

The biogeochemistry of a north-temperate grassland with native ungulates: Nitrogen dynamics in Yellowstone National Park

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Abstract. Nutrient dynamics of large grassland ecosystems possessing abundant migratory grazers are poorly understood. We examined N cycling on the northern winter range of Yellowstone National Park, home for large herds of free-roaming elk (*Cervus elaphus*) and bison (*Bison bison*). Plant and soil N, net N mineralization, and the deposition of ungulate fecal-N were measured at five sites, a ridgetop, mid-slope bench, steep slope, valley-bottom bench, and riparian area, within a watershed from May, 1991 to April, 1992.

Results indicated similarities between biogeochemical properties of Yellowstone grassland and other grassland ecosystems: (1) landscape position and soil water affected nutrient dynamics, (2) annual mineralization was positively related to soil N content, and (3) the proportion of soil N mineralized during the year was negatively related to soil C/N.

Grazers were a particularly important component of the N budget of this grassland. Estimated rates of N flow from ungulates to the soil ranged from 8.1 to 45.6 kg/ha/yr at the sites (average = 27.0 kg/ha/yr), approximately 4.5 times the amount of N in senescent plants. Rates of nitrogen mineralization for Yellowstone northern range grassland were higher than those measured in other temperate grassland ecosystems, possibly due to grazers promoting N cycling in Yellowstone.

Keywords: grasslands, nitrogen cycling, herbivory, Yellowstone National Park.

Introduction

Nutrient cycling in grasslands reflects a complex web of geologic, biotic, and climatic factors. Aeolian and fluvial processes influence nutrient cycling by creating gradients of soil texture and litter (Malo et al. 1974, Schimel et al. 1985a, 1985b, Burke 1989). At a smaller spatial scale, plant species also affect local nutrient fluxes (Burke 1989, Wedin & Tilman 1990, Hobbie 1992). Interactions of edaphic and vegetative properties with soil microclimate are important determinants of spatial and temporal patterns of nutrient dynamics (Matson and Vitousek 1981, Schimel & Parton 1986, Burke 1989).

Large herbivores also can be an important component of biogeochemical processes in grasslands (Detling 1988, Huntly 1991). Herbivores can facilitate nutrient cycling by trampling and fragmenting plant tissue, by altering soil temperature and moisture conditions (Ruess 1987), by converting low quality plant material into dung and urine in which nutrients are more readily available to soil microbes and plants (Floate 1981, McNaughton 1985, McNaughton et al. 1988), and by stimulating nutrient uptake rates by plant

roots (Ruess et al. 1983, Jaramillo & Detling 1988, Polley & Detling 1988). In addition, herbivores redistribute nutrients in landscapes (Senft et al. 1987, McNaughton 1985, Inouye et al. 1987a, b), alter plant species composition (Houston 1982, McMaughton 1985, Huntly 1991), and increase ammonia loss through volatilization (Woodmansee 1978, Ruess & McNaughton 1988, Schimel et al. 1986). Much attention has been devoted to the biogeochemical cycles of North American grasslands (e.g. Woodmansee et al. 1978, Risser & Parton 1982, Schimel et al. 1985b), including studies of nitrogen cycling on prairie dog (*Cynomys ludovicianus*) colonies grazed by bison (*Bison bison*) in mixed-grass steppe (Holland & Detling 1990, Holland et al. 1992). However, little is known about nutrient dynamics of temperate grassland ecosystems supporting large herds of free-roaming ungulates.

We examined nitrogen dynamics of a grazed watershed in Yellowstone National Park. Large herds of migratory herbivores were common to most of the Earth's vast grassland ecosystems prior to the spread of European influence (McNaughton 1989). Today, Yellowstone National Park represents one of the few remaining settings where abundant native herbivores can migrate unencumbered within a large temperate region. We performed a one-year study of pools and fluxes of nitrogen on a winter range that sustains heavy use by elk (*Cervus elaphus*) and bison for seven months of the year. There were four objectives: (1) to measure N in vegetation and soil, and N availability, including mineralization, at points along a toposequence, (2) to describe spatial and temporal variability of N dynamics and explore how they may be associated with soil properties and soil moisture patterns, (3) to compare the relative magnitudes of selected fluxes, placing the flow through grazers in perspective, and (4) to compare N mineralization rates in Yellowstone with rates reported for other semi-arid grassland and shrub-grassland ecosystems.

Methods

Study area

This study was conducted in the Blacktail Deer Creek drainage located 10.5 km east southeast of Mammoth, Wyoming (110° 42'W, 44° 59'N) on the northern winter range of Yellowstone National Park (Fig. 1). The northern winter range occupies 100,000 ha of rolling shrub-steppe within the Yellowstone and Lamar River drainages (Houston 1982). Roughly 20,000 elk and 400 bison occupy this area from October to May each year, feeding primarily on senescent vegetation during the winter and on young, green vegetation in the spring before migrating to higher elevations (Houston 1982, Meagher 1973, Frank & McNaughton 1992).

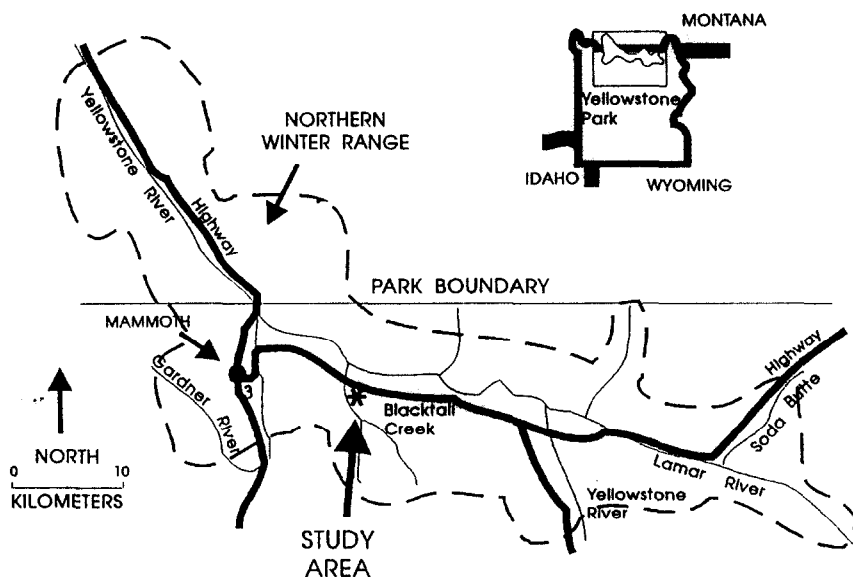


Fig. 1. Location of the study area on the northern winter range of Yellowstone National Park.

Soils of the study area were derived from glacial deposits of andesitic and sedimentary composition laid down in the late-Pleistocene. The climate is cool and dry. The thirty-year (1961–1991) mean precipitation and temperature for Mammoth are 37.9 cm and 4.6 °C (NOAA 1990), respectively. Peak precipitation occurs in May and June, and roughly 35–55% of the annual precipitation falls as rain (Despain 1990).

We measured N pools and fluxes at five topographic positions along a cross section of the Blacktail Deer drainage (Fig. 2). Four of these, ridgetop (RT), upper bench (UB), slope (S), and riparian (R), were located along a west-facing toposequence ending at Blacktail Deer Creek. The fifth, lower bench (LB), was west of Blacktail Deer Creek. The elevational difference between RT and Blacktail Deer Creek was 100 m, and LB was 1.5 m above creek level.

