

The role of cattle in the volatile loss of nitrogen from a shortgrass steppe

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Abstract. The cycling and volatile loss of N derived from cattle urine at upland and lowland sites within the shortgrass steppe of eastern Colorado was studied, using ^{15}N -labelled urea as an N source. Losses of NH_3^0 were determined by direct measurement and by difference. Losses were higher from coarse (27% summer, 12% winter) than from fine textured (0–2%) soils. Immobilization and plant uptake of N accounted for significant amounts of added N. Extrapolating our plot measurements to a typical pasture, using spatially and temporally stratified urine deposition data, losses from upland sites were calculated to be $0.016 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, while losses from lowland sites were negligible. This resulted in an average loss of $0.011 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ for a pasture divided 70:30 between uplands and lowlands. The loss of urine N calculated assuming no spatial stratification would be sevenfold higher ($0.076 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$). Losses of NH_3^0 from urine, animal biomass removal, and N_2O loss totaled only $0.07 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, or about 25% of wet deposition input. We calculated a potential loss of NH_3^0 from senescing vegetation of $0.26 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, an order of magnitude larger than all other losses combined.

Introduction

Several roles for large herbivores in grassland nutrient cycling have been suggested, including fertilization effects from urine and feces (Floate, 1982), redistribution of nutrients within a pasture (Hilder and Motterstead 1963, Senft 1982), and loss of volatile N compounds (N_2O , NH_3^0) from urine and feces (Carran et al., 1982; Limmer and Steele 1983; Mosier et al., 1981; Lockyer, 1984). The process of volatile loss is of particular interest in semiarid ecosystems, where it may be the principal pathway for N loss (Woodmansee, 1978). Hydrological output of N is thought to be unlikely in semiarid grasslands, where potential evapotranspiration often greatly exceeds actual evapotranspiration and precipitation and movement of water below

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the rooting zone is infrequent (Parton et al., 1981a). Large losses by denitrification and N_2O flux are unlikely from dry grassland soils (Mosier and Stillwell, 1979; Woodmansee, 1978). The loss of NH_3^0 from herbivore urine is potentially important for both grassland-N budgets (Floate, 1981; Lockyer, 1984) and as a control over NH_3^0 concentrations in the atmosphere (Crutzen, 1983). NH_3^0 plays a role in several important processes in the atmosphere, including NO_x - N_2O conversions and control of rainfall pH (Crutzen, 1983) and so may be important to tropospheric chemistry even at emission rates not significant to ecosystem nitrogen balances (Bolin et al., 1983).

Wide variations in urea hydrolysis and NH_3^0 -loss rates have been reported as a function of a number of soil properties, including organic matter content (O'Toole et al., 1982), H^+ buffering capacity (Ferguson et al., 1984), pH (Ernst and Massey, 1960), CEC (Campbell et al., 1984), and texture (Campbell et al., 1984). These parameters are often correlated (i.e., texture with OM content). Large variations in these properties may occur within relatively small areas (Schimel et al., 1985), so regional budgets based on small plot measurements must account for variations in loss rate within the unit of study. Such a budget must also account for nonuniform deposition of urine (Senft, 1983), since this will control the amount of N available for loss from each soil type.

The objectives of our study were, first, to compute annual losses of N as NH_3^0 from a grazed pasture of the shortgrass. We wanted to account for heterogeneity in both deposition and volatilization rates within the study unit. By including spatial heterogeneity in our study we hoped to increase its generality. Second, we wanted to compare the animal loss vectors with other losses and additions measured at this site to assess the importance of NH_3^0 loss to the site's nutrient budget.

Materials and methods

Site description

All studies were carried out at the United States Department of Agriculture, Agricultural Research Service, Central Plains Experimental Range (CPER). CPER is north of Nunn, Colorado, in Weld County. The site was a north-facing hillside near the head of a small drainage in Range 66W, Township 10N, Section 26. The base elevation was 1641 m, with 12 m of relief over 130 m. Three soils were found along the hillside. The summit, not used in this study, was a Ustic Torriorthent, the backslope was a Ustollic haplargid, and the footslope was a Pachic argiustoll (Soil Survey Staff, 1977). The dominant plant species on all slope positions was blue grama (*Bouteloua gracilis*). Selected soil properties are given in Table 1. These two soils were chosen to represent the range of variation between uplands and lowlands in shortgrass steppe soils. Summit and backslope soils are generally similar

Table 1. Properties of soils used in NH_3^0 -loss studies. Data are for surface horizons

| Soil | Surface horizon depth (cm) | Clay (%) | Organic C ($\mu\text{g} \cdot \text{g}^{-1}$) | Organic N ($\mu\text{g} \cdot \text{g}^{-1}$) |
|--------------------|----------------------------|----------|---|---|
| Ustollic haplargid | 15 | 15.0 | 5700 | 665 |
| Pachic argiustoll | 15 | 26.7 | 20400 | 1937 |

(Schimel et al., 1985a). Detailed soil and vegetation descriptions are given in Schimel et al. (1985a).

