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SMALL-SCALE SPATIAL AND TEMPORAL VARIABILITY OF N_2O FLUX FROM A SHRUB-STEPPE ECOSYSTEM

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Summary—Nitrous oxide (N_2O) is a trace greenhouse gas that catalyses ozone destruction. It is also the major gaseous loss of N from the N-limited shrub-steppe ecosystem. We examined the spatial and temporal flux of N_2O from small plots in an undisturbed shrub-steppe ecosystem having spatially heterogeneous plant cover. The N_2O flux from the soil surface and NH_4^+-N and NO_3^--N concentrations were measured periodically over 1 y from 44 points in 2.4 m^2 plots centered on individual *Artemisia tridentata* shrubs. Positive N_2O flux occurred from March to October, with no detectable flux during the winter months. The spatial (plot) variability of N_2O flux ranged from 23 to 130%, with lower variability as soil moisture increased. Temporal variability (March to October) was 171%, but decreased to 77% when calculated without the August sampling date. The measured N_2O flux correlated positively with microbial activity (CO_2 production), with moisture when the soil was fairly wet and usually with NO_3^-N concentrations. After a precipitation event on to dry soil, there was a pulse of N mineralization and N_2O flux, which strongly correlated with proximity to vegetation. The estimated N_2O flux occurring within 48 h after warm season precipitation events accounted for 20% of the total annual N_2O flux from this ecosystem. Thus, small-scale spatial and short-term temporal variations can significantly affect annual estimates of ecosystem N_2O flux and, thus, gaseous N loss from semi-arid ecosystems. Published by Elsevier Science Ltd

INTRODUCTION

Nitrous oxide (N_2O) influences the climate as a greenhouse gas (Crutzen, 1983; Dickenson and Cicerone, 1986), participates in the formation and destruction of ozone (Cicerone, 1987), and is a significant vector for the loss of N from terrestrial ecosystems (Bowden, 1986). The amount of atmospheric N_2O has increased since the 1970 s (Rasmussan and Kahlil, 1986), enhancing interest in quantifying N_2O flux from terrestrial ecosystems. Problems exist in quantifying N_2O flux from natural ecosystems because methodology to deal effectively with the high spatial and temporal variability associated with the processes responsible for N_2O formation is lacking (Folorunso and Rolston, 1984). Further complications include spatially heterogeneous plant cover in natural ecosystems resulting in varying N-cycling rates, and processes associated with different plant species and interplant areas.

Significant plant heterogeneity exists in the semi-arid shrub-steppe, which is the largest grassland region in North America, totalling over 64,500,000 ha (Rogers and Rickard, 1988). In heterogeneous plant systems trace gas flux from soil is generally measured at random locations. However, soil chemical patterns and N mineralization in patchy ecosystems, such as the shrub-steppe, have been shown to be directly related to individual plants, i.e. non-random (Charley and West, 1975, 1977; Hook *et al.*, 1991). Soil microbial biomass C and N and microbial activity are greater in shrub-steppe soil under plant canopies than inter-plant soil crust areas (Bolton *et al.*, 1993) due to the decomposition of above and below ground litter from *Artemisia* shrubs and grass plants (Halvorson *et al.*, 1993). The spatial distribution of microbial biomass and microbial processes in the shrub-steppe suggests that N_2O production would also be non-random (Smith *et al.*, 1994).

A significant contribution to N_2O flux in varying ecosystems can come from nitrification (Mosier *et al.*, 1981; Firestone and Davidson, 1989; Hutchinson *et al.*, 1993) including the shrub-steppe (Mummey *et al.*, 1994). Therefore, environmental factors that regulate nitrification also regulate N_2O flux. Soil moisture content can strongly influence N mineralization, N assimilation and nutrient diffusion that can regulate nitrification. Mummey *et al.* (1994) found that N_2O flux was most limited by soil moisture and available N and that large pulses of

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N_2O were produced when dry soil was wetted. The pulse of N_2O upon soil wetting has been commonly observed in other studies, but the cause remains unknown (Davidson, 1992; Hutchinson *et al.*, 1993). However, it might be related to the rapid release of C and N from microbial cells and physically protected soil organic matter.

An understanding of the spatial patterns of N_2O flux is important to determine annual ecosystem flux, especially if the flux is non-random across the landscape. Since soil variables controlling N_2O flux interact at the microsite scale, small-scale spatial patterns will influence ecosystem level estimates. Our objectives were to: (i) examine the small-scale spatial variability of soil N_2O flux and soil NO_3^--N and NH_4^+-N concentrations around individual *Artemisia tridentata* shrubs; and (ii) examine the temporal variability of soil N_2O flux in this shrub-steppe ecosystem.

