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Environmental controls on nitric oxide emission from northern Chihuahuan desert soils

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Abstract. A survey of nitric oxide (NO) emission from Chihuahuan desert soils found mean NO fluxes <0.1 ng NO-N cm^{-2} h^{-1} during the dry season. These fluxes were at the lower end of the range reported for temperate grassland and woodland ecosystems. NO fluxes from wet or watered soils were higher (0.1–35 ng NO-N cm^{-2} h^{-1}). Watering of black grama grassland soils produced an initial pulse of 12 ng cm^{-2} h^{-1} (12-h after 1-cm watering) with high fluxes sustained over 4 days with repeated watering. Initial pulses from shrubland soils were lower (maximum 5 ng cm^{-2} h^{-1}), and fluxes declined with repeated watering. Repeated watering of creosotebush soils depleted the soil NH_4^+ pool, and NO emissions were directly related to soil NH_4^+ concentrations at the end of the experiment. In watered and NH_4^+-fertilized creosotebush soils, NO fluxes were positively related to potential net nitrification rates. NH_4^+-fertilization boosted the initial NO pulse 15 times in the shrubland and 5 times in black grama grassland relative to watered controls. These experimental results point toward greater substrate limitation in shrublands. In this desert basin, NO emission averaged 0.12 kg N ha^{-1} y^{-1} in untreated soil and 0.76 kg N ha^{-1} y^{-1} in watered soil. We multiplied these averages by the distribution of grassland and shrubland vegetation within a 58,600-ha area of the Jornada del Muerto basin to estimate regional losses of 0.15–0.38 kg NO-N ha^{-1} y^{-1} for this area of the Chihuahuan desert.

Introduction

Nitric oxide (NO) is a trace gas that regulates the consumption and production of photochemical oxidants, e.g. ozone (O_3) and hydroxy radicals, in the troposphere (Warneck 1988). At low concentrations (<3–8 pptv NO; Crutzen & Zimmerman 1991), NO reacts with O_3 to produce NO_2 and O_2, but at higher concentrations, NO catalyzes the oxidation of CH_4, CO and volatile organic compounds (VOC) to produce O_3 (Warneck 1988). The reaction of NO with

plant-emitted VOC can be a predominant source of O_3 in rural environments (Chameides et al. 1992).

Soil-emitted NO is important to regional tropospheric O_3 production in tropical savannas (Johansson & Sanhueza 1988). Tropical savannas and forests emit high NO pulses from nitrification in soils watered at the end of the dry season (Johansson et al. 1988; Johansson & Sanhueza 1988; Davidson et al. 1991). In deserts, the wet season NO fluxes from nitrifying bacteria could be extremely high because soil ammonium (NH_4^+) accumulates during the dry season by mineralization of organic N (Fisher et al. 1987). In the southwest U.S., soil-emitted NO may react with VOC emitted from desert shrubs to produce O_3 (Guenther 1997; Kinnee et al. 1997). To our knowledge, there are no published studies of NO emission from desert soils (Davidson & Kingerlee 1997).

In the southwestern United States, large areas of grassland have been replaced by shrubland over the past century, putatively due to livestock overgrazing and drought (Schlesinger et al. 1990). This vegetation shift, a form of desertification, redistributes soil resources within the landscape. Organic matter and inorganic nutrients accumulate under shrub canopies, forming "islands of fertility" (Noy-Meir 1985; Schlesinger et al. 1996). Soil nutrients are eroded from areas between shrubs and deposited in topographic depressions (Wierenga et al. 1987; Schlesinger et al. 1999). In this study, we investigate soil moisture, temperature, inorganic N concentrations and N cycling rates as controls on NO emission, and estimate the magnitude of NO losses from a desert basin.

Materials and methods

Study site

This study was conducted at the Jornada Basin Long-Term Ecological Research (LTER) site, 40 km NNE of Las Cruces, Doña Ana County, New Mexico, USA. The Jornada LTER is located in the Jornada del Muerto basin in the northern Chihuahuan Desert (32°37′ N, 106°40′ W). Mean annual precipitation is 23 cm with 52% falling in local, convective storms during the summer (July to September). July is the warmest month (mean maximum temperature 36 °C), and January the coldest (mean maximum temperature 19 °C).

Twelve study sites were located in 5 vegetation types adjacent to or within LTER permanent plots (for UTM coordinates see Hartley 1997). These sites represent the major plant communities of the Jornada del Muerto basin: black grama (*Bouteloua eriopoda* (Torr.) Torr.) grasslands;

Table 1. Physical and chemical properties of Jornada soils.

Ecosystem	% Sand[1]	% Clay[1]	pH in H_2O[1]	Depth (cm)[1]	% Organic C[2]	% $CaCO_3$[2]
Black grama grassland	68.5	10.0	6.8	0–15	0.3	0.03
Creosote shrubland	71.0	7.5	7.6	0–18	0.4	0.20
Mesquite shrubland	90.0	7.0	7.8	0-81	0.3	0.13
Tarbush shrubland	66.0	18.0	7.9	0–15	0.5	0.63
Playa grassland	18.0	51.0	7.9	0–8	1.3	0.28

[1] Upper horizon data from Virginia and Jarrell, unpub. (sampling depth variable).
[2] Carbon data published by Gallardo and Schlesinger (1992); soils sampled to 10 cm.

shrubland communities dominated by creosotebush (*Larrea tridentata* (DC) Cov.), mesquite (*Prosopis glandulosa* (Torr. Var. Torreyana (L. Benson) M.C. Johnson) or tarbush (*Flourensia cernua* DC); and mixed grassland communities dominated by *Hilaria mutica* (Buckl.) Benth. and *Scleropogon brevifolius* Phil. in ephemeral lakebeds or playas.

The Jornada del Muerto Basin is situated within the Basin and Range physiographic province, which is characterized by parallel, fault-block mountain ranges (Gile et al. 1981). Alluvial deposits fan the base of the mountains, and ephemeral or dry lakebeds (playas) occupy the lowest topographic positions within the endorheic basins. Basin soils are classified as Aridisols, with the exception of mesquite coppice dunes which are Entisols (Gile et al. 1981). Soil physical and chemical characteristics of our sites are summarized in Table 1.

