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Denitrification in a semi-arid grazing ecosystem

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Abstract The effect of large herbivores on gaseous N loss from grasslands, particularly via denitrification, is poorly understood. In this study, we examined the influence of native migratory ungulates on denitrification in grasslands of Yellowstone National Park in two ways, by (1) examining the effect of artificial urine application on denitrification, and (2) comparing rates inside and outside long-term exclosures at topographically diverse locations. Artificial urine did not influence denitrification 3 and 12 days after application at hilltop, midslope, and slope-bottom sites. Likewise, grazers had no effect on community-level denitrification at dry exclosure sites, where rates were low. At mesic sites, however, ungulates enhanced denitrification by as much as 4 kg N ha^{-1} $year^{-1}$, which was double atmospheric N inputs to this ecosystem. Denitrification enzyme activity (DEA, a measure of denitrification potential) was positively associated with soil moisture at exclosure sites, and herbivores stimulated DEA when accounting for the soil moisture effect. Glucose additons to soils increased denitrification and nitrate additions had no influence, suggesting that denitrification was limited by the amount of labile soil carbon, which previously has been shown to be enhanced by ungulates in Yellowstone. These results indicate that denitrification can be an ecologically important flux in portions of semi-arid landscapes, and that there is a previously unsuspected regulation of this process by herbivores.

Key words Denitrification · Grassland · Herbivory · Nitrogen · Yellowstone National Park

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Introduction

Extensive research over the last two decades has documented a number of important effects of ungulates on grassland soil N cycling. For example, herbivore trampling, wasting, and grazing all reduce C/N ratios of litter, roots and soil (Floate 1981; Seastedt 1985; Ruess 1987; McNaughton et al. 1988, 1997; Day and Detling 1990; Shariff et al. 1994; Holland et al. 1992). These grazer-induced changes in organic matter quality stimulate net N mineralization and N availability to plants (Holland and Detling 1990; Shariff et al. 1994; McNaughton et al. 1997) as a consequence of increases in gross mineralization and/or reductions in microbial immobilization (Holland and Detling 1990; Holland et al. 1992; Frank and Groffman 1998).

Despite this prodigious effort to understand how large herbivores affect grassland N processes, the influence of grazers on gaseous N loss, particularly denitrification, is still poorly characterized. A large number of studies have examined short-term ammonia volatilization from soils amended with simulated urine (e.g., Musa 1968; Denmead et al. 1974; Vallis et al. 1982), and some studies have extrapolated these values to derive the influence of herbivores on annual rates of ammonia loss across grassland landscapes (Schimel et al. 1986; Ruess and McNaughton 1988; Frank and Zhang 1997). Likewise, some work has examined short-term effects of urine patches on denitrification rates in intensively managed European pastures (Ryden 1986; Monaghan and Barraclough 1993; de Klein and van Lotestijn 1994). However, there has been very little effort to understand the long-term consequences of herbivores on denitrification at the spatial scale of the community (Groffman et al. 1993), and there has been no investigation of how wild, migratory ungulates influence denitrification in native grasslands.

In this study, we determined rates and controls of denitrification in Yellowstone National Park grasslands that were grazed by large herds of migratory native

ungulates. We examined two potential influences of grazers on denitrification: (1) effects associated with small urine patches; and (2) community-wide influences of herbivores. Urine effects were studied by adding artificial urine to three sites in different topographic settings and community-wide influences were examined by comparing rates inside and outside 33- and 37-year-old exclosures at seven topographically diverse locations. We show for the first time that ungulates can dramatically increase grassland denitrification; however, this influence is strongly dependent on site soil moisture, determined in Yellowstone primarily by topographic position.

Materials and methods

Study sites and experimental design

We conducted this study on the northern winter range of Yellowstone National Park. The northern winter range is approximately 100,000 ha of rolling, grassland/shrub-grassland habitat located in the lower Yellowstone and Lamar river valleys, which is grazed October–May by large herds of migratory elk (*Cervus elaphus*) and bison (*Bison bison*). Other seasonal or year-round occupants of this range are pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), bighorn sheep (*Ovis canadensis*), and moose (*Alces alces*) (Meagher 1973; Houston 1982; Despain 1990). Elevations vary from 1616 to 1921 m.

