

Ammonia volatilization from a seasonally and spatially variable grazed grassland: Yellowstone National Park

DOUGLAS A. FRANK & YIMIN ZHANG

Biological Research Labs, Syracuse University, Syracuse, NY 13244-1220 USA; DAF phone: 315-443-4529; e-mail: dafrank@mailbox.syr.edu

Key words: ammonia volatilization, grassland, nitrogen, ungulate, Yellowstone National Park

Abstract. We measured ammonia volatilization at three topographic positions (hilltop, mid-slope, slope-bottom) on three grassland landscapes at three times during 1995 (April, May, July) on the northern winter range of Yellowstone National Park that supports large herds of native ungulates. Percent ammonia-N lost from all sites during the study ranged 1–24% of urea-N applied. Volatilization among sites was negatively related to soil cation-exchange capacity ($r = -0.85$) and rates were highest in July. We used the relationship between soil CEC and percent N volatilized from urea-amended plots to estimate annual ammonia-N volatilization from 5 sites for which annual ungulate urine inputs were previously determined (Frank et al. 1994). Estimated mean annual ammonia-N volatilized from those sites was 1.4 kg/ha/yr, which was less than a previously reported regional atmospheric deposition rate (2 kg/ha/yr; Swank 1984). Results indicate the need to understand the interaction between (1) spatially heterogeneous patterns of soil processes, and 2) nonuniform patterns of ungulate use of landscapes to determine rates of ecosystem-level N-gaseous loss. Findings also suggest that ammonia-N volatilized from urine patches should not lead to a decline in soil N in this ecosystem.

Introduction

Ammonia volatilization from ungulate urine can be a major pathway of nitrogen (N) loss in grazed grassland (Woodmansee et al. 1978; Schimel et al. 1986). Measured losses of ammonia-N mostly range 10%–40% of the urea-N added to plots; although amounts of 2–90% have been reported (e.g., Musa 1968; Stewart 1970; Denmead et al. 1974; Vallis et al. 1982; Bouwmeester et al. 1985; Schimel et al. 1986; Ruess & McNaughton 1988). High variation in ammonia loss is a complex function of several interrelated factors that include soil texture (Schimel et al. 1986), organic matter (O'Toole et al. 1982), pH (Ernst & Massey 1960), cation exchange-capacity (CEC; Campbell et al. 1984), soil micrometeorology (Sherlock & Goh 1984), and vegetation (Ruess & McNaughton 1988).

Nitrogen is a limiting nutrient in grasslands. Nitrogen fertilization increases grassland production (e.g. Woodmansee et al. 1978; Seastedt et al. 1991) and microbial biomass is strongly correlated with total soil N

(Wardle 1992), suggesting that both plant productivity and microbial biomass are under N control. In addition, N is a key component of forage quality for migratory large herbivores who track high N forage that shifts spatially through time in large ecosystems (McNaughton 1979, 1985; Frank & McNaughton 1992). Because of its role in limiting grassland processes, rates of N loss, if significant, may play an important role in the functional regulation of grasslands.

Large herds of elk (*Cervus elaphus*) and bison (*Bison bison*) in Yellowstone National Park remove a substantial amount of the annual aboveground production and return ecologically significant quantities of N to the soil. For example, among 5 sites across a grassland watershed, herbivores added an average of 27 kg-N/ha/yr, which was equivalent to 27% of the average annual net N mineralized throughout the major rooting zone among the sites (Frank et al. 1994). The large amount of N passing through ungulates implicates N loss from urine patches as a potentially important factor affecting the N budget of this grassland ecosystem.

Grassland ecosystems are characterized by high spatial variation in soil processes. Recent interest in incorporating biotic and abiotic controls of trace gas fluxes into spatially extensive (e.g., regional, global) systems models has reinforced the demand for an understanding of the spatial heterogeneity of ecosystem processes within landscapes (Sellers et al. 1988; Schimel et al. 1991; Knapp et al. 1993). Although it is clear that ammonia volatilization will vary with topography, due to variation in soil texture, organic matter, and CEC, and season, due to variation in micrometeorological conditions, spatial and seasonal effects on ammonia volatilized from grasslands grazed by large herds of migratory native herbivores are poorly understood. The objectives of this study were to: 1) determine spatial and temporal effects on ammonia loss, 2) determine soil factors that are correlated with ammonia loss in this ecosystem, and 3) compare estimates of annual rates of ammonia-N volatilization with previously reported annual rates of atmospheric-N deposition to determine the effect of ammonia volatilization from urine patches on the N budget of Yellowstone grassland.

