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EFFECTS OF WOODY VEGETATION ENCROACHMENT ON SOIL NITROGEN OXIDE EMISSIONS IN A TEMPERATE SAVANNA

ROBERTA E. MARTIN,[1,2,5] GREGORY P. ASNER,[2] R. JAMES ANSLEY,[3] AND ARVIN R. MOSIER[4]

[1]*Department of Geological Sciences, University of Colorado, Boulder, Colorado 80309 USA*
[2]*Department of Global Ecology, Carnegie Institution of Washington, Stanford, California 94305 USA*
[3]*Texas A&M Research Extension Center, Vernon, Texas 76348 USA*
[4]*USDA/ARS P.O. Box E, Fort Collins, Colorado 80522 USA*

Abstract. Woody vegetation has encroached into areas once dominated by herbaceous land cover in arid and semiarid regions of the southwestern United States and around the world, resulting in documented changes to the biophysical and biogeochemical structure of these ecosystems during the past century. In North Texas rangelands, encroaching mesquite (*Prosopis glandulosa* var. *glandulosa*), a known nitrogen (N)-fixing species, has caused changes in aboveground biomass, which, in turn, have influenced carbon (C) and N storage in surface soils. However, the effect on N oxide (nitric-NO and nitrous-N_2O oxide) emissions from the soils was unknown. We examined biotic (vegetation type and soil organic and inorganic N dynamics) and abiotic (soil moisture, temperature, and soil texture) controls over soil NO and N_2O emissions across a gradient of aboveground *Prosopis* biomass growing on two soil types. Soil N oxide fluxes were dominated by NO emissions produced during nitrification. Aboveground biomass was the best spatial predictor of NO emissions, with values increasing 20-fold (0.04–0.78 mg NO-$N \cdot m^{-2} \cdot d^{-1}$) across a 70-fold biomass gradient (5–350 g/m^2). Emissions also covaried with soil pH and clay content. Microsite position, under or between the mesquite canopies, did not influence NO emission rates. NO fluxes were four times higher from clay loam than from shallow clay soils; however, soil N properties (total organic N and extractable inorganic N) and cycling rates (mineralization and nitrification) did not differ significantly across the sites. Temporally, NO emissions and nitrification potential were positively correlated with temperature, with precipitation events elevating NO emissions fourfold over a 24-h period and producing small amounts of N_2O. We conclude that mesquite encroachment in these grasslands increases NO emissions in a spatially explicit manner influenced by the aboveground biomass and soil type, which is then temporally mediated primarily by temperature and secondarily by precipitation.

Key words: *arid and semiarid ecosystems; land-cover and land-use change; mesquite; nitric oxide; nitrogen; nitrous oxide;* Prosopis glandulosa; *savanna; Texas (USA); woody encroachment.*

INTRODUCTION

Savanna ecosystems are known sources of nitrogen (N) oxide trace gases (nitric oxide, NO and nitrous oxide, N_2O). Reported ranges of 0.6–80 ng NO-$N \cdot m^{-2} \cdot s^{-1}$ and 0.4–62 ng N_2O-$N \cdot m^{-2} \cdot s^{-1}$ indicate great uncertainty in calculating the contribution of savanna NO and N_2O fluxes to the global atmospheric N budget (Davidson and Klingerlee 1997). Savanna ecosystems may contribute up to 35% of the total NO emitted from soils globally, the most of any ecosystem, due in part to the warm, semiarid climate of these regions (Davidson and Klingerlee 1997). NO plays an important role in controlling the oxidative capacity of the troposphere, thus regulating the production and destruction of tropospheric ozone, a regionally important greenhouse gas (Prather 1995). Soil N_2O emissions from savanna systems are ~10% that of NO emissions (Scholes et al. 1997); however, N_2O has a long atmospheric lifetime (120 years) and is a globally important greenhouse gas (Bouwman et al. 1995).

Both NO and N_2O are produced in the soil during the microbial processes of nitrification and denitrification. The total N oxide efflux from soils is controlled by the rate of internal N cycling, with the relative amount of each gas primarily controlled by soil water content and diffusivity (e.g., Firestone and Davidson 1989, Davidson et al. 2000). Other factors such as soil solution pH, soil texture, temperature, pulse wetting of soil, and land-use practices are important drivers of N gas emissions from soils (Davidson and Verchot 2000, Parton et al. 2001). At regional scales, N additions to the soil pool are strongly controlled by the inputs from vegetation via litterfall (Schlesinger and Pilmanis 1998). In addition, many savanna plant species partake in associative biological N fixation, a process that likely affects N oxide emissions through increased N cycling (Villagra and Felker 1997, Geesing et al. 2000, Hartley and Schlesinger 2000, Hibbard et al. 2001).

Temperate savannas of North America extend over 50×10^6 ha (Bailey 1996). The spatial pattern and

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[5] E-mail: robin@globalecology.stanford.edu

relative abundance of herbaceous and woody plants in these savannas are dictated by complex interactions between climate, topography, soils and land-management practices. Woody encroachment has been well documented in the southwest United States, and it now threatens the livelihood of pastoral, subsistence, and commercial grazing (Archer et al. 1988, Archer 1994). Overgrazing, fire suppression, and climate change are implicated in the shift from open savanna grasslands to ecosystems now densely populated by trees and shrubs (Archer 1995, Scholes and Archer 1997). In Texas rangelands, encroaching mesquite (*Prosopis glandulosa* var. *glandulosa*) has caused an increase in aboveground woody biomass, which in turn has increased soil carbon (C) and nitrogen (N) storage (Boutton et al. 1999, Geesing et al. 2000, Archer et al. 2001, Hibbard et al. 2001; R. F. Hughes, G. P. Asner, S. R. Archer, and C. A. Wessman, *unpublished manuscript*). Mesquite is a known N fixer and has been found to contain concentrations of N in leaves three times higher when compared to non-N fixing reference plants (Shearer and Kohl 1989). Recent studies in Texas show that replacement of grassland by mesquite woodlands over the past 100 years has lead to a 1.2- and 10-fold increase in soil and plant N pools, respectively (R. F. Hughes et al., *unpublished manuscript*).

Quantification of N oxide emissions from savanna soils may depend upon the spatial distribution of woody plant canopies, and specifically upon the changes in N availability and cycling and subsequent N trace gas production as influenced by the shift from herbaceous to woody vegetation type. The objectives of this study were to quantify N oxide emissions in a temperate savanna across a gradient of aboveground *Prosopis* biomass on two dominant soil types found in the region. The study was carried out at two spatial scales including the microsite tree–grass level and the landscape level. Both biotic (vegetation type and soil organic N) and abiotic (soil type, soil pH, temperature, soil moisture, and soil inorganic N) controls were analyzed for their contributions to observed spatial and temporal variation in soil N gas fluxes.