The sites represented a spectrum of plant community types found throughout the winter range (Table 1), with varying growth form compositions (Table 2). UB burned in 1988, leaving a conspicuous patchwork of abundantly vegetated areas (UBV) and areas of sparse plant cover where large sagebrush bushes burned and killed the neighboring vegetation (UBB). We sampled 'bare' and 'vegetated' areas separately and compared N pools and fluxes within UBB and UBV with other sites. We also derived values for UB (whole-plot) from proportions of the plot covered by bare and vegetated patches deter-

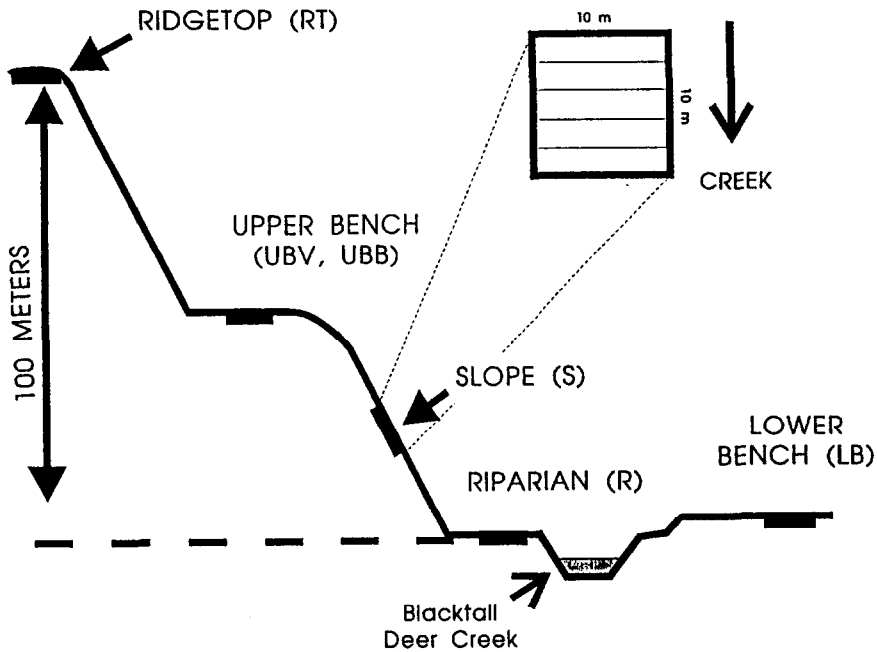


Fig. 2. Position of study sites within the watershed. The small square represents the sample plot at each site. Plant, root, resin bag, and mineralization samples were randomly located within the five 2×10 m segments, with the exception that three 3.3×10 m segments were used for mineralization samples at the Upper Bench.

mined with line transects (UBB = 70%, UBV = 30%). Plant cover at R was predominantly herbaceous with scattered groups of *Salix spp.*, which were browsed during the winter and <1 m in height. All 5 sites were grazed during this study. Elk bedded at RT during both springs.

Plant measurements

A 10×10 m plot was established within a homogeneous stand of the dominant vegetation at each site. Aboveground biomass was clipped to ground level at peak standing crop (July at RT, UB, S, LB, and August at R) and in mid-October within each of five 20×50 cm quadrats. Peak standing crop samples were sorted to species. Samples were stratified within five, 2×10 m areas to disperse measurements within each plot (Fig. 2). Clippings were dried at 65°C for a minimum of 48 hrs and weighed.

Roots were sampled with a 5.5 cm diameter core taken from the center of clipped quadrats at peak standing crop. Root core depth was 15 cm at RT and S, 20 cm at UB and LB, and 30 cm at R. A survey indicated that these

Table 1. Dominant species at study sites. Values in parentheses are percent relative biomasses.

Site	Herbaceous	Shrub
RT	<i>Agropyron spicatum</i> (28) <i>Astragalus miser</i> (18) <i>Poa sandbergii</i> (11) <i>Festuca idahoensis</i> (8)	<i>Chrysothamnus nauseosus</i> (20) <i>Tetradymia canescens</i> (9)
UBV	<i>Stipa occidentalis</i> (36) <i>Stipa viridula</i> (27) <i>Agropyron spicatum</i> (11) <i>Poa</i> sp. (18)	
UBB	<i>Achillea millifolium</i> (55) <i>Poa</i> sp. (14) <i>Chenopodium</i> sp. (10)	
S	<i>Agropyron spicatum</i> (31) <i>Chrysopsis villosa</i> (12) <i>Festuca idahoensis</i> (7)	<i>Artemisia tridentata</i> (29) ssp. <i>vaseyana</i>
R	<i>Phleum pratense</i> (26) <i>Calamagrostis canadensis</i> (19) <i>Aster</i> sp. (7) <i>Poa</i> spp. (7)	<i>Salix</i> spp.*
LB	<i>Festuca idahoensis</i> (33) <i>Stipa richardsonii</i> (26) <i>Agropyron spicatum</i> (15)	

* *S. bebbiana*, *S. geyeriana*, *S. plantifolia* present at R but not sampled.

depths included 82% (LB) to 84% (RT) of the total root biomass at the sites. Therefore, soil was sampled to approximately the equivalent functional depth at each site. Material collected from 0–10 cm and >10 cm depths was bagged separately in the field and air-dried. Roots that did not pass through a 0.5 mm screen were collected, oven-dried as above and weighed. We did not separate dead from live roots.

All plant material was ground with a Wiley Mill to pass through a 0.5 mm mesh. Carbon and N content of two to three replicates of each sample were

Table 2. Percent of peak standing crop biomass represented by major growth forms.

Site	Graminoid	Forb	Shrub
RT	48	23	29
UBV	92	8	–
UBB	22	78	–
S	31	46	23
R*	75	25	–
LB	84	16	–

* Results of line transects indicated 6% of the plot was covered by *Salix* spp.

determined with a Carlo Erba Model 1106 or LECO CHN analyzer using standard protocol.

Soil property determination

Soils were sampled with a 5.5 cm corer at four randomized locations at each site from the same depths that roots were sampled. Bulk density, pH, and percent sand, silt, clay, and field moisture, by volume, were determined using standard techniques (Page et al. 1982). Carbon and N contents of soil were measured as above for plants.

In May, 1991 Blacktail Deer Creek overflowed its bank and flooded the riparian site (R), depositing stream-transported material. We estimated the proportion of the plot covered by surface deposits with ten, 10 m line transects. The depth of deposited material was measured every 1 m along each transect ($n = 100$).

Relative N availability

We measured the relative availability of inorganic N at the sites with ion exchange resin (Binkley & Matson 1983, Binkley et al. 1986). Five nylon-mesh bags filled with two level tablespoons of mixed bed resin (Dowex MR-3, a 1:1 mixture of HCRS[H^+] and SBR[OH^-]) were placed in the soil at a depth of approximately 8–12 cm at each of the sites. Locations of resin bags were stratified in a manner similar to that for plant samples. Sequential incubations were performed to determine seasonal patterns in N availability. Incubation periods were monthly intervals from May to peak standing crop (July at RT, UB, S, and LB, and August at R), peak standing crop to October,

and October to April, 1992. After removal from the soil, resin bags were immediately placed in a cooler on ice. Samples were transported to Pocatello, Idaho, and kept refrigerated until they were washed with distilled water and air-dried within five days of being taken from the soil. Resin was extracted with 1M KCl (1 g resin / 15 ml KCl) and the extract was analyzed for NH_4^+ and NO_3^- with an Alpkem RFA300.

Net N mineralization

Net N mineralization rates were determined using a mineralization tube method (Adams and Attiwill 1986). Galvanized steel tubes, 2.5-cm diameter, were driven into the ground and incubated *in situ* for monthly intervals from June to October, 1991, for a six-month winter period between October, 1991 and April, 1992, and during May, 1992. Steel tubes were required in this study because of the rocky soil at most sites. As has been reported elsewhere (Raison et al. 1987), we found no difference in mineralization rates using steel and polyvinyl chloride tubes ($F_{1,18} = 0.058$, $P = 0.81$).

Five replicate incubations were performed at each site over the year, except at UB where three replicates were used in each of bare (UBB) and vegetated (UBV) areas. Locations for mineralization tubes were stratified in the same way as plant biomass and resin bag samples, with the exception that at UB samples were stratified within three, 3.3×10 m areas. Tube depths for sites were the same as depths of root samples at the four grassland sites (RT, UB, S, LB) and 10 cm at R. Driving 10 tubes below 10 cm at R resulted in soil compaction of up to 60%. For this reason we measured 10–30 cm mineralization rates at R with buried bags (Eno 1960). Intact soil cores were sampled with a 3.5-cm diameter corer, resulting in negligible compaction, and were buried at about 20-cm depth in sealed polyethylene bags. We compared net mineralization rates of 0–10 cm soil determined with buried bags versus mineralization tubes during September, October, November–March, and April incubations, and found no effect of method ($F_{1,35} = 0.002$, $P = 0.967$). Mean net mineralization over the four incubations was 1.4 g/m^2 using buried bags and 1.5 g/m^2 using mineralization tubes.