Methods

Study area

This study was conducted in the northern winter range of Yellowstone National Park: a 100,000 ha shrub-grassland located within the Yellowstone and Lamar River drainages (Figure 1). Approximately 20,000 elk and 400

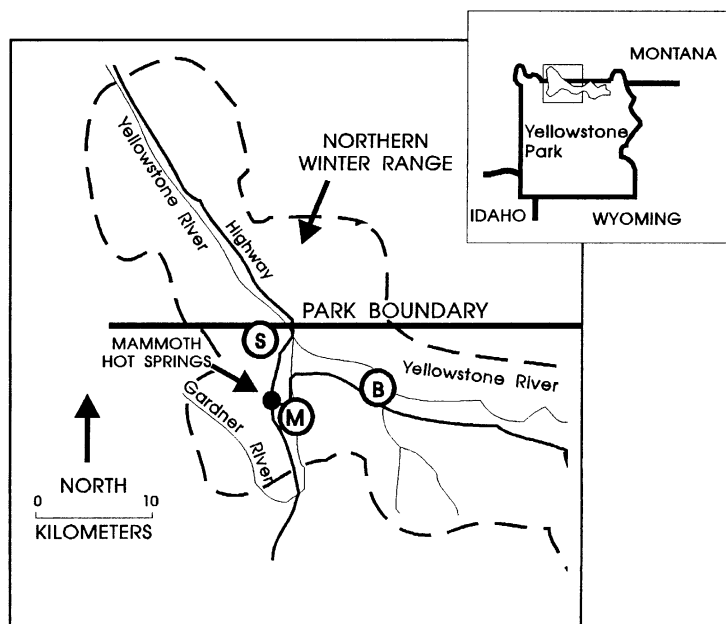


Figure 1. Locations of three landscapes, Stevens Ck (S), Mammoth (M), and Blacktail (B), on the northern winter range of Yellowstone National Park.

bison overwinter on this range, from which they begin an annual migration to the higher elevation transitional and summer ranges in April–May.

We measured ammonia volatilization at three topographic positions, hill-top, midslope, and slope-bottom, along catenas on three landscapes, Stevens Ck, Mammoth, and Blacktail (Figure 1). Mean elevations and aspects were 1631 m, NE; 1969 m, ENE; and 2062 m, SE at Steven CK, Mammoth, and Blacktail, respectively. Physiognomy of midslope sites on each of the three landscapes was shrub-glassland; otherwise all other communities were grassland (Table 1). Ammonia volatilization was measured at three times during 1995: April 20–May 2, May 15–24, and July 18–28.

Soils at Mammoth and Blacktail were typical of much of the northern winter range and were derived from andesitic and sedimentary glacial till deposited in the Pleistocene. In contrast, soils at Stevens Ck were formed from bentonite-rich material deposited by Pleistocene landslides. The climate of the northern winter range is cool and dry. Thirty-year mean precipitation and temperature for Mammoth (Figure 1) are 37.9 cm and 4.6 °C (NOAA 1990), respectively. Mean temperatures at Mammoth during our experiments in late-April, mid-May, and late- July were 1 °C, 8 °C, and 19 °C, respectively; 27 cm of snow fell during the April measurements.

Table 1. Three most abundant species at each of the study sites.

Site	Herbaceous	Shrub
Stevens Ck		
Hilltop	<i>Pseudoroegneria spicata</i> <i>Koeleria cristata</i> <i>Artemisia frigida</i>	
Mid-slope	<i>Pseudoroegneria spicata</i> <i>Bromus tectorum</i>	<i>Grayia spinosa</i>
Slope-bottom	<i>Poa compressa</i> <i>Hordeum jubatum</i> <i>Bromus tectorum</i>	
Mammoth		
Hilltop	<i>Stipa comata</i> <i>Koeleria cristata</i> <i>Artemisia frigida</i>	
Mid-slope	<i>Pseudoroegneria spicata</i> <i>Festuca idahoensis</i>	<i>Artemisia tridentata</i>
Slope-bottom	<i>Poa pratensis</i> <i>Agropyron caninum</i> <i>Stipa richardsonii</i>	
Blacktail		
Hilltop	<i>Pseudoroegneria spicata</i> <i>Festuca idahoensis</i> <i>Koeleria cristata</i>	
Mid-slope	<i>Festuca idahoensis</i> <i>Pseudoroegneria spicata</i>	<i>Artemisia tridentata</i>
Slope-bottom	<i>Festuca idahoensis</i> <i>Stipa richardsonii</i> <i>Muhlenbergia filiformis</i>	

Ammonia volatilization measurements

Because we were interested in landscape-level dynamics of ammonia loss, we used a simple static chamber method, similar to Schlesinger & Peterjohn (1991), that provided an index of ammonia volatilization. We calibrated this method with a dynamic chamber technique (Ruess & McNaughton 1988) that provided measures of actual rates, but was too labor intensive to have simultaneously used at a large number of locations.

