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Ecology, Volume 79, Issue 7 (Oct., 1998), 2229-2241.

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UNGULATE VS. LANDSCAPE CONTROL OF SOIL C AND N PROCESSES IN GRASSLANDS OF YELLOWSTONE NATIONAL PARK

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Abstract. Within large grassland ecosystems, climatic and topographic gradients are considered the primary controls of soil processes. Ungulates also can influence soil dynamics; however the relative contribution of large herbivores to controlling grassland soil processes remains largely unknown. In this study, we compared the effects of native migratory ungulates and variable site (“landscape”) conditions, caused by combined climatic and topographic variability, on grassland of the northern winter range of Yellowstone National Park by determining soil C and N dynamics inside and outside 33–37 yr exclosures at seven diverse sites. Sites included hilltop, slope, and slope bottom positions across a climatic gradient and represented among the driest and wettest grasslands on the northern winter range. We performed two experiments: (1) a 12-mo in situ net N mineralization study and (2) a long-term (62-wk) laboratory incubation to measure potential N mineralization and microbial respiration.

Results from the in situ experiment indicated that average net N mineralization among grazed plots ($3.8 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) was double that of fenced, ungrazed plots ($1.9 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). Mean grazer enhancement of net N mineralization across sites ($1.9 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) approached the maximum difference in net N mineralization among fenced plots ($2.2 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), i.e., the greatest landscape effect observed. Furthermore, ungulates substantially increased between-site variation in mineralization; grazed grassland, $1 \text{ SD} = 2.2 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, fenced grassland, $1 \text{ SD} = 0.85 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$.

In the long-term incubation, potential microbial respiration and net N mineralization were positively related to total soil C and N content, respectively. There was greater variation in potential respiration and net N mineralization early in the incubation, when labile material was processed, compared to late in the incubation, when more recalcitrant substrate was processed, suggesting that between-site variation in labile organic matter was greater than that of recalcitrant material. Herbivores improved the organic matter quality of soil, increasing the labile fractions and reducing the recalcitrant fractions. Grazers reduced C respired/N mineralized ratios, an index of microbial N immobilization, by an average of 21%. However, the largest landscape influence on the immobilization index was 13-fold greater than the grazer effect. Given that the greatest landscape influence on in situ net mineralization ($2.2 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) was similar to the average grazer impact on that rate ($1.9 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), we hypothesize that the landscape effect on field N availability was primarily caused by variation in microbial immobilization, while the grazing effect was primarily due to stimulation of gross mineralization. These results indicate that the relative importance of ungulates in controlling soil N cycling may be more important than previously suspected for grasslands supporting large herds of migratory ungulates, and that the dominant mechanisms underlying the landscape and ungulate influences on soil mineral fluxes may differ.

Key words: carbon; grassland; grazing; herbivory; large herbivores; nitrogen; Yellowstone National Park.

INTRODUCTION

Climatic and topographic gradients are generally considered the major factors influencing soil carbon (C) and nitrogen (N) dynamics in grassland ecosystems (Jenny 1941, Aandahl 1948, Meentemeyer 1978, Paul and Clark 1989, Schimel et al. 1985a, b, Burke et al. 1989, Frank et al. 1994). Climate, which can vary among landscapes, directly affects soil temperature and

moisture, two principal determinants of microbial activity. Within landscapes, aeolian and fluvial processes along topographic gradients determine a number of important edaphic properties that influence soil processes, including texture, moisture, and nutrient content (e.g., Malo et al. 1974, Frank et al. 1994, Ruess and Seagle 1994, Turner et al. 1997). Both climatic and topographic gradients in grasslands are associated with patterns of plant production, leaf chemistry, and plant species distributions, all of which can strongly feed back on local C and N processes (Burke 1989, Schimel 1985b, Schlesinger et al. 1990, Wedin and Tilman

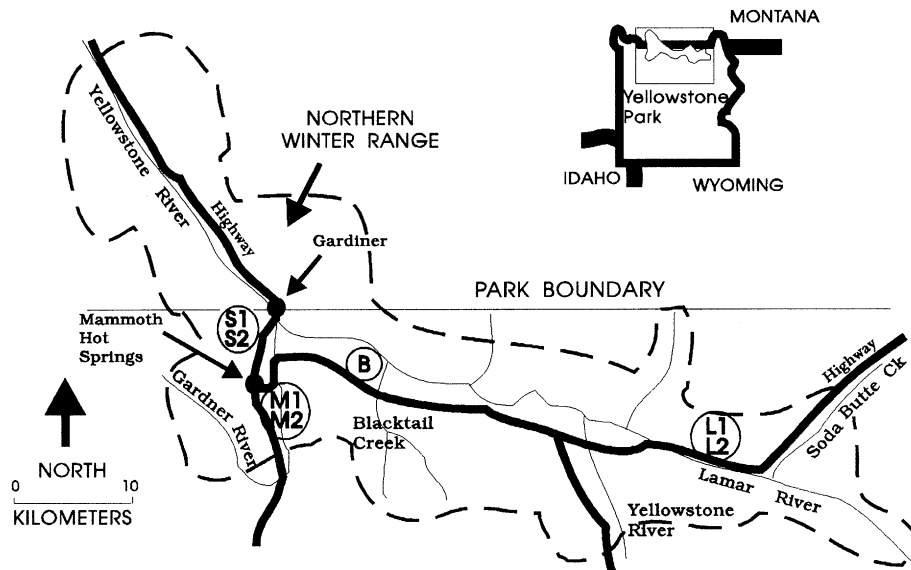


FIG. 1. Study site locations. Adapted from Frank and Evans (1997).

1990, Hobbie 1992, 1996, Vázquez de Aldana et al. 1996, Köchy and Wilson 1997).

In addition to variable site ("landscape") characteristics resulting from variation in climate and topographic position, large herbivores influence grassland soil dynamics. Grazers accelerate nutrient cycling within patches receiving their waste products (Floate 1981, McNaughton 1985, McNaughton et al. 1988, Day and Detling 1990, Jaramillo and Detling 1992, Seagle and McNaughton 1992, Hobbs 1996, Frank and Evans 1997). Herbivores also increase decomposition rates by reducing C/N ratios of plant shoots and roots (Risser and Parton 1982, Coppock et al. 1983, Seastedt 1985, McNaughton et al. 1988, Seastedt et al. 1988, Holland et al. 1992, Shariff et al. 1994). Furthermore, plants often respond to defoliation by decreasing root production (e.g., Weaver and Zink 1946, Jameson 1963, Caldwell et al. 1981, Ingham and Detling 1984, Richards 1984, Holland et al. 1992, Miller and Rose 1992) that can result in reduced soil C and C/N ratios (Holland et al. 1992). Lower C/N ratios in grazed plant material and soils increases net N mineralization by reducing microbial demand for N (i.e., microbial immobilization) during decomposition (Holland and Detling 1990, Holland et al. 1992, Shariff et al. 1994).