Methods

Study area

The study site was located on the Kite Camp Research Area of the Waggoner Ranch in the Red River Valley of North Texas (33°50′ N, 99°02′ W). Climate is temperate (mean annual temperature is 17°C) with a growing season (March–November) of ~220 days. Mean monthly air temperature ranges from 36°C in July to −2.5°C in January. Mean annual precipitation (640 mm) is bimodally distributed, with peaks in May and September. Topography of the region is gentle to moderately sloping (<4%); elevation ranges from 355 to 370 m. Soils on lowland areas are fine, mixed thermic, Typic Paleustolls of the Tillman association, developed from Permian clay and shale parent material (SCS 1962). Upland soils are dominated by shallower Vernon series clay loams and intermittently exposed red-bed clays and shales.

The Waggoner Ranch has experienced cattle grazing at stocking rates of ~10–12 ha per head over the last 20 years; prior to this, stocking rates were as high as 2 ha per head (Teague et al. 1997). Historical vegetation of the region was grassland and open savanna (Teague et al. 1997, Ansley et al. 2001). By the 1950s, the density of the native arborescent legume *Prosopis glandulosa* had increased to the point where brush management efforts were employed throughout the region (Fisher et al. 1959). These efforts have continued to the present (Teague et al. 1997), producing landscape mosaics of grassland, savanna (<800 stems/ha) and woodland (up to 7100 stems/ha) (R. F. Hughes et al., *unpublished manuscript*).

P. glandulosa is the dominant woody plant of the study region (>95% of all woody cover and density [R. F. Hughes et al., *unpublished manuscript*]). The density and stature of *P. glandulosa* stands are typically greater on the deeper Tillman soils compared to those of the shallower Vernon soils. Riparian corridors and intermittent drainages contain *P. glandulosa* along with some *Celtis*, *Populus*, and *Quercus* spp. Herbaceous cover consists of C_3 and C_4 grasses with various herbaceous dicots. The dominant C_3 grasses are *Nassella leucotricha* [Trin. & Rupr.] Barkworth and Japanese brome (*Bromus japonicus* Thunb. [Diggs et al. 1999]). Dominant C_4 grasses include sideoats grama (*Bouteloua curtipendula* (Michx.) Torr. var. *curtipendula*) and buffalograss (*Buchloë dactyloides* (Nutt.) Engelm.).

Six field campaigns (mid-May, early July, late August, late November 2000, and mid-January and late March 2001) were conducted on nine 60 × 60 m sites spanning a range of landscape units that have been previously characterized for soil texture, plant canopy cover, and aboveground mesquite biomass through remote sensing and ground-based measurements (Table 1; Asner et al. 1998; R. F. Hughes et al., *unpublished manuscript*). Each N trace gas measurement campaign extended over five days during which two sites (one located on shallow clay soils, the other on clay loam) were measured each day. Six chambers were measured at each site with a total measurement time of approximately two hours. To capture the effect of temperature each site was measured in the morning between 0800 and 1200 hours. Sites were resampled in the afternoon from 1300 to 1700 hours local time. Local variability at a given site was examined through stratified measurements beneath tree canopies ($n = 3$) and in grass interspaces between canopies ($n = 3$). There were no areas on the clay loam sites to place ''grass'' anchors farther than 10 m from a tree canopy. One site (CL5) contained a regionally unique stand of ''old growth'' *P. glandulosa*, with a known age of >70 years, verified with historical aerial photographs (G. P. Asner, *unpub-*

TABLE 1. Physical and chemical properties of North Texas soils.

Site	Soil class†	Sand (%)	Clay (%)	Bulk density (Mg soil/m^3)	pH in H_2O	Total organic N (%)	Total organic C (%)	Biomass‡ (g/m^2)
SC1	shallow clay (soil series: Vernon)	21	46	1.30 (0.04)	9.2 (0.4)	0.10 (0.05)	0.5 (0.1)	5.4
SC2		21	34	1.07 (0.03)	8.0 (0.4)	0.30 (0.06)	2.3 (0.6)	34.2
SC3		22	37	1.29 (0.05)	8.3 (0.2)	0.21 (0.06)	1.4 (0.7)	60.0
SC4	very rocky soil	55	23	1.35 (0.04)	7.2 (0.4)	0.16 (0.01)	0.8 (0.1)	114.3
CL1	clay loam (soil series: Tillman)	36	26	1.30 (0.03)	8.0 (0.1)	0.30 (0.01)	2.3 (0.)	251.0
CL2		31	24	1.22 (0.04)	6.4 (0.2)	0.18 (0.01)	1.0 (0.1)	284.1
CL3		28	26	1.35 (0.04)	6.1 (0.3)	0.18 (0.01)	1.0 (0.1)	305.0
CL4		22	32	1.25 (0.03)	7.2 (0.3)	0.26 (0.03)	1.2 (0.3)	359.3
CL5		34	22	1.20 (0.04)	6.6 (0.4)	0.21 (0.08)	1.3 (0.9)	2462.9

Notes: All soil characteristic were measured in the top 10 cm of the soil; $n = 3$ for bulk density, total organic N and C; $n = 6$ for pH. Standard errors (1 SE) are given in parentheses.

† Soil class was determined from soil survey maps for Wilbarger County, Texas (SCS 1962).

‡ Aboveground *Prosopis* biomass from Asner et al. (2003).

lished data). Although this age class is regionally insignificant, it provided an opportunity to assess the long-term potential (e.g., maximum) effects of *Prosopis* encroachment on soil N oxide emissions and other processes.

Trace gas analysis

Seasonal survey field measurements.—Soil NO measurements were made following the procedure of Martin et al. (1998), using a portable Scintrex LMA-3 chemiluminescent instrument and its LNC converter modified with an extra drier attached to the nafion tubing assembly to decrease air sample humidity (Scintrex/Unisearch, Concord, Ontario, Canada; Hutchinson et al. 1999). At each site, six soil NO measurements were collected by consecutively fitting a 9.2-L chamber (lined with Teflon to inhibit chemical transformation of NO) onto separate polyvinyl chloride (PVC) pipe anchors. Approximately 30 min before measurement, the anchors were installed in the soil just deep enough to solidly hold a seal, 1–3 cm. Steady increases in NO concentration were observed 1–8 min after the chamber was placed on the anchor. NO concentration was recorded every minute over a 6-min interval. NO fluxes from a given chamber over time were calculated using the following equation:

$$r = \frac{F(C_t - C_0)}{(1 - e^{-Ft/V})} \times \frac{M_{\text{mol}}}{V_{\text{mol}}} \times 10^9 \qquad (1)$$

where r is the rate of NO emission (nanograms NO-N per square meter per second), F is the flow rate through the chamber (cubic meters per second), C_{chamber} is the concentration of NO (liters per 10^9 liters) measured from the chamber at a given time t, C_{ambient} is the ambient concentration of NO in the atmosphere at the location of the inlet port (liters per 10^9 liters), M_{mol} is the molecular mass of nitrogen (grams per mole), V_{mole} is the molar volume of NO (cubic meters per mole) at a given air temperature, V is the chamber volume (cubic meters), A is the area of soil covered by the chamber (square meters), t is a finite time after chamber closure(s), and 10^9 converts grams to nanograms so the flux may be expressed in the usual range of nanograms per square meter per second (Martin et al. 1998). This is the analytical solution to the equation

$$\int_0^t v(t) = \frac{VRt}{F} - \frac{V^2R}{F}(1 - e^{-Ft/V}) \qquad (2)$$

where v is the volume of NO within the chamber (cubic meters), t is a finite time after chamber closure (s), and R is the volumetric rate of NO release from the soil (cubic meters per second) (or in terms of concentration $R = FC/(1 - e^{(-Ft/V)})$). For comparability to other N indexes, fluxes are expressed as milligrams per square meter per day, except for the instantaneous response to wetting where the units remain nanograms per square meter per second. The instrument was calibrated in the field with a five-point calibration (range 2.95–12.98 parts per 10^9 parts) using a standard of 0.1 parts NO per 10^9 parts N_2 before and after each set of measurements (Hutchinson and Livingston 2002).

