking) effects on %N and $\delta^{15}N$ (Sokal and Rohlf 1995), although we used the sum of squares provided by the analysis to calculate the proportion of variation explained by site effects. Two, one-way ANOVAs were used to test for site effects on grazed and ungrazed plant $\delta^{15}N$ separately. A grazer effect on plant $\delta^{15}N$ was analyzed with a paired t test of plot means. We performed separate two-way ANOVAs to examine effects of (1) urine and soil depth and (2) dung and soil depth on soil $\delta^{15}N$. Relationships between (1) herbivore use (dung) and the ^{15}N enrichment by grazers and (2) plant $\delta^{15}N$ and soil $\delta^{15}N$ were explored with correlation and regression analyses. Results indicated that relationships between plant and soil ^{15}N were qualitatively the same for all soil intervals. Therefore, to simplify the presentation, we only report findings associated with 0–10 cm soil.

RESULTS

Site properties

Soil properties and dung quantity varied considerably among the sites (Table 1). The two mesic sites, M1 and L1, had lower bulk density and sand content, and higher water-holding capacity and clay content than the four hilltop and slope sites; an exception was the high soil clay content at S, which was probably due to the clay-rich parent material from which soils were derived at that site (Keefer 1987). There was no consistent fencing effect on any of the variables. Dung varied by fivefold, indicating large differences in herbivore activity among the sites.

Soil %N and $\delta^{15}N$

Soil %N was highest at the mesic sites, M1 and L1 (e.g., 0–5 cm; 0.8–1.0%), compared to the dry sites (e.g., 0–5 cm; 0.07–0.5%) (Fig. 2a). Soil (0–20 cm)

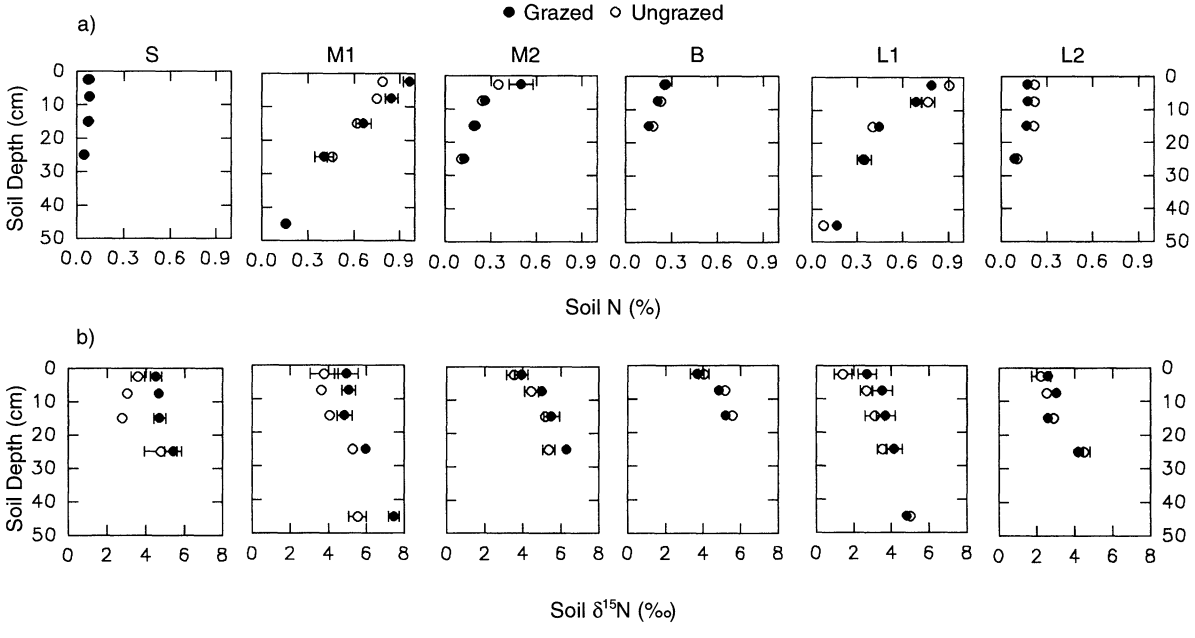

FIG. 2. Soil N and $\delta^{15}N$ at sites. Values are graphed at midpoints of soil intervals. Bars denote ±1 SE.