Trace gas analysis

All measurements of NO flux followed the method of Davidson et al. (1991), using a portable chemiluminescent detector of NO_2 (Scintrex LMA-3; Ontario, Canada). LMA-3 scale readings were externally calibrated at the beginning and end of each sampling period with a standard containing 0.1 ppm NO in N_2. At each site, 25-cm diameter PVC rings were inserted into the soil 2–3 cm, the soil was allowed to equilibrate for 10 min, and molded plastic chamber lids (10-cm high) were placed on the PVC rings. For each flux measurement, NO concentrations of chamber air were measured every 15 s for 5 min.

Soil analysis

After each flux measurement, a 20-cm soil core was removed from nearby, but outside, the 25-cm gas sampling ring, using 5.1-cm diameter PVC pipe. In the watering and fertilization experiments, soil cores were removed from

identically treated soils within a second 25-cm diameter PVC ring. In the laboratory, soil samples were sieved (2-mm), and a 100-g subsample was oven-dried at 105 °C for 48 h to determine gravimetric soil moisture content. Water-filled pore space (WFPS) was calculated using the formula in Davidson and Schimel (1995):

$$\%\text{WFPS} = [100 \times (\theta_g \times \text{BD}]/[1 - (\text{BD}/\text{PD})],$$

where θ_g is gravimetric soil moisture content (g H_2O g^{-1} oven-dried soil), BD is bulk density (g dry soil cm^{-3}) and PD is particle density (assumed to be 2.65 g dry soil cm^{-3}).

Two 20-g soil subsamples were used to estimate NH_4^+ and NO_3^- concentrations, potential net N mineralization and potential net nitrification rates. Fifty ml of 2 N KCl was added to one 20-g subsample on the day of collection. The second subsample was incubated aerobically at room temperature in the dark for 14 days before adding 50 ml KCl. After adding KCl, soil extracts were shaken and allowed to equilibrate. Approximately 10 ml of supernatant was poured off after 24 h, frozen and mailed to Duke University for colorimetric analysis on a TRAACS autoanalyzer (Bran & Luebbe 1996). The difference between final (14-d incubated) and initial NH_4^+ and NO_3^- concentrations was used to estimate potential net N mineralization rates. The difference between final and initial NO_3^- concentrations was used to estimate potential net nitrification rates.

Experimental design

We hypothesized that soil moisture was the primary factor limiting NO emission from desert soils, and conducted a series of observations and experiments with two objectives: to investigate soil moisture and N availability as controls on NO emission and to study the spatial and temporal variability of NO fluxes from Jornada basin soils.

A survey of NO emission from Jornada basin soils

In 1993, we surveyed NO fluxes from Jornada soils before (May and June) and after the start of the rainy season (August) at 2–3 sites within each of the 5 vegetation types. Gas fluxes were measured at 6 PVC rings within a 5-m^2 area at each site. These rings were randomly positioned except in the shrubland where sampling was stratified (3 under and 3 between shrub canopies).

To examine the effect of landscape position on NO emission, we also measured fluxes at 3 sites along the Jornada LTER permanent transect, which extends from a black grama grassland at the base of a mountain (Grassland-S) through creosotebush shrubland (Creosotebush-S) to a playa grassland

(Playa-C). Fluxes were measured 2 days before, 1 and 4 days after a 9.4-mm rain on 25 May 1993.

Potential NO emission from grassland and shrubland soils

To compare grassland and shrubland NO pulses at the end of the dry season, we measured fluxes from soils at 3 sites (Grassland-S, Creosotebush-S and Tarbush-W) 10 and 30 minutes after infiltration of a 2-cm simulated rain (25 June 1992). The 6 PVC rings at each site were randomly positioned in the grassland, but stratified in the shrubland – 3 under shrub canopies and 3 between shrubs.

In a second experiment during the summer of 1993, we watered soils repeatedly to determine the extent to which soil moisture and inorganic N limit NO emission from desert soils. We treated soils at Grassland-S, Creosotebush-S, Tarbush-W and Mesquite-N (between-shrub only) with a 1-cm simulated rain for up to 4 consecutive days. Pre-treatment fluxes were measured on Day 1 of the experiment. Soils in Treatment groups 1–4 were watered on the evening of Day 1, Treatment groups 2–4 on Day 2, Treatment groups 3–4 on Day 3 and Treatment group 4 on Day 4. NO fluxes were measured from these rings and control (unwatered) rings in the early morning, approximately 12 h after each watering. All soils were allowed to dry between Days 4 and 10. On Day 10, NO fluxes were measured and soils in Treatment groups 1–4 were watered in the evening. Final NO fluxes were measured on Day 11.

We measured the magnitude of NO emission from soils under mesquite shrub canopies in an abbreviated version of the above experiment (Mesquite-N on 22–25 July 1995). Soils adjacent to and under a mesquite shrub were watered on 4 consecutive days, and NO fluxes measured as described above. Each treatment group consisted of 3 replicates from which NO fluxes were sampled on consecutive days.

To test the effect of soil NH_4^+ availability on NO emission, we treated black grama grassland, creosotebush and tarbush shrubland soils (between shrubs only) with a 2-cm simulated rain or the same volume of water containing NH_4Cl (8.8 g N m^{-2}). The first experiment was conducted on 03 July 1992 in Grassland-S where the first treatment was applied at 0600 h on Day 1 and a second treatment applied at 0600 h 4 days later. NO fluxes were measured on 3 replicate PVC rings in each treatment and 3 untreated chambers before treatments were applied, then again at 1 and 24 h after each treatment. Soils were sampled at shrubland sites only. Similar experiments were conducted on 06 June 1994 in Creosotebush-S and 8 June 1994 in Tarbush-E.