Briefly, the static chamber was a 10 cm diam, 20 cm long PVC pipe pounded 5 cm into the soil and covered with aluminum foil secured with a rubber band. Ammonia volatilized within the chamber was trapped in 10 ml of 4% boric acid contained in a 20 ml vial.

The dynamic chamber method involved drawing air with a vacuum pump through a chamber with holes drilled in the side, then through an in-line acid trap containing 150 ml of 4% boric acid. Ruess & McNaughton (1988) previously showed this method was 97.1% efficient at absorbing ammonia volatilized in the chamber. The chamber (25.4 cm diam $\times$ 18 cm long) was driven 5 cm into the soil and covered with aluminum foil, secured with a rubber band. Silicon grease was used to make an airtight seal between the chamber and foil and air flow was set with flow meters at 6.4 l min^{-1} . Results were distorted to an unknown extent by inevitable effects of the chamber system on air mixing, temperature, and moisture (Black et al. 1985; Ruess & McNaughton 1988).

Calibrations were determined on 24 hr incubations in April, May, and July, 1995. This required changing the trapping solution every 4–5 hrs for the dynamic method to avoid saturation. To explore the relative effectiveness of each method at trapping volatilized ammonia within a range of rates observed in the field, we manipulated rates of ammonia loss by applying different amounts of urea in a 0.23 M solution to paired static and dynamic chambers. The volume of solution added to paired chambers was adjusted for the different chamber sizes so that each chamber received the same amount of urea per unit area. Urea-N added to the chambers ranged from 0 to 50 g/m^2 . We performed the calibrations in two grasslands, one dry and one mesic, during April, May and July. Temperatures during the calibrations ranged from -1°C in April and May to 28°C in July. Ammonia-N absorbed by the traps was determined by back-titrating 10ml of boric acid solution with 0.01 N or 0.005N HCl to a point of color change (pH 3.8) using bromocresol green dye.

Experimental conditions

We applied 4 L of an artificial ungulate urine mixture (Stillwell 1983) to three 0.5 m^2 quadrats (51 g urea-N/m^2) at each of the nine sites ($n = 27$) at each of the three times of year. Little is known about the natural levels of urea-N deposited by native ungulates, so this rate was selected to approximate urea-N deposition measured for domesticated cattle (Stillwell 1983) and is similar to levels used in other grassland studies (e.g., Schimel et al. 1986; Ruess & McNaughton 1988; Day & Detling 1990). The solution was added slowly with a sprinkling can and the quadrat was enclosed with aluminum flashing buried several centimeters in the soil to limit leakage from the quadrat. Static chamber traps

were replaced every 24 hrs. Chambers were moved to a new location within each quadrat at the beginning of each 24 hr sampling period to limit chamber effects on soil moisture. Ammonia lost from control sites located next to urea-treated quadrats was also measured. We continued measuring volatilization from urine-treated quadrats until rates reached background, control levels. About 10% of the acid traps froze overnight during the April experiment. Although volatilization was assumed to be low during those periods, overall estimates during April may be slightly underestimated.

Site properties

Soil (0–10 cm) was collected from three random locations with a 5 cm diam corer at each site and pooled. Soil pH, bulk density, field capacity, texture, total C and N, and cation-exchange capacity (CEC) were determined on pooled samples for each site. Soil pH was measured in a 1:1, soil:deionized water paste and texture was determined with the hydrometer method (Gee & Bauder 1986). Soil C and N were measured on a Carlo Erba 1500 Analyzer and CEC was determined using the NH_4^+ saturation method (Chapman 1986). Peak aboveground plant biomass was determined from five randomly located 20×50 cm clipped quadrats at each site. Clipped plants were dried at 65°C for at least 72 hrs then weighed.

Statistical analysis

Ammonia volatilization during each 24 hr incubation was derived from the calibration between static and dynamic chamber methods (see *Results*). We analyzed the total ammonia-N lost from urine-amended soil (from urine application until rates reached background levels) with a split-plot design ANOVA with landscape (Stevens CK, Mammoth, Blacktail) and topographic position (hilltop, mid-slope, bottom-slope) considered to be main plot effects and time (April, May, July) analyzed as a subplot effect (Petersen 1985). Correlation analyses were used to explore soil and plant factors associated with ammonia loss.