^{15}N application and sampling

Microplots were established by driving 10-cm-diameter \times 30-cm-deep stainless-steel pipe over blue grama swards, leaving sufficient lip exposed to attach a cuvette. Separate microplots were established for ^{15}N -budget studies and NH_3^0 volatilization measurements. The backslope soil received two applications of ^{15}N -labelled urea, in August 1981 and January 1982 on separate sets of cores. The footslope received one application, in August 1982. The urea was 10 atom percent ^{15}N (or 50% for the NH_3^0 -loss studies) and was applied at the rate of $53.5 \text{ g N} \cdot \text{m}^{-2}$. This rate was chosen to match typical cattle urination N deposition rates (Stillwell, 1983). The higher atom percent was chosen to increase sensitivity in the NH_3^0 -loss studies. The set of microplots which began in August 1981 was sampled more intensively, with 11 sample dates over 17 months. The other sets of microplots were sampled two or three times following application of the urea to determine initial and final N distributions. In all cases, the first samples were taken within 7–20 d following application.

At each sample date, four replicate microplots were collected. They were separated into plant tops and roots and seven soil depths, 0–2.5, 2.5–5, 5–7.5, 7.5–10, 10–15, 15–20, and 20–30 cm. Coarse roots were sieved out of each depth, using a 1-mm screen, and composited across depths for analysis. A deep core, 30–40 cm, was taken at the last date of the August 1981 experiment to recover any deep ^{15}N .

NH_3^0 measurements

We measured $^{15}\text{NH}_3^0$ and $^{14}\text{NH}_3^0$ evolution following the urea application from each experiment. Ten-cm-diameter, 25-cm-high acrylic plastic, cylindrical cuvettes were attached over four urea-treated and two control microplots. Closed cuvettes have a number of problems when used in the field, especially heat loading and increases in evapotranspiration within the cuvette. We designed our cuvettes and airflow regime so that water loss rates within the cuvette were equivalent to those outside the cuvette, as determined at a nearby weighing lysimeter. We chose to match this parameter because water-loss rates have been shown to be highly correlated with NH_3^0 -flux rates (reviewed in Freney et al., 1981). Water was added in

amounts equal to precipitation following rain events. The cuvettes were designed to maximize mixing within the chamber and hinder establishment of a boundary layer that would inhibit NH_3^0 exchange. Accordingly, the air input was set at ground level and the output near the top of the cuvette. An electric powered fan situated at the top of the cuvette further increased mixing rate within the chamber. We used airflow rates of $33\text{--}67\text{ ml} \cdot \text{s}^{-1}$ in the daytime and $8\text{ ml} \cdot \text{s}^{-1}$ at night, which resulted in good agreement between within- and without-cuvette water loss rates and a maximum increase in temperature of 6°C within the cuvette. Mixing in the chamber was evaluated using two techniques. First, a smoke bomb was placed in the inlet line, and smoke patterns observed to ensure that there were no unmixed areas. Second, water loss rates from a free water surface were evaluated. Loss rates increased sharply up to $25\text{ mL} \cdot \text{s}^{-1}$. Above $25\text{ mL} \cdot \text{s}^{-1}$, loss rates increased slowly. We assumed that boundary layer effects were minimized at $25\text{ mL} \cdot \text{s}^{-1}$, and only used lower rates when necessary to match nighttime water loss rates.

The input and output airstreams from the cuvettes were passed through a packed-tower-type acid trap (Gisclard, 1945) composed of $5\text{ mol} \cdot \text{L}^{-1} \text{H}_2\text{SO}_4$. The efficiency of these traps at airflow rates used was $> 95\%$. The traps were changed frequently and analyzed colorimetrically for NH_4^+ , as below.