From 1983 to 1994, over 90% of summer rainstorms in the Jornada del Muerto basin were 2-mm or less (Jornada LTER, unpublished data). In July 1995, we measured NO emission after a simulated 2-mm rain event by watering black grama grassland (Grassland-S on 12 July 1995) and mesquite shrubland soils (between shrubs at Mesquite-N on 8 July 1995) at 1800 h and measuring fluxes at 1900 h, 2100 h, and at 2-h intervals the following day from 0600 to 2000 h. The 3 sampling points at each site were randomly positioned on bare soil. Soils were sampled for moisture and chemical analysis at 1900 and 2100 h.

Statistical analysis

Fluxes were estimated from the linear regression of increasing NO concentration (ppbv) in each chamber over time. The slope was adjusted to standard temperature and pressure, and fluxes expressed as ng NO-N cm^{-2} h^{-1}. NO fluxes from surveyed soils were correlated to soil moisture, NH_4^+, NO_3^-, potential net N mineralization and net nitrification rates using the Pearson Product-Moment, and temporal trends were analyzed by one-way analysis of variance (ANOVA) at each site. For watering experiments, we used repeated measures ANOVA on gas fluxes and two-way ANOVA on soil variables. Treatment means were compared by Scheffe post hoc tests. If necessary, data were transformed to meet the ANOVA assumptions of normality and homogeneity of variance. A nonparametric equivalent (Wilcoxon rank sum or Kruskal Wallis test) was used when data failed to meet the ANOVA assumptions. All statistical tests were performed in JMP (SAS Institute 1996) or Data Desk (Data Description Inc. 1993).

Results and discussion

Actual NO emission from Jornada basin soils

In the survey of 12 sites within the Jornada del Muerto Basin, we found low NO emission in May and June, before the start of the rainy season (< 0.1 ng NO-N cm^{-2} h^{-1}; Table 2). NO fluxes tended to be higher in August, but also after isolated storms in May and June (e.g. Creosotebush-S in June in Table 2, Creosotebush-S and Playa-C in Table 3). Monthly sampling was too infrequent to capture short-term NO losses associated with rain at all sites; therefore, the mean fluxes in Table 2 represent a conservative estimate of NO emission from Jornada soils. These fluxes fall at the low end of the range reported for grassland and woodland ecosystems (Davidson & Kingerlee 1997).

Table 2. Seasonal changes in soil NO emission (ng N cm^{-2} h^{-1}), soil moisture availability (% water-filled pore space), inorganic N pools (KCl-extractable NH_4^+ and NO_3^-; ug N g^{-1} dry soil), potential net mineralization (ug N g^{-1} soil d^{-1}) and potential net nitrification (ug NO_3-N g^{-1} soil d^{-1}). Each number represents the mean of 6 replicates. Soils were sampled before (May and June) and after (August) the start of the rainy season in 1993. Means followed by common letters are not statistically different at the 0.05 level. n.d. = not determined.

		NO	% WFPS	NH_4^+	NO_3^-	NH_4:NO_3	Net N min.	Net nitr.
Grassland Summerford	May	0.02 a	2.6 a	1.0 a	0.3 a	3.9 a	−0.07 a	0 a
(Grassland-S)	June	0.06 a	5.3 b	0.5 a	0.7 b	0.7 b	0.04 b	0.02 a
	August	0.07 a	4.5 b	0.3 b	0.6 b	0.5 b	0.02 b	0.04 a
Grassland IBP	May	0 a	1.9 a	0.5 a	0.3 a	3.3 a	−0.02 a	0.01 a
(Grassland-I)	June	0.05 a	3.0 b	0.3 a	0.5 a	0.7 b	0.02 ab	0.02 a
	August	1.74 a	3.4 b	0.1 b	0.4 a	0.2 b	0.06 b	0.06 b
Mesquite Rabbitbrush	May	0.29 a	0.7 a	0.8 a	1.4 a	0.7 a	−0.03 a	0.01 a
(Mesquite-R)	June	0.04 b	1.3 b	0.6 a	2.9 a	0.2 a	−0.07 a	−0.01 a
	August	0.51 ab	2.1 c	1.0 a	2.2 a	0.4 a	0.11 a	0.13 b
Mesquite West Well	May	0.22 a	3.6 a	2.4 a	4.3 a	1.3 a	−0.02 a	0.06 a
(Mesquite-W)	June	0.21 a	2.2 b	1.3 a	3.9 a	0.5 a	0.09 a	−0.02 a
	August	1.78 b	2.3 b	2.0 a	4.8 a	0.6 a	0.01 a	0.05 a
Creosotebush Gravel	May	0.03 a	6.3 a	1.2 a	0.4 a	3.3 a	−0.03 a	0.03 a
(Creosotebush-G)	June	0.15 b	12.8 b	0.5 a	1.0 a	0.6 b	0.11 a	0.08 a
	August	0.12 b	9.1 ab	0.6 a	1.7 a	0.4 b	−0.01 a	0.04 a
Creosotebush Sand	May	0.02 a	2.6 a	1.9 a	0.4 a	6.7 a	0.47 a	0.12 a
(Creosotebush-S)	June	1.08 b	6.9 b	0.7 ab	1.8 b	0.4 b	−0.02 a	−0.02 a
	August	0.13 c	3.2 a	0.1 b	1.8 b	0.1 c	0.10 a	0.07 a
Tarbush Taylor	May	0.11 a	2.6 a	1.4 a	1.0 a	1.4 a	−0.09 a	−0.01 a
(Tarbush-T)	June	0.03 a	2.5 a	0.6 ab	1.4 a	0.5 b	0.02 a	0.02 a
	August	0.05 a	5.5 b	0.3 b	1.9 a	0.2 b	0.14 a	0.14 a
Tarbush West	May	0.02 a	8.2 a	1.2 a	0.5 a	2.3 a	0 a	0.04 ab
(Tarbush-W)	June	0.08 b	7.4 a	0.9 a	1.4 b	0.7 b	0.14 b	0.09 ab
	August	0.60 c	9.0 a	1.0 a	1.9 b	0.6 b	0.08 b	0.13 b
Playa College	May	0.01 a	16.0 a	2.6 a	4.0 a	0.7 a	0.19 a	0.09 a
(Playa-C)	June	0.32 b	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
	August	0.29 b	15.3 a	2.0 a	7.2 b	0.3 b	−0.07 a	0.05 a
Playa Tobosa	May	0.10 a	6.6 a	1.0 a	1.2 a	1.2 a	0.02 a	0.04 a
(Playa-T)	June	0.12 a	18.5 b	1.2 b	2.6 b	0.5 ab	0.18 b	0.16 ab
	August	0.25 b	15.2 c	1.0 a	4.4 c	0.2 b	0.23 b	0.22 b
Playa Small ungrazed	May	0.03 a	10.0 a	5.4 a	19.6 a	0.3 a	−1.2 a	−1.0 a
(Playa-SU)	June	0.12 b	29.2 b	2.0 b	7.2 b	0.3 a	n.d.	n.d.
	August	0.27 c	37.2 c	1.6 c	2.9 c	0.6 b	0.2 b	0.01 b
Playa Small grazed	May	0.05 a	15.0 a	4.3 a	15.2 a	0.3 a	−0.9 a	−0.8 a
(Playa-SG)	June	0.09 a	18.6 b	2.9 a	5.0 a	0.6 b	n.d.	n.d.
	August	0.18 b	27.7 c	1.3 b	7.6 a	0.2 a	0.1 b	−0.5 a

