

## Rates and pathways of nitrous oxide production in a shortgrass steppe

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**Abstract.** Most of the small external inputs of N to the Shortgrass steppe appear to be conserved. One pathway of loss is the emission of nitrous oxide, which we estimate to account for 2.5–9.0% of annual wet deposition inputs of N. These estimates were determined from an N<sub>2</sub>O emission model based on field data which describe the temporal variability of N<sub>2</sub>O produced from nitrification and denitrification from two slope positions. Soil water and temperature models were used to translate records of air temperature and precipitation between 1950 and 1984 into variables appropriate to drive the gas flux model, and annual N<sub>2</sub>O fluxes were estimated for that period. The mean annual fluxes were 80 g N ha<sup>-1</sup> for a midslope location and 160 g N ha<sup>-1</sup> for a swale. Fluxes were higher in wet years than in dry, ranging from 73 to 100 g N ha<sup>-1</sup> y<sup>-1</sup> at the midslope, but the variability was not high. N<sub>2</sub>O fluxes were also estimated from cattle urine patches and these fluxes while high within a urine patch, did not contribute significantly to a regional budget. Laboratory experiments using C<sub>2</sub>H<sub>2</sub> to inhibit nitrifiers suggested that 60–80% of N<sub>2</sub>O was produced as a result of nitrification, with denitrification being less important, in contrast to our earlier findings to the contrary. Intrasite and intraseasonal variations in N<sub>2</sub>O flux were coupled to variations in mineral N dynamics, with high rates of N<sub>2</sub>O flux occurring with high rates of inorganic N turnover. We computed a mean flux of 104 g N ha<sup>-1</sup> y<sup>-1</sup> from the shortgrass landscape, and a flux of 2.6 × 10<sup>9</sup> g N y<sup>-1</sup> from all shortgrass steppe (25 × 10<sup>6</sup> ha).

### Introduction

Nitrous oxide (N<sub>2</sub>O) plays an important role in biogeochemistry at local and global scales (Crutzen 1983). Nitrous oxide influences the climate as a greenhouse gas, participates in the destruction of ozone (O<sub>3</sub>) and can be an important vector for loss of nitrogen from terrestrial ecosystems (Lacis et al. 1981; Crutzen 1983; Bowden 1986). Despite the importance of N<sub>2</sub>O, fluxes in and out of terrestrial ecosystems are not well known. Data are particularly scanty from ecosystems where emissions are not thought to be significant to nitrogen budgets. Such data may nonetheless be important in defining global atmospheric balances. While there are many difficulties in measuring

$\text{N}_2\text{O}$  fluxes, a key difficulty is the characteristically high degree of spatial and temporal variability. High variability in  $\text{N}_2\text{O}$  fluxes is found both within plots and between sites which vary in vegetation, soils or hydrology.

In this paper we consider variations in rates and pathways of  $\text{N}_2\text{O}$  production in the shortgrass steppe ecosystem. Inputs of N into these shortgrass ecosystems are relatively low ( $4\text{--}8 \text{ kg N ha}^{-1} \text{ y}^{-1}$ ) from wet and dry atmospheric deposition. Nitrogen fixation is generally considered to contribute little to the N balance of the ecosystem (Woodmansee 1978). Grazing influences the N budgets by N redistribution and regulation of gaseous ammonia ( $\text{NH}_3$ ) emission (Schimel et al. 1986). From previous studies in this system (Mosier et al. 1981) we found that although nitrous oxide losses from the native soil were small ( $1\text{--}2 \text{ g N ha}^{-1} \text{ d}^{-1}$ ), they accounted for about 10% of total N inputs into the system. Urine from grazing cattle may also influence nitrous oxide emission since losses from urea-treated sites were larger than from untreated soils.

Nitrous oxide is produced both by denitrification and during nitrification. Other pathways may exist but have not yet been shown to be significant (Kaplan & Wofsy 1985; Bowden 1986). Poth & Focht (1985) have recently proposed a mechanism for the production of  $\text{N}_2\text{O}$  during nitrification; "nitrifier denitrification" which may account for most  $\text{N}_2\text{O}$  production during nitrification. Both field and laboratory studies suggested that in the shortgrass soils  $\text{N}_2\text{O}$  is the primary nitrification–denitrification product when  $\text{N}_2\text{O}$  and  $\text{N}_2$  were measured; therefore, by quantifying  $\text{N}_2\text{O}$  alone, denitrification could be measured (Mosier & Parton 1985).