At the start of each sampling period, soil directly adjacent to each incubation was collected (initials). At the end of a sampling interval, incubated soil (finals) and the initials collected for the next incubation interval were immediately stored on ice in a cooler. Samples were transported to the laboratory within 24 hrs where they were refrigerated until being extracted with 1M KCl within 72 hrs of their collection in the field.

Resin bags were placed within the bottoms of the tubes to collect N leached through the tubes during the incubations. Handling of resin, and extraction and

measurement of NO_3^- and NH_4^+ accumulated on the resin were as described above.

Net nitrification was the difference in nitrate between initial and final samples. Net mineralization equalled the sum of net ammonification and net nitrification. Annual mineralization rates were calculated as the sum over all incubations during the year. The May, 1990 mineralization rate for 0–10 cm soil at R was not measured, but was assumed to equal that for 10–30 cm during that month to derive the annual rate for that site. Mineralization rates were converted to a soil volume basis with average bulk density values. Soil moisture measurements were made gravimetrically on initial and final incubation samples.

Flux of N from grazers to the soil

Elk fecal piles deposited during the 1991–92 winter were counted within each plot in April, 1992. No bison dung was found at the sites. Winter feces were easily distinguished from older feces by color. Counts were converted to fecal mass using the weight of an average oven-dried elk pellet group (92 g; Frank & McNaughton 1992). Percent N of winter and spring elk feces was determined on fresh samples collected on the northern range. Fecal N added to the sites during the winter was calculated by multiplying fecal mass by percent N of feces.

We estimated the annual rate of fecal and urinary N deposited by large ungulates at the sites from dung deposited during the winter, the relationship between winter and spring dung deposition, N content of dung, and allometric relationships for N lost by elk in feces versus urine. Dung mass added in the spring was assumed to be 96% of the winter fecal mass, the relative rate of dung input in the spring compared to that of winter at winter range sites reported elsewhere (Frank & McNaughton 1992). This probably was an underestimate of the amount of spring N deposited at RT, where elk bedded during both springs of the study and fecal deposition was high. The amount of urinary-N deposited at the sites was calculated using allometric relationships between N lost by elk in urine versus feces when fed low quality feed (%N of dry matter = 0.90–1.2%; $n = 3$), used to simulate winter forage, and high quality feed (%N of dry matter = 2.7–4.7%, $n = 3$), used to simulate spring forage (Mould & Robbins 1981, Robbins pers comm). Ratios for urinary-N/fecal-N were 1.0 in the winter and 3.33 in the spring.

Data analysis

We used an analysis of variance (ANOVA), blocked by site and split by date and depth, to analyze soil moisture, N levels of initials, and N mineralization

data (SAS 1988). We also examined the effect of soil moisture on mineralization with an analysis of covariance using soil moisture as the covariate and site and depth as treatments. Nitrogen eluted from resin bags buried in the soil was analyzed with an ANOVA blocked by site and split by sample date. Data were appropriately transformed as needed to satisfy assumptions of parametric tests.

Results

Vegetation

Aboveground, belowground, and total plant biomass and N ranged three to six-fold among sites, with the highest pools generally occurring at R (Table 3). Roots constituted the preponderance of plant biomass at all sites.

Soils

Soils were loams, except at R, which was a sandy loam. All soils were mildly acidic (Table 4). Percent C, percent N, and C/N values were consistently higher, and bulk density was consistently lower, for 0–10 cm soil compared to deeper soil.

One hundred percent of R was covered by stream-transported material as a result of the May, 1991 flood. Average depth of the sediment was 5.1 cm (SD = 3.3).

Soil moisture was highest during the spring (May, 1991, and April, 1992; Fig. 3a). There was a spike in soil moisture at all sites in September, 1991, which reflected high rainfall during August. The wet August incubation was preceded and followed by dry periods. R had the highest soil moisture of any site for each date ($P < 0.05$, Scheffe). Seventy-two percent of the variation in soil moisture during the study was explained by site ($F_{5,16} = 285$, $P < 0.0001$) and sample date ($F_{5,186} = 254$, $P < 0.0001$). An additional 9% of the variation was explained by an interaction between site and date ($F_{25,186} = 12$, $P < 0.0001$).

Resin bags

The daily adsorption of N to resin was highest in the spring (RT, UBB, S, R, LB; Fig. 3d) or the early summer (UBV), and was negligible during the late-summer, autumn, and winter, except at UBV and UBB in the winter. Although daily winter N adsorption was low, net accumulation over the six-month incubation was substantial at some sites. The percentage of annual N adsorbed to resin during the winter ranged from 5% at LB to 60% at UBB,

Table 3. Aboveground, belowground, and total plant biomass and N (g/m^2 , mean \pm SE), and root:shoot biomass ratios at peak aboveground standing crop. P values are results from Oneway ANOVAs comparing sites. NS denotes nonsignificance ($\alpha = 0.5$). Values with the same letters are not significantly different (Scheffe Test, $\alpha = 0.05$).

	Aboveground		Belowground		Total		Root: Shoot	
	Biomass	N	Biomass	N	Biomass	N	Biomass	Biomass
RT	75 \pm 15 ^A	1.5 \pm 0.31 ^A	1324 \pm 226 ^{AB}	7.2 \pm 0.9	1399	8.7	17.7	17.7
UBV	256 \pm 49 ^{BC}	5.6 \pm 0.94 ^C	2275 \pm 714 ^{AB}	6.9 \pm 3.7	2531	12.5	8.9	8.9
UBB	69 \pm 15 ^A	1.5 \pm 0.35 ^A	1303 \pm 146 ^A	3.3 \pm 1.2	1372	4.8	18.9	18.9
S	138 \pm 25 ^{AB}	2.5 \pm 0.48 ^{AB}	1607 \pm 147 ^{AB}	3.5 \pm 0.2	1745	6.0	11.6	11.6
R	310 \pm 31 ^C	4.8 \pm 0.78 ^{BC}	3911 \pm 957 ^B	10.3 \pm 3.6	4221	15.1	12.6	12.6
LB	65 \pm 11 ^A	1.0 \pm 0.17 ^A	2120 \pm 234 ^{AB}	6.8 \pm 1.2	2185	7.8	32.6	32.6
<P	0.0001	0.0001	0.04	NS	-	-	-	-

Table 4. Soil properties (mean \pm ISE). Statistical results as Table 3.