The climate of the northern winter range is cool and dry. Thirty-year mean annual temperatures and precipitation throughout the range are 2–7°C and 28–32 cm, respectively (Houston 1982). Soils were primarily derived from deposits laid down during the Pleistocene (Keefer 1987).

We examined ungulate effects on denitrification in two ways. First we measured denitrification and denitrification enzyme activity (DEA) inside and outside 2-ha exclosures established in 1958 and 1962. Soil properties on the northern range vary primarily as a function of topographic position. The exclosure sites encompassed seven topographically variable grasslands that included dry wash (S1), mid-slope (S2, M2, L2), and hilltop (B) sites, and two mesic slope-bottom (M1, L1) sites. At each site, we sampled paired fenced and grazed plots with the same slope and aspect. Soil and plant properties at the sites are described elsewhere (Frank and Evans 1997; Frank and Groffman 1998; Tracy and Frank 1998). Briefly, soil properties varied markedly: mean growing season soil moisture varied by 4 times and soil C and N content each varied by over 10 times among the sites. Several site properties were interrelated: soil moisture, C, N, and peak growing season plant biomass were all positively correlated with each other. These results reflect the extent to which topography controls soil and vegetation properties in this ecosystem.

Denitrification rates were measured five times at four of the sites in 1995 on 23 March (within 1 week after sites became snowfree), 5 April, 18 April, 31 May, and 21 August. DEA (an estimate of denitrification potential) was determined on soil collected at all seven exclosure sites, once in 1995 (26 May), and twice in 1996 (19 April and 13 May).

We also measured denitrification in simulated urine patches created at three topographic positions (hilltop, midslope, slope-bottom) along a catena. At each topographic site, three 0.5-m^2 quadrats received urine at a rate of 51 g urea-N m^{-2}, which approximates N added in natural urine patches, and levels that have been used in numerous studies examining the effects of ungulate urine on grassland plant and soil processes (Schimel et al. 1986; Ruess and McNaughton 1988; Day and Detling 1990; Frank and Zhang 1997). Urine was applied on 20 April 1995 and denitrification was measured in urine-treated and paired control quadrats 3 and 12 days after urine application. Artificial urine followed the recipe of Stillwell (1983).

At each urine application site, soil C and N content was measured on triplicate samples with a Carlo-Erba CN Analyzer Model 1500. We also determined plant biomass by clipping five 20×50 cm quadrats at each site at peak standing crop.

Denitrification rate measurements

On each sample date, we collected replicate soil cores (15 cm deep $\times$ 2.0 cm diameter): ten from within each of the paired, grazed and fenced plots at each exclosure site, and two within each 0.5-m^2 treated and control quadrat at the urine addition sites. Denitrification rates were measured using the C_2H_2-based soil core technique described by Tiedje et al. (1989) and Groffman et al. (1998). After sampling, cores were transported to the laboratory for incubation. Within 24 h of sampling, cores were sealed with rubber serum stoppers, and amended with at least 10 kPa C_2H_2. Acetylene was mixed with the soil air by repeated pumping with a 30 ml syringe. Cores were incubated for 6 h at field temperatures and gas samples were taken at 2 and 6 h. Gas samples were stored in evacuated glass vials and were later analyzed for N_2O using a Tracor model 540 gas chromatograph (GC) equipped with an electron-capture detector and a 3-m column packed with Porapak Q. Samples were introduced into the GC via a Tekmar 7050 Headspace Autosampler.

Denitrification rate was calculated as the rate of N_2O accumulation in the soil cores between 2 and 6 h. The 2-h sample was taken to ensure equilibrium of N_2O and C_2H_2 in the headspace of the cores during the time when denitrification was being measured. After incubations were completed, the internal headspace volume of each core was measured with a pressure transducer (Parkin et al. 1984).