MATERIALS AND METHODS

Study site and soil

The site was located on the Arid Lands Ecology Reserve (ALE) within the U.S. Department of Energy's Hanford site in south-central Washington. The 33,500 ha ALE site has been relatively unaltered by human disturbance since the early 1940 s and represents one of the few remnants of the shrub-steppe that is still in a nearly pristine state of vegetation (Rogers and Rickard, 1988). The dominant vegetation species are *Artemisia tridentata* (big sagebrush) inter-mixed with the perennial grasses *Elytrigia spicatum* (bluebunch wheatgrass) and *Poa secunda* (Sandburg bluegrass). A soil crust consisting of lichens, moss and algae (cryptogams) inhabits all undisturbed inter-plant areas. The soil at the study site is a coarse-silty, mixed, mesic, Xerollic Camborthid.

The ALE site has a semiarid climate, receiving 80% of the 220 mm annual precipitation between October and May (Rickard, 1988). The average annual temperature is 10.5°C, but in the winter months below-freezing temperatures for extended periods are not unusual. Evapotranspiration in the early spring causes the surface-soil moisture content to rapidly decrease and remain relatively dry until fall, except at times following sporadic rainfall (Gee *et al.*, 1988).

Sample collection and analysis

Gas samples, for N_2O analysis, were collected at 44 locations within each of three 2.4 × 2.4 m plots, centered on individual *A. tridentata* shrubs. On average the plant canopies were 0.8 × 0.8 m, covering the center third of each plot. The three identically-oriented plots were sampled monthly (14 sampling dates) for 1 y at times representative of seasonal conditions or to coincide with precipitation events.

Gas samples were obtained by inserting plastic-lined metal cans (15.2 cm dia × 7 cm height), equipped with a gas sampling port, 2 cm into the soil. The gas collection cans were open to the atmosphere for approximately 15 min after insertion, then sealed with a rubber septum. Gas samples were taken at 0 and 30–60 min after sealing and injected into evacuated vacutainer vials. Preparation of the vacutainer vials before sampling involved removing and lightly coating the rubber stoppers with high-vacuum stopcock grease re-inserted in the glass vials, and evacuated with a vacuum pump.

Gas samples were analyzed for N_2O and CO_2 content within 48 h after collection, using a Shimazu GC-8AIE GC with a Porapak Q column and a ^{63}Ni ECD. Leakage from the vacutainers was checked by injecting a range of N_2O standards into vials in the field during sampling and analyzing them at the same time as sample analysis. Gas standards were run with the samples and standard checks every 2 h of GC operation (16 samples).

For each sample date, one 2 cm dia soil core was extracted to a depth of 10 cm from around the perimeter of each gas collection can for analysis of soil moisture, NO_3^--N, and NH_4^+-N. All soil cores were transferred to cold storage at the time of collection and extracted within 24 h. Soil-gravimetric water content was determined by drying at 105°C. Nitrate and NH_4^+-N were analyzed following extraction with 2.0 M KCl, using a calorimetric continuous flow analyzer.

Statistical analysis

Sample data from each of the three plots was averaged for each date. The distributions were normal and, thus, analyzed without transformation using univariate statistics to determine mean, frequency distributions, skewness and coefficient of variation (CV). The relationship between measured variables and plant locations, including the sparse grass species, was determined by dividing sample data into groups of plant-associated and bare soil-associated data. Bivariate statistical methods were employed to determine the relationships between measured variables and position to plants.

We also characterized the spatial distribution of N_2O flux, NH_4^+-N and NO_3^--N in the 2.4 × 2.4 m plots using a spatial covariance function (Isaaks and Srivastava, 1989). For each variable a spherical model was fitted to the spatial covariance values. The models were extrapolated to zero lag (nugget variance) to provide an estimate of the extent of spatial auto-correlation between the measured points. The spatial covariance at a sample separation distance (lag) of zero is reported (Table 1) as

Table 1. Statistics for N_2O flux from the March, June and August sampling dates on an annual plot mean basis, kg N_2O-N ha^{-1} y^{-1} (n = 44 each date)

	March	June	August
Minimum	0.01	0.01	0.01
Maximum	0.41	0.87	6.74
Mean	0.17	0.21	2.67
Skewness	0.50	1.82	0.58
C.V. (%)[a]	71.0	99.0	55.0
Spatial variance[b]	20.0	60.0	90.0

[a]Coefficient of variation ×100 = %.
[b]Percent of sample population variation explained by spatial auto-correlation.

the percentage (%) of the total variance of the sample population explained by spatial auto-correlation. This is an indication of the average degree of similarity between data values as a function of their separation distance.