Site	Depth (cm)	pH* _w	Percent							CN
			Bulk density (g/cm ³)	Field capacity	Sand	Silt	Clay	C	N	
RT	0-10	6.2 \pm 0.1	0.98 \pm 0.05	25 \pm 1	45 \pm 1	38 \pm 1	17 \pm 1	2.3 \pm 0.1	0.25 \pm 0.01 ^{AB}	9.0 ^A
	10-15	6.4 \pm 0.1 ^B	1.08 \pm 0.03	23 \pm 1	44 \pm 2	32 \pm 1	24 \pm 1 ^B	1.2 \pm 0.1	<0.1	>12.0
UBV	0-10	6.2 \pm 0.1	0.93 \pm 0.14	44 \pm 8	48 \pm 2	36 \pm 4	16 \pm 2	5.9 \pm 0.5	0.52 \pm 0.04 ^B	11.3 ^A
	10-20	6.0 \pm 0.1 ^{AB}	1.07 \pm 0.01	24 \pm 1	44 \pm 6	34 \pm 4	22 \pm 2 ^{AB}	3.5 \pm 0.1	<0.1	>35.0
UBB	0-10	6.2 \pm 0.1	1.04 \pm 0.03	26 \pm 1	38 \pm 1	45 \pm 2	17 \pm 1	2.9 \pm 0.1	0.29 \pm 0.01 ^{AB}	9.8 ^A
	10-20	5.9 \pm 0.1 ^{AB}	1.03 \pm 0.01	24 \pm 2	42 \pm 2	36 \pm 3	22 \pm 1 ^{AB}	3.5 \pm 1.2	<0.1	>35.0
S	0-10	6.2 \pm 0.2	0.96 \pm 0.06	28 \pm 4	51 \pm 2	31 \pm 1	17 \pm 1	2.8 \pm 0.3	0.27 \pm 0.03 ^{AB}	10.3 ^A
	10-15	6.3 \pm 0.1 ^{AB}	1.03 \pm 0.05	28 \pm 2	47 \pm 2	32 \pm 2	22 \pm 1 ^{AB}	2.4 \pm 0.5	<0.1	>24.0
R	0-10	6.1 \pm 0.1	0.95 \pm 0.08	30 \pm 4	57 \pm 8	28 \pm 7	15 \pm 1	3.1 \pm 0.7	0.19 \pm 0.05 ^A	18.4 ^B
	10-30	5.9 \pm 0.1 ^A	1.03 \pm 0.01	26 \pm 2	55 \pm 3	28 \pm 2	17 \pm 1 ^A	3.5 \pm 0.4	<0.1	>35.0
LB	0-10	5.8 \pm 0.1	0.77 \pm 0.08	42 \pm 8	50 \pm 3	36 \pm 2	14 \pm 2	5.5 \pm 1.3	0.48 \pm 0.08 ^B	11.0 ^A
	10-20	5.7 \pm 0.1	1.05 \pm 0.04	25 \pm 2	45 \pm 1	33 \pm 2	22 \pm 1 ^{AB}	2.4 \pm 0.4	<0.1	>24.0
<P	0-10	NS	NS	NS	NS	NS	NS	0.013	0.001	0.001
	>10	0.003	NS	NS	NS	NS	0.02	0.08	-	-

* pH of water slurry (Paige et al. 1982)

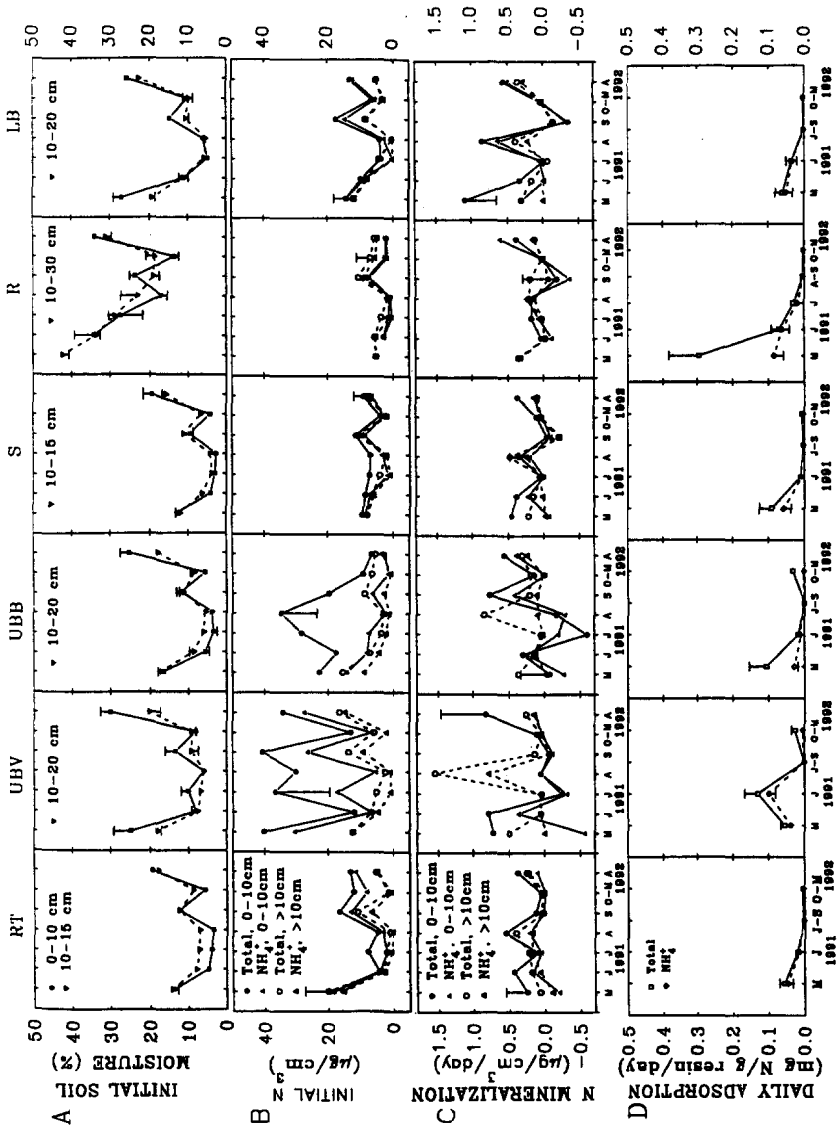


Fig. 3. (a) Soil moisture, (b) standing N pool of initials, (c) rates of N mineralization and (d) N adsorption to resin at the sites. Bars denote SE. Only the maximum SE is provided for each site in (b) and (c).

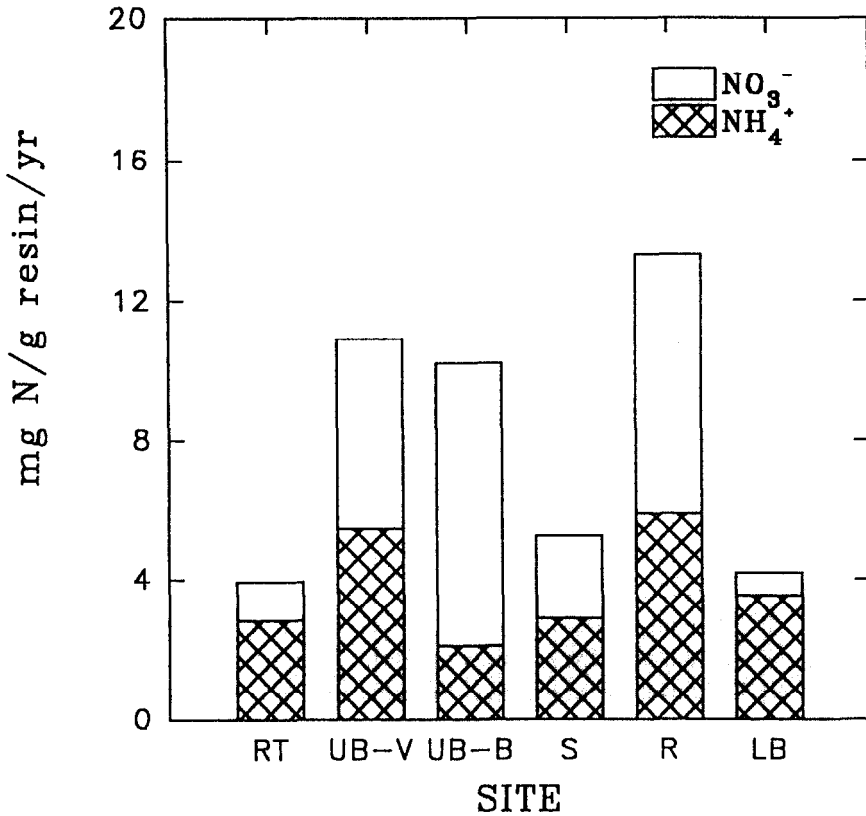


Fig. 4. Annual amounts of inorganic N accumulated to resin at the sites.

and averaged 32% across all sites. Daily N adsorption was affected by site ($F_{5,16} = 83.6$, $P < 0.0001$) and date ($F_{3,48} = 7.6$, $P < 0.005$), and there was a significant site-by-date interaction ($F_{15,48} = 6.7$, $P < 0.0001$). NH_4^+ was the dominant form adsorbed during most intervals.

N accumulated on resin varied three-fold among sites (Fig. 4). The composition of the forms of N (NH_4^+ , NO_3^-) adsorbed also differed among sites.