Table 3. NO emission from soils on the Jornada LTER permanent transect before and after a 9.4-mm rainstorm (mean of 6 replicates). Means followed by common letters are not statistically different at the 0.05 level.

	2-days pre-rain	1-day post-rain	4-days post-rain
NO emission (ng cm^{-2} h^{-1})			
Grassland-S	0.02 a	1.3 a	0.1 ab
Creosotebush-S	0.02 a	6.5 b	0.6 b
Playa-C	n.d.	4.0 ab	3.6 c
WFPS (%)			
Grassland-S	2.6 a	1.4 a	1.6 a
Creosotebush-S	2.6 a	1.6 a	1.9 a
Playa-C	n.d.	16.0 b	13.9 b
Soil NH_4-N (ug g^{-1} dry soil)			
Grassland-S	1.0 a	1.1 a	n.d.
Creosotebush-S	1.9 a	1.1 a	n.d.
Playa-C	n.d.	2.6 b	n.d.
Soil NO_3-N (ug g^{-1} dry soil)			
Grassland-S	0.3 a	0.5 a	n.d.
Creosotebush-S	0.4 a	0.7 a	n.d.
Playa-C	n.d.	4.0 b	n.d.
Potential net N mineralization (ug N g^{-1} soil d^{-1})			
Grassland-S	−0.07 a	0.14 a	n.d.
Creosotebush-S	0.47 a	0.15 a	n.d.
Playa-C	n.d.	0.19 a	n.d.
Potential net nitrification (ug N g^{-1} soil d^{-1})			
Grassland-S	0 a	0.02 a	n.d.
Creosotebush-S	0.12 a	0.04 a	n.d.
Playa-C	n.d.	0.09 a	n.d.

Potential NO emission from grassland and shrubland soils: Effects of watering and fertilization

Using watering experiments, we found pulses of NO emission from black grama grassland, cresotebush and tarbush soils at the end of the dry season. Ten minutes after a 2-cm simulated rain, NO fluxes increased by an order of magnitude at all 3 sites. The short-term response to watering was similar in grassland and creosotebush soils (5.8 and 7.0 ng NO-N cm^{-2} h^{-1}, respectively), but lower from tarbush soils (0.2 ng cm^{-2} h^{-1}). NO emission was

Table 4. Short-term response of desert soils under vs. between shrubs to 2-cm simulated rain (mean NO emission; ng cm^{-2} h^{-1}; n = 3). Time column contains time of flux measurement following infiltration of water. Means followed by common letters are not statistically significant at the 0.05 level.

Shrubland	Time		NO flux
Creosotebush-S	10 minutes	Between	1.2 a
		Under	12.9 b
Tarbush-W	10 minutes	Between	0.1 a
		Under	0.4 a
Tarbush-W	30 minutes	Between	0.4 a
		Under	2.1 b

significantly higher under shrub canopies at both shrubland sites (Table 4), but this "island of fertility" effect was was not detected in tarbush soils until 30 min after infiltration. This slower response could be related to inhibited NO diffusion or to slower recovery of microbial populations in fine-textured soils (Gallardo & Schlesinger 1995). The rapid microbial response in coarse-textured soils is similar to that observed in other ecosystems with prolonged dry seasons (cf. Davidson 1992a, 1992b). Despite an accumulation of NH_4^+ during the dry season (Table 2), NO pulses were an order of magnitude lower than the rates of 50–90 ng cm^{-2} h^{-1} observed in tropical savannas and forests watered at the end of the dry season (Johansson et al. 1988; Johansson & Sanhueza 1988; Davidson et al. 1991).

At sites that were watered repeatedly, we studied the extent to which soil moisture and inorganic N limit NO emission. Unwatered soils had 1–2% WFPS at all sites with the exception of tarbush (5%), and 4 daily 1-cm watering treatments raised WFPS to 6–12%. Grassland soils emitted a high initial NO pulse after 1-cm simulated rain and emission was sustained with repeated watering (Table 5). Even after a 5-d drydown (Days 5–10), the pulse from rewetted soils (Day 11) was double the initial pulse. In contrast, the initial pulse from shrubland soils (between shrubs) was lower (mean of 4.9 ng cm^{-2} h^{-1} in creosotebush, 3.2 ng cm^{-2} h^{-1} in tarbush and 0.3 ng cm^{-2} h^{-1} in mesquite), and fluxes declined with repeated watering. At the end of the 11-d experiment, NO fluxes from rewetted creosotebush soils were inversely related to the number of watering treatments and directly related to soil NH_4^+ concentration (R^2 = 0.49, p = 0.01). Repeated watering depleted soil NH_4^+ pool, lowering NO emission from creosotebush soils. Thus, NH_4^+ availability acts as a secondary control on NO production in shrublands. Declining emission with sequential watering or rainfall has been observed