RESULTS

Univariate and spatial variability

The univariate statistics for N_2O flux for the March and June sampling, when the soil gravimetric water content averaged 5.2% and 9.4%, respectively and the August sampling 1 h after a precipitation event (water content 12.7%), are shown in Table 1. The mean N_2O flux increased from March to August with the maximum spanning an order of magnitude. The integrated annual plot mean N_2O flux in March was 0.17 kg N_2O-N ha^{-1} y^{-1} (Table 1). The distribution of measurements exhibited a slight positive skewness (0.50) and a CV of 71%. The average soil NO_3^--N and NH_4^+-N contents were 1.6 mg-N kg^{-1} soil. The measured N_2O flux in June was similar (0.21 kg N_2O-N ha^{-1} y^{-1}) to that of the drier March sample

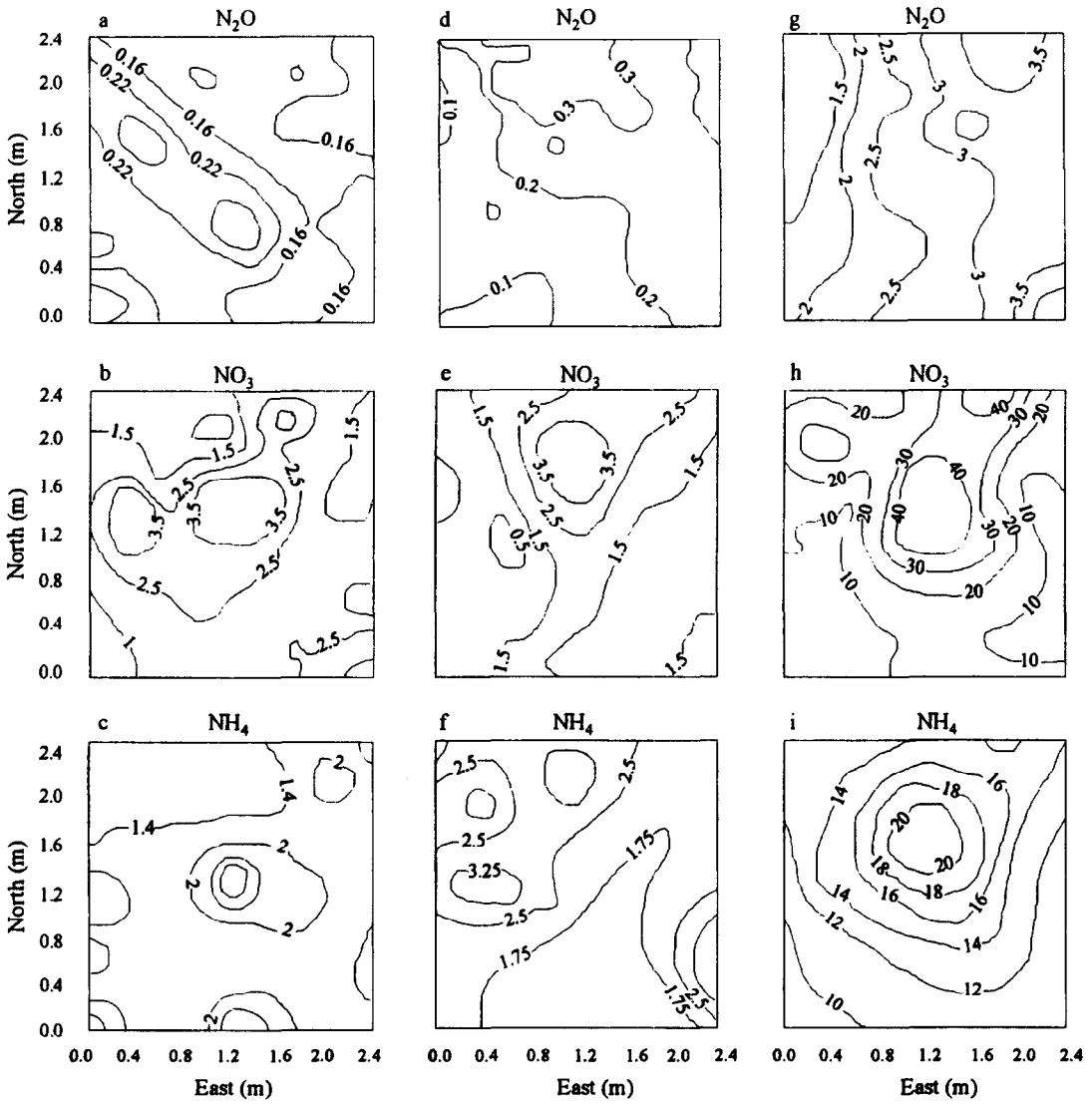

Fig. 1. Contour plots of N_2O flux (kg ha^{-1} y^{-1}), NO_3 (mg-N kg^{-1} soil) and NH_4 (mg-N kg^{-1} soil) for the March (a,b,c), June (d,e,f) and August (g,h,i) sample dates, respectively.