Chemical and isotope analysis

Total N in plants and soils was determined using the method of Nelson and Sommers (1980). Digests were analyzed for NH_4^+ colorimetrically. NH_4^+ and NO_3^- were determined colorimetrically on 2 mol/L KCl extracts using a Technicon I (Schimel et al., 1985a). Ash contents for shoot and root samples were determined by loss on ignition. Soil pH determinations were made on saturated soil pastes. Digests and KCl extracts were prepared for ^{15}N analysis using the diffusion procedure suggested by Adamsen and Reeder (1983). ^{15}N analyses were performed by Isotope Services, Inc., in Los Alamos, New Mexico. ^{15}N was determined for NH_4^+ alone and $\text{NH}_4^+ + \text{NO}_3^-$, using Devarda's alloy to reduce the nitrate. $^{15}\text{NO}_3^-$ was calculated by subtracting NH_4^+ from $\text{NH}_4^+ + \text{NO}_3^-$. Root ^{15}N was corrected for soil contamination using root-ash content as an estimate of soil contamination (Clark, 1977), using the following equation:

$$\begin{aligned} \text{Corrected root } ^{15}\text{N} = & \text{uncorrected root } ^{15}\text{N} \\ & - (\text{total root mass})(\text{ash content})(\text{soil-N content}) \\ & \quad (^{15}\text{N excess in soil}). \end{aligned}$$

Values of soil-N and $-^{15}\text{N}$ content used were average values over depths weighted by the proportion of roots from each depth. Since the majority of the roots were in the 0- to 10-cm increment, where the ^{15}N was also concentrated, this resulted in a significant correction (10–20%).

Results and discussion

Fate of ^{15}N -urea in soil

Hydrolysis of urea in shortgrass steppe soils is rapid, as is typical of undisturbed soils in general (Reynolds et al., 1985). No ^{14}N or ^{15}N urea was detected at or after the first sample date in any of the current studies, and complete hydrolysis of simulated urine urea generally occurs within 4–7 d at this site (Stillwell and Woodmansee, 1981). The urea penetrated quite deeply (7.5–15 cm), as can be seen by significant increases in pH (in the backslope) and high inorganic and organic ^{15}N values by depth at the first dates in Table 4. No increase in pH was observed at the first sample date in the rather acid (5.2) footslope soil as a result of urea hydrolysis.

Immobilization of ^{15}N into organic matter occurred rapidly after addition of urea in all experiments (Figure 1, Tables 2, 3). A stable level of ^{15}N organic matter was reached rapidly in all experiments and appeared to be a characteristic of each soil. Both summer and winter applications of ^{15}N to the backslope resulted in stable levels of about 10–11 g organic N \cdot m $^{-2}$. A pulse of immobilization, followed by rapid mineralization occurred in spring 1982

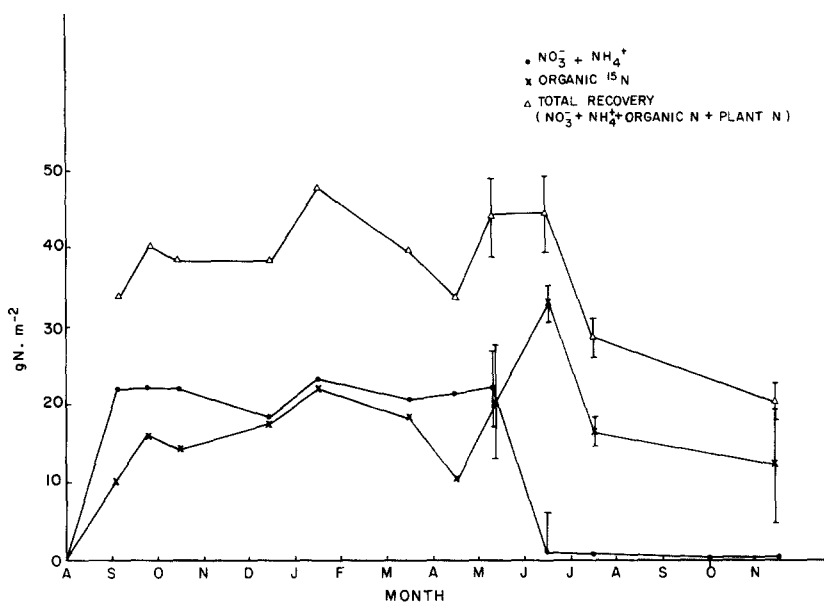


Figure 1. Time dynamics of organic ^{15}N , inorganic ($\text{NH}_4^+ + \text{NO}_3^-$) ^{15}N , and total recovery (organic + inorganic + plant uptake) in the long-term study, using the backslope soil. There were no significant differences over the first six dates and so they were averaged to yield an estimate of volatile loss. 95% confidence intervals are shown during the latter part of the experiment, where significant changes occurred.