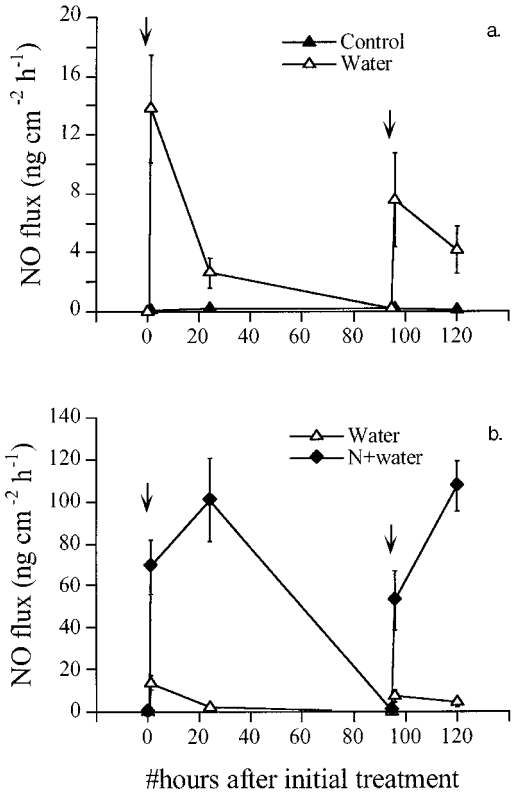

Figure 1. Effect of a) 2-cm watering and b) NH_4^+ fertilization on mean NO emission from black grama grassland soil. Treated soils received 2-cm water or the same volume of NH_4^+ solution at 0600 h on Day 1 and at the same time 4 days later (shown by arrow).

in a wide range of soil types (Slemr & Seiler 1984; Williams et al. 1987; Johansson et al. 1988; Johansson & Sanhueza 1988; Davidson 1992a). This trend was attributed to diminishing soil inorganic N supplies, except where soils were water-saturated.

In watering and NH_4^+ fertilization experiments, we detected 5 times greater NO emission from NH_4^+-treated black grama grassland soils than from watered controls 1 h after treatment (Figure 1). Grassland NO fluxes were sustained over a longer period with fertilization ($>$24 h), indicating that greater soil N availability enhanced NO production in grassland soils. A similar pattern was observed after the second treatment. In the shrubland, NO emissions from soils between shrubs were 15 times higher in fertilized and watered soils (15 vs. 0.04 ng cm^{-2} h^{-1}), but this pulse declined within 24 h (Figure 2). NO emission in creosotebush (R^2 = 0.92, p = 0.0001) and

Table 5. The effect of repeated watering on NO emission from black grama grassland, creosotebush, tarbush and mesquite shrubland soils. Bold numbers are mean NO fluxes (ng cm^{-2} h^{-1}; n = 3) measured 12 hours after a simulated 1-cm rain. TRT = Treatment or number of watering applications. n.d. = not determined.

TRT	Day 1	2	3	4	5	10	11
Grassland-S							
0	0	0	0	0	0.1	0	0
1	0	**9.9**	0.3	0.1	0.3	0	**25.7**
2	0	**17.0**	**14.9**	1.6	3.0	0	**34.6**
3	0	**16.4**	**10.1**	**13.2**	12.6	0	**28.4**
4	0	**6.1**	**7.2**	**10.7**	**15.0**	0	**9.5**
Untreated soil N = 0.6 ug NH_4- and 0.2 ug NO_3-N g^{-1} dry soil; Day 1 = JD 185							
Creosotebush-S							
0	0.1	0	0	0	0	0	0
1	0.1	**8.6**	0.3	0.1	0	0	**9.9**
2	0.1	**3.3**	**2.0**	0.3	0.2	0	**2.2**
3	0.1	**5.1**	**2.1**	**1.9**	0.4	0	**2.3**
4	0.2	**2.6**	**1.9**	**1.6**	**1.3**	0	**0.7**
Untreated soil N = 0.6 ug NH_4- and 0.6 ug NO_3-N g^{-1} dry soil; Day 1 = JD 174							
Tarbush-W							
0	0.1	0	0	0	0	0	0
1	0.1	**4.2**	0.4	0.4	0.1	0.1	**1.6**
2	0	**3.0**	**0.7**	0.7	0.1	0.1	**1.2**
3	−0.5	**2.4**	**1.5**	**1.5**	1.4	0.1	**1.4**
4	−0.3	**3.4**	**1.3**	**1.3**	**1.2**	0.1	**1.3**
Untreated soil N = 1.6 ug NH_4- and 4.6 ug NO_3-N g^{-1} dry soil; Day 1 = JD 236							
Mesquite-N							
0	n.d.	0	0	0	0	0	0
1	n.d.	**0.3**	0.1	0	0	0	**0.2**
2	n.d.	**0.4**	**0.3**	0.1	0	0	**0.3**
3	n.d.	**0.5**	**0.3**	**0.2**	0.1	0	**0.2**
4	n.d.	**0.3**	**0.5**	**0.3**	**0.2**	0	**0.2**
Untreated soil N = 0.1 ug NH_4- and 0.6 ug NO_3-N g^{-1} dry soil; Day 1 = JD 168							

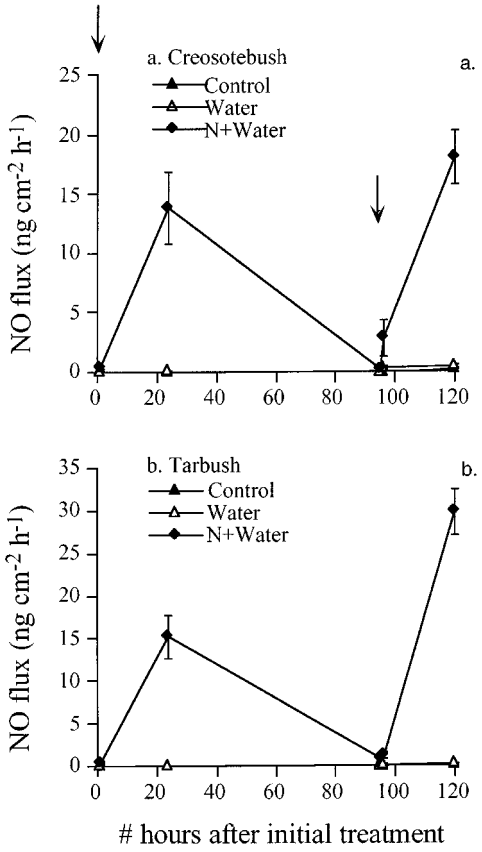

Figure 2. Effect of 2-cm watering and NH_4^+ fertilization on mean NO emission from creosotebush and tarbush soils. Treated soils received 2-cm water or the same volume of NH_4^+ solution at 0600 h on Day 1 and at the same time 4 days later (shown by arrow).