Utilizing field  $\text{N}_2\text{O}$  gas flux and soil nitrate, ammonium, water, and temperature measurements, a model was developed to describe the temporal variability of  $\text{N}_2\text{O}$  produced from nitrification and denitrification during a 2-y period. The work reported on here is a continuation of an overall study (see Mosier & Parton 1985; Schimel et al. 1986) on gas fluxes from the Shortgrass Steppe, that emphasizes the role of herbivores in modifying gas fluxes.

## Materials and methods

### *Field measurements*

The study site was located in the Central Plains Experimental Range, 56 km northeast of Fort Collins, Colorado. The site and experimental methods are explained in detail by Mosier & Parton (1985). Individual plots were established in blue grama (*Bouteloua gracilis* Lag.) swards that were as similar

Table 1. Selected soil properties for surface horizons of midslope and swale soils (from Schimel et al. 1985).

Position depth (cm)	Clay (%)	Organic C (mg/kg)	Organic N (mg/kg)	Net N Mineralization (kg/ha)
Midslope	15.0	5700	665	41
Swale	28.2	20400	1937	55

as possible in cover, exposure, and soil type at two slope positions. Plots were established at a midslope (July 1981) and a swale (May 1982) site on a northwest-facing slope having a 6% slope. The midslope soil was classified as a Ustollic Haplargid with a solum depth of 25 cm. The swale soil was an Aridic Argiustoll with a solum depth greater than 1 m. The soils differed significantly in organic carbon and N content, texture, and N mineralization rate (Table 1). The slope positions also differed in observed gravimetric water contents, ranging from 3 to 13% in the midslope and 6 to 23% in the swale. To determine the effects of urine deposition on nitrous oxide flux, urea equivalent to 450 kg N ha<sup>-1</sup> in 1.5 cm H<sub>2</sub>O (0.76 g urea in 120 ml H<sub>2</sub>O) was added uniformly to the surface of each treated plot. Nothing was added to control plots. Four replicate urea-amended and untreated plots were sampled at each sampling period. Adjacent to each of the plots, a 5-m<sup>2</sup> area was treated with natural <sup>15</sup>N abundance urea at the same rate as the amended plots to allow intensive sampling of soil NH<sub>4</sub><sup>+</sup>, NO<sub>3</sub><sup>-</sup>, and NO<sub>2</sub><sup>-</sup> at each N<sub>2</sub>O flux measuring date (see Mosier & Parton 1985).

### Laboratory experiments

A laboratory study was conducted to evaluate effects of soil moisture on the contribution of nitrification and denitrification to nitrous oxide flux. Unfertilized soils were collected from both the midslope and bottom sites to 15-cm depth and passed through a 2-mm sieve to remove plant material and stones. On the day that the soils were collected, powdered KNO<sub>3</sub> or (NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> was added to 500-g portions of sieved soils to attain a NO<sub>3</sub>-N or NH<sub>4</sub><sup>+</sup>-N content of 100 mg N/g soils and mixed thoroughly in a twin-shell blender. Soils were incubated at a range of gravimetric water contents from 2.5 to 30% (Fig. 1). This represents the range of water contents observed in the field, plus saturated conditions. Ten-gram portions of the field-moist, N-amended soil were placed in 125-ml serum bottles. Water was added to the desired moisture content, and the bottles were sealed with rubber serum stoppers and incubated 1 to 7 d at 25 °C. The flask air was amended with 0.1 l/l acetone-free acetylene in some treatments to block the nitrification process