Evaluation of limiting factors

For the May 1995 sample date, after the incubation described above, water was added to half of the cores from each site to simulate a 2-cm rainfall event. The cores were left to stand overnight and denitrification rate was measured the following day as described above.

Nitrate and carbon limitations of denitrification were tested using samples collected in May 1996. Sieved samples were amended with either (1) distilled water, (2) distilled water and nitrate (100 mg N kg^{-1}), or (3) distilled water with nitrate (100 mg N kg^{-1}) and glucose (1000 mg C kg^{-1}). Samples were incubated under anaerobic conditions, in the presence of C_2H_2, for 90 min. Gas samples were taken at 30 and 90 min, stored in evacuated glass tubes and analyzed for N_2O by electron capture gas chromatography.

Other measurements

Denitrification enzyme activity was determined with the short-term anaerobic method of Smith and Tiedje (1979). Soil moisture was measured on composite samples (three replicates) taken from each soil at each sample date. Moisture was quantified by drying at 105°C for 24 h. Nitrate was extracted with 1 M KCl from composite samples (three replicates) taken from each soil on each date when denitrification rate was measured. Extracts were analyzed colorometrically using a Perstorp continuous flow analyzer.

Data analysis

Herbivore effects on denitrification were determined with paired-t tests and an analysis of covariance to control for soil moisture. Relationships of denitrification with DEA, and denitrification and

Table 1 Cummulative 1995 denitrification, denitrification enzyme activity (*DEA*, mean ± 1 SE), and soil pool NO_3^- (mean ± 1 SE) at exclosure sites (*S1* is a dry wash; *S2, M2*, and *L2* are dry, midslope sites; *B* is a dry hilltop; and *M1* and *L1* are mesic sites)

Site	Denitrification (kg N ha^{-1})		DEA (μg N kg^{-1} h^{-1})		$N0_3^-$ (kg N ha^{-1})	
	Inside	Outside	Inside	Outside	Inside	Outside
S1	1.12	0.19	36 ± 6	29 ± 3	1.0 ± 0.3	1.9 ± 0.7
S2	0.18	0.42	4 ± 2	17 ± 3	0.3 + 0.1	0.9 + 0.2
M1	2.71	6.82	583 ± 46	1249 ± 157	3.2 ± 0.4	6.6 ± 1.7
M2	0.52	0.83	63 ± 3	97 ± 50	0.7 ± 0.1	0.7 ± 0.1
B	–	–	32 ± 15	83 ± 14	–	–
L1	–	–	281 ± 89	518 ± 239	–	–
L2	–	–	37 ± 16	18 ± 5	–	–

DEA with soil moisture were examined with least squares regressions. Denitrification during the 1995 growing season was derived by summing rates over sampling intervals. Rates during the intervals 23 March–5 April, 5–18 April, 18 April–31 May, and 31 May–21 August were calculated by multiplying the daily rate of denitrification, estimated as the average of the two samples bracketing the interval, by the number of days of the interval. The last interval (21 August–30 September) was calculated from 21 August rates. The effect of artificial urine on denitrification for each date was examined with an analysis of variance (ANOVA) blocked by site. Variables were log-transformed when necessary to achieve normal distributions.

Results

Denitrification and DEA measurements

Estimated 1995 growing season denitrification and mean DEA varied from 0.18 to 6.82 kg N ha^{-1} and 4 to 1249 μg N kg^{-1} h^{-1}, respectively (Table 1). Grazers increased the soil NO_3^- pool by an average of 94% ($t_3 = 3.4$, $P = 0.04$; Table 1). There was a positive, linear association between May 1995 denitrification and May 1995 DEA (Fig. 1). This relationship indicates that DEA is a valid index of actual denitrification rates in these soils. DEA was positively related to soil moisture (Fig. 2).