tarbush (R^2 = 0.60, p = 0.001) soils was negatively related to potential net N mineralization, and NO emission was positively related to potential net nitrification in creosotebush soils (R^2 = 0.89, p = 0.0001; Figure 3). These experimental results suggest that black grama grassland soils have higher potential for NO production than shrubland soils, and that NO production in desert soils is limited primarily by water and secondarily by NH_4^+ availability.

Putative controls on NO emission from desert soils

Davidson (1993) hypothesized that NO emission would reach a maximum at field capacity, approximately 60% WFPS. His hypothesis is based in part on work by Linn and Doran (1984), which showed that up to ~60%

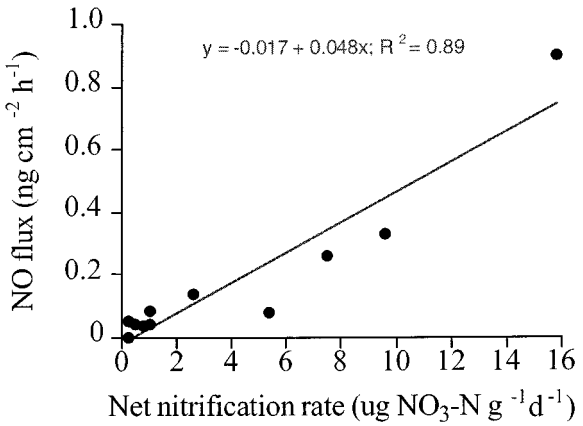

Figure 3. Relationship between soil NO emission and potential net nitrification rates (14-d laboratory incubation) in untreated, watered and NH_4^+-fertilized creosotebush soils.

WFPS, microbial reactions are limited by substrate diffusion in soil water films. Above 60%, aerobic reactions such as nitrification are inhibited by low oxygen concentrations. In our study, NO fluxes in repeatedly watered, coarse-textured soils increased exponentially up to 10% WFPS (Grassland-S: R^2 = 0.60, p = 0.0001; Mesquite-W: R^2 = 0.53, p = 0.0001; Creosotebush-S: R^2 = 0.60, p = 0.0001). NO was positively, linearly related to moisture in fine-textured playa soils, where WFPS spanned 5 to 40% (Playa-SU and -SG; R^2 = 0.68, p = 0.0001). Linear increases in NO emission up to 30–56% WFPS have been reported in other seasonally dry ecosystems (Cárdenas et al. 1993; Parsons et al. 1996). We found no evidence of a parabolic relationship between NO emission and WFPS, presumably because soil moisture rarely exceeds field capacity.

Temperature interacts with soil moisture to regulate NO emission and the direction of this relationship is time-dependent. Soil temperature ranged from 19 to 60 °C during the summer survey, but NO fluxes were strongly related to temperature only at the wettest sites (Playa-SG and -SU, R^2 = 0.40, p = 0.0001). The negative relationship between soil temperature and playa NO could indicate inhibition at high temperatures, but in this case, the effect of soil temperature is confounded by moisture because soils tend to be cooler during the wet season. Diel trends in NO emission show a stronger temperature dependence in wet soils than in dry (Figure 4), as documented in other seasonally dry ecosystems (Johansson & Sanhueza 1988; Johansson et al. 1988; Anderson & Poth 1989; Meixner et al. 1997). Grassland NO fluxes varied directly with soil temperature until soils dried, although diel

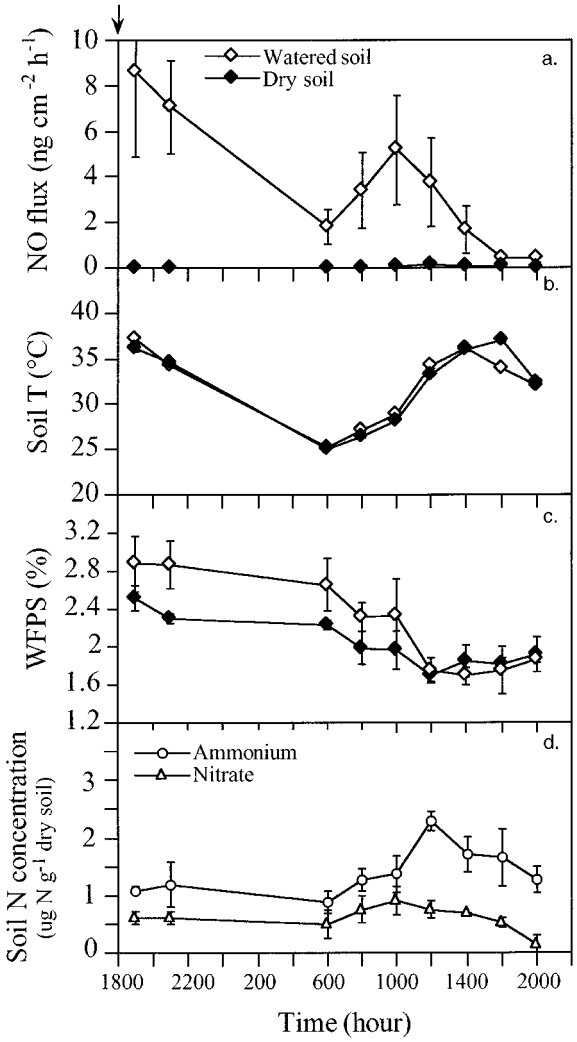

Figure 4. Diel trends in mean NO emission, soil temperature (2-cm depth) and percent water-filled pore space after 2-mm simulated rain (n = 6). Figures (a–d) display data from a black grama grassland and Figures (e–h) from a mesquite shrubland (between shrubs). Treated soils (open symbols) were watered at 1800 h (shown by arrow). Closed symbols represent unwatered controls.

trends were also evident in mesquite soils where moisture did not change significantly.