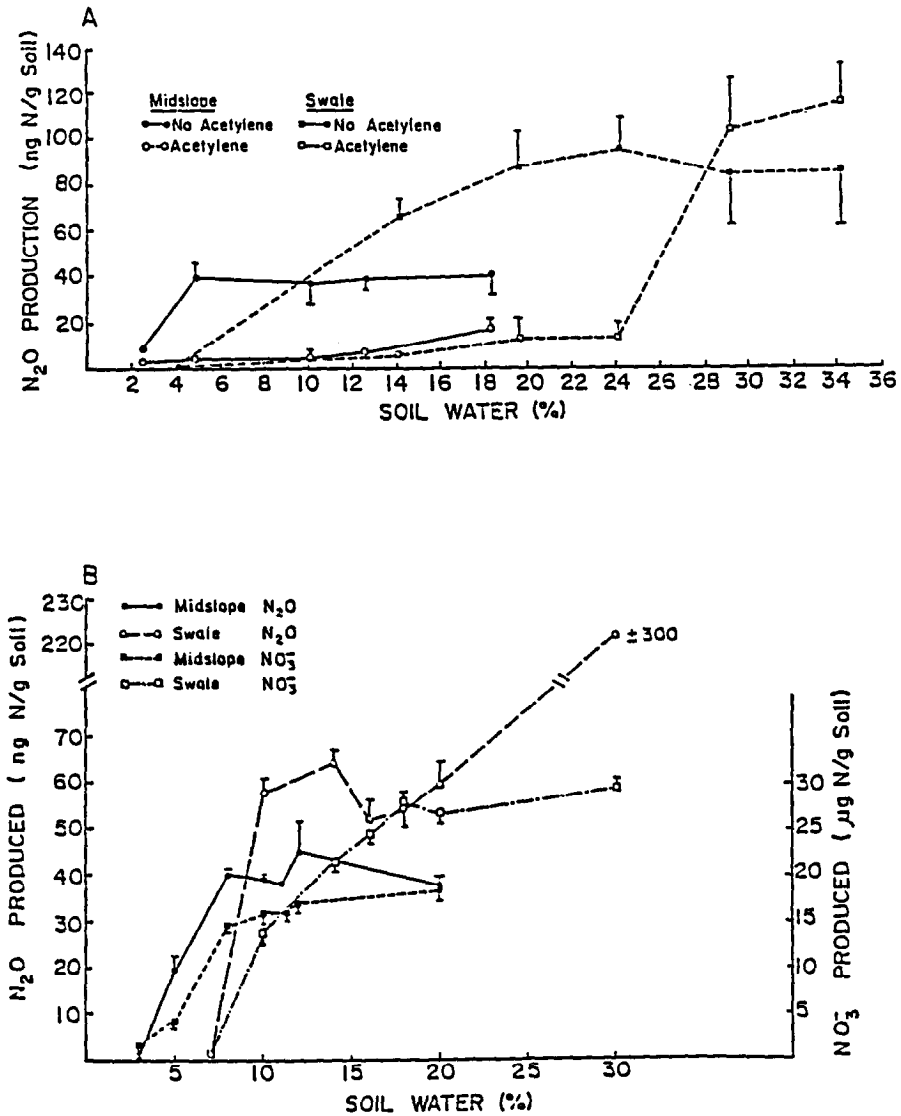


Fig. 1. (A) N<sub>2</sub>O production after 7-d incubation with NO<sub>3</sub><sup>-</sup> added for midslope and swale soils with and without acetylene. Standard error bars are included for each data point. (B) Effect of soil water content on the production of NO<sub>3</sub><sup>-</sup> and N<sub>2</sub>O from NH<sub>4</sub><sup>+</sup>-amended shortgrass midslope and swale soils during 7-d of laboratory incubations. Standard error bars are included for each data point.

and N<sub>2</sub>O production associated with that process (Walter et al. 1979) Headspace N<sub>2</sub>O concentration was determined by gas chromatography (Mosier & Mack 1980) and total N<sub>2</sub>O production was corrected for solubility in soil H<sub>2</sub>O. At the end of the desired incubation period the soils were

extracted with 50 ml of 2 M KCL and the extract analysed for  $\text{NO}_3^-$  and  $\text{NH}_4^+$  as described above.

## Results

### *Effects of soil water on nitrification/denitrification*

The effect of increasing soil water content on  $\text{NO}_3^-$  and  $\text{N}_2\text{O}$  production in  $\text{NH}_4^+$ -amended soils (see Fig. 1b) was to greatly enhance  $\text{N}_2\text{O}$  and  $\text{NO}_3^-$  production as water content increased to 5% and 7% for midslope and swale soils. Little change was observed in  $\text{N}_2\text{O}$  production as water content increased from 10% to 20% for both soils. At 30%  $\text{H}_2\text{O}$  (6% greater than was ever observed in the field), the swale soil  $\text{NO}_3^-$  recovery was not increased but  $\text{N}_2\text{O}$  production increased markedly. The midslope soil behaved similarly. Nitrate and  $\text{N}_2\text{O}$  production rates were highly correlated ( $R^2$  of 0.88), and maximum  $\text{N}_2\text{O}$  production occurred when the soil water content exceeded 50% of available soil water (8 and 15% for the midslope and swale soils).

Two soils were amended with  $\text{NO}_3^-$  and incubated in the absence and presence of acetylene (Fig. 1a). The data for both soils at water content less than 28% shows  $\text{C}_2\text{H}_2$  addition reduces  $\text{N}_2\text{O}$  production by approximately 80%. Because  $\text{C}_2\text{H}_2$  inhibits nitrification, this suggests that 80% of  $\text{N}_2\text{O}$  production comes from nitrification and 20% from denitrification. At 28%  $\text{H}_2\text{O}$  above, the  $\text{C}_2\text{H}_2$ -treated soil produced more  $\text{N}_2\text{O}$  than did the non- $\text{C}_2\text{H}_2$ -treated soil, suggesting the dominance of the denitrification process. These data suggest that nitrification (or nitrifier denitrification) is dominant over denitrification until soils become very wet. In addition, nitrification must be the main source of  $\text{N}_2\text{O}$  in the field, since observed water contents never exceeded 24%.