The goal of this study was to examine how large herbivores and landscape factors affect soil C and N dynamics in grasslands of Yellowstone National Park. We believe this investigation is unusual in two respects. First, although many studies have examined landscape and large herbivores influences on soil processes, these efforts usually investigated either landscape parameters or herbivores separately; few studies (Holland and Detling 1990) have compared the relative roles of herbivores and landscape in controlling soil processes in a

grassland ecosystem. Second, no other study has examined how native migratory ungulates affect soil energy and nutrient fluxes in a large, temperate reserve where animals move freely throughout their seasonal ranges. We compared landscape and grazer effects by measuring soil dynamics inside and outside 33–37 yr old exclosures at seven topographically diverse sites that were located along a temperature and moisture gradient in grassland of Yellowstone National Park. We were particularly interested in how landscape properties (under topographic and climatic control) and large herbivores influenced two important features of the soil system: (1) net N mineralization, determined in a field study, and (2) soil organic matter quality, inferred from a long-term laboratory incubation experiment.

MATERIAL AND METHODS

Site description

This study was conducted on the northern winter range of Yellowstone National Park, USA (44°55' to 45°10' N and 110°10' to 110°50' W), which is operationally defined as habitat grazed by the park's northern herds of elk (*Cervus elaphus*) and bison (*Bison bison*) during the winter (approximately November–April), and includes 100 000 ha of grassland and shrub-grassland lying athwart the northern park boundary with Montana (Fig. 1). Recent northern elk and bison population estimates for this area are 21 000 and 300–700, respectively (Singer and Mack 1993). Smaller numbers of pronghorn (*Antilocarpa americana*), bighorn sheep (*Ovis canadensis*), and mule deer (*Odocoileus hemionus*) also graze the winter range.

Long-term effects of ungulates on soil dynamics were determined by comparing soil processes in grazed

vs. fenced, ungrazed grassland. Exclosures were 2 ha (100×200 m) and have fenced out all ungulates since 1958 or 1962. We sampled seven sites at four exclosures located at Stevens Creek (S1, S2), Mammoth (M1, M2), Blacktail (B), and Lamar (L1, L2; Fig. 1). Stevens Creek and Lamar sites were 45 km apart. Elevation on the winter range increases from the park boundary eastward, and at our sites, from 1620 m at Stevens Creek to 2000 m at Lamar (Fig. 1). Study sites were selected to include the widest range of topographic positions and as much of the dry to mesic habitat gradient as possible. At each site, we sampled 8×8 m or 10×10 m paired plots inside and outside fences with the same slope and aspect. S1 was an alluvial outwash dominated by *Stipa comata* and *S. viridula*. S2, M2, and L2 were slopes and B was a hilltop; S2, L2, and B were grasslands dominated by *Festuca idahoensis* and *Pseudoroegneria spicata*, and M2 was a shrub-grassland site with *Artemisia tridentata*, *F. idahoensis*, and *P. spicata* dominating. M1 and L1 were slope-bottom sites dominated by *Poa pratensis*. Grazers have been shown to reduce shrub cover on the northern range (Houston 1982). This was evident at two sites, S1 and L1, where shrubs occurred inside (*A. tridentata* and *Atriplex spinosa* at S1 and *Pentaphylloides floribunda* [formerly *Potentilla fruticosa*] at L1) and were negligible outside the exclosures.

Climate of Yellowstone's northern winter range is cool and dry, with mean annual temperatures declining up-valley from $\sim 7^\circ\text{C}$ at Gardiner, Montana, to 2°C in the Lamar Valley, and mean annual precipitation increasing from ~ 28 cm to 32 cm along the same gradient (Houston 1982). Therefore, the study sites were located along a climate gradient from warmer and drier Stevens Creek to cooler and moister Lamar. Soils for much of the winter range were derived from glacial till deposited during the Pleistocene. Those at Stevens Creek were exceptional, having been formed from a bentonite clay-rich substrate deposited during a Pleistocene landslide (Keefer 1987).

In situ net N mineralization rates

We measured net N mineralization of 0–10 cm soil from May 1995 through April 1996 with buried polyethylene bags (Eno 1960). A previous study of soil N cycling on the northern range (Frank et al. 1994) indicated that this soil interval was where the bulk of the net N mineralization occurred. Soils were incubated monthly during the growing season (May–September 1995 and April 1996) and once during a 6-mo winter period (October–March). At the beginning of each incubation, a 2.5 cm diameter \times 10 cm soil core was collected to determine initial, i.e., preincubation, levels of NH_4^+ and NO_3^- . A second core was collected directly adjacent to the first. The second sample was placed in a 470- cm^3 (16-ounce whirlpak bag, then sealed and buried. These “final” soil samples were retrieved at the end of the incubation. We incubated five randomly

located replicate soil cores within each plot. Because shrubs can affect soil nutrient dynamics (Charley and West 1977, Burke 1989, Schlesinger et al. 1990), we sampled soil below shrubs and in grassland openings separately (5 replications each) in plots where shrubs occurred (S1, fenced; M2, fenced and grazed; L1, fenced). All soil samples were kept on ice in the field immediately after collection and were transferred to a refrigerator until extraction with 1N KCl within 48 h. A subsample of soil was oven-dried to determine soil moisture content in order to calculate flux variables on a unit dry soil-mass basis. Extract samples were shipped to Syracuse University and kept frozen at -20°C until analysis with a Perstorp Flow Injection Analyzer (Perstorp Analytical, Wilsonville, Oregon). Net N mineralization was calculated as the difference between NH_4^+ plus NO_3^- at the end of the incubation and that sum at the beginning of the incubation.

Potential microbial respiration and net N mineralization

We performed long-term, 25°C laboratory incubations on soil collected from grazed and ungrazed grassland (soils under shrubs at sites S1, M2, and L1 were not included) in September 1995, using the procedure outlined by Stanford and Smith (1972) and the incubation chambers designed by Nadelhoffer (1990). Nine replicate samples of 0–10 cm soil were randomly collected from each plot where in situ net N mineralization was measured. Samples were shipped overnight to Syracuse University and kept refrigerated until incubations were started within 1 wk after soils were collected. Mineralized NH_4^+ and NO_3^- were leached during week 2, 6, 12, 19, 28, 40, and 62 with 0.01 mol/L CaCl_2 , followed by a nutrient solution devoid of N (Pastor et al. 1993). The experiment was initiated by leaching the soil with the same solutions to remove ambient NH_4^+ and NO_3^- . Soil extracts were kept frozen at -20°C until analysis with a Perstorp Flow Injection Analyzer.

Microbial respiration was determined 4 d postleaching through week 28, yielding five time points. Chambers were completely flushed with CO_2 -free air and sealed. After five hrs, an air sample was drawn from the chamber headspace. Samples were analyzed on a Tracor 540 gas chromatograph (Tracor Analytical, Austin, Texas) equipped with a thermal conductivity detector. Microbial respiration (C respired per gram of soil) was calculated by multiplying the CO_2 -C per cubic centimeter by the chamber headspace volume and dividing by the soil dry mass.