Results

Method calibration

Ammonia absorbed by the static method was strongly and linearly related to that absorbed by the dynamic method (Figure 2) and the relationship did not appear to differ between the dry and mesic grassland sites. This

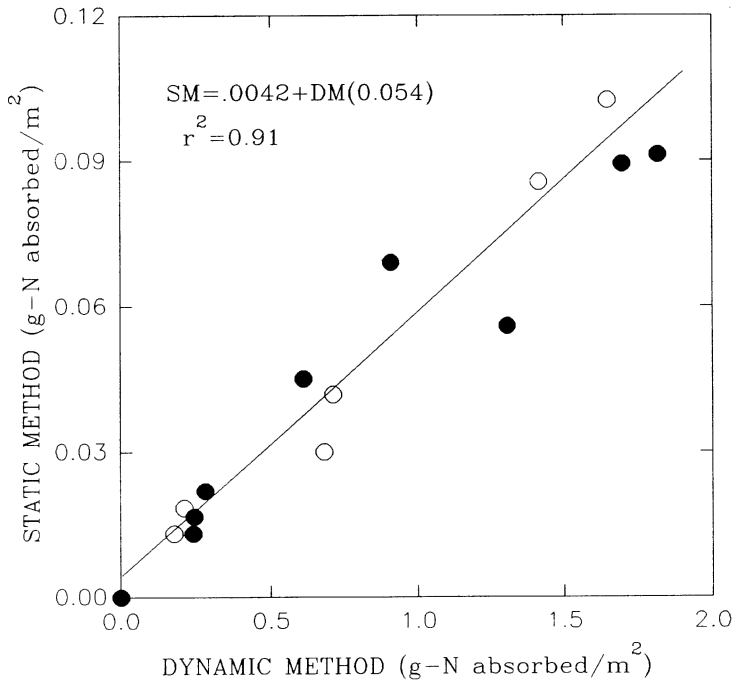


Figure 2. Relationship of ammonia trapping efficiency between static and dynamic chamber methods. Closed and open circles are dry and wet grasslands, respectively.

result indicated that the trapping efficiency of the methods was not affected by rates of ammonia volatilized from the plots, and, most importantly, the static method could be used as a reasonable indirect measure of ammonia volatilization. Rates of ammonia loss reported below are determined from static chamber measures that have been adjusted with this calibration.

Site properties

Soils were sandy loams, except those at Stevens Ck, which had higher clay contents. Bulk density, percent clay, C, N, CEC, and plant biomass tended to increase downslope; although Stevens Ck was again exceptional with respect to clay content and CEC (Table 2).

Ammonia volatilization rates

Background levels of ammonia loss were reached within 11 days after urine was applied (Figure 3). During the April and May experiments, ammonia loss increased through day 3, then declined. In contrast, in July, rates monotonically

Table 2. Study site soil characteristics.

Site	pH	Bulk density (g/cm ³)	Field capacity (% H ₂ O)	USDA texture categories (%)			Soil classification	C (%)	N (%)	CEC (cmol/kg soil)	Plant biomass (gm ²)
				Sand	Silt	Clay					
Stevens Ck											
T	8.0	1.3	30.0	48.9	12.8	38.3	Sandy clay	0.77	0.07	48.9	58
M	7.1	1.4	18.0	63.1	15.3	21.6	Sandy clay loam	1.3	0.12	25.8	71
B	6.4	1.2	30.9	42.6	21.5	35.9	Clay loam	2.6	0.25	38.7	105
Mammoth											
T	7.5	1.4	17.8	67.6	17.1	15.3	Sandy loam	3.0	0.30	23.7	51
M	6.6	1.3	20.9	60.1	21.1	18.7	Sandy loam	3.1	0.28	29.5	54
B	8.0	1.1	29.2	56.1	23.2	20.7	Sandy loam	6.5	0.58	46.0	310
Blacktail											
T	7.2	1.4	15.9	61.5	24.3	14.3	Sandy loam	1.8	0.18	13.2	70
M	6.8	1.4	16.6	71.5	17.3	11.2	Sandy loam	2.2	0.20	20.0	54
B	5.6	1.0	28.6	57.3	24.4	18.3	Sandy loam	4.1	0.26	30.7	134