### *Revised model*

Because of the data presented above, we reevaluated a model presented earlier (Mosier & Parton 1985) to estimate  $\text{N}_2\text{O}$  production from denitrification and nitrification using microclimate and mineral data (Fig. 2) in control and urine-amended soils. We omitted several sample dates from the data because analysis of field data indicated that the error terms for predicted versus observed  $\text{N}_2\text{O}$  flux were quite high soon after the studies were initiated in both slope positions. We suspect that the high soil pH and high  $\text{NH}_4^+$  level during the first week after urea was added reduced microbial

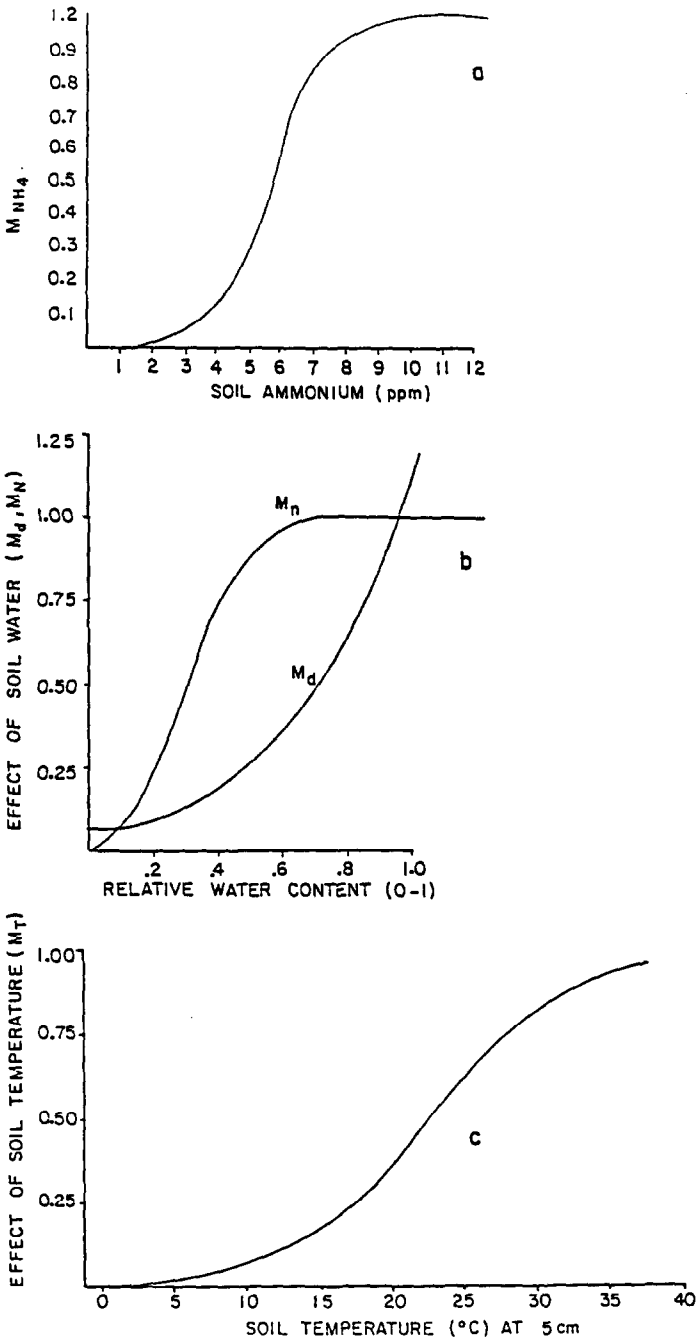


Fig. 2. The effect of soil NH<sub>4</sub><sup>+</sup> level on nitrification (a), the effect of relative water content on nitrification and denitrification (b), and the impact of soil temperature on nitrification and denitrification (c).