Table 2. Linear correlation matrix for N_2O-N and CO_2-C flux and soil NO_3-N, NH_4^+-N, water concentrations for March and June sample dates (mean water contents 5 and 9.5%, respectively) and the August sampling after a precipitation event (mean water content of 13%) (n = 44 each date)

	N_2O-N	CO_2-C	NO_3-N	NH_4^+-N
		March		
CO_2-C	0.34*			
NO_3-N	0.32*	0.18		
NH_4^+-N	0.12	−0.25	0.46**	
H_2O	0.05	0.17	−0.23	−0.17
		June		
CO_2-C	0.37*			
NO_3-N	0.06	−0.20		
NH_4^+-N	0.25	−0.19	0.14	
H_2O	−0.04	−0.17	0.15	0.12
		August		
CO_2-C	0.39**			
NO_3^--N	0.39*	0.04		
NH_4^+-N	0.41**	−0.01	0.74***	
H_2O	0.27	0.06	−0.15	−0.06

*Significant correlation at P = 0.05.
**Significant correlation at P = 0.01.
***Significant correlation at P = 0.001.

date (Table 1) even though the water content was twice as great (9.5 vs 5.2% H_2O wet/wt). The June samples showed a much larger positive, but not significant, skewness (1.82) and a CV of 99%. Despite the significant increase in moisture content in June the soil NO_3^--N and NH_4^+-N contents were similar to March averaging 1.6 and 2.3 mg-N kg^{-1} soil, respectively.

The August sampling, after a precipitation event, had an order of magnitude greater N_2O flux (2.67 kg N_2O-N ha^{-1} y^{-1}) than the March or June sampling dates (Table 1). The August sample distribution exhibited only a slight positive skewness (0.58) and had a lower CV (55%) than the other dryer sampling dates. Twelve hours after the August precipitation event the soil NO_3^--N and NH_4^+-N averaged 19.8 and 13.5 mg-N kg^{-1} soil, respectively.

The spatial distributions of N_2O flux, NO_3^- and NH_4^+ from March, June and August are shown in Fig. 1. In each figure the coordinate 1.2 east and 1.2 north is centered on an *A. tridentata* plant. Contour maps of N_2O flux for March and June are presented in Fig. 1(a,d), respectively. The N_2O flux for March [Fig. 1(a)] appears to be more spatially random when compared with the wetter June sampling [Fig. 1(d)]. The spatial variance or the degree of spatial correlation between samples is 20% for the March sampling and 60% for the June sampling (Table 1). The August sampling shows a more uniform N_2O flux pattern across the plot [Fig. 1(g)] and a higher spatial correlation between samples (90%; Table 1). The order of magnitude increase in N_2O flux in August compared with March and June is consistent across the 2.4 × 2.4 m plot [Fig. 1(g)].

The NO_3^--N and NH_4^+-N spatial patterns [Fig. 1(b,c,e,f,h,i)] show a close spatial correlation with the *A. tridentata* plant centered in the plot (1.2 × 1.2 m). After the precipitation event in August these patterns become even more distinctive [Fig. 1(h,i)]. The spatial variance of the inorganic N pool (NO_3^--N and NH_4^+-N) for March, June and August was 75, 50 and 80%, respectively, reflecting less than 50% random variability of samples at any one time.

There was a significant positive correlation between N_2O flux and microbial respiration on all sample dates (Table 2), with the highest significance on the wetter August sampling. There was also a significant positive correlation between N_2O flux and soil NO_3^--N in March and August and NH_4^+-N in August. Microbial respiration showed consistent negative correlation to NH_4^+-N concentration, in contrast NO_3^--N showed a highly positive correlation to NH_4^+-N in the March and August sampling. Water content showed no significant correlation to gas flux or inorganic N on any of the three sampling dates (Table 2). However, there was a strong positive relationship with gas flux for the August sampling date (r = 0.27, P < 0.09).

Table 3. Mean values and significant differences (t-test) of N_2O-N and CO_2-C flux and soil NO_3^--N and NH_4^+-N concentrations for soil samples associated with plants vs bare soil associated samples. Units for N_2O-N and CO_2-C are kg ha^{-1} y^{-1} and mg-N kg^{-1} soil for NO_3^--N and NH_4^+-N (n = 44 each date)

	March		June		August	
	Plant	Bare	Plant	Bare	Plant	Bare
N_2O-N						
Mean	0.19	0.15	0.22	0.12	3.18	1.80
t	0.13		3.23**		3.87***	
CO_2-C						
Mean	1220	970	8900	5900	38 000	36 400
t	1.31		2.62*		1.93	
NO_3^--N						
Mean	2.30	1.60	1.64	1.29	25.90	9.37
t	1.44		1.34		4.20***	
NH_4^+-N						
Mean	1.67	1.41	2.50	1.80	15.80	9.66
t	1.00		2.17*		3.75**	

*Significant difference between values at P = 0.05.
**Significant difference between values at P = 0.01.
***Significant difference between values at P = 0.001.