Soil and plant properties

Five random soil samples (0–10 cm depth) were gathered from each grassland plot, and, where shrubs occurred, five samples were obtained from shrub and grassland patches each. Soil C and N were measured on each sample with a Carlo Erba Model 1500 (Carlo Erba Instruments, Milan, Italy). Soil pH, bulk density,

and texture were determined on bulked samples for each plot, except for shrub–grassland plots where under-shrub and grassland opening soils were bulked separately for analysis. Current year peak aboveground biomass was measured with six, 20×50 cm clipped quadrats in grassland, and six, 20×20 cm quadrats in shrub patches. Both herbaceous and shrub (leaf only) biomass was clipped within quadrats. At the same time, 0–10 cm root cores (5.5 cm diameter) were obtained from the center of each quadrat. Roots that did not pass through a 500- μm (number 35) sieve were collected by hand. Live and dead roots were not separated.

Data analysis

Paired *t* tests were used to examine effects of grazers ($df = 6$) on soil properties, plant biomass, in situ net N mineralization, and potential net N mineralization and microbial respiration. We did not explicitly test for a landscape effect. Rather, we assumed that variation among fenced plots reflected a range in site properties influenced by climatic and topographic variation in this ecosystem. Our study sites included among the driest and wettest grassland and grassland/shrub communities on the range, and processes of fenced plots were assumed to reflect this broad variation in site characteristics.

Seasonal patterns of in situ net N mineralization were examined for grassland soils. Soils under shrubs at sites S1, M2, and L1 were omitted from this analysis in order not to confound seasonal effects with those of vegetation structure (herbaceous vs. shrub). Whole-plot mineralization for each shrub–grassland plot was derived by multiplying mineralization (N mass per unit area) in grassland and shrub patches by respective weighting factors representing the proportion of the plot occupied by each vegetation type, determined with nine line transects at each plot (Frank and McNaughton 1992, Frank et al. 1994). Least squares regressions were used to examine relationships of potential microbial respiration with soil C content, potential net N mineralization with soil N content, and potential rates of microbial respiration and net N mineralization with week of incubation. One-way analysis of variance (ANOVA) was used to examine shrub effects on plant biomass and soil properties in each shrub–grassland plot. Throughout the paper, $\alpha = 0.10$ is used for statistical significance. N mineralization and C respiration are expressed on a mass of dry soil and per unit area basis.

RESULTS

Soil properties and plant abundance

Soil and plant properties varied markedly among sites, reflecting a combination of topographic position and climatic effects (Table 1). Slope-bottom sites, M1 and L1, had higher soil moisture, N, C, and plant biomass and lower soil bulk density than the hilltop and

slope sites S2, M2, B, L2. Climatic influences were exhibited at Stevens Creek sites S1 and S2, on average the warmest and driest of our study sites, which had the lowest soil N and C, and plant biomass levels; although note that soil moisture at S1 and S2 during this particular year of study was comparable to that of other slope and hilltop sites (Table 1). The variation among sites was substantial, ranging by an order of magnitude for total plant biomass and soil C and N content, and by a factor of 4 for average soil moisture during the snow-free year. This reflects the wide spectrum of sites we examined in the study. Correlation analyses among grassland soils ($n = 14$, omitting soils under shrubs in shrub–grassland plots) revealed positive relationships between (1) pH and clay ($r = 0.65$, $P = 0.01$); (2) moisture and N ($r = 0.84$, $P < 0.001$), C ($r = 0.90$, $P < 0.001$), and shoot biomass ($r = 0.89$, $P < 0.001$); (3) percent N and C ($r = 0.93$, $P < 0.001$), shoot biomass ($r = 0.84$, $P < 0.001$), and combined shoot and 0–10 cm root biomass ($r = 0.57$, $P < 0.033$); and (4) soil C and shoot biomass ($r = 0.94$, $P < 0.001$). There was a surprising lack of correlation between soil C and the sum of root and shoot biomass, the sources of C to that interval of soil.

Grazers had no effect on any grassland soil or plant variable, with the exception that ungulates lowered the average gravimetric soil moisture (paired *t* test omitting shrub microsites in shrub–grassland plots, $P < 0.056$).

Aboveground plant biomass was greater in shrub than grassland patches in each of the four shrub–grassland plots (Table 1). Root biomass (0–10 cm) was lower under shrubs than in open grass areas at S1; similar nonsignificant trends were found at the other three shrub–grassland plots. The combination of positive and negative shrub effects on above- and belowground biomass, respectively, led to a significant difference in total plant (shoot and root) biomass at only one plot (M2, fenced). Soil moisture was higher under shrubs than under grasses at three of four plots (Table 1).

In situ net N mineralization

Net N mineralization ranged widely during the study, from 0 at ungrazed plots in June (S1, L1) and August (M1) to $1.2 \mu\text{g N} \cdot (\text{g soil})^{-1} \cdot \text{d}^{-1}$ in grazed grassland at M1 in July (Table 2). Ungulates increased net N mineralization in grassland soil (shrub microsites omitted) in May by 450%, in June by 75%, and in July by 72% (Fig. 2).

The presence of shrubs had variable effects on mineralization rates. In fenced shrub–grassland plots S1 and L1, net mineralization during some intervals was greater under shrubs than in grassland openings, while the opposite occurred during incubation intervals at grazed M2 (Table 2). Over the 12-mo study, shrubs reduced and increased annual mineralization at grazed M2 and ungrazed L1, respectively, and had no effect on mineralization at S1 and ungrazed M2 (Fig. 3).

Whole-plot annual mineralization (including shrub

TABLE 1. Soil properties and plant abundance (mean, one standard error in parentheses) at study sites in Yellowstone National Park.