Soil nutrient status is often invoked to explain differences in N trace gas emission across sites. In the summer survey, low inorganic N concentrations and N cycling rates appear to cause the low NO losses from desert soils (Table

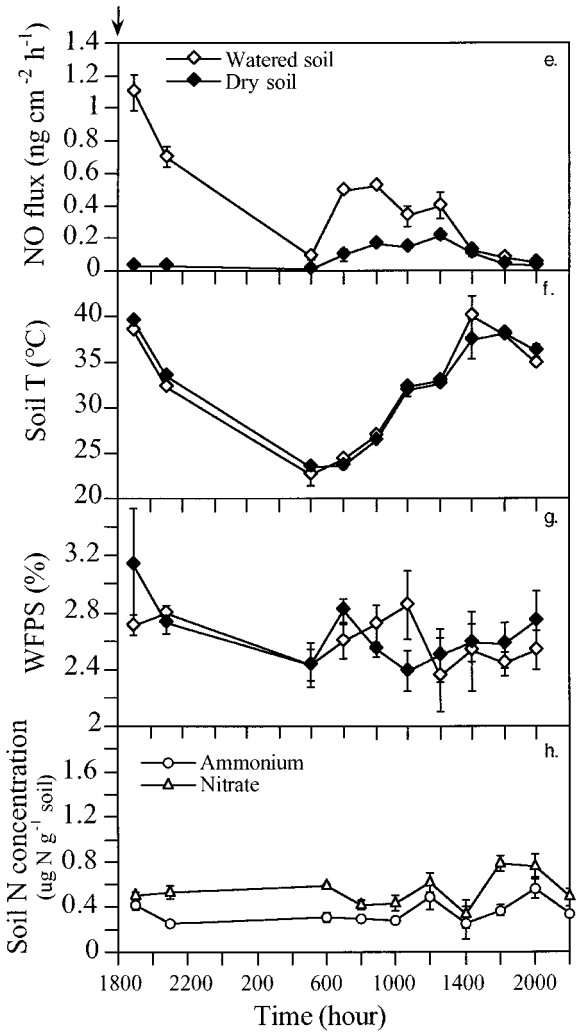

Figure 4. Continued.

2). However, inorganic N pools were poor predictors of NO emission potential at the site level. Grassland soils with the lowest inorganic N demonstrated a high capacity for NO production (Table 5), while tarbush soils with higher inorganic N emitted low NO. At a smaller scale, within shrublands, higher inorganic N concentrations (36% higher under shrub canopies, averaged over shrubland sites in Table 2, $p = 0.01$) may have caused the higher NO fluxes from watered soils under shrub canopies (Table 4).

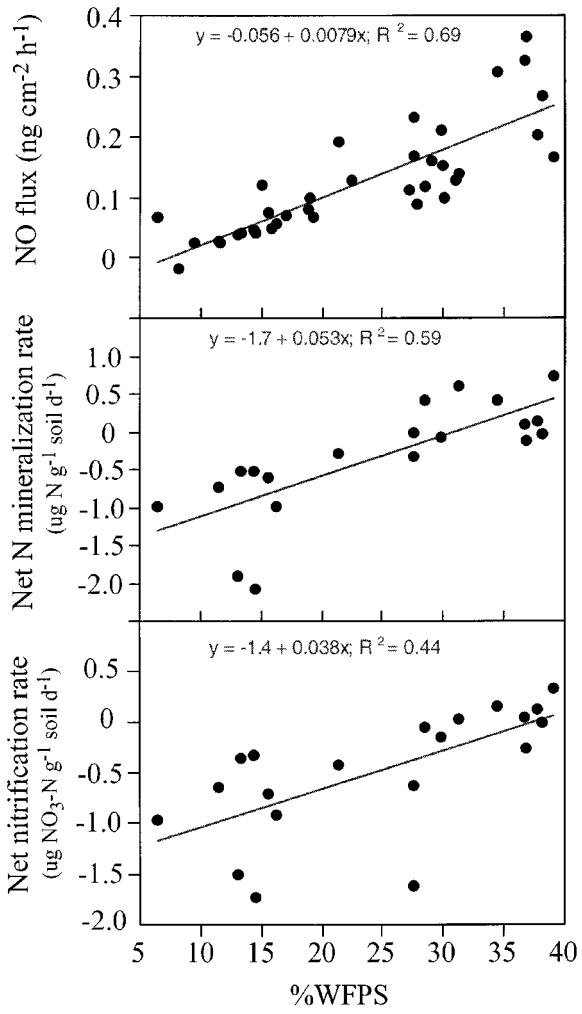

Figure 5. Summer-time increases in NO emission and soil nitrogen cycling rates as a function of increasing soil moisture in grazed and ungrazed playa grassland soils.

Watering and fertilization experiments yielded the most compelling evidence that substrate regulates NO emission. Despite low initial N concentrations, differentially watered creosotebush soils showed a positive relationship between NO fluxes and NH_4^+ availability (Creosotebush-S, Table 5). Direct NH_4^+ additions enhanced NO losses from grassland and shrubland soils (Figures 1 and 2), as in other field experiments involving NH_4^+ fertilization (Slemr & Seiler 1984; Hutchinson & Brams 1992).

In simplified form, soil N transformations include organic N conversion to NH_4^+ (mineralization or ammonification), NH_4^+ oxidation to NO_3^- (nitrification) and NO_3^- reduction to N_2O or N_2 (denitrification). Emissions of nitrogen gases are regulated by the rate of soil N cycling, which determines the total amount of N gases produced. Studies have demonstrated a strong positive relationship between potential net N mineralization and N trace gas emission in tropical soils (Matson & Vitousek 1987; Verchot et al. 1999). We found a direct relationship between potential net N mineralization and NO emission only at the wettest desert site (Figure 5).