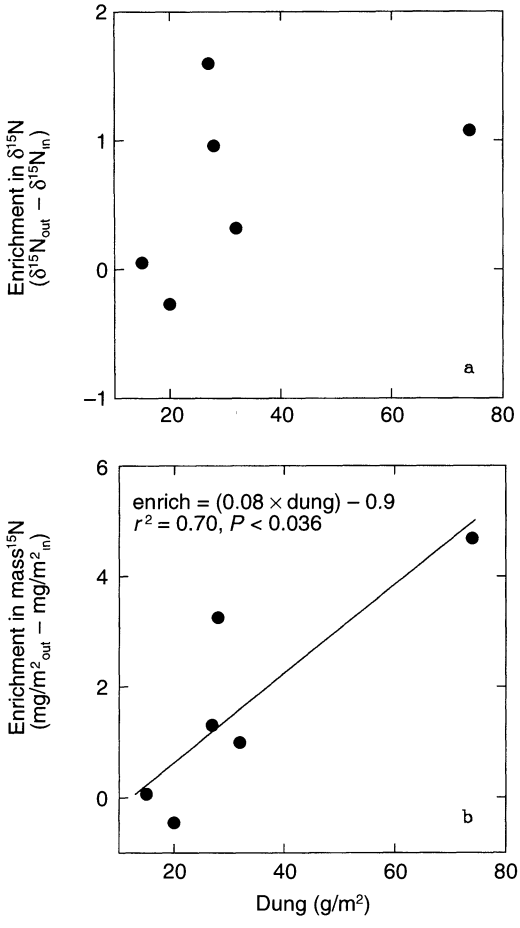

FIG. 3. Relationship of (a) $\delta^{15}N$ enrichment by grazers and dung and (b) mass ^{15}N enrichment and dung.

%N declined with depth ($F_{2,27} = 11.13$, $P < 0.004$), but was unaffected by grazing ($F_{1,27} = 0.16$, $P < 0.697$). Inspection of the sums of squares indicated that depth and site (the blocking factor), contributed 7 and 86% of the variation in %N, respectively.

Soil $\delta^{15}N$ ranged from +1.4 (0–5 cm, ungrazed, L1) to +7.9‰ (40–50 cm, grazed, M1). Soil (0–20 cm) $\delta^{15}N$ increased with depth ($F_{2,27} = 6.36$, $P < 0.006$) and grazers ($F_{1,27} = 13.99$, $P < 0.008$) (Fig. 2b). Site, soil depth, and grazing explained 62, 9, and 10% of the variation in $\delta^{15}N$, respectively. On average, grazers increased soil $\delta^{15}N$ (0–20 cm) by 0.7‰, a substantial amount considering that values for ungrazed soil among the six topographically diverse sites differed by 2.4‰ (2.4–4.8‰). Furthermore, the magnitude that herbivores increased ^{15}N varied considerably among sites (Fig. 2b). Grazed soils at sites S, M1, and M2 had elevated ^{15}N levels relative to those of ungrazed soils throughout their entire soil profiles, while at other sites, the response was not consistent with soil depth (L1, L2), or was counter to the statistically significant pattern (B).

We explored the relationship between the amount

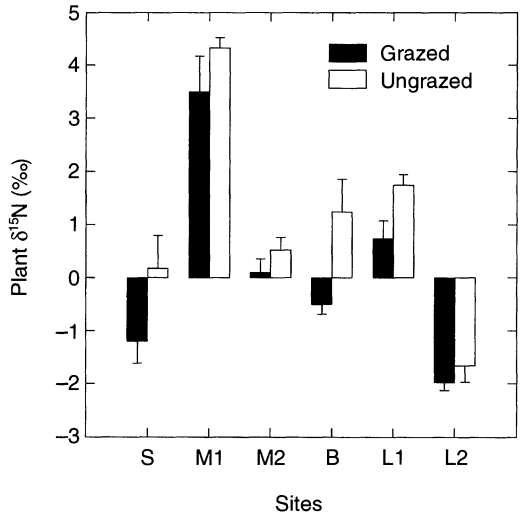

FIG. 4. $\delta^{15}N$ (mean + 1 SE) of dominant grass species at sites.

that grazers increased soil ^{15}N and the grazer activity at the sites (dung) by first relating the per mil (‰) grazer enrichment with dung deposited at the sites during the study. This analysis was performed on the $\delta^{15}N$ values for 0–20 cm soil, derived from 0–5, 5–10, and 10–20 cm $\delta^{15}N$ measurements, weighted by %N values. We found no relationship ($P < 0.367$) between dung deposition and $\delta^{15}N$ enrichment by herbivores (Fig. 3a).