Site	Treatment	pH	Bulk density (g/cm ³)	Gravimetric moisture [‡] , § (%)	USDA texture categories (%)			N (%)	C (%)	C/N [§]	Plant biomass (g/m ²) [§]		
					Sand	Silt	Clay				Shoot	Root	Total
S1	Fenced, grass	7.0	1.2	13.5	47.0	28.1	24.9	0.13 (0.01)	1.5 (0.1)	11.1 (0.4)	47 (15)*	364 (101)†	411 (100)
	Fenced, shrub	7.1	1.0	13.5	31.5	39.2	29.3	0.13 (0.01)	1.4 (0.1)	10.7 (0.1)	254 (61)	133 (21)	387 (76)
	Grazed	7.1	1.2	11.2	43.8	27.0	29.2	0.13 (0.01)	1.3 (0.2)	10.7 (0.3)	52 (6)	47 (5)	99 (7)
S2	Fenced	7.3	1.3	13.7	50.0	21.1	28.9	0.09 (0.01)	1.0 (0.1)	10.9 (0.4)	35 (6)	71 (39)	106 (40)
	Grazed	7.2	1.3	11.0	55.8	17.6	26.6	0.09 (0.01)	1.0 (0.1)	11.0 (0.5)	30 (5)	113 (48)	143 (52)
M1	Fenced	7.9	0.75	45.7	35.1	34.1	30.8	0.86 (0.03)	16.2 (0.7)	18.9 (0.8)	293 (34)	250 (90)	543 (97)
	Grazed	7.8	0.77	43.2	32.1	37.8	30.1	0.79 (0.04)	15.0 (0.7)	19.2 (1.0)	293 (34)	285 (50)	578 (60)
M2	Fenced, grass	6.5	1.1	14.3*	46.5	35.9	17.6	0.34 (0.01)	3.8 (0.2)	11.1 (0.2)	41 (3)*	275 (73)	316 (75)†
	Fenced, shrub	6.7	1.2	15.3	36.0	59.0	5.0	0.33 (0.02)	4.0 (0.3)	12.1 (0.5)	269 (36)	260 (80)	529 (73)
	Grazed, grass	6.3	1.1	14.5*	44.6	36.8	18.6	0.38 (0.02)	4.3 (0.3)	11.2 (0.3)	75 (8)*	483 (233)	558 (237)
	Grazed, shrub	6.2	1.1	15.2	44.4	35.2	20.4	0.37 (0.02)	4.3 (0.3)	11.6 (0.2)	258 (54)	302 (64)	560 (81)
B	Fenced	6.7	1.2	12.0	45.5	38.4	16.1	0.27 (0.01)	3.0 (0.1)	10.9 (1.1)	78 (6)	605 (121)	683 (122)
	Grazed	6.7	1.2	12.3	44.7	39.2	16.1	0.29 (0.01)	3.3 (0.2)	11.2 (0.3)	55 (8)	907 (239)	962 (236)
L1	Fenced, grass	6.6	0.9	26.5*	35.0	41.7	23.3	0.95 (0.03)	10.7 (0.4)	11.2 (0.1)	140 (6)*	609 (130)	749 (133)
	Fenced, shrub	6.8	1.1	28.5	32.0	46.9	21.1	1.07 (0.06)	11.8 (0.7)	11.1 (0.1)	374 (47)	51 (112)	725 (47)
	Grazed	6.8	0.9	26.7	33.5	42.3	24.2	0.82 (0.04)	9.4 (0.5)	11.5 (0.2)	238 (24)	1147 (276)	1385 (268)
L2	Fenced	7.6	1.3	13.5	45.5	34.8	19.7	0.25 (0.02)	3.3 (0.2)	14.3 (1.5)	70 (17)	445 (124)	515 (131)
	Grazed	7.7	1.4	11.5	48.5	28.2	23.3	0.17 (0.08)	3.0 (0.2)	18.4 (1.6)	59 (11)	307 (102)	366 (99)

Note: Data for pH, bulk density, and texture values for grassland soils, except S1, have appeared previously (Frank and Evans 1997).

* $P < 0.05$; † $0.05 < P \leq 0.10$.

‡ Gravimetric moisture measurements are annual averages calculated from "initial" in situ incubation samples.

§ Values that are statistically different between shrub and grassland patches are in bold.

patches in shrub-grassland plots) was $1.8 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ greater in grazed vs. ungrazed plots, which was equivalent to a twofold herbivore-induced increase (Fig. 4). This average effect of ungulates approached the range of rates measured among ungrazed plots ($2.2 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), reflecting the maximum landscape effect (due to variation in topographic position and climate) observed in the study. Herbivore promotion of mineralization varied substantially among the sites, ranging by $4.9 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ ($0.6\text{--}5.5 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$). This was more than twice the range of values measured among fenced plots, which contributed to the greater between-site variation among grazed ($1 \text{ SD} = 2.2$) vs. ungrazed habitat ($1 \text{ SD} = 0.85$).

Potential rates of microbial respiration and net N mineralization

Temporal patterns during the laboratory incubation.—Potential microbial respiration declined for soil of each site (Fig. 5, top), displaying a sharply decreasing curvilinear relationship with week of incubation among plots (Fig. 6a). Extrapolating the best fit line

for all plots to the beginning of the incubation, daily respiration declined from $12.3 \text{ mg C/g soil C}$ at day 1 to $2.3 \text{ mg C/g soil C}$ at day 14 (week 2) to $1.2 \text{ mg C/g soil C}$ at day 42 (week 6). The steep initial reduction reflects the rapid exhaustion of relatively labile soil C that microbes utilize quickly, leaving more recalcitrant forms of C. Variation in respiration, measured as one standard deviation, was much greater early in the incubation (week 2, $1 \text{ SD} = 1.79 \text{ mg}$) compared to later in the incubation (week 28, $1 \text{ SD} = 0.44 \text{ mg}$) (Fig. 6a). This suggests higher spatial variability in labile compared to recalcitrant soil C across this grassland ecosystem. When considering variation relative to the mean, however, coefficient of variation (cv) was similar in week 2 ($\text{cv} = 0.58$) and week 28 ($\text{cv} = 0.65$).

In contrast to the monotonic declines observed for respiration at each of the sites, daily net N mineralization exhibited an initial increase during the second and third sample periods at many of the sites, before declining (Fig. 5, bottom). Potential net N mineralization was negatively and linearly related to week of incubation among sites (Fig. 6b). Variation in potential

TABLE 2. Mean daily in situ net N mineralization rates, in $\text{ng N} \cdot (\text{g soil})^{-1} \cdot \text{d}^{-1}$ (one standard error in parentheses).

Site	Treatment	Sampling dates					
		May	June	July	August	September–March	April
S1	Fenced, grass	116 (70)	0*	8 (3)†	59 (20)	23 (6)	87 (40)
	Fenced, shrub	17 (9)	42 (14)	74 (34)	30 (8)	25 (9)	37 (21)
	Grazed	352 (120)	26 (20)	24 (10)	9 (9)	15 (3)	93 (27)
S2	Fenced	41 (8)	2 (2)	2 (1)	20 (13)	12 (2)	42 (19)
	Grazed	168 (79)	12 (11)	21 (8)	4 (2)	41 (14)	68 (32)
M1	Fenced	44 (24)	243 (229)	601 (336)	0	8 (5)	118 (55)
	Grazed	414 (259)	718 (327)	1217 (734)	346 (335)	78 (58)	132 (46)
M2	Fenced, grass	112 (61)	383 (94)	96 (27)	41 (15)	12 (5)	51 (31)
	Fenced, shrub	504 (304)	523 (446)	143 (58)	25 (8)	28 (1)	52 (22)
	Grazed, grass	345 (136)*	300 (91)†	161 (34)	33 (11)	11 (2)	104 (38)
	Grazed, shrub	28 (17)	106 (27)	181 (31)	48 (12)	8 (1)	52 (15)
B	Fenced	49 (21)	139 (66)	239 (60)	42 (11)	21 (5)	108 (37)
	Grazed	237 (25)	165 (31)	306 (58)	39 (19)	89 (53)	48 (21)
L1	Fenced, grass	16 (16)	0	31 (18)	148 (68)	7 (2)*	28 (16)
	Fenced, shrub	120 (80)	189 (139)	182 (156)	185 (132)	21 (6)	22 (12)
	Grazed	306 (280)	116 (54)	8 (5)	22 (1)	6 (2)	9 (7)
L2	Fenced	17 (13)	94 (41)	84 (37)	28 (20)	25 (5)	50 (27)
	Grazed	75 (29)	167 (84)	97 (24)	52 (30)	32 (6)	42 (12)

Note: Values that are statistically different between shrub and grassland patches are in bold.

* $P < 0.05$; † $0.05 < P \leq 0.10$.

net N mineralization, measured as 1 SD and CV, was much greater early (week 2: 1 SD = 0.50 mg, CV = 1.16) compared to later (week 62: 1 SD = 0.04 mg, CV = 0.14) in the incubation.