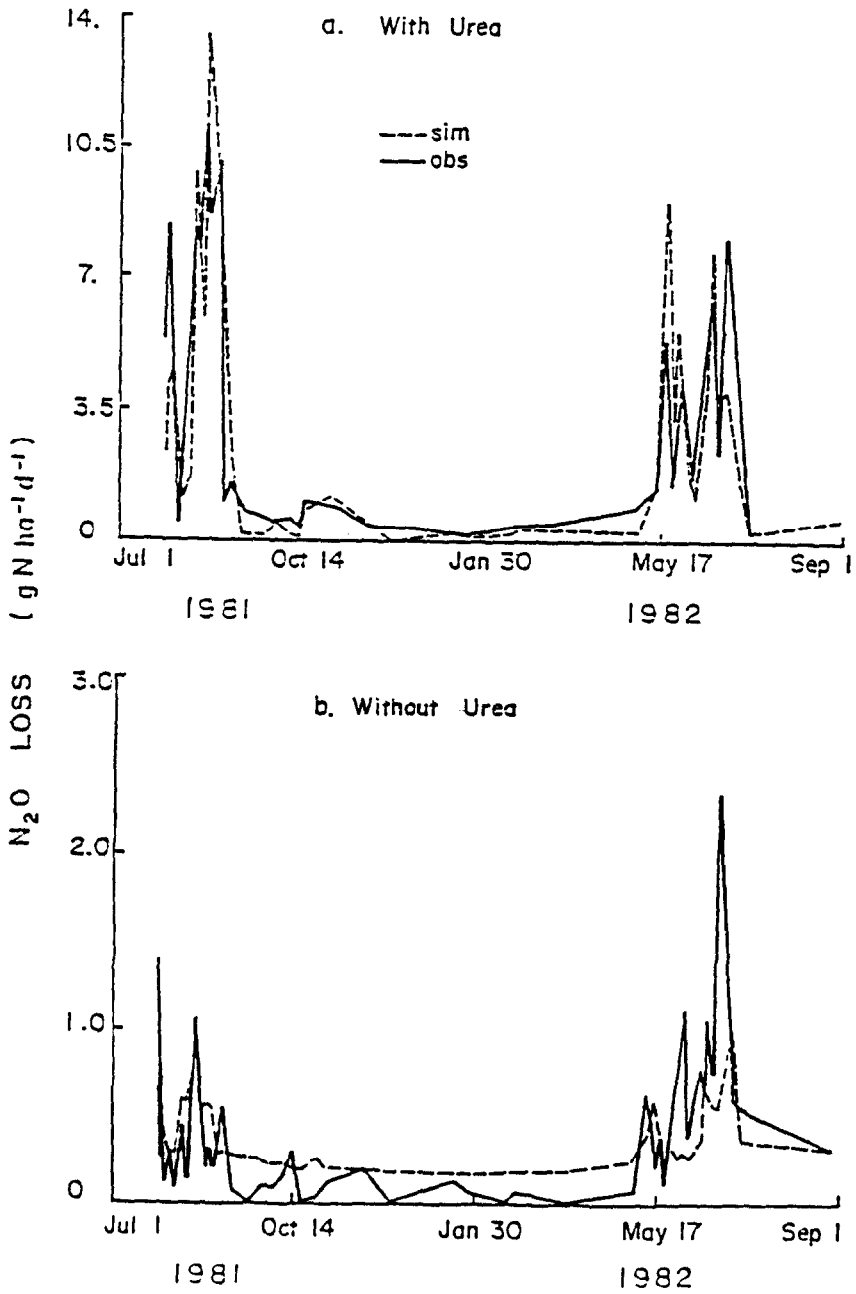


Fig. 3. Comparison of simulated and observed  $\text{N}_2\text{O}$  loss for the midslope site with (a) and without (b) urea-N addition.