Results from paired *t*-tests for 1995 denitrification ($t_3 = 0.457$, $P = 0.851$) and mean DEA ($t_6 = 1.49$, $P = 0.187$) data suggest that grazers had no effect on denitrification. However, a grazer influence emerged when accounting for soil moisture (Fig. 2). Ungulates increased DEA when soil moisture was treated as a covariate (analysis of covariance; $F_{1,36} = 5.6$, $P = 0.0236$). Moreover, grazer stimulation of growing season denitrification and mean DEA (calculated for both variables by subtracting fenced from grazed measurements) was a function of soil moisture; ungulates increased denitrification and DEA in soils with mean moisture > approximately 20% (Fig. 3).

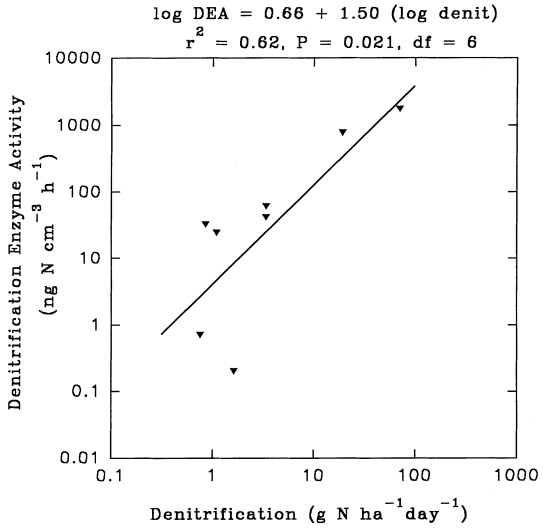

Fig. 1 Relationship between denitrification enzyme activity (DEA) and denitrification inside and outside fences at four sites in May 1995

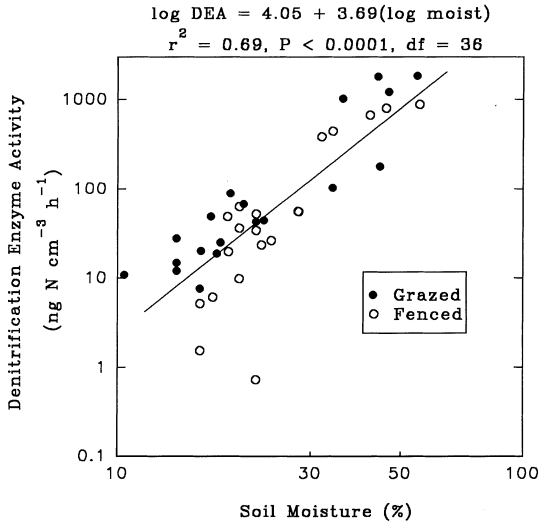

Fig. 2 Relationship between DEA and soil moisture for grazed and fenced soils collected at all sampling dates

Limiting factors

A simulated 2-cm rainfall increased May denitrification by 2.7-fold among plots ($t_7 = 2.24$, $P = 0.06$; Table 2). Nitrate amendments had no effect on denitrification ($P = 0.46$; Table 3). However, glucose additions stimulated denitrification rates by 10 times ($t_{13} = 5.24$, $P = 0.0002$; Table 3). There was no difference in the

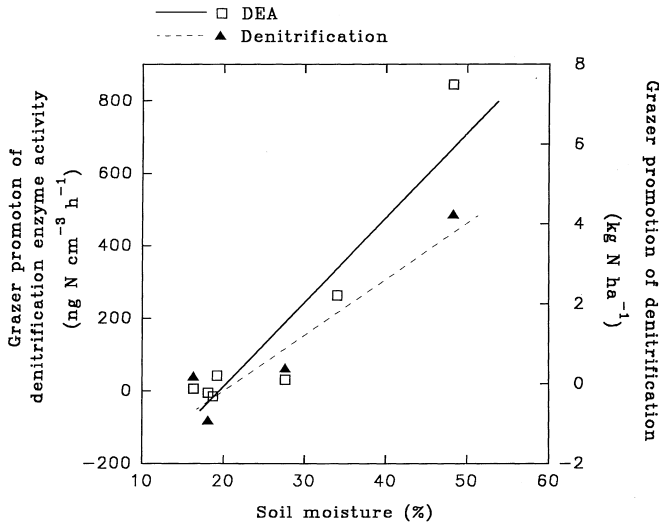

Fig. 3 Relationships between grazer promotion of DEA and denitrification (denit) and mean percent soil moisture (moist). DEA = 25.4(moist)–494; $r^2 = 0.89$; $P = 0.0014$; $df = 5$. Denit = 0.15(moist)–3.1; $r^2 = 0.91$; $P = 0.047$; $df = 2$