Soil N_2O emissions were measured following the NO measurements by sampling air from closed chambers four times over a 30-min period using a syringe. These samples were transferred to evacuated 12-mL vials. For quality assurance, two samples of a certified standard (0.1 and 0.5 parts per 10^9 parts) as well as two samples of ambient air collected at chamber height were packaged in the field during each measurement period. Samples were analyzed for N_2O using a gas chromatograph equipped with an electron capture detector (GC-14, Shimadzu Scientific Instruments, Columbia, Maryland). Changes in N_2O concentration within the chambers were within the range of the analytical error (3–5 parts/10^9 parts), and therefore could not be used to calculate N_2O flux rates from the soil.

Field wetting experiments.—To examine the short-term effects of rainfall on soil N oxide emissions, field wetting experiments were conducted in June 2001 on two sites representing the dominant soil types: a clay loam (CL2) with moderate aboveground biomass, and shallow clay (SC1) with low biomass. Based on daily

rainfall measurements collected from 1 May 2000 through 31 May 2001, 75% of the rain events averaged 10 mm, while 5% of the events were 30–35 mm. Soils inside four anchors at each site were wet with 1.5 L to simulate a large (30 mm) but typical rain event (R. J. Ansley, *unpublished data*). In addition a 2.0-m^2 area surrounding the anchors was wet to minimize dry-down effects at the edge of the anchors. Soil NO and N_2O emissions were measured at 0, 0.5, 2, 4, 6, 8, 12, and 22 h following wetting. Three additional anchors at each site were wet with purified water for soil core collections (0–10 cm) for moisture and N content (NH_4^+ and NO_3^-). Soil cores were collected concurrently with each trace gas sampling. The experiment was replicated beneath (four anchors) and between *Prosopis* canopies ($n = 4$) on CL2, where there was sufficient canopy cover. A replicated dry anchor was installed matching each anchor that was wetted. Soil N gas emissions, N content, and moisture were measured from the four dry anchors at 0, 4, 12, and 22 h following the beginning of the wetting.

Soil analysis

Soil physical and chemical properties.—Soils from each site were analyzed for total organic C and N. Six soil samples from each site (three tree, three grass) were collected in late July 2000, using PVC soil cores from 0–10 cm depth, oven-dried at 70°C for 48 h, and ground to a fine powder. Carbonates were removed from the soils using 0.5 mol/L HCl followed by repeated rinsing (Midwood et al. 1998). Total soil organic C and N were determined for three subsamples using a combustion autoanalyzer (EA-1108, Carlo Erba, Milan, Italy). Soil solution pH was determined from these same soils for each site using three replicates of 10 g of dry soil added to 20 mL of deionized water. The pH values were determined after 30 min using a portable pH meter. The soil physical and chemical characteristics averaged by site (tree and grass combined) are presented in Table 1.

Temperature and soil water content measurements were made once in conjunction with each set of flux measurements. Air and soil temperature (5 cm depth) data were collected with a hand-held probe. Soil samples (0–10 cm) were weighed, oven-dried at 110°C for 24 h, and reweighed to calculate the percent volumetric water content (VWC):

$$\text{VWC} = \text{GMC} \times \text{BD} \quad (3)$$

where GMC is gravimetric moisture content and BD is the soil bulk density.

Bulk density was measured using bulk density tins of 113.4 mL in volume that were inserted ~2.5 cm into a newly exposed soil face just below the litter layer, sampling to 8 cm depth. Intact samples were weighed at initial moisture content, oven-dried at 105°C for 48 h, and reweighed. Bulk density was calculated as dry soil mass divided by tin volume (Parent and Coran 1993).

Extractable soil NH_4^+, NO_3^-, and N cycling rates.—One set of four soil cores (0–10 cm) was collected in conjunction with each set of flux measurements and combined for analysis of soil N availability via aerobic laboratory incubations and nitrification potential assays. One soil subsample (10 g) from each site was immediately extracted in 50 mL of 2 mol/L KCl, while two subsamples (50 g) were weighed into flasks. Deionized water was added to one set of flasks to adjust the gravimetric water content to just above field capacity. Field capacity values were estimated based on texture: 21.5% GMC for clay loam and 22.6% GMC for clay texture classes (Donahue 1990). To ensure that field capacity was reached, but not overly exceeded, water was added to reach 25% GMC. Water content was maintained during the incubation through periodic wetting, with the amount of water addition needed again determined by mass loss. No water was added to the second set. Both sets were incubated at 26°C for 14 d. After incubation, 10 g of soil were extracted in 50 mL of 2 mol/L KCl. All samples were assayed for NH_4^+ and NO_3^- on a segmented-flow colorimetric autoanalyzer (ALKEM Chemicals, Little Island, Cork, Ireland). The difference between the final and the initial $NH_4^+ + NO_3^-$ concentrations yielded an index of net N mineralization, while the difference between the final and the initial NO_3^- concentration alone provided an index of net nitrification.

Nitrification potential.—Subsamples of soil (25 g) from each series were added to a 100-mL nitrification potential medium (ammonium as $(NH_4)_2SO_4$ and phosphorous as K_2HPO_4 and KH_2PO_4) in 125-mL Erlenmeyer flasks covered with parafilm that was pierced to allow air exchange and placed on a shaker at 350 rpm. Aliquots of the slurry (10 mL) were taken after 2, 5, 12, and 24 h. The samples were centrifuged and the solution was filtered into vials for NO_3^- analysis on a segmented-flow colorimetric autoanalyzer (ALKEM Chemicals). The rate of $NO_3^- + NO_2^-$ accumulation was determined by linear regression and expressed as NO_3^--N·m^{-2}·$soil^{-1}$·d^{-1}. Nitrate generated by the microbial nitrifier population under optimal conditions yields an estimate of population size and potential nitrification rate (Hart et al. 1994).

Prosopis *aboveground biomass and canopy cover*

Aboveground *Prosopis* canopy cover (crown area, stem basal diameter, and plant number; R. F. Hughes et al., *unpublished manuscript*) and aboveground (AG) *Prosopis* biomass (derived from harvest studies; Asner et al., 2003) were measured at each site. The AG biomass on SC and CL 1–4 ranged from 5.4 to 359.3 kg/m^2, while the CL5 or ''old growth'' site averaged 2462.9 kg/m^2 (Table 1).