However, the effect that ungulates have on soil $\delta^{15}N$ is, in part, a function of the size of the soil N pool into which that effect is diluted. For example, the equivalent level of herbivore activity should be diluted more at a fertile (high soil N) site, and, therefore, alter soil $\delta^{15}N$ less, than at an infertile site. Consequently, we calculated the mass-^{15}N required to increase grazed soil (with its characterized N content) by the observed ‰. $^{15}N/^{14}N$ ratios were converted to milligrams ^{15}N/per square meter values using soil %N and bulk density measurements. Mass ^{15}N-enrichment at each site was calculated as the difference in milligrams ^{15}N/per square meter between grazed and ungrazed soils. We found mass ^{15}N/per square meter enrichment was positively related to dung, explaining 70% of the variation in the observed difference in ^{15}N inside vs. outside the exclosures (Fig. 3b).

Plant $\delta^{15}N$

Plant $\delta^{15}N$ ranged from −1.98 to +4.32‰ (Fig. 4). Surprisingly, grazers reduced plant $\delta^{15}N$ among sites ($t_5 = 3.09$, $P < 0.027$, paired t test) (Fig. 4). The highest values among both grazed and ungrazed sites were for the two mesic sites, M1 and L1, where *P. pratensis* was collected. One-way ANOVAs indicated that plant $\delta^{15}N$ differed among both grazed ($F_{6,23} = 17.99$, $P < 0.001$) and ungrazed ($F_{6,23} = 27.34$, $P < 0.001$) sites. However, since these analyses included two species, *P. pratense* and *P. spicata,* and, therefore, may have con-

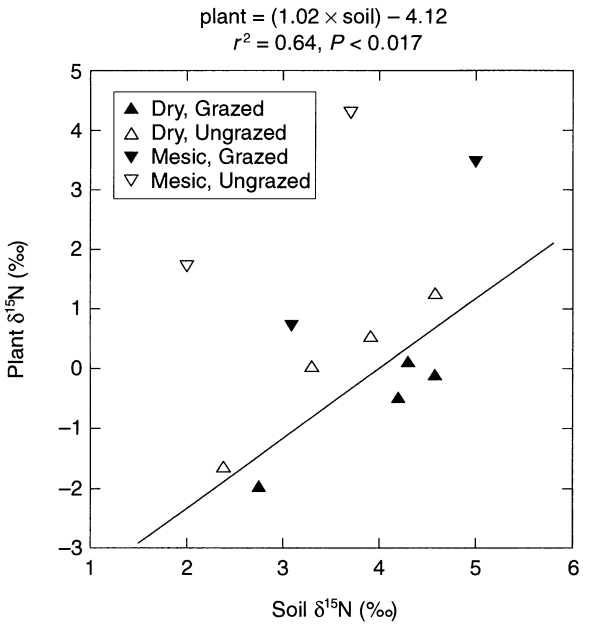

FIG. 5. Relationship between mean plant $\delta^{15}N$ and soil $\delta^{15}N$ (0–10 cm). The regression line was calculated using values for dry sites.

founded site and plant species effects, we performed a second analysis on sites S, M2, B, and L2, where only *P. spicata* was collected. Here too we found differences among sites (grazed: $F_{3,16} = 11.63$, $P < 0.001$; ungrazed: $F_{3,16} = 7.57$, $P < 0.003$).

There was a positive relationship between plant $\delta^{15}N$ and soil $\delta^{15}N$ for the four dry sites (S, M2, B, L2) (Fig. 5). An analysis of covariance, with soil $\delta^{15}N$ as the covariate, indicated a significant grazing effect on plant $\delta^{15}N$ ($F_{1,5} = 34.31$, $P < 0.003$), which is clearly evident in Fig. 5. For the two mesic sites (M1, L1), a similar positive relationship between plant $\delta^{15}N$ and soil $\delta^{15}N$ was apparent, but plants were isotopically heavier relative to the dry sites, probably as a result of the deeper rooting zones at the mesic sites allowing plants to acquire N from ^{15}N-enriched depths.