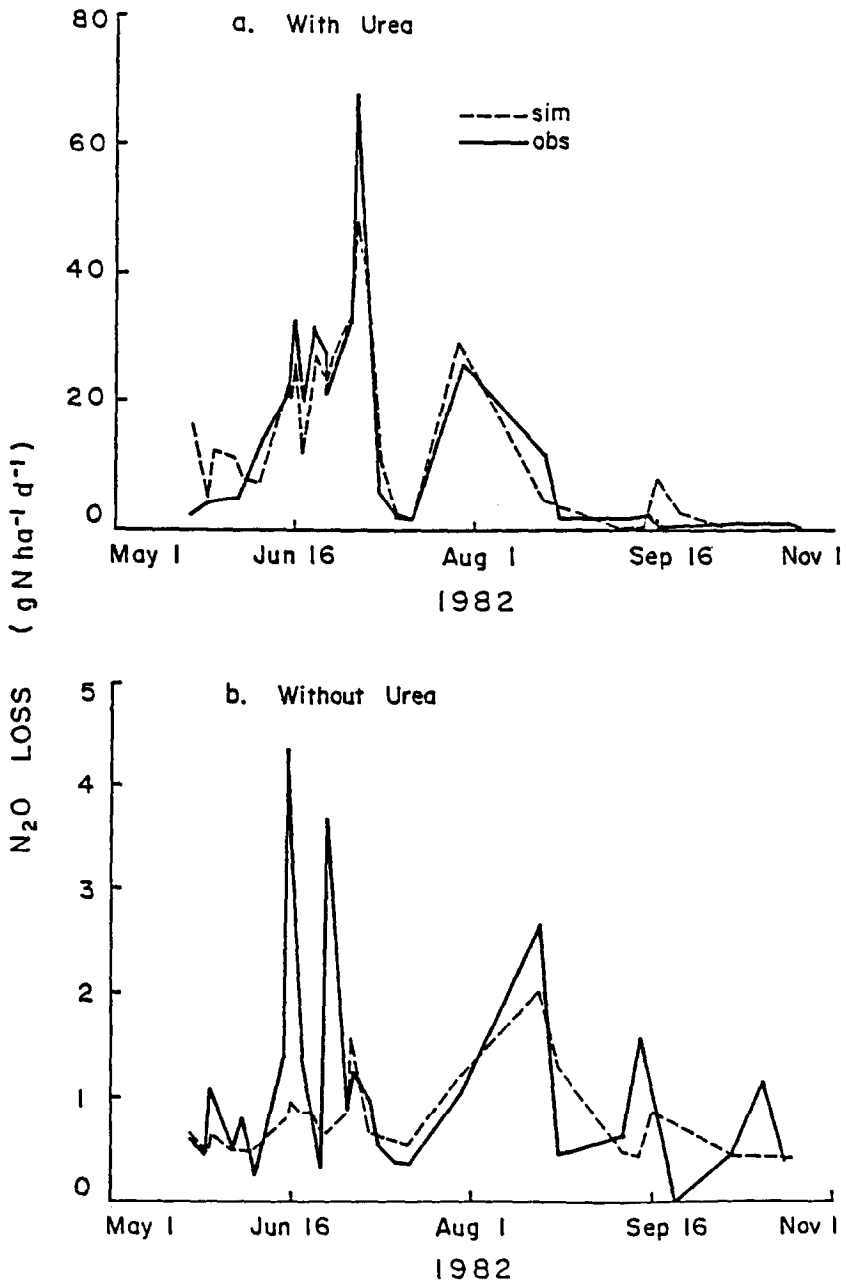


Fig. 4. Comparison of simulated and observed  $N_2O$  emission from the swale site with (a) and without (b) urea-N addition. Note the change in scale on the ordinate between (a) and (b).



activity for this brief period (Schimel et al. 1986), although other explanations are possible. The new model cannot be used to estimate N gas fluxes under such conditions.

Using this rationale we omitted the data for the first five data collection periods for each slope position and refitted the model parameters (see Eq. (1), Table 2). As a result, the agreement between observed and simulated  $N_2O$  flux density was greatly improved ( $R^2$  was increased from 0.57 to 0.82; Figs. 3, 4).

We used slightly different models to simulate  $N_2O$  flux from urine amended and control soils. In urine-amended soils, inorganic N levels were high. We used measured concentrations of inorganic N species to drive simulations of  $N_2O$  flux from the urine treated soils. Inorganic N levels in untreated shortgrass soils were consistently low and probably do not reflect levels of flux through mineral pools (see estimates of mineralization in Schimel et al. 1985; Schimel & Parton 1986). Since we did not have appropriate field data on flux through mineral N pools in control soils, we used a single empirical parameter to reflect the fact that the swale site had higher mineral N turnover rates than the midslope (Schimel et al. 1985).

The  $N_2O$  production equation for urine-amended soils (Mosier & Parton 1985) is shown in Eq. (1), where the  $N_2O$  produced by nitrification and denitrification ( $^pN_2O$ , in  $g\ N\ ha^{-1}\ d^{-1}$ ) are represented by separate functions that are dependent on soil water content, soil temperature (C),  $NO_3^-$  level ( $mg\ g^{-1}$ ), and  $NH_4^+$  level ( $mg\ g^{-1}$ ).

$$\text{Denitrification} \qquad \text{Nitrification} \qquad (1)$$

$$^pN_2O = [(a \cdot NO_3 \cdot M_T \cdot M_D) + (b \cdot M_{NH_4} \cdot M_T \cdot M_N) + C] \cdot S,$$

where  $M_T$  is the soil temperature term (Fig. 2c),  $M_D$  and  $M_N$  are the effect of relative water content (actual water content minus the minimum water content divided by the difference between maximum and minimum water content) on denitrification and nitrification (Fig. 2b), respectively,  $M_{NH_4}$  and  $M_{NO_3}$  are the effects of soil  $NH_4^+$  and  $NO_3^-$  levels on nitrification (Fig. 2a), and  $S$  is the site term, which is equal to one except when slope positions are combined, when  $S$  is equal to 3.25 and 1 for the swale and midslope, respectively. The parameter values in Eq. (1) were determined using a nonlinear data-fitting routine (Powell 1965), which minimizes the difference between the observed and simulated  $N_2O$  loss data (1981–1982) from the swale and midslope soils. The importance of nitrification in the production of  $N_2O$  is shown (see Table 2) by the fact that a version of Eq. (1) that does not include denitrification has a substantially higher  $r^2$  than a version of the

Table 2. Summary of the error terms and values of the parameters in Eq. (1) for urine amended soils.