Statistical analysis

Field measurements of soil NO, soil temperature, and soil moisture as well as laboratory measurements of

TABLE 2. Correlation matrix of data averaged by site between soil NO flux and spatially distributed parameters.

	Soil NO flux (mg NO-N·m^{-2}·d^{-1})	AG biomass (g/m^2)	pH	Clay (%)	Soil solution (g/m^2)	
					NO_3^--N	NH_4^+-N
Soil NO flux	···	0.89	−0.91	−0.64	0.73	0.80
		<0.01	<0.01	0.09	0.41	0.02
AG biomass		···	−0.76	−0.63	0.70	0.59
			0.03	0.10	0.05	0.12
pH			···	0.81	−0.67	−0.88
				0.02	0.07	<0.01
Clay				···	−0.59	−0.70
					0.12	0.05
NO_3^-					···	0.71
						0.05
NH_4^+						···

Notes: Parameters are: aboveground *Prosopis* biomass (AG biomass), soil solution pH (in water), soil clay content, and soil solution N. The old-growth site is not included in the statistical analysis. Correlation coefficients and *P* values are given; $n = 8$.

soil N properties (soil extractable NH_4^+, and NO_3^-, nitrogen mineralization and nitrification rates and nitrification potential), pH, and texture were tested for normality using Kolmogorov-Smirnov tests. For statistical uniformity of sample size, data collected during the May, July, and August samplings were averaged by site to examine spatial patterns in NO emissions and soil N properties. Data were log-transformed to satisfy the requirements of normality (NO emissions as log(NO + 1)). Analysis of variance (ANOVA) with Tukey mean comparison test was used to determine intersite differences in NO emissions, AG *Prosopis* biomass, pH, clay content, and soil N properties. ANOVA was also applied to test for intrasite differences from soils located under the tree canopy or within the grass interspaces between canopies at a given site as well as differences on shallow clay soils or clay loam soils in a given sampling period. Relationships between spatially distributed variables of soil NO emissions, AG biomass, pH, soil clay content, and soil N properties as well as temporal relationships between soil NO emissions, soil temperature and moisture, and soil N properties were evaluated using Pearson product-moment correlations and regression analysis. Correlations were also assessed within a given soil type; however, the number of sites was then reduced to only four, thus greatly reducing the power of these analyses. We conducted the same analyses while including the regionally unique *Prosopis* ''old growth'' site (CL5). These results were compared and contrasted with those calculated from the other eight regionally common sites.

Manipulative wetting experiments were performed on two sites in the field in June 2001. Repeated Measures Analysis was used to examine differences between soil NO and N_2O emissions observed under *Prosopis* canopies and in intercanopy spaces. The analyses were repeated in clay loam and shallow clay soils.

RESULTS AND DISCUSSION

Spatial variation

Soil NO emissions.—NO at all sites and on all sampling dates dominated soil N oxide emissions. A small, short-term pulse in N_2O emission was generated only through artificial wetting of he soil (discussed in *Effects of water additions*). Therefore, only NO flux data were used to examine spatial and temporal variations across the sites.

The mean soil NO flux from eight sites and all sampling dates (not including the ''old growth'') was 0.9 kg NO-N·ha^{-1}·yr^{-1} (range = 0.1–1.7kg NO-N·ha^{-1}·yr^{-1}). This flux was within the range summarized for tropical savanna/woodland: 0.1–10 kg NO-N·ha^{-1}·yr^{-1} (Davidson and Kingerlee 1997). In particular, studies have measured similar emission rates in South African savannas, with values ranging from 0 to 6.2 kg NO-N·ha^{-1}·yr^{-1} (Levine et al. 1996, Otter et al. 1999, Kirkman et al. 2001). The only NO emissions reported for a temperate savanna woodland vary between 0.1 and 1.2 kg N·ha^{-1}·yr^{-1} from south-central Texas (Cole et al. 1996). Emissions reported for a desert scrubland in New Mexico containing *Prosopis* were lower, at 0.1 kg N·ha^{-1}·yr^{-1} (Hartley and Schlesinger 2000). The large range of emissions in our work and in the literature highlights the need for spatially and temporally extensive studies.

Effects of woody vegetation encroachment on soil NO emissions.—The spatial distribution of soil NO emissions from North Texas soils were correlated with AG *Prosopis* biomass and soil properties (Table 2, Fig. 1). For statistical uniformity of sample size, NO emissions from the ''summer'' sampling periods (May, July, August) were grouped to calculate mean NO emissions from each site for examination of spatial patterns. These fluxes comprised 80% of the total NO emissions measured during this study. Historical increases in this N-fixing species throughout the southwestern United

States have been shown to increase both above- and belowground C and N stores (Connin et al. 1997, Boutton et al. 1999). High tissue N concentrations have been documented in *Prosopis*, likely due to additional N inputs via biological fixation (Virginia et al. 1984, Shearer and Kohl 1989, Johnson and Mayeux 1990). This added N enters the soil organic N pool through litterfall, increasing the rate of N cycling and availability in soils (Hibbard et al. 2001). In most soils, NH_4^+ availability is the most important proximal factor controlling autotrophic nitrification rates (Robertson et al. 1989), while NO_3^- accumulation is indicative of a ''leaky'' nitrogen cycle that is often associated with increased N oxide (Davidson et al. 2000). Although savanna systems are often thought to be N limited and thus maintain a closed N cycle with minimal N oxide losses, a change in N status caused by *Prosopis* appears, from our studies, to have relaxed this limitation to some degree.

Soil NO emissions increased from 0.04 to 2.81 $mg \cdot m^{-2} \cdot d^{-1}$ (0.4–8.7 ng $NO\text{-}N \cdot m^{-2} \cdot s^{-1}$) across a 70-fold increase (5–350 kg/m^2) in AG biomass, the positive linear relationship ($P = 0.003$) accounting for 79% of the variation in NO flux among the sites (Table 2; Fig. 1A, B). Similarly, Sanhueza et al. (1990) reported a 10-fold difference in NO emissions from two savanna sites associated with a doubling of soil organic matter and total soil N. NO emissions measured from soils in the Krueger Park, South Africa were 3.5 and 8.0 ng $NO\text{-}N \cdot m^{-2} \cdot s^{-1}$ from sites with total N contents of 450 and 900 μg N/g dry soil, respectively (Levine at al. 1996, Parsons et al. 1996). In contrast, there was no significant difference in N trace gas emission rates from two sites in the Nylsvley Reserve, South Africa that differed in N content (total N, available NO_3^-, and N min potential) as well as biomass (Scholes and Walker 1993, Scholes et al. 1997). Higher NO emissions from a midsuccessional forest in Puerto Rico were attributed to increased N cycling as a result of higher quality litter from an N-fixing legume (Erickson et al. 2001).