Table 4. Mean N_2O flux, soil water content and NH_4^+-N and NO_3^--N concentrations for each sample date with positive N_2O flux (n = 44 each date)

Date	N_2O-N(kg ha^{-1} y^{-1})	H_2O(%)	NH_4^+-N(mg kg^{-1} soil)	NO_3^--N (mg kg^{-1} soil)
18 March	0.54 (0.21)*	9.2	1.8	0.5
27 March	0.17 (0.06)	5.2	1.6	1.6
3 April	0.08 (0.06)	5.1	1.7	0.4
17 June	0.21 (0.08)	9.4	2.3	1.6
29 June	0.08 (0.07)	4.2	2.1	2.4
16 July	0.12 (0.16)	2.1	1.0	2.5
23 August	2.67 (0.97)	12.7	13.5	19.8
15 September	0.39 (0.09)	6.1	2.0	2.4
27 October	0.12 (0.07)	2.3	1.0	8.2

*Mean and SEM of all samples at each time period.

The N_2O flux from soil associated with plants was significantly greater than from inter-plant soil for the June and August sampling, but not for the drier March sampling (Table 3). The order of magnitude increase in N_2O flux for the August sampling compared with the March and June sampling is consistent for both plant and bare associated soil. In addition, the August sampling had significantly greater soil NO_3^--N and NH_4^+-N in the plant associated soil (Table 3). There was little significance (June) in CO_2 evolution between the plant and bare soil associations, even when the mean flux varied significantly from March to August.

Temporal variability

For the nine sampling dates with positive N_2O flux the annual plot N_2O flux and concentrations of moisture, NH_4^+-N and NO_3^--N are shown in Table 4. Over the 1-y period (14 dates) the highest N_2O flux occurred following soil wetting during the warm season from March to September. There was no detectable N_2O production from November to February when soil temperature was low and moisture was not limiting. The annual plot means calculated at each sampling time ranged from 0.08 to 2.67 kg N_2O-N ha^{-1} y^{-1}. Without the August sample date the N_2O flux remained below 0.5 kg N_2O-N ha^{-1} y^{-1} throughout the year. The CV of the temporal N_2O flux during the year was 171% for the nine sample dates, but 77% without the August sampling date included. The within date (spatial) CVs ranged from 23 to 130% (Table 4).

The inorganic N in this ecosystem is generally low, ranging from 1 to 3 mg-N kg^{-1} soil except immediately after precipitation where it can increase by an order of magnitude within hours (August; Table 4). Except for periodic precipitation events, the moisture content in this soil is low ranging from 10 to 60% of field capacity (−33 kPa).

DISCUSSION

We have found that in this shrub-steppe ecosystem nutrient inputs and factors regulating microbial processes, such as N_2O production, are not spatially or temporally random. These non-random spatial patterns, usually on a small-scale, govern ecosystem-level estimates of N_2O flux.

Small-scale spatial patterns of N_2O flux are controlled by interacting abiotic and biotic factors, such as plants, microorganisms, precipitation and nutrients. These factors may vary on an annual basis having a significant effect on the magnitude of N_2O flux. Thus, on a temporal basis we would expect N_2O flux to vary spatially depending on the dominant controlling factor. For the spatial analysis we evaluated N_2O as a mean plot flux and as influenced by plants. We present in detail three sampling times representative of seasonal water contents during the temporal window where the highest N_2O flux occurs.

The N_2O flux for the March sample date [Fig. 1(a)] is typical of the spatial distribution of N_2O flux when soil moisture contents were low, being relatively random with no strong spatial relationships visually detectable (Fig. 1). The soil NH_4^+ and NO_3^- concentrations for March are also typical for dry, warm season sample dates that were not influenced by precipitation. Even though the soil at the late June sampling was twice as moist (9.5%) as the March sampling the N_2O flux and inorganic N concentrations were not significantly different (Tables 1 and 4). This indicates that moisture is a controlling factor only on initial wetting, after which the substrates (C and N) become limiting. The flush of N_2O upon wetting and subsequent control by NH_4^+ substrate has been shown for this soil under controlled laboratory conditions (Mummey *et al.*, 1994).