Effects of urine and dung on soil %N and $\delta^{15}N$

Soil %N was the same on and off urine ($P < 0.580$) and dung ($P < 0.155$) patches (Fig. 6a). In contrast, urine increased soil $\delta^{15}N$ ($F_{1,12} = 5.04$, $P < 0.044$); particularly the top 0–5 cm (site × depth interaction; $F_{2,12} = 4.95$, $P < 0.028$) (Fig. 6b). Soil $\delta^{15}N$ was also increased by dung ($F_{1,12} = 9.40$, $P < 0.020$) (Fig. 6b).

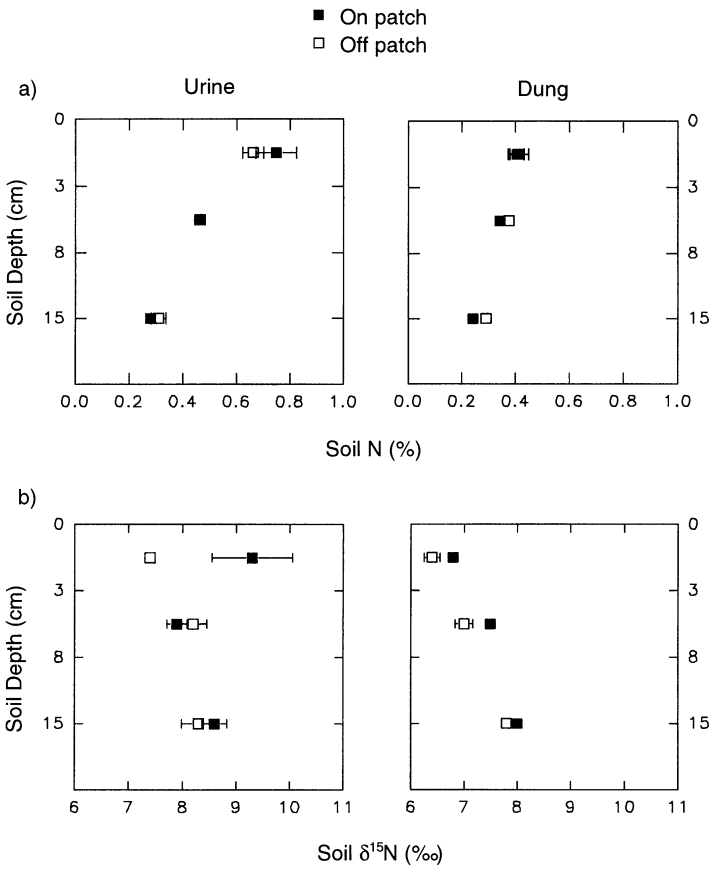

FIG. 6. Soil N (a) and $\delta^{15}N$ (b) on and off urine and dung patches.

We found that dung of both Yellowstone elk (+3.4 ± 1.0‰, mean ± 1 SE) and bison (+4.0 ± 0.4‰) were isotopically heavy relative to elk urine (−1.2 ± 0.2‰).

Discussion

Soil $\delta^{15}N$

Site and soil depth factors contributed to the variation in soil $\delta^{15}N$ observed in Yellowstone grassland, similar to results from other ecosystems (Shearer et al. 1978, Mariotti et al. 1980, Karamanos et al. 1981, Steele et al. 1981, Ledgard et al. 1984, Tiessen et al. 1984, Shearer and Kohl 1986, Nadelhoffer and Fry 1988, Evans and Ehleringer 1993, Sutherland et al. 1993). However, this study is the first that we are aware of to document that consumers also can determine soil ^{15}N abundance. Grazers accounted for 10% of the variation in 0–20 cm soil $\delta^{15}N$ across our study sites. This magnitude of a herbivore effect was substantial, considering that topographic influences, the preeminent determinant of soil $\delta^{15}N$ in this system, accumulated over thousands of years of soil genesis in Yellowstone, while measured grazer effects accrued over only 32–36 yr, since exclosures were erected.