Although an increase in soil NO emissions was observed across an intersite increase in AG biomass, we found no significant intrasite (or microsite) difference in fluxes or other soil properties measured under vs. between tree canopies, as has been found in other arid ecosystem studies. Hartley and Schlesinger (2000) found NO emissions were significantly higher under shrub canopies of mesquite, tarbush, and creosotebush following artificial wetting, suggesting that ''islands of fertility'' contribute to higher N oxide fluxes. However, emissions from their site were generally very low (<0.28 ng $NO\text{-}N \cdot m^{-2} \cdot s^{-1}$), so no significant ''natural state'' differences in NO emissions could be detected. Cole et al. (1996) found summer NO emissions were 50 times greater from soils under *Prosopis* than from those measured under the herbaceous layer between canopies. The higher emissions were associated with greater rates of N mineralization and total soil N content (Hibbard et al. 2001).

Other studies have documented increases in soil nutrients, as well as differences in soil temperature and moisture, beneath plant canopies in comparison to canopy interspaces; however, soil N oxide emissions were not measured (Goldberg and Turner 1986, Burke 1989, Schlesinger et al. 1990, Virginia et al. 1992, Schlesinger et al. 1996). In our study, the lack of microsite differences in NO emissions and other soil parameters may result from the fact that while measurements were made 5–10 m from the nearest *Prosopis* canopy, we could not place anchors beyond the influence of tree roots. *Prosopis* trees growing in this region have expansive root systems reaching 8 m beyond the canopy crown, precluding the establishment of the original herbaceous ''system'' (M. Simmons and S. Archer, *unpublished data*). Connin et al. (1997) found that *Prosopis* affected SOM properties at least 3 m beyond its canopy edge.

Effects of soil type on NO emissions.—The continuous variation in AG biomass and related NO emissions is overlain on a landscape stratified by two dominant soil types, the Tillman (clay loam) and the Vernon series (shallow clay). These soils developed from the shales of Permian red-bed clays (200 × 106 yr BP) that first weathered to red amorphous, highly calcareous shallow clays (Vernon series). In slightly concave or broad-level topographic positions on the landscape, these soils developed further to the darker colored soils of the Tillman series (SCS 1962). This spatial variation in soil type governs differences in soil texture and carbonate content that regulate water-holding capacity, diffusivity, and pH. These are significant factors governing the emission of N trace gases through N availability (plant growth and subsequent litter turnover) and physical constraints of emissions (Firestone and Davidson 1989, Robertson et al. 1989). Increased clay content decreases the porosity of the soil and increases

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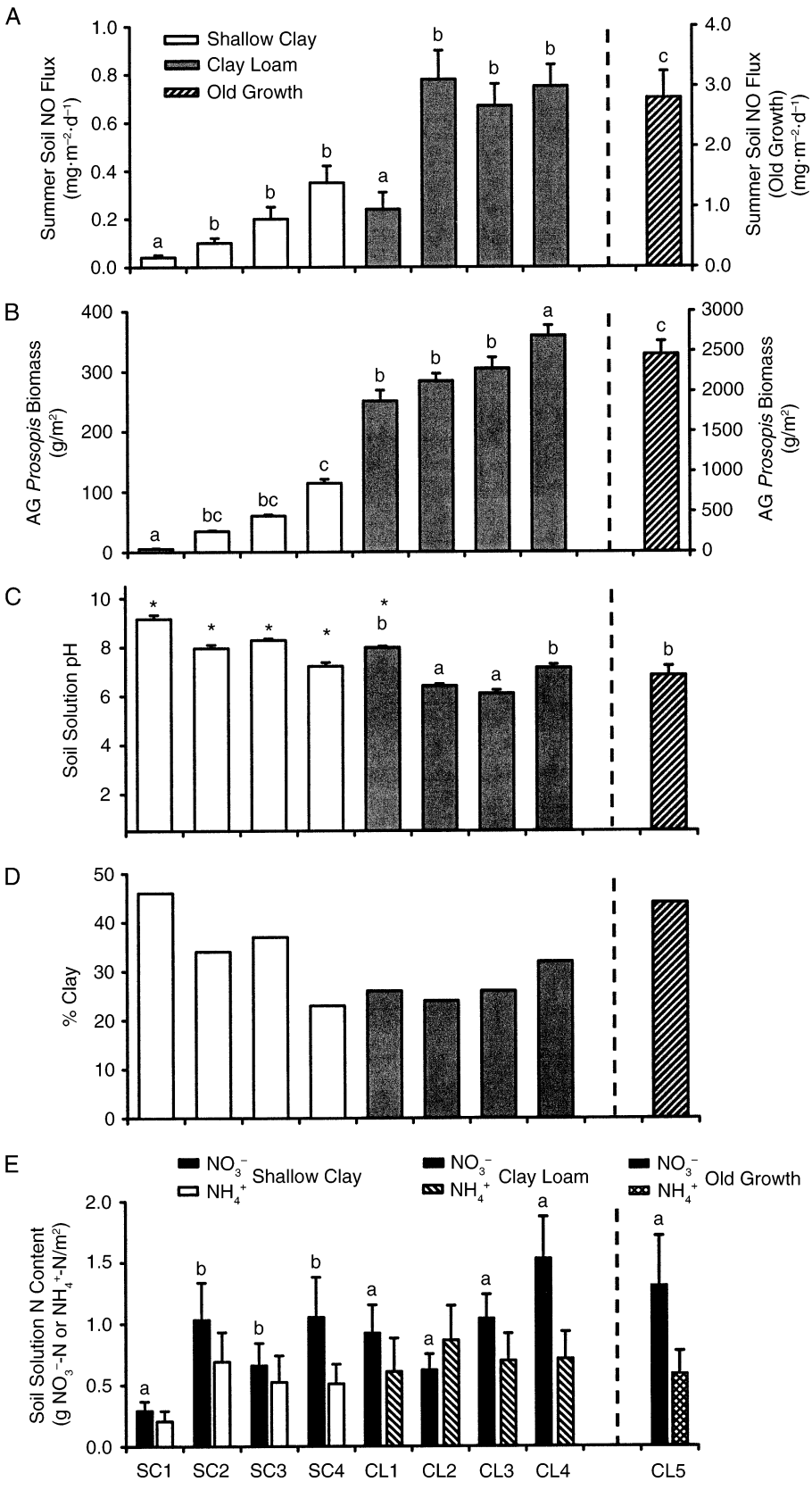
FIG. 1. Soil NO emissions and associated landscape parameters from nine sites in North Texas organized by site: (A) summer average soil NO emissions; (B) aboveground *Prosopis* biomass; (C) soil solution pH (an asterisk indicates carbonates); (D) soil clay content; and (E) soil inorganic $NO_3^- + NH_4^+$ content. Data are means from summer sampling periods at each site with one standard error. For each variable, different lowercase letters within each soil type (SC and CL) indicate significantly different means ($P < 0.05$) using Tukey multiple comparisons tests after one-way ANOVA. Statistical analyses and correlations were done on log-transformed data; means and one standard error are shown as nontransformed data to facilitate comparison with other studies. Axis labels and numbers to the right of the dashed line refer only to the ''old growth'' (CL5) site.