The August sampling was made within hours of a precipitation event on to warm soil that caused a significantly greater N_2O flux and inorganic N flush than on the previous sampling dates (Table 4). In addition, this precipitation event on to dry soil resulted in distinct spatial patterns of N_2O flux [Fig. 1(g)]. Pulses of N_2O and N mineralization (inorganic N production) following wetting of dry soil are thought to be due to the release of readily decomposable organic matter. These substrates are released from non-living organic matter and from

the death of microorganisms due to rapid changes in water potential (Kieft *et al.*, 1987; Groffman and Tiedje, 1988; Burke, 1989). Organisms surviving dessication rapidly utilize these substrates causing rapid CO_2 and N_2O production.

According to Allison and Prosser (1991) ammonium-oxidizing bacteria survived for more than 3 months in air-dried soil that may provide them with a competitive advantage for utilizing substrates on re-moisturising. In addition it has been suggested that microorganisms with fast growth rates are more susceptible to desiccation than slower growing ones (Van Gestel *et al.*, 1993), which would include nitrifying bacteria. Thus, it would appear that conditions exist, (plentiful substrates, moisture conditions and a surviving population) for rapid oxidation of NH_4^+ and production of N_2O immediately after a precipitation event.

Several investigators have reported large fluxes of N oxides after wetting of dry soil in various ecosystems, such as grass pasture (Hutchinson *et al.*, 1993), shortgrass prairie (Mosier *et al.*, 1981), agricultural soil (Van Kessel *et al.*, 1993), as well as laboratory studies (Davidson, 1992; Mummey *et al.*, 1994). However, enhanced N_2O flux and N mineralization after wetting dry soil are short-lived. A laboratory study using soil from this shrub-steppe (Mummey *et al.*, 1994) showed that after wetting the spike of N_2O decreased rapidly after 24 h. Soil inorganic N concentrations also returned to pre-wet levels within days after wetting. This suggests that intense microbial competition for inorganics rapidly reduced NH_4^+-N availability for nitrification. Therefore, nitrous oxide flux from this ecosystem is likely limited by N availability, except immediately after precipitation on to dry soil.

Another major influence of wetting a dry soil is the effect on the spatial distribution of substrates and N_2O flux. Wetting a dry soil rapidly releases and distributes substrates from SOM and microbial biomass that mitigates substrate hot spots by producing more uniform conditions throughout the soil. The variability of N_2O flux was less for the August sampling, due to more uniform moisture conditions, compared with the patchiness of the March and June samplings (Fig. 1). This was also reflected in the lower spatial variability (CV% = 55; Table 1) and higher explained variation between samples (90%; Table 1) for N_2O flux in the August sampling. Even though the variability of inorganic N at the March, June and August samplings was similar, the percentage of the total variation explained by spatial auto-correlation was significantly greater for the August sampling (data not shown, see Fig. 1).

Generally N_2O flux correlated with respiration (CO_2-C), but little else in the March and June sampling. For the wetter August sampling there were also significant correlations between N_2O and NH_4^+-N and NO_3^--N (Table 2; Fig. 1). The correlation between microbial respiration and N_2O flux suggests that N_2O flux is greater in areas of high microbial activity, but not necessarily related to water content. Water content is less variable in these plots (CV% = 16–25) compared with NO_3^--N and NH_4^+-N (CV% = 50–90). Inorganic N may cause hot spot activity and the subsequent low correlation between moisture and microbial activity as measured by N_2O and CO_2-C. In a topogradient covering several ecosystems Ambus and Christensen (1995) found that N_2O varied over time within sites but was not correlated to inorganic N, temperature or moisture. However, in our study it appears that the distribution of substrates, caused by moisture, may be responsible for the inter-relationships of processes at the microsite level.

The spatial relationships between microbial processes and substrates are also influenced by vegetation, e.g. an *Artemisia* shrub. Correlation between N_2O flux and plant associated soil generally increased with increasing soil-water content (Table 3). This may be due to increased microbial access to inorganic N when water contents are greater, since plant associated soil has higher concentrations of inorganic N than inter-plant soil (Table 3). In addition, after precipitation the larger microbial biomass of plant associated soil decomposes more organic matter into the soil environment than inter-plant soil, resulting in relatively greater increases in inorganic N, and subsequently N_2O production (Table 3). This hypothesis is supported by the change in the ratio of soil inorganic N (extractable NO_3^--N and NH_4^+-N) from plant associated soil to soil inorganic N from samples farther away. This ratio was 1.7 for the dry March sampling, 1.2 for the wetter June sampling and 2.7 after the precipitation event in August.

Temporal sampling showed nitrous oxide flux measurements were generally highest when the water contents were above 6.0%. During the late spring and summer, when the soil dried between precipitation events N_2O flux rates were relatively low and constant except after precipitation events (Table 4). During the colder winter months N_2O flux was below detection limits even though soil moisture contents were relatively high and soil NO_3^--N and NH_4^+-N averaged as high as 3.6 and 5.3 mg kg^{-1} soil, respectively. This indicates that N_2O production is limited by low temperatures during the winter months. This is in contrast to other studies that found significant N_2O production under cold conditions (Sommerfeld *et al.*, 1993). Though conditions under snow and spring thaw are much different to bare frozen soil which is common in this shrub-steppe soil.