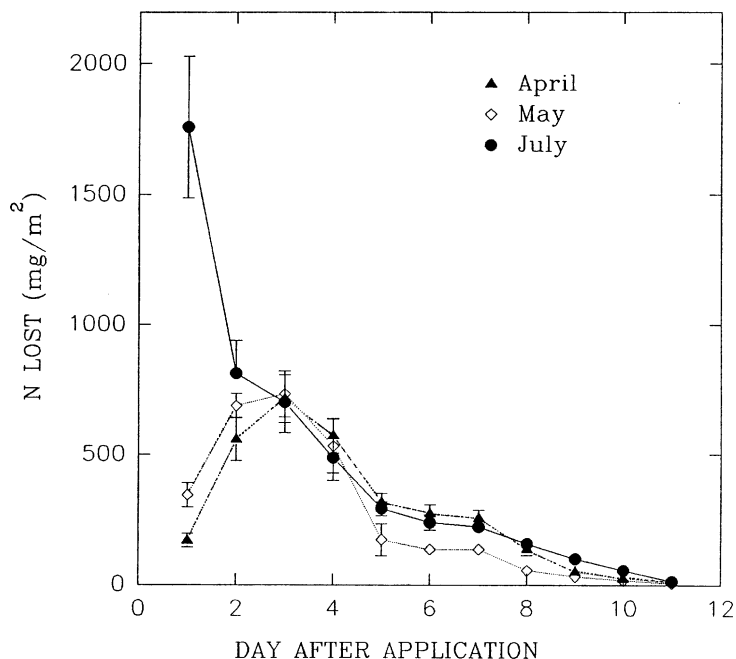


Figure 3. Average 24 hr rates of ammonia volatilization during the April, May, and July experiments. Bars are $\pm$ one standard error.

cally declined after day 1, which were the highest 24 hr rates observed during the study.

The amount of ammonia-N volatilized among the sites varied considerably, ranging from 0.6 g-N/m² at Stevens Ck hilltop during April to 12.2 g-N/m² at Blacktail hilltop during July (Figure 4). These values represent 1% and 24% of the urea-N added, respectively. ANOVA results indicated that ammonia loss was affected by landscape ($F_{2,18} = 15.4$, $P < 0.0001$), topographic position ($F_{2,18} = 47.4$, $P < 0.0001$), and season ($F_{2,36} = 62.7$, $P < 0.0001$); strong landscape*topographic position ($F_{4,18} = 51.57$, $P < 0.0001$) and season*landscape ($F_{4,36} = 25.6$, $P < 0.0001$) effects were also observed. These statistical results are reflected in Figure 4: (1) The Blacktail sites averaged the highest rates of ammonia loss among the sites during the study, (2) July rates tended to be highest, (3) ammonia loss declined from hilltop to slope-bottom, except at Stevens Ck, and (4) there was a particularly large efflux of ammonia from the Blacktail sites in July relative to earlier measurements. Note that the high ammonia loss at Blacktail in July was due to unusually elevated rates during day 1 of that experiment, which was largely responsible for the high day 1 value averaged across all sites in July (Figure

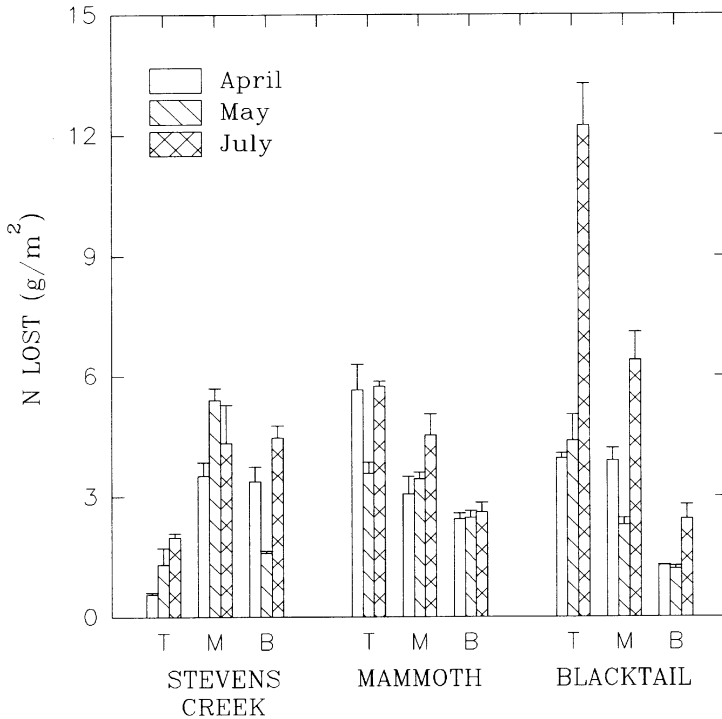


Figure 4. Ammonia loss from hilltop (t), mid-slope (m) and slope-bottom (b) sites on 3 landscapes during the 3 seasonal experiments. Bars denote one standard error.

3). The unexplained (residual) error was 4% of the measured variation in the study, indicating that variation at the microsite scale (0.5 m^2) contributed little to the spatial heterogeneity of ammonia loss across this grassland.