Site	a	b	c	+R <sub>a</sub> (g N ha <sup>-1</sup> d <sup>-1</sup> )	r <sup>2</sup>
Combined data					
Urine amended	0.32	14.62	-0.15	2.47	0.86
Swale					
Urine amended	0.66	54.6	-0.52	4.4	0.82
Without nitrification	2.59	-	0.57	7.1	0.56
Without denitrification	-	58.9	0.55	4.84	0.72
Midslope					
Urine amended	0.56	12.85	0	1.24	0.73
Without nitrification	1.97	-	0	1.56	0.53
Without denitrification	-	15.36	0.11	1.32	0.68.

$$+R_a = \frac{\sum_{i=1}^N \text{ABS}(x_i^o - x_i^s)}{N},$$

where N = number of data points,  $x_i^s$  = simulated data, and  $x_i^o$  = observed data.

model that includes only denitrification. This pattern is shown for both data sets and the relative contribution to N<sub>2</sub>O flux by nitrification and denitrification for the combined version of Eq. (1) was 0.75 and 0.25, respectively. Adding the denitrification term to the swale site model results in a greater increase in the r<sup>2</sup> than including this term to the midslope site model and suggests that denitrification may be slightly greater on the fine-textured, high organic matter swale soils.

The N<sub>2</sub>O production equation for untreated soils is shown in equation 2:

$${}^c\text{N}_2\text{O} = (a' \cdot M_d \cdot M_T + b')S', \quad (2)$$

Where  ${}^c\text{N}_2\text{O}$  is the N<sub>2</sub>O loss (g ha<sup>-1</sup> d<sup>-1</sup>), a' and b' are coefficients given in Table 3 for the two sites, and S is the site multiplier. The site multiplier accounts for differences in inorganic N supply when data are not available and is equal to 1 for all cases except the combined site equation, where it is equal to 2.42 for the swale site. Comparison of the site coefficients for the

Table 3. Summary of the error terms and values of the parameters in Eq. (2); untreated soils.

Site	a'	b'	R <sub>a</sub> (g N ha <sup>-1</sup> d <sup>-1</sup> )	r <sup>2</sup>
Swale	2.87	0.39	0.58	0.075
Midslope	2.46	0.17	0.23	0.27
Combined	2.46	0.29	0.40	0.30

two sites shows that the  $N_2O$  flux rates are higher for the swale site and reflect the higher mineralization and nitrification rates (see Fig. 1; Schimel et al. (1985); Schimel & Parton (1986) and greater denitrification potentials in the swale (see Fig. 2).

A comparison of the observed and simulated  $N_2O$  data for the midslope (Fig. 3) and swale (Fig. 4) shows that the model compares well with observed data for the urine amended case, while the comparison for the control data is substantially poorer. The poorer fit to control data is probably caused by the greater measured errors for the lower flux rates and because the model did not include the temporal variation in soil  $NO_3^-$  and  $NH_4^+$  levels (Table 3).

## Model results

### *Simulated annual losses*

Annual  $N_2O$  losses were estimated using a soil water flow model (Parton 1978) and a soil temperature model (Parton 1984) to simulate daily soil water content (0–15 cm) and average daily soil temperature 5-cm depth) from 1950 through 1984. The models were used to calculate soil temperature and moisture from the long-term climatic record of air temperature and precipitation. Driving variables for the models were the monthly mean value of live and dead standing plant biomass (plant biomass differs between the two sites), daily precipitation and maximum and minimum air temperatures at 2 m. Daily soil water and soil temperature simulated by the models were used as inputs into Eq. (1 and 2) to calculate  $N_2O$  fluxes under control and urine-amended conditions at the two sites. The  $N_2O$  loss from a urine patch was simulated using the daily soil temperature and soil water content as inputs into Eq. (1) and using the observed time series of  $NO_3^-$  and  $NH_4^+$  levels (0- to 15-cm depth) for the 1981 urine addition at the midslope site as the inputs for the  $NO_3^-$  and  $NH_4^+$  levels in the soil. This assumption is crude, but we had no basis for making other assumptions from our data. Initial  $NH_4^+$  levels were greater than  $150 \text{ mg g}^{-1}$  and declined to less than  $5 \text{ mg g}^{-1}$  at the end of the time series, while  $NO_3^-$  increased rapidly after application of urine to greater than  $30 \text{ mg m}^{-1}$  and then declined to near zero at the end of the time series. During most of the time series  $NO_3^-$  and  $NH_4^+$  levels were greater than  $20 \text{ mg g}^{-1}$ .