The spatial variability at each sampling time ranged from 23 to 130% CV (Table 4), which is similar to trace gas flux variability reported in other field

studies (Folorunso and Rolston, 1984; Parsons *et al.*, 1991). The temporal variability over the March to October period was 171% CV, however, excluding the August sampling date reduced the variability to 77%. We found no temporal stability for N_2O flux from nitrification during the warm season. In contrast, Christensen *et al.* (1990) found temporal stability in N_2O produced from denitrification. Significant temporal correlations between the variables shown in Table 4, excluding August date, were found between N_2O flux and water content ($r = 0.67$, $P < 0.07$) and NH_4^+-N and water content ($r = 0.74$, $P < 0.04$). This is in contrast to the spatial data for March, June and August, where water content was uncorrelated with processes or pools.

Knowledge of the magnitude and duration of N_2O flux following warm season precipitation events has important implications for determining N_2O fluxes that are representative of seasonal conditions. Integration of N_2O flux estimates for sample dates not following precipitation yielded an estimate from these soils of 0.12 kg N_2O-N ha^{-1} y^{-1}. Integration of N_2O flux estimates for sample dates following precipitation events greater than 0.4 cm, which occurred when soil temperatures at 5 cm depth were greater than 15°C, was estimated to contribute 0.03 kg N_2O-N ha^{-1} y^{-1} to the annual plot N_2O flux. Addition of the estimated N_2O-N flux after warm season precipitation events to the annual plot estimate yields a total estimate of 0.15 kg N_2O-N ha^{-1} y^{-1}. Therefore, N_2O flux, from this ecosystem, occurring within 48 h of precipitation events may be responsible for 20% of the total N_2O flux to the atmosphere.

While our estimate is based on data from a small undisturbed region of the shrub-steppe, it does suggest that undisturbed shrub-steppe ecosystems make relatively small contributions to global N_2O atmospheric contributions when compared with wetland ecosystems or temperate or tropical forests (Bowden, 1986 Matson *et al.*, 1990). None the less, our study demonstrates the importance of considering spatial variability and warm season precipitation events when estimating N_2O flux from shrub-steppe ecosystems.

This small-scale study of N_2O flux from a shrub-steppe ecosystem suggests that if local spatial variability and the temporal factors affecting this variability are unknown it is virtually impossible to make ecosystem N_2O flux estimates by simply sampling over larger scales.

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REFERENCES

Allison S. M. and Prosser J. I. (1991) Survival of ammonia oxidising bacteria in air-dried soil. *FEMS Microbiological Letters* **79,** 65–68.

Ambus P. and Christensen S. (1995) Spatial and seasonal nitrous oxide and methane fluxes in Danish forest-, grassland-, and agroecosystems. *Journal of Environmental Quality* **24,** 993–1001.

Bolton H. Jr., Smith J. L. and Link S. O. (1993) Soil microbial biomass and activity of a disturbed and undisturbed shrub-steppe ecosystem. *Soil Biology & Biochemistry* **25,** 545–552.

Bowden W. B. (1986) Gaseous nitrogen emissions from undisturbed terrestrial ecosystems: an assessment of their impacts on local and global nitrogen budgets. *Biogeochemistry* **2,** 249–279.

Burke I. C. (1989) Control of nitrogen mineralization in a sagebrush steppe landscape. *Ecology* **70,** 1115–1126.

Charley J. L. and West N. E. (1975) Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology* **63,** 945–964.

Charley J. L. and West N. E. (1977) Micro-patterns of nitrogen mineralization activity in soils of some shrub-dominated semi-desert ecosystems of Utah. *Soil Biology & Biochemistry* **9,** 357–365.

Christensen S., Simkins S. and Tiedje J. M. (1990) Temporal patterns of soil denitrification: their stability and causes. *Soil Science Society of America Journal* **54,** 1614–1618.

Cicerone R. J. (1987) Changes in stratospheric ozone. *Science* **237,** 35–42.

Crutzen P. J. (1983) Atmospheric interactions–homogeneous gas reactions of C, N, and S containing compounds. In: *The Major Biogeochemical Cycles and Their Interactions* (B. Bolin and R. B. Cook, Eds), pp. 67–114. John Wiley and Sons, New York.

Davidson E. A. (1992) Sources of nitric oxide and nitrous oxide following wetting of dry soil. *Soil Science Society of America Journal* **56,** 95–102.