Landscape effects.—Cumulative (28 wk) respiration increased with soil C content (Fig. 7a), an edaphic property under topographic position and climatic control in this ecosystem. However, the percentage of total

carbon that was respired was negatively related with soil C (Fig. 7b). Notice that in the latter relationship, 80% of the variation in respiration occurred among sites with soil C contents of <5%.

In a similar fashion, cumulative net N mineralization during the incubation (62 wk) was positively related to soil N content (Fig. 7c), another soil property closely associated with topographic position and climate, while

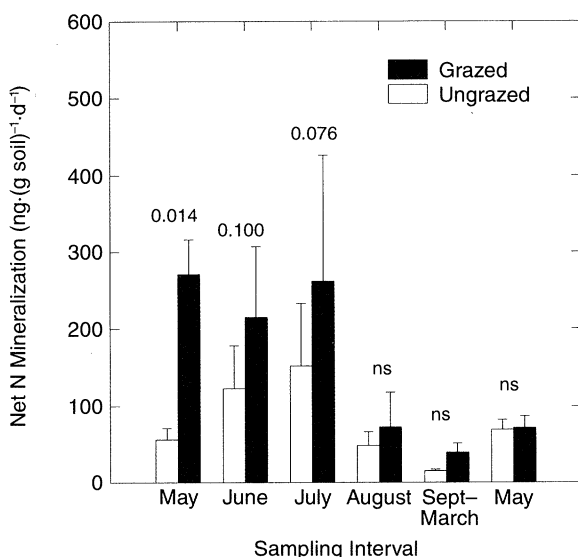


FIG. 2. Mean net N mineralization in grassland soil (omitting soil under shrubs) during each of the in situ incubations. Bars represent + 1 standard error. The probabilities resulting from paired t tests ($df = 6$) are indicated above bars; “ns” denotes no significance ($\alpha = 0.10$).

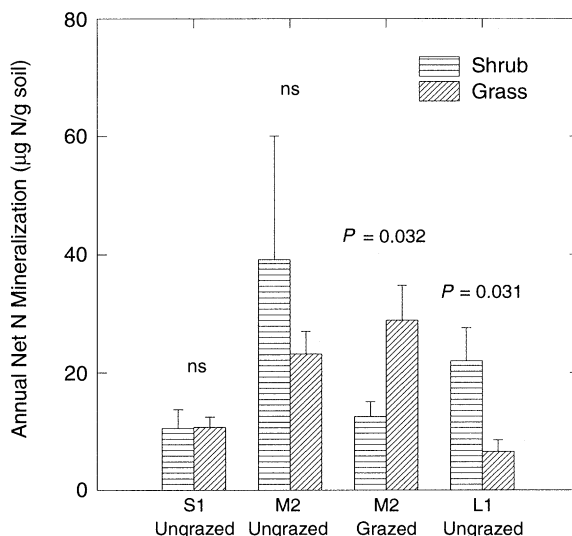


FIG. 3. Annual net N mineralization under and between shrubs at four shrub/grassland plots. Bars denote + 1 standard error. Probabilities resulting from one-way ANOVAs ($df = 1,8$) are indicated above the bars; “ns” denotes no significance ($\alpha = 0.10$).

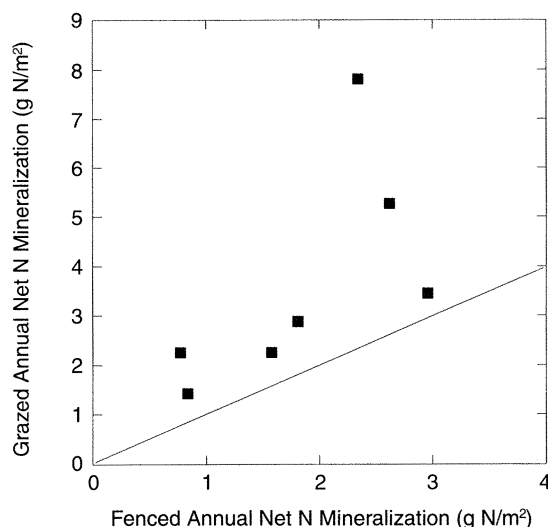


FIG. 4. The relationship between grazed and fenced "whole-plot" annual net N mineralization. Diagonal line denotes equality.

percent soil N mineralized during the experiment was negatively related to soil N (Fig. 7d). Most (71%) of the dynamics in percent N turnover were observed among soils with $\leq 0.4\%$ soil N (Fig. 7d).

Grazer effects.—Herbivores had a significant but variable impact on potential microbial respiration. Paired *t* tests conducted on daily rates for each time point during the incubation revealed that herbivores enhanced potential respiration (Fig. 8a) and N mineralization (Fig. 8b) early in the incubation when labile material was processed by microbes, and reduced rates late in the incubation when substrates were more recalcitrant. These results indicate that grazers altered the quality of soil organic matter, increasing the labile fraction and decreasing the more recalcitrant fraction of soil.

Microbial immobilization.—The ratio of C respiration: net N mineralization can be used as an index of microbial N immobilization (Schimel 1986, Burke et al. 1989, Holland and Detling 1990, Ruess and Seagle 1994). This ratio was positively associated with soil C content among sites throughout the incubation (each timepoint, $P < 0.01$). Grazers had an effect on immobilization only during the first 2 wk, reducing it by an average of 71 mg C respired/mg N mineralized, or 21% (paired $t = 2.8$, $df = 6$, $P = 0.032$) (Fig. 9). During this same period, the largest landscape effect measured, i.e., range among fenced plots, was much more dramatic; immobilization varied by 920 mg C respired/mg N mineralized among ungrazed grasslands.

DISCUSSION

Although large herbivores are well known to influence soil processes (Woodmansee 1978, Risser and Parton 1982, Coppock et al. 1983, Seastedt 1985, Mc-

Naughton et al. 1988, 1997, Seastedt et al. 1988, Huntly 1991, Holland et al. 1992, Shariff et al. 1994), variation in landscape factors, i.e., topographic position and climate, are generally considered the predominant variables affecting soil C and N dynamics in grassland ecosystems (Jenny 1941, Aandahl 1948, Schimel et al. 1985a, b, Burke 1989, Frank et al. 1994). Our results indicate that herbivores can play a larger role in soil dynamics than previously suspected. Despite a fourfold variation in average growing season soil moisture and a >10 -fold variation in soil C and N content among sites, we found that mean grazer enhancement of net N mineralization ($1.9 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) approached the range of rates measured among ungrazed plots ($2.2 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$), the greatest landscape effect observed. This average promotion by herbivores created a twofold increase in N availability to plants across the ecosystem.