Correlations of ammonia loss with site properties

Correlations between ammonia loss and soil properties across all landscapes and positions were qualitatively the same for each seasonal measurement, so we present relationships for mean seasonal measurements only. Ammonia loss was negatively correlated with CEC (Figure 5). CEC was a function of a combination of soil clay and carbon content. Plant biomass positively influenced CEC through its effect on soil C content. Unlike several other studies (e.g., Ernst & Massey 1960; Ruess & McNaughton 1988), we did not find soil pH to be associated with ammonia volatilization ($P > 0.87$).

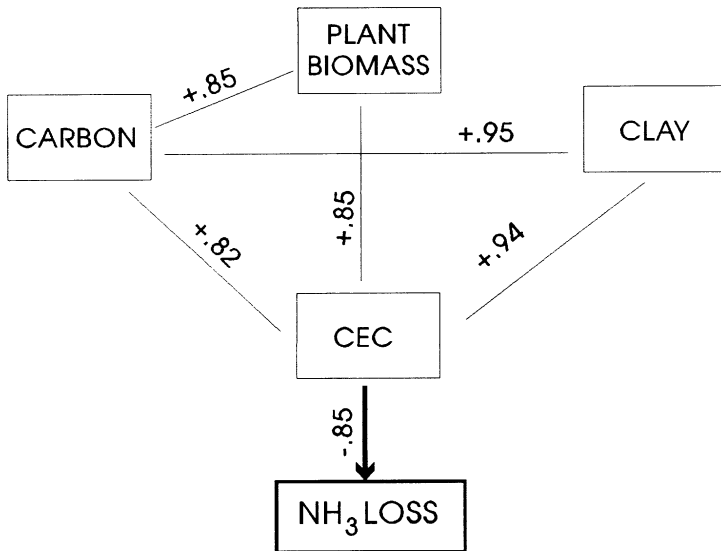


Figure 5. Correlations ($P < 0.05$) between ammonia-N volatilized from urine patches (g/m^2) and CEC, and among soil properties that directly or indirectly determine CEC. Numbers are coefficients.

Discussion

These results indicate large spatial and temporal variation in ammonia loss from urine patches in Yellowstone Park grassland. Ammonia volatilization varied 24-fold among sites during the three sampling periods, indicating seasonal and topographic effects are important when considering landscape level rates of gaseous N loss.

Ammonia loss was elevated in July when relatively high temperatures likely increased rates of urea hydrolysis. Volatilization was strongly and negatively related to soil CEC (Figure 5), which has been shown to contribute to reducing ammonia loss in other grasslands (Campbell et al. 1984; Ruess & McNaughton 1988), probably by increasing NH_4^+ adsorption to exchange sites. Clay and organic matter content, two components of CEC, are influenced by topography, usually increasing from hilltop to slope-base in Yellowstone grassland (Frank 1990), explaining the effect of topography on ammonia loss. This pattern was observed at Mammoth and Blacktail, where soils represent those typical of most of the northern winter range, and ammonia loss tended to decline from the top to bottom of slopes (Figure 3). In contrast, ammonia loss at Stevens CK was lowest on the hilltop, presumably in part due to the relatively high clay content at that site.

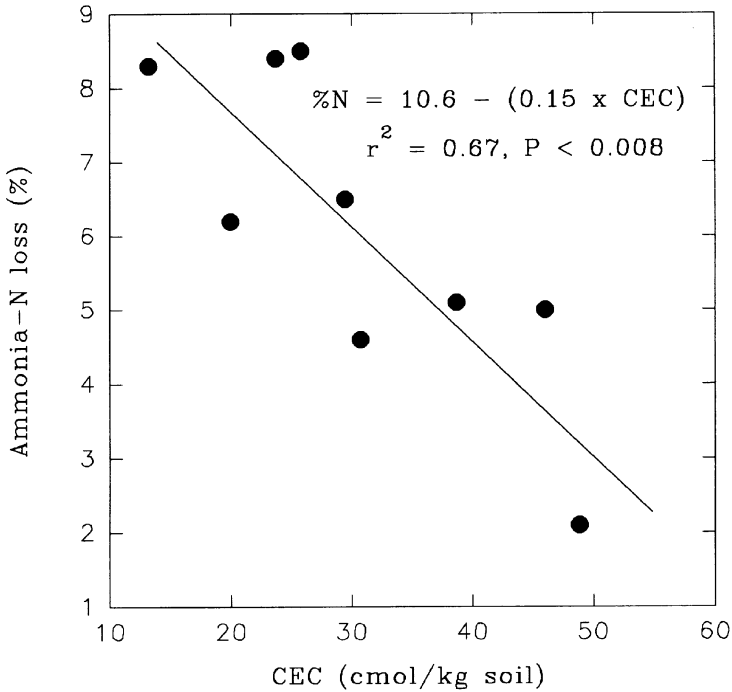


Figure 6. The relationship between percent ammonia-N volatilized of N applied to urine-amended plots and CEC.