Table 2. Long-term experiment using the backslope depth distributions of organic N, NO_3^- , NH_4^+ and pH at selected dates, showing depth of urea penetration and springtime leaching of $^{15}\text{NO}_3^-$. Values are ^{15}N recovery in a pool divided by the enrichment of the added urea (10%). ^{15}N -urea was added on 08/18/81

| Depth | Organic ^{15}N (g added $\text{N} \cdot \text{m}^{-2}$) | | | | Depth | $^{15}\text{NO}_3^-$ (g added $\text{N} \cdot \text{m}^{-2}$) | | | |
|-------------|---|------|-------|------|-------------|--|------|------|------|
| | S81** | F82 | J82 | Jy82 | | S81 | F82 | J82 | N82 |
| 0 - 2.5 | 2.00 | 6.00 | 4.40 | 2.40 | 0 - 2.5 | 0.20 | 0.60 | ND | 0.10 |
| 2.5 - 5.0 | 1.40 | 2.00 | 4.60 | 1.90 | 2.5 - 5.0 | 0.30 | 0.60 | ND | 0.20 |
| 5.0 - 7.5 | 2.90 | 6.70 | 11.00 | 3.40 | 5.0 - 7.5 | 0.50 | 1.70 | ND | 0.10 |
| 7.5 - 10.0 | 3.00 | 7.00 | 4.90 | 2.50 | 7.5 - 10.0 | ND | ND | 2.30 | ND |
| 10.0 - 15.0 | 0.50 | 1.50 | 2.50 | 1.10 | 10.0 - 15.0 | ND | ND | 1.40 | ND |
| 15.0 - 20.0 | 0.60 | 1.00 | 3.90 | 2.00 | 15.0 - 20.0 | ND | ND | ND | ND |
| 20.0 - 30.0 | 0.30 | 0.00 | 1.50 | 2.90 | 20.0 - 30.0 | ND | ND | ND | 1.20 |
| 30.0 - 40.0 | * | * | * | * | 30.0 - 40.0 | * | * | * | * |
| pH | | | | | | | | | |
| Depth | $^{15}\text{NH}_4^+$ (g added $\text{N} \cdot \text{m}^{-2}$) | | | | Depth | $^{15}\text{NH}_4^+$ (g added $\text{N} \cdot \text{m}^{-2}$) | | | |
| | S81 | F82 | J82 | Jy82 | | S81 | F82 | J82 | N82 |
| 0 - 2.5 | 7.5 | 7.1 | 5.7 | 5.3 | 0 - 2.5 | 6.30 | 4.40 | 0.40 | 0.10 |
| 2.5 - 5.0 | 7.8 | 7.2 | 5.6 | 5.0 | 2.5 - 5.0 | 5.90 | 4.40 | ND | 0.30 |
| 5.0 - 7.5 | 7.5 | 7.1 | 5.6 | 5.1 | 5.0 - 7.5 | 8.90 | 8.30 | ND | 0.50 |
| 7.5 - 10.0 | 7.2 | 6.8 | 5.9 | 5.4 | 7.5 - 10.0 | ND | ND | ND | ND |
| 10.0 - 15.0 | 6.9 | 6.9 | 6.5 | 6.3 | 10.0 - 15.0 | ND | ND | ND | ND |
| 15.0 - 20.0 | 7.2 | 7.2 | 6.9 | 6.9 | 15.0 - 20.0 | ND | ND | ND | ND |
| 20.0 - 30.0 | 7.4 | 7.5 | 7.5 | 7.4 | 20.0 - 30.0 | ND | ND | ND | ND |
| 30.0 - 40.0 | * | * | * | * | 30.0 - 40.0 | * | * | * | * |

* Not sampled

** September, February, June, July, November

ND = Not detected.