A
Shallow Clay
Clay Loam
Old Growth
Summer Soil NO Flux (mg·m⁻²·d⁻¹)
Summer Soil NO Flux (Old Growth) (mg·m⁻²·d⁻¹)
B
AG Prosopis Biomass (g/m²)
AG Prosopis Biomass (g/m²)
C
Soil Solution pH
D
% Clay
E
NO3⁻ Shallow Clay
NH4⁺
NO3⁻ Clay Loam
NH4⁺
NO3⁻ Old Growth
NH4⁺
Soil Solution N Content (g NO3⁻-N or NH4⁺-N/m²)
SC1 SC2 SC3 SC4 CL1 CL2 CL3 CL4 CL5

the water-holding capacity, which increases soil organic matter turnover (Schimel and Parton 1986, Burke et al. 1989). Higher clay content also increases the diffusional path length of soils, which decreases the escape efficiency of N trace gases (Conrad 1996, Godde and Conrad 2000). Moreover, the role of diffusion rate is more important for NO emissions than N_2O emissions because NO is more reactive (Remde et al. 1989).

The purely physical effects of decreased clay content are convolved with the concurrent increase in AG biomass, which increases organic matter inputs and contributes to increased turnover, while decreasing pH and adding NH_4^+ (Schimel and Parton 1986). Increases in nitrification due to increased N availability also contribute to decreases in pH. Without controlled manipulative experiments and the invocation of a full biogeochemical model, it is hard to determine the relative contributions of these driving factors to NO production. However, correlations with AG biomass and soil type lend themselves readily to spatial extrapolation.

Soil clay content (%) followed the soil taxonomic classification (SCS 1962), with greater clay contents in the shallow clay soil than in the clay loam (35% and 26% clay, respectively; Fig. 1D). Soil clay content was well correlated with soil solution pH, which varied from 6.1 to 9.2 across the sites ($r = 0.81$, $P = 0.02$; Table 2, Fig. 1C, D). All shallow clay soils, as well as the CL1 site, tested positive for soil carbonates.

Averaging by soil type, summer NO fluxes were lower from the sites on shallow clay areas (0.03–0.3 mg NO-N·m^{-2}·d^{-1}) than clay loams (0.2–0.8 mg NO-N·m^{-2}·d^{-1}), and did not differ at each site within a soil type (Fig. 1A). This difference is also enhanced by the additional AG biomass on clay loam vs. shallow clay soils (81 ± 27 and 23 ± 8 g/m^2 [mean ± 1 SE], respectively). On a site-by-site basis within a soil type, NO emissions were lower from SC1 than from SC4 (shallow clay soils), and emissions from CL5 were greater than all sites located on clay loam soils (Fig. 1A). All other sites were statistically similar within a soil type. Correlations of NO fluxes with AG biomass, soil pH, and % clay remained significant ($P < 0.05$) for fluxes measured from shallow clay soils alone, while they were no longer significant ($P = 0.20$ for AG biomass and pH and $P = 0.69$ for % clay) for fluxes measured from clay loams (not shown), indicating that the changes in soil properties caused by increases in AG biomass may mask the purely physical effects of texture on NO emissions. Similar changes in NO emissions associated with the increase in coarseness of soil texture have also been found in savanna (Johansson et al. 1988), grassland (Martin et al. 1998), and tropical forest soils (Bakwin et al. 1990).

While the secondary controlling soil property of clay content was not as highly correlated with AG biomass ($r = -0.63$, $P = 0.10$) or NO flux ($r = -0.64$, $P = 0.09$; Table 2), the primary property of soil solution pH, was correlated with both parameters across the sites ($r = -0.76$, $P = 0.03$; and $r = -0.91$, $P = <0.01$; respectively; Table 2). NO emissions decreased with increasing pH across the sites (Fig. 1A, C). Nagele and Conrad (1990) showed that NO release from agricultural soils increased as pH was reduced from 7.8 to 6.5, but the trend did not continue as the pH was reduced to 4.

Chemodenitrification is often invoked as a mechanism for NO production with changing pH (Davidson 1993). Historically, chemodenitrification is believed to occur more readily in acid soils (Van Cleemput and Baert 1984, Blackmer and Cerrato 1986). Venterea and Rolston (2000) showed recently that NO production was stimulated in soils ranging in pH value from 3.8 to 5.3, measured in 0.01 mol/L $CaCl_2$. The difference between values determined in a water solution vs. $CaCl_2$ may be as great as 1.5 (Peech 1965), lowering our lower pH values into this range. While under these field conditions it is not possible to know if NO was produced from nitrification or chemodenitrification, soil NO production is ultimately controlled through the initial oxidation of NH_4^+; therefore either mechanism links emission rates to NH_4^+ supply.

Effects of soil nitrogen properties on NO emissions.—Extractable (2 mol/L KCl) soil NO_3^- and NH_4^+ averaged 7.4 ± 0.8 and 5.0 ± 0.6 μg N/g dry soil, respectively. These NO_3^- concentrations are within the range determined for South African and Venezuelan savannas: 4–24 μg N/g dry soil (Johansson and Sanhueza 1988, Sanhueza et al. 1990, Scholes et al. 1997). Measured concentrations are higher than those found in a mesquite shrubland in New Mexico (Hartley and Schlesinger 2000). However, the proportion of NO_3^- to NH_4^+ concentration, roughly 1:2 (1.4 and 3.2 μg N/g dry soil, respectively), was similar to that observed in our study. NO_3^- tends to be the dominant species in the presence of high nitrification rates, exceeding uptake requirements by plants and microbes (Firestone and Davidson 1989). As discussed earlier, higher NO_3^- than NH_4^+ content is indicative of a ''leaky'' nitrogen cycle from which there are often greater losses via NO and N_2O (Davidson et al. 2000).

Extractable (2 mol/L KCl) soil NO_3^- and NH_4^+ content measured during the ''summer'' sampling periods followed similar trends as NO emissions, but did not differ statistically between most sites or vegetation cover type (Fig. 1E). The distribution of soil NH_4^+ content was most strongly related to NO emissions ($r = 0.80$, $P = 0.02$; Table 2), while soil NO_3^- content was related to AG biomass across the sites ($r = 0.70$, $P = 0.05$; Table 2). Similarly, soil NH_4^+ was positively correlated with NO emissions and nitrification rates in a south Texas grassland (Hutchinson et al. 1993). In many soils, NH_4^+ availability is the most important proximal factor controlling nitrification rates (Robertson et al. 1989). However, the high degree of spatial covariance among AG biomass, soil pH, and clay content with soil N content again illustrates the interrelated

influences of these parameters on soil N properties and subsequent NO production across these gradients.