In a previous study of N cycling on the northern winter range (Frank et al. 1994), the flux of ungulate urea-N to the soil at five topographically diverse sites in a watershed (hilltop, benches, slope, riparian) on the Blacktail Plateau was estimated from the levels of fecal-N deposited and the allometric relationship for the proportions of N lost from ungulates in urine vs feces. Here we estimated the annual rate of ammonia-N volatilized from these five sites using the relationship between the percent of urine-N lost and soil CEC, determined in this study (Figure 6). This relationship was calculated using April and May measurements only, since the preponderance of herbivores were off the winter range in July. In other words, the amount of urea-N volatilized from the sites was calculated by multiplying the urine-N deposited at the sites by the proportion of that N volatilized, derived with CEC values for the sites and the regression in Figure 6.

Ammonia-N lost from these five Blacktail sites ranged 0.4–2.4 ka/ha/yr. Most of the variation between sites was due to variability in urine-N deposited (6–26 kg/ha/yr), as opposed to variation resulting from differences in CEC (22.7–29.5 cmol/kg soil). This indicates the importance of understanding spatially nonuniform patterns of ungulate use in heterogeneous grassland

landscapes to determine ecosystem-level rates of gaseous N loss. Mean annual ammonia-N lost from the five sites was 1.4 kg/ha/yr. Although not a true landscape-level estimate, since it does not include the spatial extent of each of the types of sites in the calculation, this value does suggest that ammonia lost from urine patches in this ecosystem is at least compensated by atmospheric N deposition (2 kg N/ha/yr; Swank 1984). In addition, because ungulates concentrate on the lower winter range, where the Blacktail Plateau is located, during the 7 mo. winter (Houston 1982), the flux of urea-N to the soil is probably higher on the Blacktail Plateau than much of the rest of the northern range, including transitional and summer ranges (Frank 1990). Therefore, if effects of soil CEC are equal throughout the northern range, annual rates of ammonia volatilization from the Blacktail Plateau sites likely overestimate ecosystem-level rates. Interestingly, in the Serengeti Ecosystem of East Africa, the only other grassland with abundant free-roaming native ungulates where ammonia volatilization has been measured (Ruess & McNaughton 1988), the rate of ammonia-N volatilized from urine patches was also at least compensated by atmospheric N deposition.

The spatiotemporal variation in ammonia loss from grassland is a combination of (1) soil and micrometeorological factors that influence volatilization, and (2) the interaction of ungulates with their forages that produces nonuniform deposition of urine across landscapes, suggesting the importance of considering spatiotemporal linkages between soils and herbivores to understand N gaseous loss from grazed grassland. Although N passing through herbivores can be substantial in Yellowstone grassland (Frank et al. 1994), N volatilized from urine patches is probably at least balanced by atmospheric deposition. Similar findings in the Serengeti Ecosystem suggest that, in general, ammonia volatilization from urine patches should not lead to a decline in soil N in grasslands that support large herds of native ungulates.

Acknowledgements

We are indebted to S. J. McNaughton for use of his dynamic chamber equipment and R. Ruess for invaluable guidance on the method. Comments by S. J. McNaughton, W. Peterjohn, and D. S. Schimel assisted substantially in efforts to improve early drafts of the paper. Help from L. G. Schlenker was critical in making field measurements. This study was supported by NSF grant DEB-9408771.