Table 2 Denitrification (mean ± 1 SE, g N ha^{-1} day^{-1}) in May 1995 in control and irrigated soil to simulate a 2-cm rainfall event. Sites as in Table 1

Site		Control	Irrigated
S1	Inside	0.9 ± 0.4	18.7 ± 14.6
	Outside	1.1 ± 0.4	0.3 ± 0.2
S2	Inside	0.7 ± 0.3	2.0 ± 1.3
	Outside	1.6 ± 0.3	25.5 ± 15.8
M1	Inside	19.2 ± 7.5	62.1 ± 27.4
	Outside	70.6 ± 24.0	257.1 ± 127.0
M2	Inside	3.4 ± 0.6	4.4 ± 2.0
	Outside	3.4 ± 2.1	6.0 ± 4.0

response to water, nitrate, or glucose amendments between grazed and fenced soils.

Artificial urine patches

Soil C and N and peak plant aboveground biomass varied markedly among topographic sites where artificial urine was applied (Table 4). Denitrification was unaffected by simulated urine addition (day 3; $F_{1,14} = 1.62$, $P = 0.22$: day 12; $F_{1,14} = 0.95$, $P = 0.36$: Fig. 4).

Discussion

Large herbivores have profound and well documented effects on a number of grassland soil N processes. In this study, we show for the first time that herbivores can also influence denitrification. In Yellowstone, ungulates had no effect on denitrification at dry sites, which dominate this semi-arid ecosystem. However, at mesic sites, grazers increased denitrification by as much as

Table 3 Denitrification from soil ammended with (1) distilled water (*DI*), (2) DI and KNO_3, and (3) DI, KNO_3, and glucose. Units are μg N kg^{-1} h^{-1}. Sites as in Table 1

	Site	DI	DI + KNO_3	DI + KNO_3 + glucose
S1	Inside	16.1	7.7	40.6
	Outside	0.1	0.6	25.0
S2	Inside	0.1	0.1	0.9
	Outside	2.7	0.1	0.3
M1	Inside	53.6	106.4	596.3
	Outside	205	18	1395
M2	Inside	17.1	17.7	68.8
	Outside	23.3	33.4	46.9
B	Inside	12.7	1.8	6.2
	Outside	7.3	2.8	58.9
L1	Inside	4.4	1.1	395.1
	Outside	15.5	13.0	93.2
L2	Inside	53.6	106.4	596.3
	Outside	0.74	1.8	10.7

Table 4 Peak aboveground plant biomass and soil carbon and nitrogen content at hilltop, midslope, and slope-bottom sites where the artificial urine study was conducted. Values are mean ± 1 SE

Site	Plant biomass (g m^{-2})	Percent soil	
		C	N
Top	50 ± 3	2.8 ± 0.3	0.28 ± 0.1
Mid	50 ± 6	5.1 ± 1.4	0.35 ± 0.1
Bottom	310 ± 40	6.7 ± 0.7	0.59 ± 0.1

4 kg N ha^{-1} year^{-1}, or double the estimated rate of atmospheric N deposition (2 kg N ha^{-1} year^{-1}; Swank 1984). Thus, denitrification, and grazer effects on denitrification, are important to community-level, and, potentially, landscape- and ecosystem-level N budgets in Yellowstone. As has been shown in previous studies, denitrification can be high in semi-arid grassland (and even desert) in early spring when soils are wet (Peterjohn 1991; Groffman et al. 1993; Zaady et al. 1996). Our results for Yellowstone show that grazers can be important regulators of denitrification, but in a way that is constrained by prevailing soil moisture conditions (Figs. 2, 3).