Table 3. Results from winter application (12/07/81) of ^{15}N urea to a backslope soil, showing initial recovery and subsequent losses. Values are ^{15}N recovery \div enrichment of added urea (10%)

| | Date | |
|---|--|-----------------|
| | 12/14/81 | 11/03/82 |
| | ---- (g added N \cdot m $^{-2}$) ---- | |
| Shoot ^{15}N | 0.26 ± 0.04 | 1.38 ± 1.12 |
| Root ^{15}N | 0.60 ± 0.18 | 5.84 ± 0.78 |
| Inorganic ^{15}N ($\text{NO}_3^- + \text{NH}_4^+$) | 36.2 ± 2.4 | 0 |
| Organic ^{15}N | 10.6 ± 3.4 | 11.4 ± 1.0 |
| NO_3^- ^{15}N | 0 | 0 |
| Total | 47.66 | 18.62 |

of the long-term study (Figure 1). This may have resulted from immobilization into recently dead roots, followed by rapid decomposition and release of that N, much of which may have been leached. The higher organic matter foot-slope soil (Table 1) immobilized more N, 20–30 g organic N \cdot m $^{-2}$, than the backslope did, presumably because of higher carbon stocks available for microbial growth and lower organic-N turnover rates (Schimel et al., 1985).

Inorganic-N levels in the long-term study were stable throughout the winter at levels of 20–23 g N \cdot m $^{-2}$ until May 1982, when they declined rapidly. At that time, high rates of nitrification occurred. The high rates of NO_3^- production were accompanied by a marked decline in soil pH (Figure 2) resulting from the release of H^+ associated with NH_4^+ oxidation. Much of the NO_3^- produced may have leached below our cylinders, as can be seen in Table 4, where $^{15}\text{NO}_3^-$ can be seen moving deeper into the profile over time. We cannot account for all springtime N losses from the footslope soil (\sim g \cdot m $^{-1}$) by leaching, but N_2O losses from urine patches have been shown to be negligible (Mosier et al., 1981). This method is probably not sensitive enough to quantitatively measure leaching. Leaching may be more important than previously thought at this site. The steady incorporation of ^{15}N into organic matter at depth (Table 4) is further evidence for downward movement of N as NO_3^- . Labelled N may also have been translocated in growing roots. In any case, NO_3^- leached below our cylinder probably moved laterally downslope and, since roots are found as deep as 1 m, probably did not constitute a loss to the system. A similar leaching of NO_3^- apparently occurred following the winter application to the backslope (Table 2), but not in the finer-textured footslope, where substantial inorganic N remained at the end of the study (Table 3).

Plant uptake accounted for about 10 g N \cdot m $^{-2}$ by July 1982, with the majority of the N in the roots (Figure 3). During fall 1982, 2.5 g N \cdot m $^{-2}$ was lost from aboveground plant parts (Fig. 3). A maximum of 1 g N \cdot m $^{-2}$ reappeared in the roots, suggesting translocation; but 1.5 g N \cdot m $^{-2}$ was

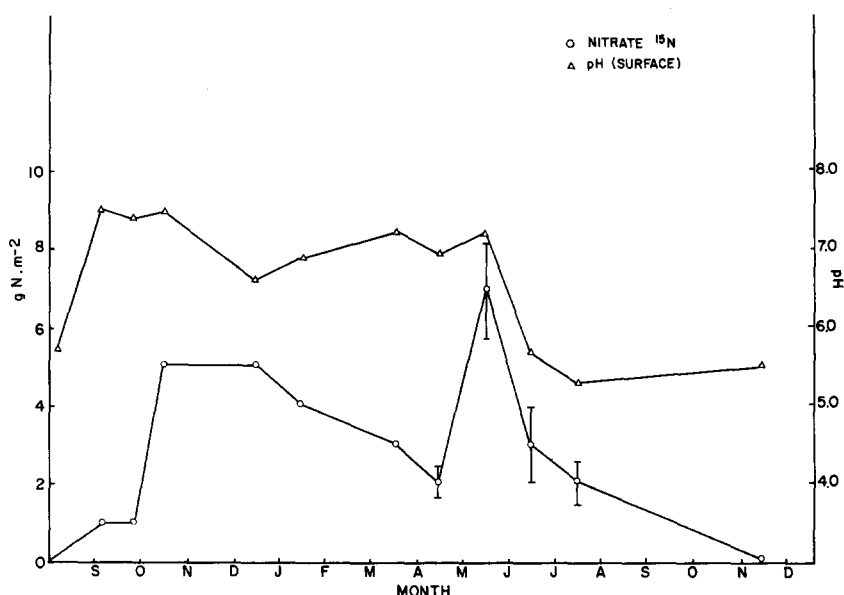


Figure 2. Total NO_3^- and surface pH, showing the correlation between nitrification and decline in pH during spring for the long-term study, using the backslope soil. Note the initial increase in pH resulting from urea hydrolysis. 95% confidence intervals for NO_3^- are shown when significant changes occurred. Initial and springtime changes in pH were significant at $P < 10^{-3}$.

lost, perhaps as NH_3^0 (Farquhar et al. 1979). There was no significant loss of shoot mass during this interval, so this loss could not have been due to grazing or shattering. Less loss was apparent in the footslope ($0.65 \text{ g N} \cdot \text{m}^{-2}$), and translocation of $1.5 \text{ g N} \cdot \text{m}^{-2}$ occurred (Table 3).