Laboratory assays of net N mineralization and nitrification were highly variable and did not vary statistically across the sites or by canopy cover type (data not shown). When data from all sites and sampling dates were combined, both averaged 0.7 ± 0.1 g N as (NH_4^+ + NO_3^-) or (NO_3^-)·g dry soil^{-1}·d^{-1} at field capacity. These values were 50% lower when assayed at field-moist conditions with mean values of 0.3 ± 0.1 g N as (NH_4^+ + NO_3^-) or (NO_3^-)·g dry soil^{-1}·d^{-1}, indicating the pronounced effect of water limitation in this system.

Temporal variation

Soil NO emissions.—NO emissions and soil properties measured six times throughout the year were averaged by soil type to examine temporal variations among variables. NO fluxes varied temporally from nearly zero to as high as 2.5 mg NO-N·m^{-2}·d^{-1}, following changes in temperature (Fig. 2A, D). Few field studies have measured NO emissions beyond the growing season to determine emissions in the cooler months (Martin et al. 1998, Verchot et al. 1999, Erickson et al. 2001). Past studies have measured NO emissions from wet and dry seasons (Johansson and Sanhueza 1988, Johansson et al. 1988, Davidson et al. 1991), and many relationships have been established between temperature and soil moisture in laboratory and field studies during the warm growing season periods (Williams et al. 1992, Davidson 1993). Our measured NO emissions were significantly higher in July and August than in all other months, but were not different from each other ($P < 0.01$). Diel measurements of NO emissions, taken over a 22-h period concurrent with the field wetting experiment, showed no significant variation (data not shown). However, the temperature was generally high and only varied between 19° and 35°C, and soil moisture was low (5.8 ± 0.5 % VWC).

Temporal changes in temperature and water control the short-term N supply via plant growth and are key determinants of N cycling rate and subsequent N gas production. Temporally, soil NO emissions were correlated with temperature ($r = 0.63$) and soil NO_3^- concentration ($r = 0.59$) but not with soil moisture content (Table 3). Given adequate soil moisture (water-filled pore space >20%), there was a positive exponential relationship between NO flux with air and soil temperature. The resulting equations were: log(NO flux) $= -0.93 + [0.29 \times$ (air T)]; $r^2 = 0.48$, $P = 0.01$ and log(NO flux) $= -0.74 + [0.27 \times$ (soil T)], $r^2 = 0.40$, $P = 0.03$. Similar exponential relationships are documented from savanna soils in both laboratory and field studies from around the world (Johansson et al. 1988, Scholes et al. 1997, Otter et al. 1999, Godde and Conrad 2000).

Nitrate is the resultant soil solution N product following nitrification. NO_3^- will accumulate in the soil if denitrification does not proceed, as found in semiarid systems limited by water availability (Hartley and Schlesinger 2000). Soil available NO_3^- content was lowest in May when the growth rate of plants is high and thus plant uptake of soil-available N is also high (Fig. 2C). NO_3^- content was maximal in August, indicating increased nitrification. This result was supported by observed maximum nitrification potentials and significant soil NO emissions in August (Fig. 2A, B). While there have been numerous studies documenting temporal variations in N mineralization rates and available soil N content (Bernhard-Reversat 1982, Ruess and Seagle 1994, Kieft et al. 1998, Hibbard et al. 2001), NO emissions have rarely been measured simultaneously. Baumgartner and Conrad (1992) showed significant correlations between NO production measured from laboratory soil cores and temporal changes in NH_4^+, as well as in situ temperatures.

Effects of water additions on N oxide emissions.—The short-term effects of precipitation on N trace gas emissions from soils were evaluated through artificial wetting of field soils in June 2001. Wetting caused large but transient pulses in both NO and N_2O emissions from the soil (Fig. 3A, B). Soil NO emissions from the clay loam soils peaked ~2 h following wetting, reaching 167.5 ± 8.6 and 114.0 ± 12.7 ng NO-N·m^{-2}·s^{-1} under and away from canopies, respectively, but were not significantly different from each other over the full time series. NO fluxes from the shallow clay soils did not exhibit a rapid response to wetting, and were significantly lower than from clay loam soils (repeated measures $P = 0.003$), reaching only 12.6 ± 2.0 ng NO-N·m^{-2}·s^{-1} (Fig. 3A).

Soil N_2O emissions were more variable than NO emissions, peaking at 0.5–2.0 h following wetting of the clay loam soils under (1.2 ± 0.3 ng N_2O-N·m^{-2}·s^{-1}) and away (2.0 ± 0.3 ng N_2O-N·m^{-2}·s^{-1}) from canopies, respectively (Fig. 3B). Pulse N_2O emissions did not peak on the shallow clay soils until 6 h following wetting; this peak averaged 3.8 ± 0.7 ng N_2O-N·m^{-2}·s^{-1}. N_2O emissions were not statistically different between shallow clay and clay loam soils measured over the duration of the experiment (Fig. 3B). These types of pulses have been widely observed from many other savanna soils (Sanhueza et al. 1990, Scholes et al. 1997, Hartley and Schlesinger 2000, Otter et al. 2001). Johansson and Sanhueza (1988) measured NO emissions that were 10–30 times greater than those from dry control plots in Venezuela, whereas water addition increased emissions 5–10 times over background levels in a South African savanna (Scholes et al. 1997).

The measured soil moisture content reached 35% VWC and 29% VWC on shallow clay and clay loam soils respectively, above the field capacity of both soils calculated from texture (~23% VWC). The moisture level in the clay loam soil may not have been high enough or had a long enough duration to sustain denitrification, believed to be the greatest source of N_2O