How did grazers increase soil ^{15}N abundance? Soil $\delta^{15}N$ depends on the isotopic composition of N inputs, outputs, and transformations occurring in the soil (Nadelhoffer and Fry 1994). Grazers could have enriched soils with ^{15}N by affecting the isotopic composition of N input in three ways, each of which we believe is implausible. (1) Herbivores added ^{15}N enriched waste. This appears not to be the case according to spring $\delta^{15}N$ values for urine-N, representing 50–95% of the N lost by ungulates (Mould and Robbins 1981, Ruess 1987, Frank et al. 1994), and dung, although seasonal variation in $\delta^{15}N$ of ungulate waste needs to be explored. Moreover, because herbivores are enriched in ^{15}N relative to their diet (Gaebler et al. 1966, Miyake and Wada 1967, Steele and Daniel 1978, Macko et al. 1982, Minegawa and Wada 1984, Schoeninger and DeNiro 1984, Ambrose and DeNiro 1986), total N excreted by ungulates in urine and dung must be isotopically light relative to that of the forage removed, which in Yellowstone is depleted in ^{15}N compared to the soil. Soil directly affected by the isotopically heavy ungulate corpses themselves represents a negligible proportion of this range and, therefore, could not explain range-level effects observed in this study. (2) Ungulate migration patterns result in a net removal of isotopically light plant N from the winter range and its deposition in depleted forms on other seasonal ranges, i.e., net movement of N by grazers from low to high elevation ranges. This is not supported by the results of the study indicating that soil %N inside and outside the exclosures did not differ across sites. Moreover, it has been argued (Frank and McNaughton 1992, Frank et al. 1994) that grazers should move N in the opposite direction, from spring and summer ranges where animals graze N-rich forage and gain condition, to winter range where animals consume senesced plants and lose mass. This may explain the higher soil N content outside relative to inside the Mammoth exclosure (M1, M2), where animals congregate during the winter. (3) We also do not believe that grazers increased soil ^{15}N by reducing N_2-fixation rates, a process that would have incorporated isotopically light N into the soil (Shearer and Kohl 1986). We were careful not to include sites with legumes or cryptobiotic crust; the latter is rare in Yellowstone grassland (D. A. Frank, *personal observation*). Furthermore, if asymbiotic fixation were occurring at our sites, we would expect grazers to have the opposite effect on fixation, i.e., increase it, since grazers reduce standing dead and litter in Yellowstone grassland (Coughenour 1991), and, therefore, should indirectly increase soil irradiation and, consequently, N_2 fixation (Bazely and Jefferies 1989, Eisele et al. 1989).

Instead, we believe grazers increased soil ^{15}N abundance by facilitating one or more of three pathways of N loss from the soil system: leaching, NH_3 volatilization, and/or denitrification. Because ^{15}N is discriminated against during mineralization, nitrification, NH_3 volatilization, and denitrification, N lost from the soil system will be isotopically light, resulting in soil ^{15}N enrichment.

The finding that ungulate urine and dung increased soil ^{15}N abundance (Fig. 6b), indicates that grazers promoted N loss from those patches. Furthermore, since the urine effect was restricted to 0–5 cm soil, leaching can be eliminated as a mechanism responsible for the ^{15}N shift of that soil. Ammonia volatilization and/or denitrification at the soil surface, therefore, caused the increase in ^{15}N on urine patches. The isotopically heavy N of the top 5 cm presumably would be leached to lower depths over time.

A number of studies have reported NH_3 volatilization from urea-N amended plots, serving as simulated urine patches (e.g., Woodmansee et al. 1978, Schimel et al. 1986, Ruess and McNaughton 1988). That work is corroborated by results of this study using natural ^{15}N abundance, indicating gaseous N loss from natural ungulate urine patches, although direct measurements would be required to determine what proportion of the observed isotopic shift was due to ammonia volatilization vs. denitrification. These findings also indicate N losses from dung patches may be of ecological importance, which is usually ignored in grassland N cycling studies.

In addition to waste products causing microsite increases in soil ^{15}N, we suspect grazers also had a more spatially extensive effect on soil isotopic composition. We already discussed how herbivores can increase net N mineralization rates via trampling (Ruess 1987) and by inducing grazed plants to narrow litter and soil C:N ratios (McNaughton et al. 1988, Holland et al. 1992). The acceleration of N turnover and, consequently, the

increased production of NH_4^+ and NO_3^- throughout the grazed grassland may promote rates of inorganic N leaching, ammonia volatilization, and/or denitrification that would contribute to ^{15}N enrichment of Yellowstone grassland. Enhancement of these processes by N fertilization appears to have caused an increase in soil $\delta^{15}N$ in a Norway spruce forest (Johannisson and Högberg 1994).