The magnitude of ungulate effects on N dynamics varied markedly among sites. This is not surprising, because grazers strongly interact with topographic gradients. Landscape preferences are displayed by numerous large herbivores, including bison (Coppock et al. 1983, Norland et al. 1985), feral horses (Turner and Bratton 1987), eastern grey kangaroos, and wallaroos (Taylor 1984). Herbivores select landscapes according to forage quality (Senft et al. 1987, McNaughton 1990) and quantity (Frank and McNaughton 1992), water availability (Valentine 1947, McNaughton and Georgiadis 1986), and the presence of mineral licks (Jones and Hanson 1985, Tracy and McNaughton 1995). In this study, we found that herbivore promotion of net mineralization in Yellowstone varied from 0.6 to $5.5 \text{ g N} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$. This resulted in considerably higher variation in net mineralization rates among grazed compared to fenced grasslands.

Grazer-induced increases in the spatial heterogeneity of mineral cycling within grassland communities is well documented (Floate 1981, McNaughton 1985, McNaughton et al. 1988, Day and Detling 1990, Jaramillo and Detling 1992, Seagle and McNaughton 1992, Hobbs 1996, Frank and Evans 1997). Nitrogen cycling is accelerated in urine and fecal patches, relative to the rest of the community. Greater N availability to plants growing in urine patches results in greater tissue N and a higher probability that these areas will be regrazed compared to the surrounding community (Day and Detling 1990), and, therefore, a greater likelihood that the patch will receive additional excretory inputs (Hobbs 1996). Our findings for Yellowstone indicate that grazers also can increase heterogeneity of N cycling at a larger spatial scale, the landscape, i.e., among communities.

Nitrogen availability in grasslands is a principal limiting resource of primary production (Vitousek and Howarth 1991) and a major determinant of species composition (Tilman 1988). Consequently, the doubling of N availability by grazers in Yellowstone grassland may be an important contributing factor underlying the pre-

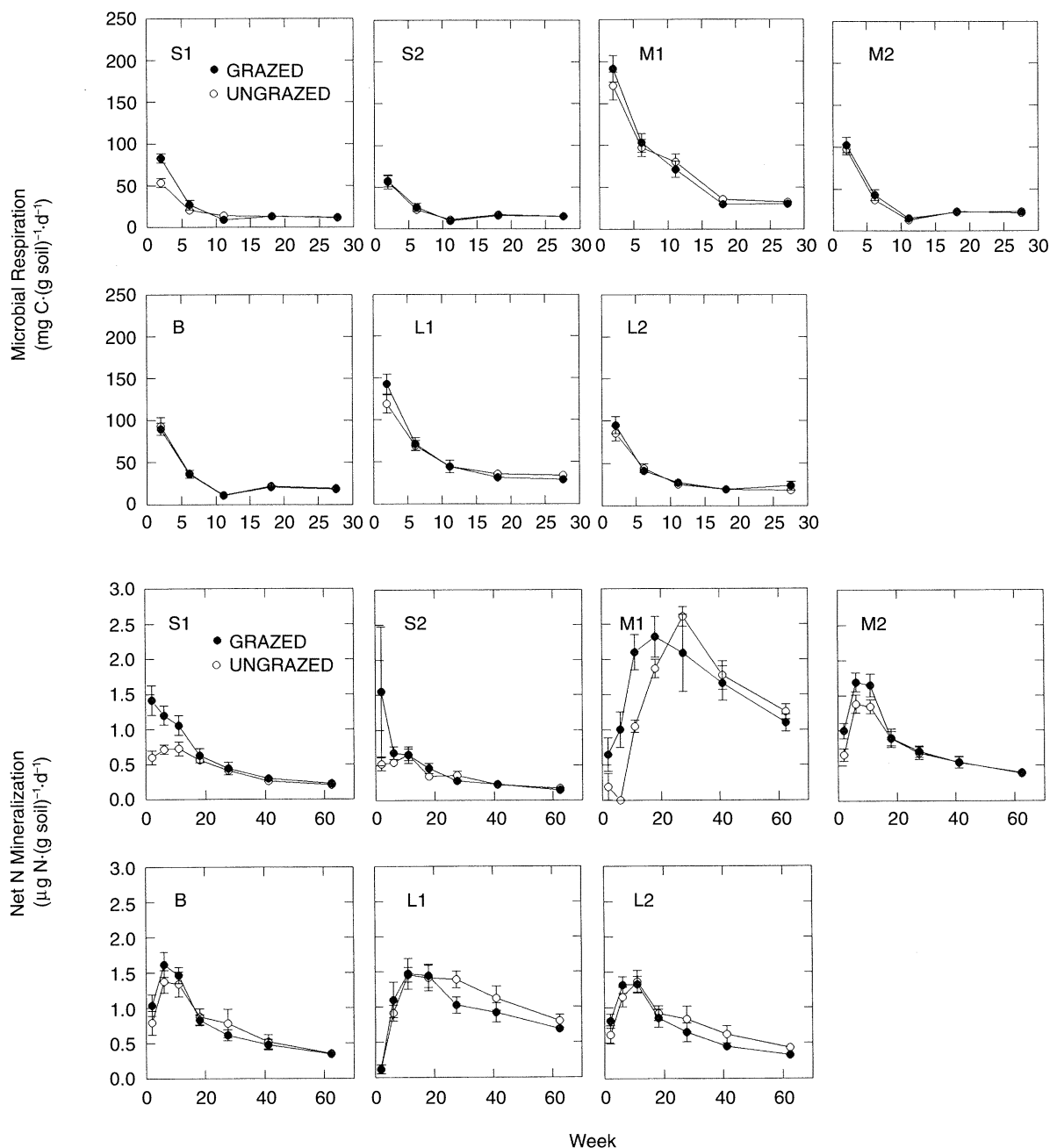


FIG. 5. Potential microbial respiration (top) and net N mineralization (bottom) during the laboratory incubation experiment for grazed and fenced soils collected at each site. Bars are ± 1 standard error.

viously documented promotion of aboveground primary production by ungulates in Yellowstone (Frank and McNaughton 1993). Furthermore, based on our results, grazers should increase between-site variation in primary productivity and species composition in this ecosystem.

Mechanisms

We found large variation and intercorrelation among soil chemical and physical characteristics in Yellow-

stone's northern winter range, similar to other grassland ecosystems (Schimel 1985a, b, Burke 1989, Ruess and Seagle 1994). These differences in edaphic properties produce variability in soil microclimate (e.g., Jenny 1941) and resource availability (Table 1, Fig. 7) that interact in complex ways to determine nutrient cycling (Burke 1989). In contrast, ungulates had no influence on any measured soil property, except soil moisture, yet their average impact on soil N cycling was similar to the greatest landscape effect measured in the study.