N losses from the shortgrass ecosystem

Nitrogen-recovery values were calculated for each replicate core and mean values calculated. The first six dates were averaged for the long-term study, since no trend was observed during that period. In all other studies, recovery at the first sample dates were used. Significant effects ($P < 0.05$) of time of year and soil type on ^{15}N recovery occurred, based on the difference between initial recovery and amount added. Highest initial losses of N occurred from the summer application of urea to the backslope, next highest from the winter application, and lowest from the footslope. The initial losses computed were 27, 12, and 0%, respectively. Losses derived from NH_3^0 scrubbers were comparable at 30, 8.0, and 1.7%. Measurements of loss based on recovery of $^{14}\text{NH}_3^0$ and $^{15}\text{NH}_3^0$ in scrubbers were not significantly different (Figure 4). These proportional losses are comparable to those reported elsewhere (Vallis et al., 1982; Ball et al., 1979). Several factors may account

Table 4. ^{15}N distribution following addition (on 07/25/82) of labelled urea to a foot-slope soil. Values are ^{15}N recovery \div enrichment of added urea (10%)

| | Date | | |
|---|--------------------------------|-----------------|----------------|
| | 08/03/82 | 08/11/82 | 11/03/82 |
| | (g added N \cdot m $^{-2}$) | | |
| Shoots | 0.90 ± 0.75 | 3.15 ± 1.0 | 1.0 ± 0.40 |
| Roots | 2.20 ± 0.25 | 3.5 ± 0.5 | 5.0 ± 0.75 |
| Inorganic ($\text{NO}_3^- + \text{NH}_4^+$) | 21.0 ± 1.0 | 22.5 ± 4.5 | 21.5 ± 3.0 |
| Organic | 19.5 ± 3.0 | 30.0 ± 7.0 | 33.0 ± 3.0 |
| NO_3^- | 4.5 ± 3.0 | 15.0 ± 11.0 | 21.5 ± 3.5 |
| Total | 43.6 | 59.15 | 60.5 |

for the spatial and temporal variations, including water-loss rate, CEC, rate of uptake by organic matter and microorganisms, water dynamics, and depth of penetration (Parton et al., 1981b). In our study these factors were confounded in that one soil had high OM, high CEC, low pH, and high microbial activity, while the other had the opposite characteristics. We cannot separate the relative importance of these effects, since they acted in concert to

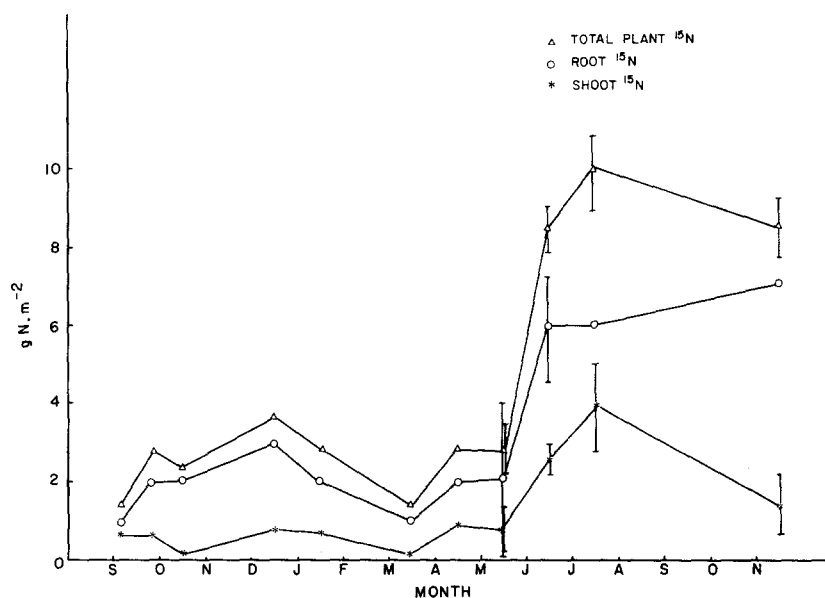


Figure 3. Dynamics of ^{15}N in plant parts for the long-term study, using the backslope soil. No significant uptake occurred until spring. Retranslocation and loss of plant N can be seen between August and November of the study. 95% confidence intervals are shown when significant changes occurred. Note that changes in root ^{15}N during 6/82–11/82 were not significant.