References

- Black AS, Sherlock RR, Cameron KC, Smith, NP & Goh KM (1985) Comparison of three field methods for measuring ammonia volatilization from urea granules broadcast on to a pasture. *Journal of Soil Science* 36: 271–280
- Bouwmeester RJB, Vlek PLG & Stumpe JM (1985) Effect of environmental factors on ammonia volatilization from urea-fertilized soil. *Soil Science Society of America Journal* 49: 376–381
- Campbell CA, Myers RJK, Vatchpoole VR, Vallis I & Weier KL (1984) Laboratory study of transformation and recovery of urea-N in three Queensland soils. *Australian Journal of Soil Research* 22: 433–441
- Chapman HD (1986) Cation-exchange capacity. In: Klute A (Ed) *Methods of Soil Analysis*. Second Edition. Agronomy Monograph 9, Part 2 (pp 891–901). Soil Science Society of America, Madison, Wisconsin, USA
- Day, TA & Detling JK (1990) Grassland patch dynamics and herbivore grazing preference following urine deposition. *Ecology* 71: 180–188
- Denmead OT, Simpson JR & Freney JR (1974) Ammonia flux into the atmosphere from a grazed pasture. *Science* 185: 609–610
- Ernst JW & Massey HF (1960) The effect of several factors on volatilization of ammonia formed from urea in the soil. *Soil Science Society of America Proceedings* 24: 87–90
- Frank DA (1990) Interactive ecology of plants, large mammalian herbivores and drought in Yellowstone National Park. Dissertation. Syracuse University, Syracuse, NY
- Frank DA & McNaughton SJ (1992) The ecology of plants, large mammalian herbivores and drought in Yellowstone National Park. *Ecology* 73: 2043–2058
- Frank DA, Inouye RS, Huntly N, Minshall GW & Anderson JE (1994) The biogeochemistry of a north-temperate grassland with native ungulates: Nitrogen dynamics in Yellowstone National Park. *Biogeochemistry* 26: 163–188
- Gee GW & Bauder TW (1986) Particle size analysis. In: Klute A (Ed) *Methods of Soil Analysis*. Second Edition. Agronomy Monograph 9, Part 1 (pp 283–311). Soil Science Society of America, Madison, Wisconsin, USA
- Knapp AK, Fahnestock SP, Hamburg LB, Statland LB, Seastedt TR & DS Schimel (1993) Landscape patterns in soil-plant water relations and primary production in tallgrass prairie. *Ecology* 74: 549–560
- Houston, DB (1982) *The Northern Yellowstone Elk: Ecology and Management*. Macmillan Publishing, New York
- McNaughton SJ (1979) Grassland-herbivore dynamics. In: Sinclair ARE & Norton-Griffiths M (Eds) *Serengeti: Dynamics of an Ecosystem* (pp 46–81). University of Chicago Press, Chicago
- McNaughton SJ (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55: 259–295
- Musa MM (1968) Nitrogenous fertilizer transformations in the Sudan Gezira soils: I. Ammonia volatilization losses following surface application of urea and ammonium sulfate. *Plant and Soil* 28: 413–421
- NOAA [National Oceanic and Atmospheric Administration] (1990) Climatological data for Wyoming. United States Department of Commerce, Washington, DC, USA
- O'Toole P, Morgan MA & McAleese DM (1982) Effects of soil properties, temperature and urea concentration on patterns and rates of urea hydrolysis in some Irish soils. *Irish Journal of Agricultural Research* 21: 185–197
- Petersen RG (1985) Design and Analysis of Experiments. Statistics: Textbooks and Monographs, Vol. 65. Marcel Dekker Inc., New York, New York
- Ruess RW & McNaughton SJ (1988) Ammonia volatilization and the effects of large grazing mammals on nutrient loss from East African grasslands. *Oecologia* 77: 382–386

- 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
- Schimel DS, Kittel TGF, Knapp AK, Seastedt TR, Parton WJ & Brown VB (1991) Physiological interactions along resource gradients in a tallgrass prairie. *Ecology* 72: 672–684
- Schlesinger WH & Peterjohn WT (1991) Processes controlling ammonia volatilization from Chihuahuan desert soils. *Soil Biology and Biochemistry* 23: 637–642
- Seastedt TR, Briggs JM & Gibson DJ (1991) Controls of nitrogen limitation in tallgrass prairie. *Oecologia* 87: 72–79
- Sellers PJ, Hall FG, Asrar G, Strebel DE & Murphy RE (1988) The first ISLSCP field experiment (FIFE). *Bulletin of the American Meteorological Society* 69: 22–27
- Sherlock RR & Goh KM (1984) Dynamics of ammonia volatilization from simulated urine patches and aqueous urea applied to pasture. I. Field experiments. *Fertilizer Research* 5: 181–195
- Stewart BA (1970) Volatilization and nitrification of nitrogen from urine under simulated cattle feedlot conditions. *Environ Sci Technol* 4: 579–582
- Stillwell MA (1983) Effects of bovine urinary nitrogen on the nitrogen cycle of a shortgrass prairie. Dissertation. Colorado State University, Fort Collins, CO
- Swank WT (1984) Atmospheric contributions to forest nutrient cycling. *Water Resources Bulletin* 20: 313–321
- Vallis I, Harper LA, Catchpoole VR & Weier KL (1982) Volatilization of ammonia from urine patches in a subtropical pasture. *Aust J Agric Res* 33: 97–107
- Wardle DA (1992) A comparative assessment of factors that influence microbial biomass carbon and nitrogen levels in soil. *Biological Review* 67: 321–358
- Woodmansee RG, Dodd JL, Bowman RA & Clark FE (1978) Nitrogen budget of a shortgrass prairie ecosystem. *Oecologia* 34: 363–376