Simulated annual  $N_2O$  fluxes over 24 years from the urine amended treatments were three to four times greater than control  $N_2O$  losses and the variation between years was substantially greater from urine-amended soils

(see Table 4). Annual  $\text{N}_2\text{O}$  fluxes ranged from a low of  $172 \text{ g N ha}^{-1} \text{ y}^{-1}$  to a high of  $1432 \text{ g N ha}^{-1} \text{ y}^{-1}$  for urine-amended treatment in the swale. The ratio of  $\text{N}_2\text{O}$  flux to N added was small in all treatments, ranging from 6 to 14% in midslope and swale, respectively. Even though fluxes from urine patches can be high, they do not contribute significantly to the total  $\text{N}_2\text{O}$  flux from a pasture because less than 1% of the area of a typical pasture is affected by urine each year (Senft 1983).

Simulated nitrous oxide fluxes (Table 4) from unamended soils ranged from  $82 \text{ g N ha}^{-1} \text{ y}^{-1}$  for the midslope to  $161 \text{ g N ha}^{-1} \text{ y}^{-1}$  for the swale. Variations between years were fairly small, with estimated  $\text{N}_2\text{O}$  fluxes ranging from a minimum of  $73 \text{ g N ha}^{-1} \text{ y}^{-1}$  to a maximum of  $100 \text{ g N ha}^{-1} \text{ y}^{-1}$  for the midslope site.  $\text{N}_2\text{O}$  fluxes were highest during wet years and lowest during dry years. The flux rates were highest for all sites in 1979, when the precipitation was 40 cm, and lowest in 1964, when precipitation was 10 cm.  $\text{N}_2\text{O}$  fluxes were approximately twice as great from the swale as from the midslope site.

## Conclusions

Nitrification appears to be the dominant source of nitrous oxide in the Shortgrass Steppe, contributing 60 to 80% of the total flux. Rates of emission were not high, but accounted for a measureable fraction of annual precipitation inputs. Simulated control (non-urine-amended)  $\text{N}_2\text{O}$  losses from the two sites as a percentage of the atmospheric N inputs (NADP 1982) ranged from 5.1 to 8.5% for the swale and from 2.4 to 4.8% for the midslope. Nitrous oxide production in urine is a minor pathway. While these fluxes are not large, in the long-term they influence the site's steady state N levels (Parton et al. 1987).

Differences in  $\text{N}_2\text{O}$  production seasonally and between sites were closely coupled to mineral N dynamics. Soil  $\text{NO}_3^-$  concentration, nitrification and mineralization rates all peak in June, along with the  $\text{N}_2\text{O}$  production rate (Schimel 1982; Schimel et al. 1985; Schimel & Parton 1986). Because much  $\text{N}_2\text{O}$  flux occurs at water contents which do not favor denitrification, we suggest that patterns of temperature and water availability have their effect on  $\text{N}_2\text{O}$  production by controlling N mineralization and nitrification. The formation of oxygen stressed microenvironments during very wet periods may also be of importance.

The significant spatial heterogeneity observed must be considered in calculating the average  $\text{N}_2\text{O}$  flux from a shortgrass steppe ecosystem. The average flux from the shortgrass, assuming the same ratio of upland to

Table 4. Simulated annual  $\text{N}_2\text{O}$  loss ( $\text{g N ha}^{-1} \text{y}^{-1}$ ) for two soil types with (+ N) and without urine amendment from a 24-year simulation. Standard deviations reflect variability between simulated years.

Site	Mean loss $\pm$ SD	Highest annual loss	Lowest annual loss
Midslope	82 $\pm$ 7	100	73
Midslope + N	295 $\pm$ 112	614	85
Swale	161 $\pm$ 9	178	151
Swale + N	690 $\pm$ 290	1432	192

lowland (70:30) is in Schimel et al. (1986) and assuming that the sites chosen for intensive study were representative, would be  $104 \text{ g N ha}^{-1} \text{y}^{-1}$ . This flux is small relative to the standing pools and inputs of N to the system but could be a significant input of  $\text{N}_2\text{O}$  to the atmosphere. The Shortgrass Steppe would contribute  $2.6 \times 10^9 \text{ g N}_2\text{O N y}^{-1}$  to the atmosphere, assuming approximately 25 000 000 ha of shortgrass steppe worldwide (Milchunas, pers. comm.). This suggests lower fluxes from worldwide grasslands and steppes than those presented in Bowden (1986) or Banin et al. (1984).

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