Previously we reported that ungulates increased net N mineralization and soil labile carbon levels in Yellowstone grasslands (Frank and Groffman 1998). Given that NO_3^- additions had no effect on denitrification, and glucose additions increased denitrification, we hypothesize that grazer stimulation of this rate, within the constraints imposed by soil moisture, is associated with ungulates increasing labile C in soils.

Landscape-scale topographic factors that control inherent soil wetness appear to have much more influence on denitrification than site-specific urine deposition by grazers. Neither simulated urine nor NO_3^- amendments stimulated denitrification, although irrigation did. Apparently, in situ levels of NO_3^- were high enough to support the activity of the denitrifier populations at the different sites, given the existing soil

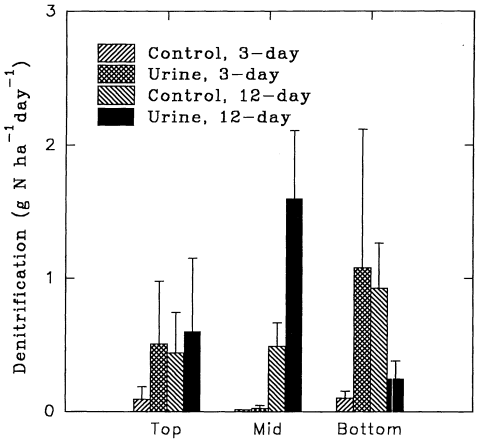

Fig. 4 Denitrification in urine-amended and control plots at three topographic positions

water conditions, and these populations are not stimulated by N addition. These results reinforce the idea that denitrification activity is confined to inherently wet, N-rich, mesic sites within the Yellowstone landscape. The fact that we observed a significant response to glucose additions further supports this idea by showing that denitrifier populations are linked to C availability in soil and will thus be larger in mesic areas with higher plant production and soil organic matter levels. It is important to note that native grazers do not use the Yellowstone landscape uniformly, but rather concentrate their activities at mesic sites that support relatively high forage biomass (Frank and McNaughton 1992; Frank et al. 1998). Thus grazer effects on denitrification are likely to be greatest in the areas with the highest denitrification potential. These results suggest that grazer regulation of denitrification is secondary to the primary influences of climate and topography on soil moisture.

Previous work in grasslands has suggested that there is high annual variation in denitrification in these ecosystems controlled by spring rainfall (Groffman et al. 1993). The positive response to irrigation that we observed suggests a similar pattern in Yellowstone grasslands, i.e. annual denitrification will fluctuate according to rainfall. It is interesting to note that strong spring rainfall control of annual denitrification is less common in temperate areas with higher fall and/or winter precipitation where soils are more reliably wet in spring (Groffman and Tiedje 1989).

It is also interesting to note that our results further support the idea that denitrification is not necessarily lower in semi-arid or even arid ecosystems than in more temperate ecosystems (Peterjohn 1991; Zaady et al. 1996). For example, many temperate forests have very low denitrification (<1 kg N ha^{-1} year^{-1}) due to high competition for N or coarse soil texture (Davidson et al. 1990; Vermes and Myrold 1992). Because denitrification can proceed at high rates during brief seasonal windows of high water and nitrate availability, this process can be of comparable importance in a wide range of ecosystems, even those with relatively low rainfall. Moreover, denitrification can be markedly high at mesic sites with elevated levels of available NO_3^- and carbon that are located in otherwise semi-arid landscapes.

Ungulates increase grassland organic matter quality, which has reverberating consequences on mineral cycling (Holland and Detling 1990; Holland et al. 1992; Shariff et al. 1994; McNaughton et al. 1997; Frank and Evans 1997; Frank and Groffman 1998). In this study, we show that grazers can dramatically increase denitrification in Yellowstone grassland and present evidence for ungulate-induced changes in organic matter as the underlying mechanism. Because this putative mechanism for grazers increasing denitrification in Yellowstone is a well documented response of grasslands to large herbivores in general, stimulation of denitrification by ungulates may be an unrecognized common feature of the N budgets of grazed grasslands.

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