Pool N (Initials)

Inorganic N pools at most sites were highest when soils were wet, during the spring months, and in September, 1991, after a wet August (Fig. 3b). UB-V and UBB were exceptions. NH_4^+ generally was the dominant form. Inorganic-N was more abundant in the 0–10 cm depth, except at R, where 10–30 cm soil consistently had larger N pools. Twenty-seven percent of the variation in soil pool N was due to site ($F_{5,16} = 8.0$, $P < 0.0001$) and depth ($F_{1,20} = 42.2$, $P <$

0.0001). Interactions of site and depth ($F_{5,20} = 9.3$, $P < 0.0001$), site and date ($F_{25,186} = 1.82$, $P < 0.02$), and site, date, and depth ($F_{25,186} = 1.73$, $P < 0.03$) explained an additional 17% of the variation.

Mineralization

Nitrogen leached from tubes

Nitrogen accumulated on resin placed at the bottom of tubes during incubations was 2–6% of the total N mineralized in the tubes at the upland sites (RT, UBV, UBB, S, LB). NH_4^+ represented 49–78% of the N adsorbed to resin at these sites. Since NH_4^+ is less mobile in the soil than NO_3^- , we expected higher proportions of NO_3^- adsorption if resin was sampling N leaching through the tubes. The large relative amount of NH_4^+ adsorption suggested that resin was not primarily accumulating inorganic N leached from upper levels in the tube, but was sampling soil it was in contact with. At R, resin adsorbed 6.0 times the amount mineralized in the tubes, likely due to resin sampling saturated soil below the mineralization tube. Since including N accumulated to resin at R would have led to inflated values for N mineralized in tubes, we derived mineralization rates only from soil extractable N for all sites. This should not have resulted in significant error in estimating mineralization rates.

Net N mineralization

Daily mineralization rates were high in spring and August at each of the sites. Mineralization during these periods was greater in 0–10 cm soil compared to deeper soil, except at UBB, UBV, and S in August (Fig. 3c). Immobilization occurred at each site, except RT, for at least one incubation, usually during dry periods. Net N mineralization varied among dates ($F_{5,192} = 19.6$, $P < 0.0001$), sites ($F_{5,18} = 3.38$, $P = 0.006$), and there were interactions between site and depth ($F_{5,192} = 7.3$, $P < 0.0001$) and site, date, and depth ($F_{25,192} = 3.07$, $P < 0.0001$), which together explained 37% of the variation (Fig. 3c).

To separate the effects of soil moisture from those of site and soil depth, we analyzed the daily rates of N mineralization during the growing season (excluding the winter incubation) with an analysis of covariance (ANCOVA), using soil moisture as the covariate and site and depth as treatments. Soil moisture and site explained 13% ($F_{1,59} = 9.3$, $P < 0.0035$) and 15% ($F_{5,59} = 2.1$, $P < 0.08$) of the variation, respectively. Depth was not significant. The modest amount of variation in mineralization explained by soil moisture was surprising given the high rates of N mineralization in the watershed during spring and August when the soils were wet and the low rates during intervals when soils were dry (Fig. 5). The analysis may have underestimated the effect of soil moisture on N mineralization, because soil moisture values were

Table 5. Annual net mineralization and nitrification at sites. Units are $\mu\text{g}/\text{cm}^3/\text{yr}$.

Site	By depth			Percent soil N mineralized	Across depth
	Depth	NO_3^-	Total-N		Total-N
RT	0–10	48	62	2.52	55
	10–15	18	42	–	
UBV	0–10	78	80	1.65	83
	10–20	48	85	–	
UBB	0–10	27	45	1.49	69
	10–20	56	89	–	
S	0–10	44	64	2.47	54
	10–15	22	33	–	
R	0–10	19	27	1.49	27
	10–30	13	27	–	
LB	0–10	39	82	2.22	58
	10–20	18	34	–	

taken from initial measurements, which did not always accurately reflect the average soil conditions during incubations, i.e. wet August and dry September incubations.

Annual net mineralization varied by approximately 3-fold among sites for both soil depths (Table 5). Net mineralization rates were higher for 0–10 cm soil than >10 cm soil at all sites, except UBV and UBB. Since mineralization tubes were not capped, inorganic N may have leached below 10 cm during the incubations. Therefore, N transformation rates for 0–10 cm may be underestimates, and those for >10 cm may be overestimates. Annual net mineralization over the entire soil profile sampled ranged from 27–83 $\mu\text{g}/\text{cm}^3$ (Table 5).

The proportion of annual N mineralization that occurred during the wet August incubation ranged from 0% at UBB to 33% at LB for 0–10 cm; and 22% at R to 58% at UBV for >10 cm. On average 27% of the annual net N mineralization occurred during August. Nitrogen mineralized during the winter accounted for 4% at R to 55% at UBB of the annual rates for 0–10 cm;

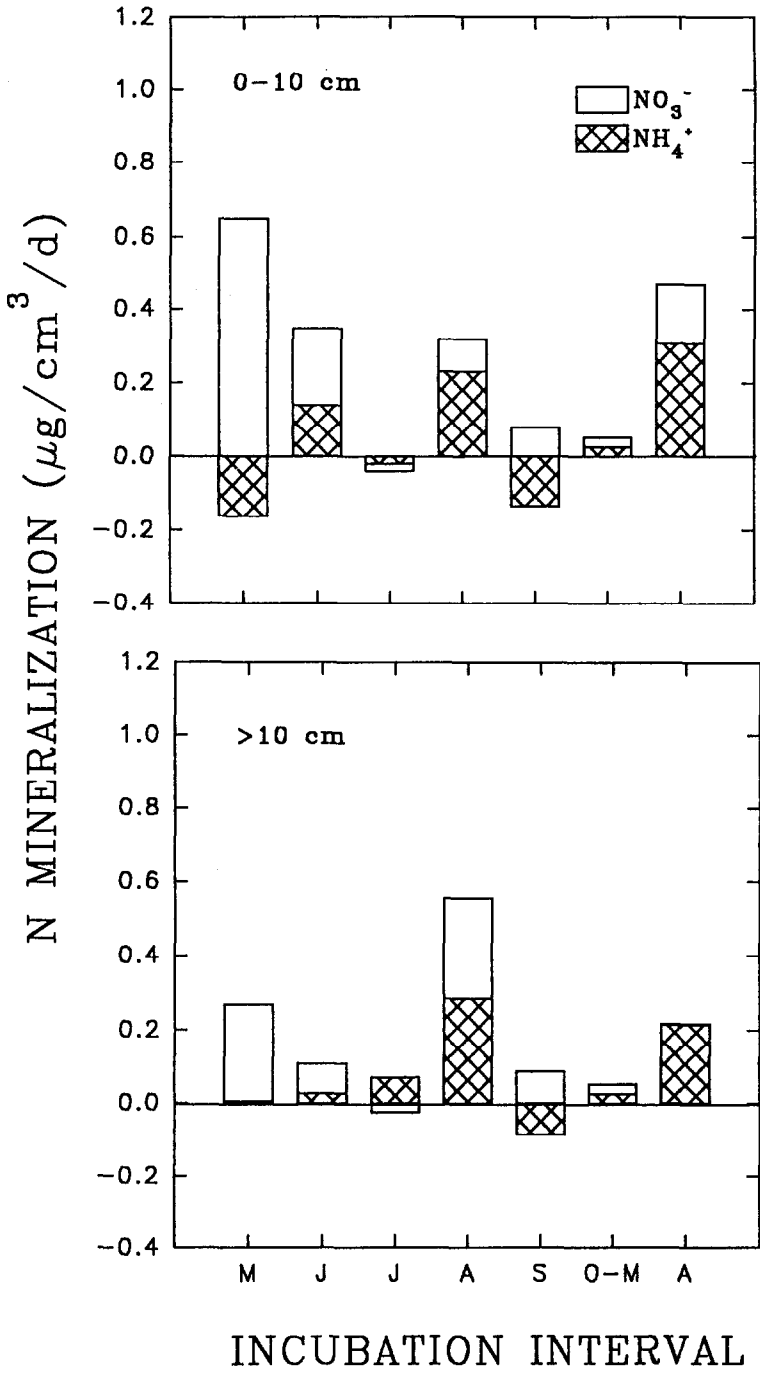


Fig. 5. Seasonality of N mineralization. Average daily rates of net N mineralization among sites during incubations for 0-10 cm and >10 cm soil.