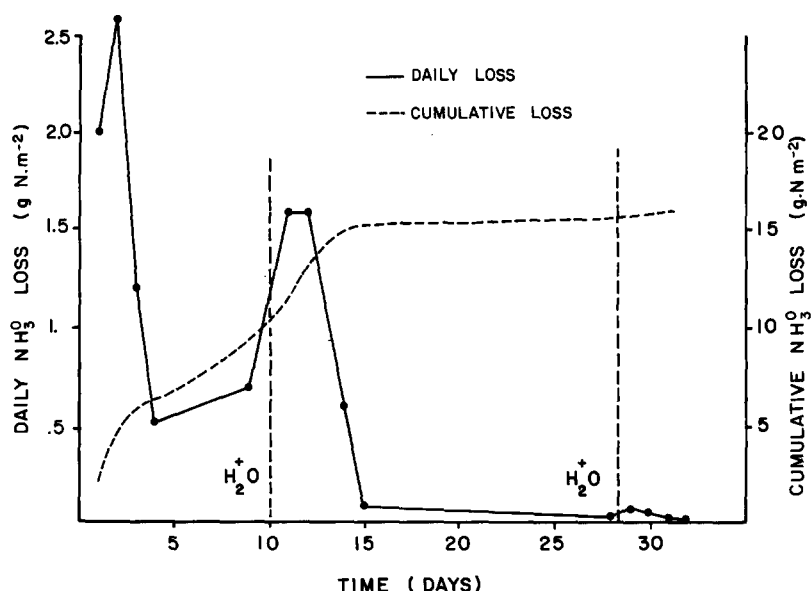


Figure 4. Cumulative and daily loss rates of NH_3^0 for the first 35 days of the long-term experiment, using the backslope soil. Data are derived from scrubbers. Water in amounts equal to natural precipitation was added on days 10 and 30.

produce the observed contrast. Additions of water stimulated NH_3^0 emission at 10 d after application but not at 30 d. We do not have sufficient soil data during this interval to explain this difference (Fig. 4).

We extrapolated the NH_3^0 losses observed in this study to a typical pasture of the shortgrass steppe, using seasonal rates of urine and feces deposition, stratified by landscape position, obtained by Senft (1982) and Stillwell (1983). Cattle responses to microclimate and forage availability result in differential use of upland and lowland areas of pastures. These patterns are described in detail in Senft et al. (1983, 1985). Urine deposition was higher during the growing season, when forage-N levels were higher (Senft 1982), and highest in lowland soils (Table 5). We used our rates for the footslope and the backslope as representative of lowland and upland (slope plus hill-tops) areas, respectively. We assumed the backslope rates were applicable to hilltops because soil properties, plant production, and cattle behavior are generally similar in these two landscape components. We assumed that losses of NH_3^0 were negligible in lowland soils and that rates of loss from upland soils were 27 and 12% in the growing and dormant seasons. This yielded estimates of NH_3^0 loss for the lowlands of $0 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ and for the uplands of $0.016 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ (0.015 summer and 0.001 winter). We assume that losses from feces are low relative to urine losses. The study

Table 5. Temporal and spatial partitioning of cattle urine and feces deposition for use in loss calculations (after Senft 1983). Maximum deposition was found in sites where loss rates are negligible.

| Season | N deposition by landscape component ($\text{g N} \cdot \text{m}^{-2}$) | | | |
|-------------------|--|-------|--------|-------|
| | Lowland | | Upland | |
| | Urine | Feces | Urine | Feces |
| Growing (Apr–Oct) | 0.211 | 0.146 | 0.059 | 0.041 |
| Dormant (Nov–Mar) | 0.036 | 0.072 | 0.011 | 0.023 |
| Total | 0.247 | 0.218 | 0.070 | 0.064 |

pasture was approximately 70% uplands (Schimel et al., 1985b), so an average annual value for the entire pasture would be $0.011 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$. This loss is less than the estimated N_2O flux rate for this region of $0.05 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ (Mosier et al., 1981; Mosier and Parton, 1985). The loss rates of NH_3^0 and N_2O combined account for approximately 25% of wet deposition of N at this site, which averages $0.30 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ (NADP 1982). Loss rates would be higher from a pasture lacking substantial areas of lowland soils and vegetation. If all urine deposition in our study pastures had occurred on upland sites, losses of NH_3^0 would have been $0.076 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, or 25% of wet deposition. This number is sevenfold higher than the value calculated above and is the value we would have arrived at had we not included spatial patterns of deposition and loss in our study. Studies of gaseous emissions may be particularly vulnerable to this type of error, since volatile losses may occur intermittently and be patchily distributed in space.