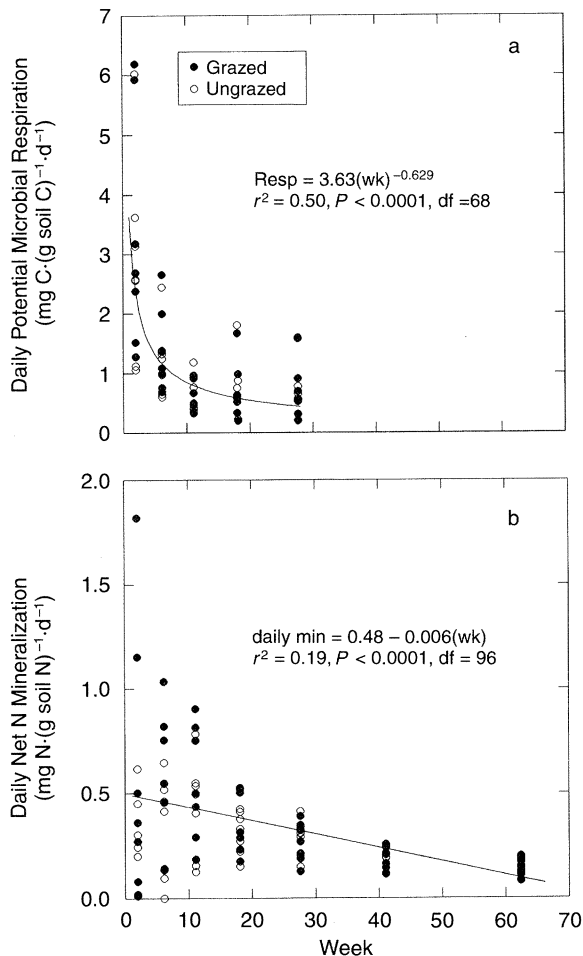


FIG. 6. Relationships between daily rates of potential microbial respiration (a) and net N mineralization (b) on week of incubation. Symbols are plot means.

Large herbivores increase N cycling in grasslands by two related mechanisms. First, the N added by ungulates in excrement is in forms more available to plants and soil microbes than N in the original forage (Floate 1981, McNaughton 1985, McNaughton et al. 1988, Day and Detling 1990, Jaramillo and Detling 1992, Seagle and McNaughton 1992, Hobbs 1996). Second, grazers lower C/N ratios of plant litter, roots, and soil organic matter (Risser and Parton 1982, Coppock et al. 1983, Seastedt 1985, Seastedt et al. 1988, McNaughton et al. 1988, Holland et al. 1992, Shariff et al. 1994). Narrower C/N ratios reduce microbial immobilization of N during decomposition, and, consequently, increase rates of net N mineralization (Holland and Detling 1990, Holland et al. 1992).

Our laboratory incubation findings support the notion that herbivores promote in situ mineralization rates in Yellowstone grassland by improving organic matter quality; labile organic matter was greater and recalcitrant organic matter was less in grazed compared to

fenced, ungrazed soil, respectively (Fig. 8). This herbivore-induced shift in organic matter quality was not reflected in a change in soil C/N ratios, suggesting that the entire-soil C/N ratio may not reliably index the portion of soil that is turned over in the field, or other factors, e.g., lignin content, may be important in controlling turnover rates of grassland soil organic matter (Schimel et al. 1996). Grazers increased net N mineralization by 81% during the first 2 wk of the laboratory incubation, a period that is probably most reflective of in situ processes (Wedin and Pastor 1993). This approaches the level (100%) that herbivores increased rates of in situ mineralization.

Another way in which herbivores may promote soil N cycling is by changing soil temperature and/or moisture regimes. Moisture was not involved in herbivore stimulation of soil N cycling, because grazed soils were drier than fenced soils (Table 1). This could have been a result of a mulching effect from the accumulation of standing dead and litter inside fences (Coughenour 1991; D. Frank, *personal observation*). However, the mulch also may have reduced the rate of soil warming during the spring, which if true, would have lowered microbial activity during that period and contributed to the 4.5-fold greater rate in net N mineralization outside vs. inside exclosures in May of this study (Fig. 2).

Net N mineralization is a result of two simultaneous processes, gross N mineralization and microbial N immobilization. Herbivore stimulation of net N mineralization has been shown to be associated with declines in N immobilization in mixed-grass prairie (Holland and Detling 1990). In this study, grazers lowered the immobilization index, C respired : net N mineralized, by 21% during the first 2 wk of the incubation. This suggests that a reduction in immobilization also played a role in ungulates increasing net N mineralization in Yellowstone grassland.

However, we believe that understanding the variability of in situ net N mineralization in Yellowstone requires interpreting herbivore and landscape effects on gross mineralization, in addition to immobilization. The greatest difference in the C respired/N mineralized ratio among ungrazed plots, i.e., the maximum landscape effect observed in the study, was 13-fold greater than the overall 21% reduction by grazers (Fig. 9). The accumulation of soil C at mesic, slope-bottom sites likely was involved in the markedly higher rates of immobilization measured at those sites relative to dry, hilltop and slope sites. Despite this dramatic difference in the magnitude at which landscape factors and grazers influenced immobilization, average ungulate and maximum landscape influences on in situ net N mineralization rates were similar. Consequently, we hypothesize that differences in net mineralization rates among our sites were primarily controlled by variation in immobilization, and conversely, changes in gross N mineralization were the primary factor behind the grazer

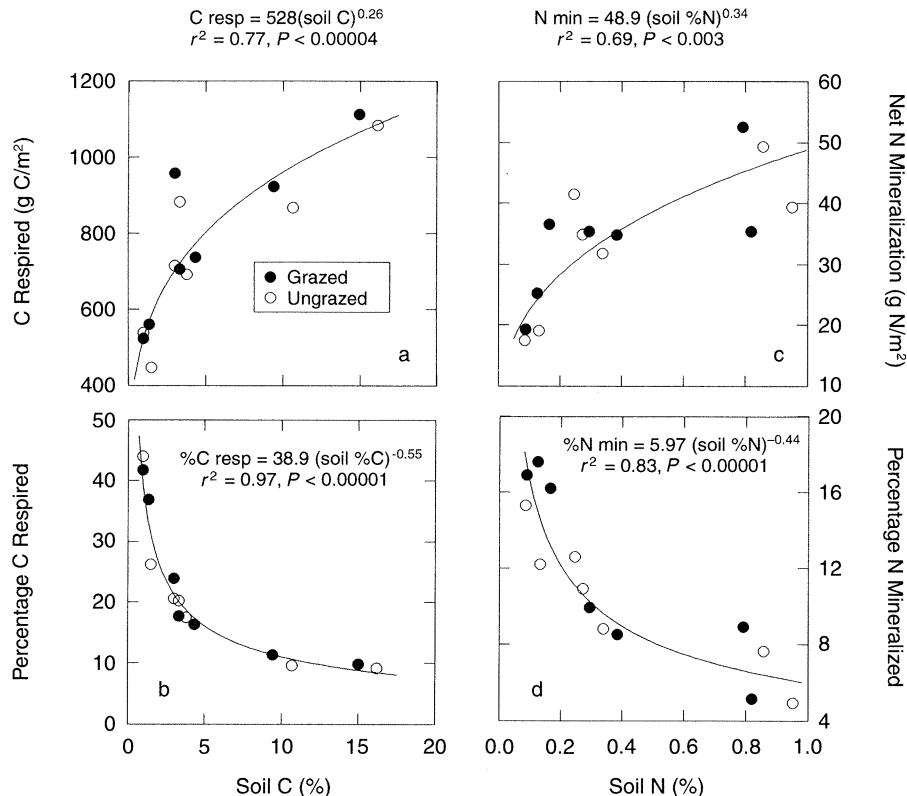


FIG. 7. Relationships between cumulative rates during the incubation and soil elemental content: (a) potential microbial respiration and (b) the percentage of soil C respired vs. soil C content; (c) potential net N mineralization and (d) percentage of soil N mineralized vs. soil N content. Symbols are plot means.

effect, although, as discussed above, herbivores also influenced immobilization. These predictions could be examined with ^{15}N dilution experiments.