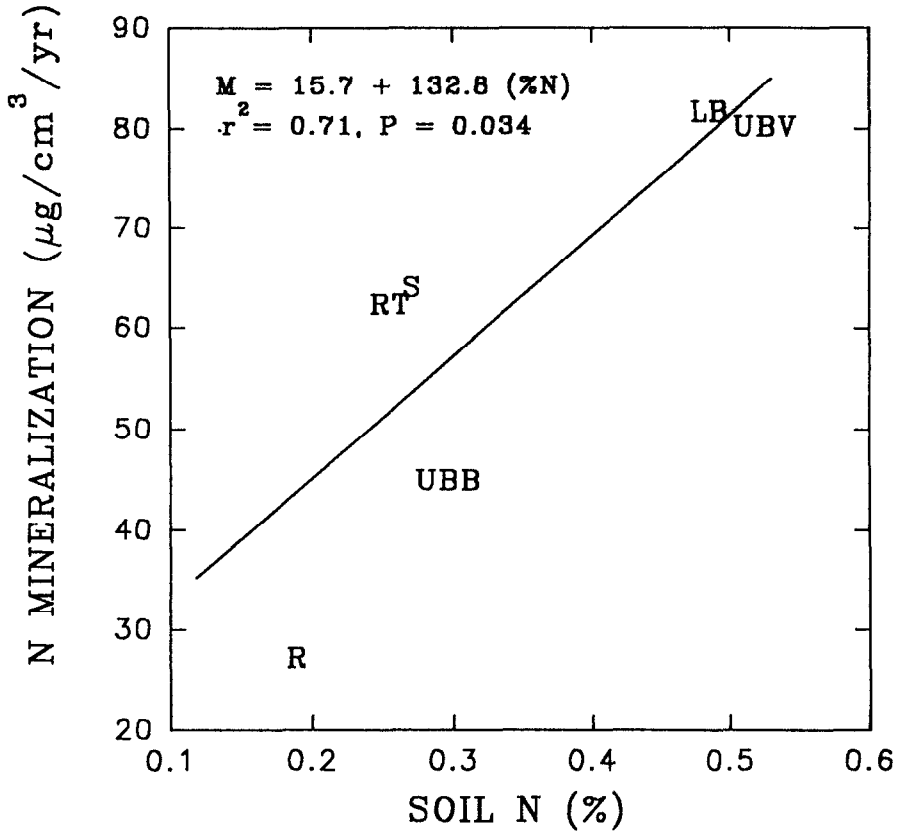


Fig. 6. Relationship of annual N mineralization (M_{0-10}) and percent soil N ($N\%_{0-10}$) in the top 10 cm.

and from 2% at RT to 35% at UBB of annual rates for >10 cm. Averaged over both depths, 18% of the annual N mineralization occurred during the winter.

Within the 0–10 cm soil depth, annual net mineralization was positively related to soil percent N ($N\%_{0-10}$; Fig. 6). $N\%_{0-10}$ was also weakly related to annual mineralization of the whole soil profile ($M = 23.7 + 101.8 * N\%_{0-10}$; $r^2 = 0.54$, $P = 0.09$, $df = 4$).

The proportion of soil N that was mineralized during the year-long study ranged from 1.49% to 2.52%, and, omitting UBB, was negatively related to C/N of the 0–10 cm soil (Spearman rank correlation $r_s = -1.0$, $P < 0.00001$).

The daily rate of nitrification (NO_3^- produced per day) varied through the year (date: $F_{5,303} = 8.32$, $P < 0.0001$; date * site: $F_{25,303} = 2.11$, $P < 0.003$; date * depth: $F_{5,303} = 7.72$, $P < 0.0001$; date * site * depth: $F_{25,303} = 2.48$, $P < 0.0003$). These factors together explained 47% of the variation in nitrification (Fig. 3c, 5). The proportion of annual mineralized N that was NO_3^- ranged

Table 6. Fecal-biomass and fecal-N deposited during the winter at the sites.

Site	Pellet groups	Calculated mass deposited (g/m ²)	Fecal-N (mg/m ²)
RT	28	25.8	307
UB	31	28.5	339
S	7	6.3	75
R	39	35.6	424
LB	9	8.3	99

from 48% at LB to 98% at UBV for 0–10 cm; and from 43% at RT to 66% at S for >10 cm (Table 5).

Dung

Dung input varied widely among sites. The number of elk pellet groups counted within the plots during the 1991–92 winter ranged from 7 at S to 39 at R (Table 6). Estimated dry-mass of dung at the sites ranged from 6.3–35.6 g/m².

Nitrogen content of fresh winter and spring/summer elk dung was 1.19% ($n = 11$, SE = 0.03) and 2.52% ($n = 10$, SE = 0.19), respectively. Nitrogen added as winter dung varied markedly among sites; ranging from 75–424 mg/m² (Table 6).

Relationships between N pools and fluxes

We compared annual net N mineralization with the annual N flows to the soil from herbivores and senescent plants (Table 7). Values for excretal-N (H) are estimates of N in both feces and urine. Litter N (L) was calculated by multiplying %N by the aboveground standing crop of October clippings; although not measured, leaf fall prior to the October clipping appeared to be negligible. These values are upper limits of the N returned to the soil by plants, since ungulates removed some of this plant material during the winter. Mineralization rates (M) reflect estimates for N mineralized in the entire soil profile sampled.

The amount of N added to sites by ungulates relative to that mineralized (H/M) varied more than six-fold, and averaged 27% across the sites (Table 7). The amount of N in standing dead at the end of the growing season was

Table 7. Derived N fluxes and relationships among them.

Site	Herbivore to soil (kg/ha/yr) (H)	Plant litter to soil (kg/ha/yr) (L)	Mineralization (kg/ha/yr) (M)	Percent	
				H/M	L/M
RT	33.4	3.0	83	40	4
UB	37.3	14.0	142	26	10
S	8.1	3.3	81	10	4
R	45.6	3.6	81	56	4
LB	10.7	6.8	116	9	6
Average	27.0	6.1	101	27	6

small in relation to N mineralized (L/M), averaging 6%. The contributions of ungulates were roughly 10-fold greater than those of litter at RT and R.

Discussion

Spatial and temporal patterns of N cycling

Yellowstone grassland is similar to other temperate grasslands with respect to several spatial and temporal controls of N cycling. Topography plays an important role in determining the spatial distribution of nutrient pools and rates of fluxes in several grassland ecosystems. Benches, depressions, and the base of slopes typically have higher levels of soil organic matter and N than do steep slopes and ridgetops (e.g. Jenny 1980, Barnes & Harrison 1982, Schimel et al. 1985b). In Yellowstone, two grassland bench sites (UBV, LB) had higher soil N and C levels than the ridgetop (RT) and slope (S) sites (Table 4). Soil N and C of the top 10 cm were markedly less within bare patches at UB (UBB) compared to vegetated patches (UBV), likely because of N volatilization that occurred when sagebrush bushes burned in 1988, creating bare areas. Furthermore, annual N mineralization in Yellowstone was positively related to soil N content (Fig. 6), and the proportion of soil N that was mineralized during the year was negatively associated with soil C/N ratio. Therefore, low mineralization at R likely was due to low soil N and high C/N ratios of soil at that site (Table 4). These results are consistent with observations in shortgrass steppe (Schimel et al. 1985b) where the annual rate

of mineralization is related to the amount of soil N, and the rate of N turnover is associated with soil organic matter quality.

Results from Yellowstone also corroborate findings from other grasslands indicating the importance of soil microclimate on mineralization rates (Schimel & Parton 1986, Fisher et al. 1987, Burke 1989). In this study, mineralization rates were related to soil moisture. N mineralization was high during the spring when soils were moist after snowmelt. In addition, N mineralization was high during the wet month of August, except at R, which had the highest soil moisture of any of the sites throughout the study. The strong mineralization response to increased soil moisture in August after a month-long dry period is suggestive of the 'Birch effect' (Birch 1958), i.e. a promotion of mineralization rates when dry soils are wetted beyond the rates observed if the soils had remained moist. The large amount of N mineralized during August, 28% of the annual rate across sites, suggests that variation in climate may produce significant inter-annual variability in N mineralization in this grassland ecosystem.