Plant $\delta^{15}N$

The isotopic relationship between plants and soils in Yellowstone is comparable to that of other ecosystems studied. We found that plants in Yellowstone were depleted in ^{15}N relative to the soil in which they grew, similar to other reports (e.g., Virginia and Delwiche 1982, Vitousek et al. 1989, Gebauer and Schulze 1991, Handley and Raven 1992, Johannisson and Högberg 1994), although some exceptions exist (Pate et al. 1993). Since little if any discrimination occurs during plant NH_4^+ and NO_3^- uptake (Mariotti et al. 1982; Shearer and Kohl 1986, Evans et al. 1996), plants must become ^{15}N depleted as a result of ^{15}N discrimination during ammonification and nitrification that yield isotopically light NH_4^+ and NO_3^- (Nadelhoffer and Fry 1994) relative to soil organic N. In addition, the positive relationship between plant and soil ^{15}N abundance in Yellowstone (Fig. 5) also has been reported elsewhere (Gebauer and Schulze 1991, Garten 1993, Evans and Ehleringer 1994*b*, Johannisson and Högberg 1994).

It was a surprise that grazers reduced plant $\delta^{15}N$ in Yellowstone, given that they had the opposite effect on soil ^{15}N abundance. We believe there are three potential explanations for this response. First, grazers reduced the rooting depth of plants and, consequently, the ^{15}N abundance of N available for plant assimilation. However, according to root biomass measurements for grasslands inside and outside the Yellowstone exclosures (D. A. Frank, *unpublished data*), grazers had no effect on the absolute or proportional rooting depths of plants. Similarly, Milchunas and Lauenroth (1989) found that cattle had no effect on rooting depth in a shortgrass steppe ecosystem. Therefore, differences in rooting depth cannot explain grazer effects on plant ^{15}N abundance in Yellowstone grassland.

A second mechanism is that grazers increased microbial immobilization. Shearer et al. (1974) have shown that relative immobilization rates (immobilization/gross mineralization) should be inversely related to ^{15}N abundance of inorganic N. However, since grazers, in general, are considered to increase N availability in grasslands (McNaughton et al. 1988), herbivores should, in fact, reduce relative immobilization rates, as documented by Holland and Detling (1990) in bison-grazed, mixed-grass steppe. In Yellowstone, net N mineralization rates are markedly higher than other temperate grassland ecosystems that have been studied, presumably due to facilitation of this rate by abundant herbivores (Frank et al. 1994). Therefore, we believe that the depletion in ^{15}N in plants is not a result of grazers increasing microbial immobilization relative to ungrazed grassland.

The third potential mechanism responsible for the grazer-induced reduction in plant $\delta^{15}N$ is that plants exploit different N pools in grazed vs. ungrazed grassland. Higher rates of net N ammonification caused by grazers (McNaughton et al. 1988, Holland and Detling 1990) may increase nitrification rates and, therefore, the availability of NO_3^-. Because nitrification discriminates against ^{15}N, NO_3^- should be isotopically lighter than NH_4^+ (Feigin et al. 1974). Consequently, if grazed plants in Yellowstone assimilate proportionally more NO_3^- than NH_4^+, grazed vegetation will be isotopically lighter than ungrazed vegetation. This is how we believe grazers depleted plant ^{15}N in Yellowstone grassland.

A shift towards a more NO_3^--based plant N economy would have important ramifications for grazed vegetation. Because NO_3^- is mobile and, therefore, more readily delivered to roots by diffusion and mass flow relative to NH_4^+ (Clarke and Barley 1968, Barber 1984), plants in grazed grassland need not invest in as much root growth to acquire N compared to those in ungrazed grassland. This would be particularly critical to defoliated plants needing to recoup shoot material, which is often considered to occur at the expense of root growth (Evans 1973, Hodgkinson and Baas Becking 1977, Holland et al. 1992). Elevated NO_3^- availability may be an unexplored indirect mechanism contributing to grazers increasing aboveground production in Yellowstone grassland (Frank and McNaughton 1993) and other grassland ecosystems (McNaughton 1985, McNaughton et al. 1996).