In the South Dakota mixed-grass prairie, Holland and colleagues (Holland and Detling 1990, Holland et al. 1992) found, similar to our results for Yellowstone, that bison increased net N mineralization. Parameterizing the CENTURY model (Parton et al. 1987, 1988) with data for bison effects on plant growth and soil C and N dynamics, they showed that bison stimulation of mineralization was primarily due to herbivores reducing microbial immobilization. This was, to a great extent, a consequence of animals lowering soil C/N ratios by indirectly reducing root productivity, and therefore soil C input. Their results indicated that after 25 yr of bison grazing, soil C in this mixed-grass prairie declined by 6–16%, depending on the level of bison grazing and on whether sites on or off prairie dog colonies were modelled. We think it is important to emphasize that after 33–37 yr of exclusion in Yellowstone Park, soil C content did not diverge between grazed and ungrazed grassland, nor did we find that grazers affected soil C/N ratios. This suggests that mechanisms responsible for the grazer increase of net N mineralization in Yellowstone Park are different from those proposed for mixed-grass prairie.

Shrub effects

We also observed plant growth form effects on soils. Shrubs have been shown to increase total and available soil nutrients, microbial biomass, net mineralization, microbial immobilization, and reduce soil surface temperatures in other ecosystems (Charley and West 1977, Lajtha and Schlesinger 1986, Klopatek 1987, Burke et al. 1989, Schlesinger et al. 1990). We found that soil moisture was higher below shrubs than in grassland interspaces at three of the four shrub–grassland plots (Table 1). Furthermore, in two shrub–grassland plots, annual net N mineralization was significantly different under shrubs, compared with the grassland interspaces—greater under shrubs at L1 and lower under shrubs at M2, grazed (Fig. 3). It is unclear why shrubs differentially affected N mineralization at these plots, but in as much as shrub species were different, the answer may lie in variation in the quality of litter produced by the plants. Unlike studies that have documented greater accumulations of soil C and/or N in shrub relative to grassland patches (Burke 1989, Schlesinger et al. 1990), we found that soil C and N did not differ under the two types of vegetation. Together then, these results indicate that the effects of shrubs on mineral cycling may vary among grasslands and not always increase

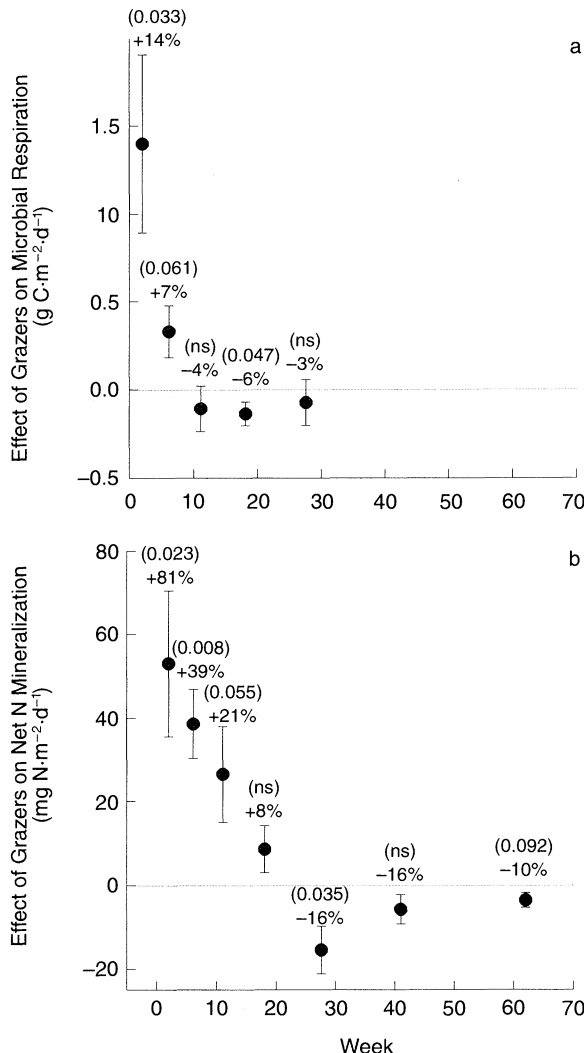


FIG. 8. Herbivore effects on organic matter quality. Average differences ($n = 7$) between grazed and fenced rates of potential microbial respiration (a) and potential net N mineralization (b) at time points during the lab incubation. Values above zero represent grazer enhancement, and values below zero, grazer inhibition. Bars denote ± 1 SE. Percent change due to herbivores and probabilities resulting from paired *t* tests (parentheses) are indicated above bars; "ns" denotes no significance ($\alpha = 0.10$).

nutrient pools and flows, as has been indicated by previous work.

Conclusion

Climatic and topographic variation within large grassland ecosystems have profound effects on soil genesis, leading to gradients in a large number of interrelated edaphic properties that are important determinants of nutrient cycling. In contrast, the principal effect of grazers is to change plant litter and soil organic matter quality. In Yellowstone, both (1) landscape factors and (2) herbivores were important con-

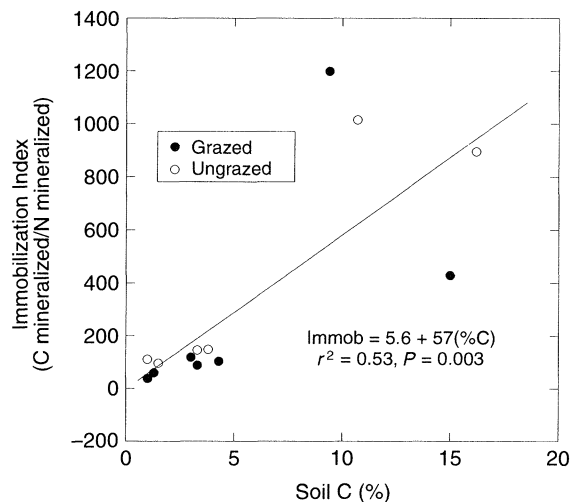


FIG. 9. Relationship between immobilization index, calculated for first 2 wk of incubation, and soil C content.

trols on soil N cycling, although the primary mechanisms underlying their effects probably differed. Our findings suggest that variation in net N mineralization among diverse sites is principally a function of differences in immobilization rates, while effects of grazers on net mineralization may primarily be due to variation in gross mineralization. We found that grazers doubled average net N mineralization and dramatically increased between-site variation of that rate. Gradients of topography and climate are generally considered to be the major determinant of nutrient cycling in grasslands. Our findings indicate that the regulatory influences of herbivores on soil N dynamics may be underestimated, particularly for grasslands supporting large herds of ungulates.

ACKNOWLEDGMENTS

We wish to thank L. Schlenker and Y. Zhang for field assistance. M. Dyer, S. J. McNaughton, and B. F. Tracy kindly commented on an early draft of the paper. We also thank S. J. McNaughton for access to his CN analyzer. This study was funded by NSF grant DEB-9408771.

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