Interestingly, high mineralization rates during the spring months of this study were coincident with intense grazing at our study area before ungulates migrated to higher elevations. This suggests synchronous large pulses of N from microbes to plants and from plants to herbivores. Since elk and bison typically graze sites across the northern range within the first two months after snowmelt (Frank & McNaughton 1992), simultaneous pulses of N from soil to plants, and from plants to grazers, may characterize Yellowstone's northern range. High availability of N at precisely the time that vegetation is grazed may play an important role in allowing grazed plants to regrow in Yellowstone (Frank & McNaughton 1993).

Relationships among fluxes

Although spatial and temporal controls of N cycling in Yellowstone are similar to those in other grasslands, Yellowstone is unique among temperate grasslands where N cycling has been studied in that it possesses large, migratory herds of native ungulates. Large herbivores can have profound effects on nutrient dynamics of grasslands (Detling 1988, McNaughton et al. 1988). We did not attempt to study all effects of herbivores on the biogeochemical processes of grassland. However, we did compare the deposition of excretal-N with other N flows in Yellowstone winter range grassland.

Estimates for N added to the sites by ungulates demonstrate the important role that grazers play in the N budget of Yellowstone grassland. The average annual rate of N excreted was 27% of the annual N mineralized (Table 7), a substantial flow of N to the soil when considering it was 4.5 times the amount of N in senescent plant tissue (Table 7), considered the primary source of

soil N in some grasslands (Woodmansee et al. 1978, Parton et al. 1988). Although we did not measure grazing in this study, we calculated N removed by ungulates using an average consumption rate (28%) reported elsewhere for three winter range grasslands (Frank & McNaughton 1992), and the average N in peak aboveground biomass at the sites (Table 3: 2.5 g/m²). The estimated rate of N removal from the sites was 10 kg/ha/yr, or 37% of the estimated rate of N added (27 kg/ha/yr). These results suggest that there was a net movement of N over the year from high elevation summer range, where ungulates gain body mass, to winter range, where body mass is lost.

Together, the two flows of N to the soil that we examined, from aboveground plant tissue and from ungulates, accounted for only 33% of the total N mineralized at the sites. Atmospheric deposition of N, which was subsumed in the N mineralization measurements due to the uncapped incubation tubes, was probably low (2 kg/ha/yr; Swank 1984). Therefore, several unmeasured fluxes must have been significant sources of mineralizable N. Root turnover probably was important given the relatively large amount of root N (Table 3). Other animals, including pocket gophers (*Thomomys talpoides*), ground squirrels (*Spermophilus armatus*), voles (primarily *Microtus montanus*), and grasshoppers (Orthoptera: Acrididae), were conspicuous in the study area. Nitrogen consumed by these and other herbivores before peak standing crop and cycled to the soil via excretion and death was not accounted for in this study and may have represented a significant source of N for microbes. Finally, N₂ fixation rates for Yellowstone grassland are unknown. Vascular plant associated N₂ fixation likely was negligible, since no nodulating plant species was found in the study area (personal obs, DAF, RSI, NH). N₂ fixation by cyanobacteria, both free-living and symbiotic with lichens and mosses, can be significant in some arid to semi-arid habitats (West 1990), and may be an important N source in Yellowstone grassland.

N cycling in Yellowstone versus other grassland ecosystems

The annual rate of N mineralized in Yellowstone grassland/shrub-grassland (RT, UB, S, LB) was high relative to field-measured rates for other western grassland or shrub-grassland ecosystems (Table 8). The highest rate at sites on a Colorado shortgrass prairie (Schimel et al. 1985b) and Wyoming sagebrush grassland (Burke 1989) were below the lowest rate we measured for Yellowstone grassland; although the Burke (1989) study did not include the top 5 cm of soil, likely a productive soil interval. Several factors may contribute to the relatively high rates of N turnover in Yellowstone grasslands, including differences in temperature, moisture, and geology among the areas. An additional hypothesis is that large herbivores in Yellowstone Park facilitate N mineralization. Large herbivores directly (Day & Detling 1990)

Table 8. Annual net N mineralization in grassland and shrub-grassland ecosystems.

Study	Soil depth	rate (kg/ha/yr)	Ecosystem	Method
This study	0–10	62–81	Yellowstone Shrub-grassland	Mineralization Tube
Schimel et al. 1985	0–10	30–55	Colorado Shortgrass Prairie	Buried Bag
Burke 1989	5–15	7–22	Wyoming Shrub-grassland	Buried Bag

and indirectly (Holland & Detling 1990) increase N cycling in shortgrass steppe. Therefore, grazers may be involved in the high rates of mineralization measured in this study.

Gaseous N loss from Yellowstone grasslands may be significant. Ammonia volatilization from urine patches can vary according to meteorological conditions and soil and vegetation properties; however, most values range from 20 to 40% of the urea-N applied (see Ruess & McNaughton 1988). Soil pool NO_3^- at the sites was greatest when soils were wet, precisely when redox conditions of soils would be most suitable for denitrification to occur. Peak Yellowstone soil NO_3^- pools were roughly 2–4 times higher than the maximum level reported for 0–15 cm soil of tallgrass prairie (Groffman et al. 1993) and approached an order of magnitude greater than the maximum level reported for 5–15 cm depth soil of Wyoming sagebrush steppe (Burke 1989). The substantial N transferred to the soil from herbivores as excrement and the high soil NO_3^- levels suggest that ammonia volatilization and denitrification rates may be particularly important pathways for N loss from Yellowstone's northern winter range.

The watershed as a unit of biogeochemical study

The high rates of both N deposition from ungulates and mineralization, and the high levels of soil NO_3^- , a relatively mobile form of inorganic N, suggest that N leaching may be important in Yellowstone. For this reason it was surprising that inorganic N accumulated on resin placed at the bottoms of

incubation tubes was only 2 to 6% of the annual rate of mineralization at the grassland sites. Since incubation tubes did not include live plant roots, the actual amount of N leached out of the rooting zones at the sites likely was less.

Inorganic N accumulated onto resin buried in the soil (Fig. 4), showed higher N availability at the riparian site than at grassland sites. This does not follow from mineralization rates at the sites, since R had the lowest annual rate among sites (Fig 7). Therefore, there must have been a supplemental source of N for the riparian site. Most of the N that accumulated to resin at R occurred during peak snowmelt in May, 1991, when Blacktail Deer Creek overflowed its banks and the riparian site was flooded (Fig. 3d). This suggests that a large portion of the N budget at that site may have been exogenously provided by overland flow and/or subsurface leaching from upland habitat directly above and up-drainage from the site in the spring when soils were saturated; the latter being carried to the site by the stream. Although N leaching from upland grassland may be a small percentage of the N mineralized during the year, as discussed above, the cumulative effect of low rates of N leaching from extensive grassland may have resulted in a substantial N input into the narrow riparian zone within this watershed. When we fertilized patches of riparian vegetation adjacent to site R with N ($10 \text{ g/m}^2 \text{ N as NH}_4\text{NO}_3$), aboveground production was stimulated by 22% ($F_{1,8} = 4.6, P < 0.06$). This result indicates that the riparian zone was N-limited. Furthermore, this finding suggests that the riparian zone within this watershed was not a passive conduit through which nutrients move, but, instead, biologically responded to biogeochemical processes occurring upslope and upstream from it (Gregory et al. 1991).

The results of this study indicate that soil microclimate and topographically-mediated variation in soil organic N at our Yellowstone grassland generally play similar roles in controlling the spatial and temporal dynamics of N cycling as they do in other grassland ecosystems. However, mineralization rates were higher than in other similar grassland studies, possibly due to grazers facilitating N cycling in Yellowstone.