Several other loss vectors occur. Removal of N in animal biomass at a light-moderate stocking rate, corrected for additions in supplemental feed of $0.015 \text{ g N} \cdot \text{m}^{-2}$, is about $0.009 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$ (Senft 1983). The largest remaining potential loss is volatilization of NH_3^0 from non-urine-affected plants (Farquhar et al., 1980). We calculated this potential loss rate as follows:

$$\begin{aligned} \text{Average plant biomass above ground} &= 86 \text{ g m}^{-2} \\ [200 \text{ g m}^{-2} \text{ for lowlands}] &\quad (\text{Schimel et al., 1985a}) \end{aligned}$$

$$\begin{aligned} \text{Average change in plant N concentration above ground between} \\ \text{peak biomass and senescence} &= 0.4\% \end{aligned}$$

$$\begin{aligned} \text{Fraction of above ground N translocated to roots} &= 0.4 \\ [0.7 \text{ for lowlands}] &\quad (\text{to account for translocation}) \end{aligned}$$

$$\text{NH}_3^0 \text{ loss} = 86 [200] \cdot 0.004 \cdot (1-0.4) [(1-0.7)].$$

The average plant N concentration varies from 1.5% N at peak standing biomass to 0.9–1.1% in late fall, resulting in the mean decline of 0.4% (Senft, 1983). These assumptions result in an estimated loss of $0.2 \text{ g N} \cdot \text{m}^{-2}$ from

upland and $0.24 \text{ g N} \cdot \text{m}^{-2}$ from lowland vegetation. The pasture average value would be $0.21 \text{ g N} \cdot \text{m}^{-2}$, assuming a 70:30 distribution of uplands and lowlands. While this flux is based on a series of assumptions, it is worthy of some attention since it is an order of magnitude larger than the sum of other losses. These results appear to contradict Clark's 1977 report of constant recovery of ^{15}N for four years; however, regressing Clark's ^{15}N recovery data against time (Clark, unpublished data) showed a relationship ($R^2 = 0.4, P < 0.1$), which predicted an annual loss of $0.04 \text{ g } ^{15}\text{N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$. It is difficult to convert this value to a ^{14}N loss because it is not evident what enrichment value should be used; assuming a mean $^{14}\text{N}:^{15}\text{N}$ ratio of 18 for dead aboveground foliage (Clark, 1977) yields an estimate of $0.72 \text{ g} \cdot ^{14}\text{N} \cdot \text{m}^{-2} \cdot \text{y}^{-2}$. This is the same order of magnitude as our value of $0.21 \cdot \text{g} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$. It is also possible that the proportional losses of plant N were higher in our study because of a fertilizer effect. We have no way of evaluating that except for comparison with the above calculations, based on Clark's (1977) data.

Conclusions

Ammonia volatilization from urine patches does not appear to be an important loss vector for nitrogen in the shortgrass prairie and is an order of magnitude less than originally suggested for our site (Woodmansee, 1978). Losses of NH_3^0 at moderate stocking rates can range from 0.01 to $0.08 \cdot \text{g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$, depending on the proportion of urine deposition occurring in low versus high loss potential sites. The pattern of soil and forage properties within a pasture influence cattle behavior and urine deposition and so result in variations in the proportion of total deposition vulnerable to loss. These variations are predictable, given sufficient information, but make the computation of regional budgets difficult. The magnitude of losses from urine patches relative to potential losses from senescing vegetation suggests that the latter pathway is worthy of significant attention in grasslands, both as a loss vector for N and as a source of atmospheric NH_3^0 .

Assuming no loss from vegetation, the shortgrass prairie would be accumulating nitrogen under the current N loss regime at a rate of $0.23 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$. If all urine N deposition occurred on sites of maximum loss potential, the system would still be accumulating N at the rate of $0.16 \text{ g N} \cdot \text{m}^{-2} \cdot \text{y}^{-1}$. If N is in fact lost from senescent plant tissue at the rate estimated above, then the system would be in steady state within the precision of our measurements.

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