The unique contribution of natural ^{15}N abundance to the study of N cycling is the information on transformations of intact, undisturbed systems that would be difficult or impossible to determine using standard rate-measurement techniques. Results of this study indicate that herbivores promote N loss from Yellowstone grassland via multiple pathways: (1) from urine patches, generally considered to be the major pathway of N loss from grazed grasslands (Woodmansee et al. 1978, Schimel et al. 1986), (2) from dung, which largely has been ignored in studies examining effects of grazers on grassland N budgets, and (3) possibly from grazed grassland throughout as a result of herbivores indirectly increasing N cycling. This suggests that values for grazer-mediated N loss from grasslands derived solely from NH_3 volatilization from urine patches (Bouwmeester et al. 1985, Schimel et al. 1986, Ruess and McNaughton 1988) may underestimate the composite effects that large herbivores have on grassland N loss. Furthermore, findings indicate that grazers probably increased NO_3^- availability to plants. Therefore, not only do consumers enhance availability of N to plants by increasing N cycling (Floate 1981, Ruess 1987, McNaughton et al. 1988, Holland and Detling 1990, Holland et al. 1992), ungulates additionally may promote

N availability to plants by altering the form in which inorganic N exists. Both would have positive effects on the primary productivity of this ecosystem.

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ERRATUM

The article by William L. Kendall et al. entitled "Estimating temporary emigration using capture–recapture data with Pollock's robust design," published in *Ecology* 78(2):563–578, was printed with several errors, as itemized below.

Page 565, first column, definition of X^{ω}_{hi}.—In the last line of this definition, $X^{\omega}_{i} = \Sigma_{h=0}^{i-1} X^{\omega}_{hi}$ should be replaced by $X^{\omega}_{\cdot i} = \Sigma_{h=0}^{i-1} X^{\omega}_{hi}$.

Page 565, first column.—The following line should be inserted after the definition of R_i: "r_i = number of R_i animals captured subsequent to primary period i."

Page 566, first column.—Expression L_2 in Eq. 2 should be replaced by:

$$L_2 = \prod_{i=2}^{k} \binom{u_i}{X^{10}_{0i}, X^{01}_{0i}, X^{11}_{0i}} \left[\prod_{h=1}^{i-1} \binom{m_{hi}}{X^{10}_{hi}, X^{01}_{hi}, X^{11}_{hi}} \right] \times \left(\frac{p_{i1} q_{i2}}{p^*_i} \right)^{X^{10}_i} \left(\frac{q_{i1} p_{i2}}{p^*_i} \right)^{X^{01}_i} \left(\frac{p_{i1} p_{i2}}{p^*_i} \right)^{X^{11}_i}.$$

Page 568, second column, section on Completely random emigration: estimator selection.—The first line should read "Selection of an estimator (from the full-likelihood approach or Eq. 5, or Eqs. 9 or 11) . . . ."

Page 578, Table A2.—The cell probabilities for release in years 1 and 2, recapture in year 5 are incorrect. The corrected table appears below.

TABLE A2. Multinomial cell probabilities.

Year of release	Year of recapture			
	2	3	4	5
1	$\phi_1(1 - \gamma''_2)p^*_2$	$\phi_1\mathbf{f}_2\phi_2\mathbf{d}_3p^*_3$	$\phi_1\mathbf{f}_2\phi_2\mathbf{G}_3\phi_3\mathbf{d}_4p^*_4$	$\phi_1\mathbf{f}_2\phi_2\mathbf{G}_3\phi_3\mathbf{G}_4\phi_4\mathbf{d}_5p^*_5$
2		$\phi_2(1 - \gamma''_3)p^*_3$	$\phi_2\mathbf{f}_3\phi_3\mathbf{d}_4p^*_4$	$\phi_2\mathbf{f}_3\phi_3\mathbf{G}_4\phi_4\mathbf{d}_5p^*_5$
3			$\phi_3(1 - \gamma''_4)p^*_4$	$\phi_3\mathbf{f}_4\phi_4\mathbf{d}_5p^*_5$
4				$\phi_4(1 - \gamma''_5)p^*_5$