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References

- Adams MA & Attiwill PM (1986) Nutrient cycling and mineralization in eucalypt forests of south-eastern Australia. 1. Nutrient cycling and nitrogen turnover. *Plant and Soil* 92: 319–339
- Barnes P & Harrison AT (1982) Species distribution and community organization in a Nebraska Sandhills mixed prairie as influenced by plant-soil-water relations. *Oecologia* 52: 192–202
- Binkley, D (1984) Ion exchange resin bags: factors affecting estimates of nitrogen availability. *Soil Sci Soc Am J* 48: 1181–1184
- Binkley D & Matson P (1983) Ion exchange resin bag method for assessing forest soil nitrogen availability. *Soil Sci Soc Am J* 47: 1050–1052
- Binkley D, Aber J, Pastor J & Nadelhoffer K (1986) Nitrogen availability in some Wisconsin forests: comparisons of resin bags and on-site incubations. *Biol Fert Soils* 2: 77–82
- Birch HF (1958) The effect of soil drying on humus decomposition and nitrogen availability. *Plant and Soil* 10: 9–31
- Burke IC (1989) Control of nitrogen mineralization in a sagebrush steppe landscape. *Ecology* 70: 1115–1126
- Day TA & Detling JK (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* 71: 180–188
- Despain, DG (1990) *Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting*. Roberts Rinehart Publishers, Boulder, CO
- Detling JK (1988) Grasslands and savannas: regulation of energy flow and nutrient cycling by herbivores. In: Pomeroy LR & Alberts JJ (Eds) *Concepts of Ecosystem Ecology: A Comparative View* (pp 131–148). Ecological studies 67. Springer-Verlag, New York
- Eno CF (1960) Nitrate production in the field by incubating the soil in polyethylene bags. *Soil Science Society of America Proceedings* 24: 277–279
- Fisher FM, Parker LW, Anderson JP & Whitford WG (1987) Nitrogen mineralization in a desert soil: interacting effects of soil moisture and nitrogen fertilizer. *Soil Science Society of America Journal* 51: 1033–1041
- Floate MJS (1981) Effects of grazing by large herbivores in agricultural ecosystems. In: Clark FE, Rosswall T (Eds) *Terrestrial nitrogen cycles*. *Ecological Bulletins-NFR* 33: 585–601
- Frank DA & McNaughton SJ (1992) The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology* 73: 2043–2058
- Frank DA & McNaughton SJ (1993) Evidence for the promotion of aboveground grassland production in Yellowstone National Park. *Oecologia* 96: 157–161
- Gregory SV, Swanson FJ, WA Mckee & KW Cummins (1991) An ecosystem perspective of riparian zones. *Bioscience* 41: 540–551
- Groffman PM, Rice CW & Tiedje JM (1993) Denitrification in a tallgrass prairie. *Ecology* 74: 855–862
- Hobbie SE (1992) Effects of plant species on nutrient cycling. *Trends in Ecology and Evolution* 7: 336–339
- Holland EA & Detling JK (1990) Plant response to herbivory and belowground nitrogen cycling. *Ecology* 71: 1040–1049
- Holland EA, Parton WJ, Detling JK & Coppock DL (1992) Physiological responses of plant populations to herbivory and other consequences of ecosystem nutrient flow. *American Naturalist* 140: 685–706
- Houston DB (1982) *The Northern Yellowstone Elk: Ecology and Management*. Macmillan Publishing, New York
- Huntly, N (1991) Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics* 22: 477–503
- Inouye RS, Huntly NJ & Tilman D (1987a) Pocket gophers (*Geomys bursarius*), vegetation, and soil nitrogen along a successional sere in east-central Minnesota. *Oecologia* 72: 178–184

- Inouye RS, Huntly NJ, Tilman D & Tester, JR (1987b) Responses of *Microtus pennsylvanicus* to fertilization of plants with various nutrients, with particular emphasis on sodium and nitrogen concentrations in plant tissues. *Holarctic Ecology* 10: 110–113
- Jaramillo VJ & Detling JK (1988) Grazing history, defoliation, and competition: effects on shortgrass production and nitrogen accumulation. *Ecology* 69: 1599–1608
- Jenny H (1980) *The Soil Resource: Origin and Behavior*. Ecological Studies, Volume 37. Springer-Verlag, New York, New York, USA
- Malo DD, Worcester BK, Cassel DK & Matzdorf KD (1974) Soil-landscape relationships in a closed drainage system. *Soil Science Society of America Proceedings* 38: 813–818
- Matson PA & Vitousek PM (1981) Nitrogen mineralization potentials following clearcutting in the Hoosier National Forest, Indiana. *Forest Science* 27: 781–791
- McNaughton SJ (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55: 259–295
- McNaughton SJ (1989) Interactions of plants of the field layer with large herbivores. Symposium of the Zoological Society of London. 61: 15–29
- McNaughton SJ, Ruess RW & Seagle, SW (1988) Large mammals and process dynamics in African ecosystems. *Bioscience* 38: 794–800
- Meagher MM (1973) *The Bison of Yellowstone National Park*. National Park Service Scientific Monograph Series Number 1. United States Department of the Interior, Washington DC
- Mould ED & Robbins CT (1981) Nitrogen metabolism in elk. *Journal of Wildlife Management* 45: 323–334
- Page, AL, Miller RH & Keeney DR. (1982) *Methods of Soil Analysis*. Part 2. Chemical and Microbiological Properties. 2nd ed. American Society of Agronomy, Inc. and Soil Science Society of America, Inc., Madison, WI
- Parton, WJ, Stewart JWB & Cole CV (1988) Dynamics of C, N, P and S in grasslands soils: a model. *Biogeochemistry* 5: 109–131
- Polley HW & Detling JK (1988) Defoliation, nitrogen, and competition: effects on plant growth and nitrogen nutrition. *Ecology* 70: 721–727
- Raison RJ, Connell MJ & Khanna PK (1987) Methodology for studying fluxes of soil mineral-N *in situ*. *Soil Biology and Biochemistry* 5: 521–530
- Risser PG & Parton WJ (1982) Ecosystem analysis of the tallgrass prairie: nitrogen cycle. *Ecology* 63: 1342–1351
- Ruess RW (1987) The role of large herbivores in nutrient cycling of tropical savannahs. In: Walker BH (Ed) *Determinants of Tropical Savannahs* (pp 67–91). IRL Press Limited, Oxford
- Ruess RW & McNaughton SJ (1988) Ammonia volatilization and effects of large grazing mammals on nutrient loss from East African grasslands. *Oecologia* 77: 382–386
- Ruess RW, McNaughton SJ & Coughenour MB (1983) The effects of clipping, nitrogen source and nitrogen concentration on the growth responses and nitrogen uptake of an East African sedge. *Oecologia* 59: 253–261
- SAS (1988) *SAS/STAT 6.03* SAS Institute, Cary, NC, USA
- Schimel DS & Parton WJ (1986) Microclimatic controls of nitrogen mineralization and nitrification in shortgrass steppe soils. *Plant and Soil* 93: 347–357
- Schimel DS, Coleman DC & Horton KA. (1985a) Soil organic matter dynamics in paired rangeland and cropland toposequences in North Dakota. *Geoderma* 36: 201–214
- Schimel DS, Stillwell MA & Woodmansee RG (1985b) Biogeochemistry of C, N, and P on a catena of the shortgrass steppe. *Ecology* 66: 276–282
- Schimel DS, Parton WJ, Adamsen FJ, Woodmansee RG, Senft RL & Stillwell MA (1986) The role of cattle in the volatile loss of nitrogen from a shortgrass steppe. *Biogeochemistry* 2: 39–52
- Senft RL, Coughenour MB, Bailey DW, Rittenhouse LR, Sala OE & Swift DM (1987) Large herbivore foraging and ecological hierarchies. *Bioscience* 37: 789–799
- Swank, WT (1984) Atmospheric contributions to forest nutrient cycling. *Water Resources Bulletin* 20: 313–321

- Wedin DA & Tilman D (1990) Species effects on nitrogen cycling: a test with perennial grasses. *Oecologia* 84: 433–441
- West NE (1990) Structure and function of microphytic soil crusts in wildland ecosystems of arid to semi-arid regions. *Advances in Ecological Research* 20: 179–223
- Woodmansee RG (1978) Additions and losses of nitrogen in grassland ecosystems. *Bioscience* 28: 448–453
- Woodmansee RG, Dodd JL, Bowman RA & Dickinson CE (1978) Nitrogen budget in a shortgrass prairie ecosystem. *Oecologia* 34: 363–376