Dickenson R. E. and Cicerone R. J. (1986) Future global warming for atmospheric trace gases. *Nature* **319,** 109–115.

Firestone M. K. and Davidson E. A. (1989) Microbial basis of NO and N_2O production and consumption in soil. In *Exchange of Tracegasses Between Terrestrial Ecosystems and the Atmosphere* (M. O. Andreae and D. S. Schimel, Eds), pp. 7–21. John Wiley, New York.

Folorunso O. A. and Rolston D. E. (1984) Spatial variability of field-measured denitrification gas fluxes. *Soil Science Society of America Journal* **48,** 1214–1219.

Gee G. W., Beedlow R. L. and Skaggs R. L. (1988) Water balance. In *Shrub-Steppe Balance and Change in a Semi-arid Terrestrial Ecosystem* (W. H. Rickard, L.E. Rogers, B. E. Vaughan and S. F. Liebetrau, Eds), pp. 61–84. Elsevier, New York.

Groffman P. M. and Tiedje J. M. (1988) Denitrification hysteresis during wetting and drying cycles in soil. *Soil Science Society of America Journal* **52,** 1626–1629.

Halvorson J. I., Bolton H. Jr., Smith J. L. and Rossi R. E. (1993) Geostatistical analysis of resource islands under *Artemisia tridentata* in the shrub-steppe. *Great Basin Naturalist* **54,** 313–328.

Hook P. B., Burke I. C. and Lauenroth W. K. (1991) Heterogeneity of soil and plant N and C associated with individual plants and openings in North American shortgrass steppe. *Plant and Soil* **138,** 247–256.

Hutchinson G. L., Guenzi W. D. and Livingston G. P. (1993) Soil water controls on aerobic soil emission of gaseous nitrogen oxides. *Soil Biology & Biochemistry* **25,** 1–9.

Isaaks E. H. and Srivastava R. M. (1989) *An Introduction to Applied Geostatistics*. Oxford University Press, New York.

Kieft T. L., Soroker E. and Firestone M. K. (1987) Microbial biomass response to a rapid increase in water potential when dry soil in wetted. *Soil Biology & Biochemistry* **19,** 119–126.

Matson P. A., Vitousek P. M., Livingston G. P. and Swanberg N. A. (1990) Sources of variation in nitrous oxide flux from Amazonian ecosystems. *Journal of Geophysical Research* **95,** 16789–16798.

Mosier A. R., Stillwell M., Parton W. J. and Woodmansee R. G. (1981) Nitrous oxide emissions from a native shortgrass prairie. *Soil Science Society of America Journal* **45,** 617–619.

Mummey D. L., Smith J. L. and Bolton H. Jr. (1994) Nitrous oxide flux from a shrub-steppe ecosystem: sources and regulation. *Soil Biology & Biochemistry* **26,** 279–286.

Parsons L. L., Murray R. E. and Smith M. S. (1991) Soil denitrification dynamics: spatial and temporal variations of enzyme activity, populations and nitrogen gas loss. *Soil Science Society of America Journal* **55,** 90–95.

Rasmussan R. A. and Kahlil M. A. K. (1986) Atmospheric trace gases: trends and distributions over the last decade. *Science* **232,** 1623–1624.

Rickard W. H. (1988) Climate of the Hanford site. In *Shrub-Steppe Balance and Change in a Semi-Arid Terrestrial Ecosystem* (W. H. Rickard, L. E. Rogers, B. E. Vaughan and S. F. Liebetrau, Eds), pp 13–21. Elsevier, New York.

Rogers L. E. and Rickard W. H. (1988) Introduction: Shrub-steppe lands. In *Shrub-Steppe Balance and Change in a Semi-Arid Terrestrial Ecosystem* (W. H. Rickard, L.E. Rogers, B. E. Vaughan and S. F. Liebetrau, Eds), pp. 1–12. Elsevier, New York.

Smith J. L., Halvorson J. J. and Bolton H. Jr. (1994) Spatial relationships of soil microbial biomass and C and N mineralization in an and shrub steppe ecosystem. *Soil Biology & Biochemistry* **26,** 1151–1159.

Sommerfeld R. A., Mosier A. R. and Musselman R. C. (1993) CO_2, CH_4 and N_2O flux through a Wyoming snowpack and implications for global budgets. *Nature* **361,** 140–142.

Van Gestel M., Merckx R. and Vlassak K. (1993) Microbial responses to soil drying and rewetting: the fate of fast- and slow-growing microorganisms in soils from different climates. *Soil Biology & Biochemistry* **25,** 109–123.

Van Kessel C., Pennock D. J. and Farrell R. E. (1993) Seasonal variations in denitrification and nitrous oxide evolution at the landscape scale. *Soil Science Society of America Journal* **57,** 988–995.