Experimental manipulation of shrubland soils produced the opposite trend: potential net N mineralization decreased progressively with watering and fertilization. The decline in net N mineralization indicates that inorganic N is lost from the soil – by microbial consumption or volatilization – faster than the rate at which N is mineralized. In this arid climate, N mineralization and nitrification are at least partially decoupled in time. NH_4^+ gradually accumulates from slow rates of N mineralization during dry periods (Fisher et al. 1987), and then nitrification and denitrification (and NH_3 volatilization) deplete the NH_4^+ pool rapidly during wet periods. Although mineralization provides the inorganic N that is used for NO production, the correlation in watered soils is negative.

A positive relationship between potential net nitrification and NO emission was detected only at the wettest desert site (Figure 5). With experimental NH_4^+ fertilization, NO emission from black grama grassland and shrubland soils increased dramatically (Figures 1 and 2). Under these conditions, net nitrification was positively related to NO emission from creosotebush soils (Figure 3). These results offer strong evidence that soil moisture and NH_4^+ availability regulate NO emission by increasing nitrification rates.

Changes in soil NO_3^- pool can be used as an index of nitrification potential in field soils. Rain increased soil NO_3^- six-fold in Grassland-S (Table 3). NO_3^- concentrations were 2–4 times higher at the end of the summer in 5 of the 12 survey sites (Table 2). The ratio of NH_4^+ to NO_3^- decreased significantly at 8 sites, indicating that NO_3^- had become the dominant form of inorganic N by the end of the summer. NH_4^+ was largely transformed to NO_3^-, but some of the NO_3^- was lost by leaching or denitrification. The wettest sites in the basin (Playa-SU, -SG) showed no significant change in NH_4:NO_3, but a depletion in the total inorganic N. High inputs of moisture accelerate N losses, depleting inorganic N, as observed after repeated watering of creosotebush soils.

Extrapolation of field NO fluxes

We estimated fluxes from 4 major vegetation types (excluding playas which cover a small land area) using 2 emission scenarios. The first “actual emis-

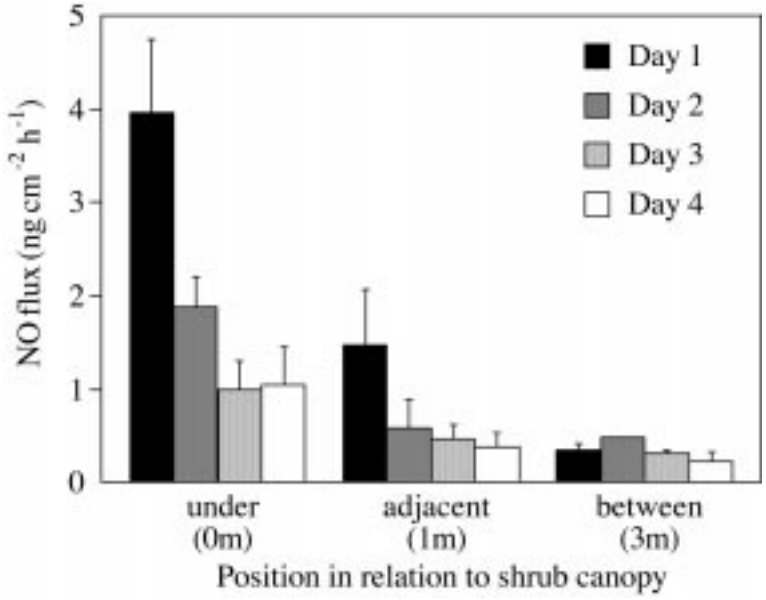

Figure 6. Effect of repeated 1-cm watering on mean NO emission from soils under a mesquite shrub canopy, adjacent to and between mesquite shrubs (n = 3).

sion" scenario uses the dry and rainy-season fluxes in Table 2. Mean annual NO emission was computed as the weighted mean of a 90-day rainy season and a 275-day dry season using August and May fluxes, respectively. We assumed that night-time and winter-time NO fluxes are negligible. In a second "potential emission" scenario, we used the mean NO fluxes from soils watered 1-cm on 4 consecutive days in each vegetation type. The mesquite shrubland mean was weighted 50% under and 50% between shrubs using data in Figure 6. We used the ratio of NO emitted under and between shrubs in Table 4 to convert under-shrub fluxes in the creosotebush and tarbush sites to areal estimates for the year.

Using these "actual" and "potential emission" scenarios, we extrapolated mean annual NO emission to the area occupied by each vegetation type within a 58,600-ha area of the basin designated the Jornada Experimental Range. We multiplied mean annual NO flux (kg N ha^{-1} y^{-1}) by the areal extent of each vegetation type in 1858 and 1963 (Table 6). Using "actual" NO fluxes, there is no indication that mean NO fluxes have changed during the past century. The "potential emission" scenario suggests that NO fluxes may have declined with the conversion of grassland to shrubland. As in 1963, mesquite shrubland is the dominant vegetation type within Jornada basin, which reinforces the trend toward lower emission; however, other factors have changed over the past century. Changes in emission over time can only be speculated in this study;

Table 6. Estimated regional NO emission at the Jornada Experimental Range, 1858–1963.

	Mean NO emission (ng N cm^{-2} h^{-1})						Regional NO emission (kg N y^{-1})			
	Actual	Potential	Areal extent (ha)[1]		Areal extent (%)		Actual NO emission		Potential NO emission	
	NO flux	NO flux	1858	1963	1858	1963	1858	1963	1858	1963
Black grama grassland	0.20	1.07	33,800	0	58	0	0.12	0	0.62	0
Mesquite shrubland	0.21	0.12	15,500	37,800	27	65	0.06	0.14	0.03	0.08
Creosotebush	0.02	1.23	400	7,500	1	13	0	0	0.01	0.16
Tarbush	0.06	0.62	8,700	13,100	15	22	0	0.01	0.09	0.14
Unweighted mean	**0.12**	**0.76**				**Total**	**0.18**	**0.15**	**0.75**	**0.38**

[1] Buffington & Herbel 1963.

however, it appears that the Jornada del Muerto basin would be a greater source of biogenic NO today if black grama grassland were more widespread.

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