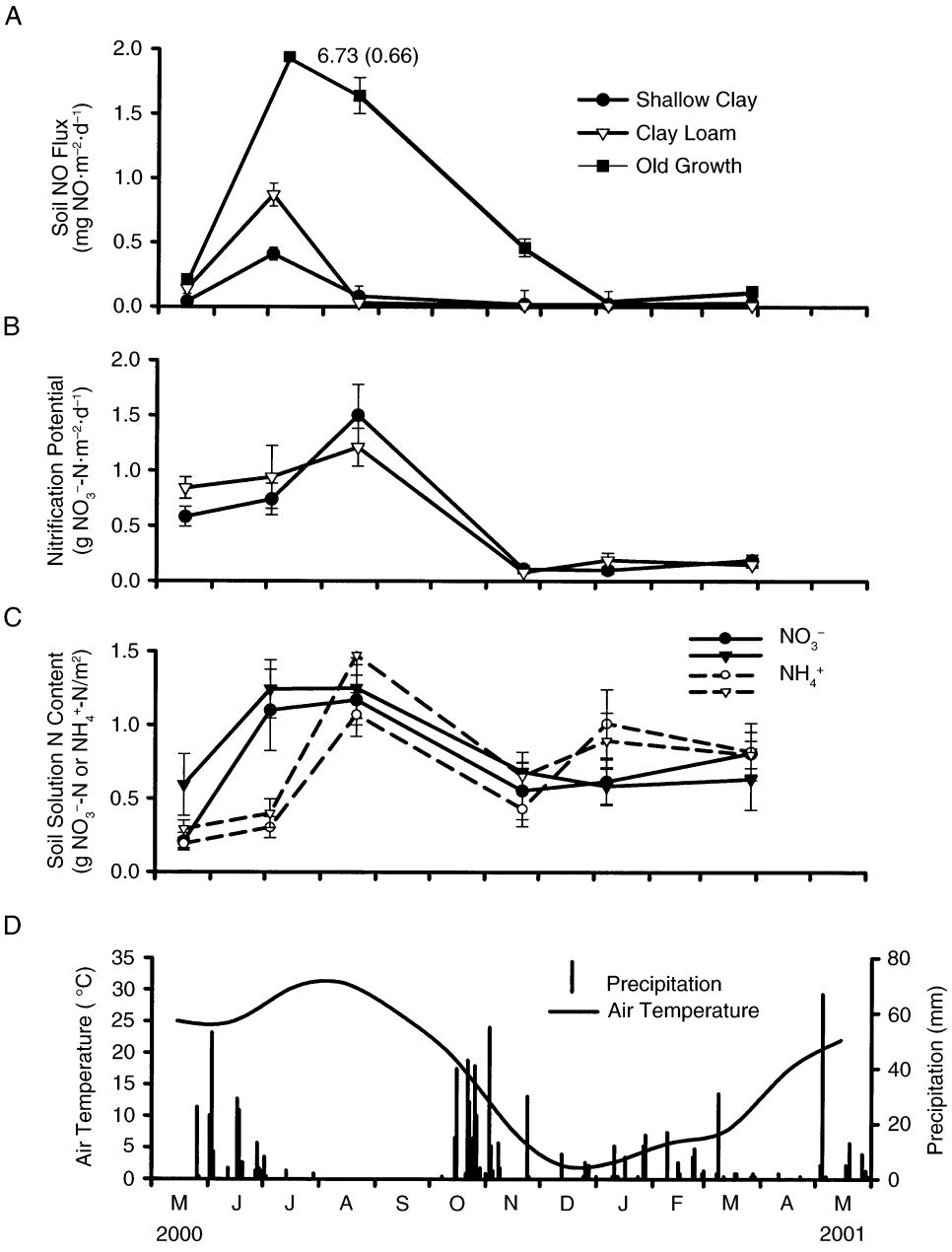


FIG. 2. Field and laboratory measurements of soil NO emissions and related soil nitrogen properties as they vary with air temperature and precipitation: (A) soil NO emissions; (B) soil solution N concentration; (C) soil nitrification potential; (D) air temperature and precipitation. Data are means calculated from all sites in each soil type and each sampling period (±1 SE in panels A–C). Correlation analyses were performed including all the data and within a soil type using log-transformed data; means and standard errors are shown as nontransformed data to facilitate comparison with other studies.

(Firestone and Davidson 1989). Conversely, diffusion of NO may have been limited by water in the shallow clay, increasing the likelihood of conversion to N_2O (Davidson 1993). The sum of these processes may explain the difference in N oxide emissions from the different soil types in this study.

NO fluxes, stimulated by wetting and integrated over 24 h from each soil type, were four times greater than average summer NO emissions. The May to September period encompasses the season when temperatures are high and water is most limiting. When multiplied by the average number of precipitation events of similar magnitude for this time period (four, mean of 7-yr precipitation record for Lake Kemp, Texas [USACE 1994]), NO pulses added ~50 mg NO-N/m^2 over five months, doubling the NO emissions from this time pe-

TABLE 3. Correlation matrix of data averaged by soil type and sampling date between soil NO flux and temporally varying parameters.

Parameter	Soil NO flux (mg NO-N·m^{-2}·d^{-1})	Soil temperature (°C)	Soil moisture (% volumetric water)	Nitrification potential (g NO_3^--N·m^{-2}·d^{-1})	Soil solution NO_3^- (g/m^2)
Soil NO flux	···	0.63	−0.25	0.53	0.59
		(0.03)	(0.43)	(0.08)	(0.04)
Soil temperature		···	−0.80	0.96	0.28
			(<0.01)	(<0.01)	(0.38)
Soil moisture			···	−0.76	−0.14
				(<0.01)	(0.68)
Nitrification potential				···	0.20
					(0.54)
Soil solution NO_3^-					···

Notes: Parameters are: soil temperature, soil moisture, nitrification potential, and soil solution N. The old-growth site is not included in the statistical analysis. Correlation coefficients are given (with *P* values in parentheses); $n = 12$.

riod. Soil N_2O emissions totaled ~3 mg N_2O-N/m^2 for the five months. Wetting of a dry, warm soil results in the largest responses from the soil microbial community. The magnitude and duration of N oxide pulses often increases in proportion to the number of antecedent dry days (Davidson et al. 1993). In addition, soil N_2O emissions may be stimulated in the winter months when soils are moist, but low temperatures would limit the gas production rate (Davidson 1993).

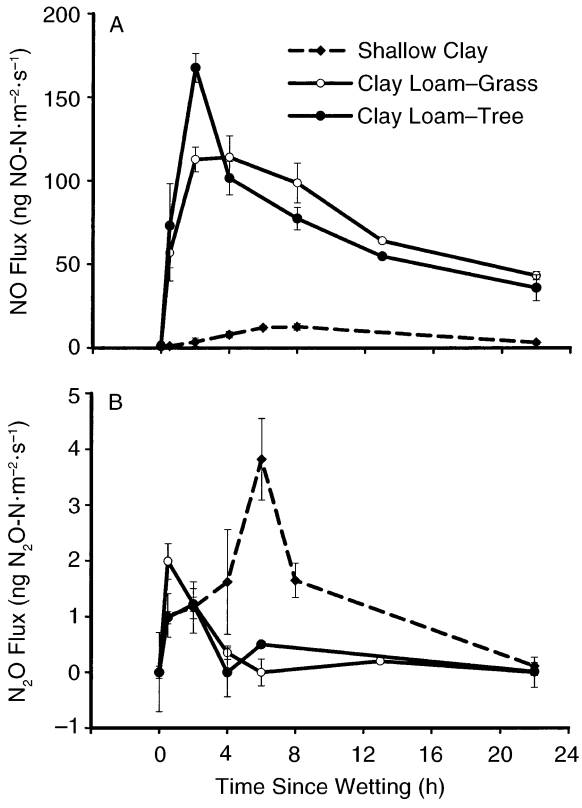


FIG. 3. Effect of in situ watering on (A) NO and (B) N_2O emissions from shallow clay and clay loam soils. Data are means calculated from four anchors at each sampling period on each soil and vegetation type. Error bars represent ±1 SE.

Multiple wetting experiments throughout the experiment were not performed to assess these effects.

Conditions following long-term woody vegetation accumulation.—While most semiarid savannas in the southwestern United States are routinely managed using pyric, herbicidal, and mechanical treatments (Fisher et al. 1959, Teague et al. 1997), it is valuable to examine the biogeochemical changes that could occur if *Prosopis* grew unchecked for long periods following establishment. Seventy years of unmanaged woody vegetation growth resulted in a sevenfold increase in AG biomass at the *Prosopis* old-growth site (Asner et al. 2003, R. F. Hughes et al., *unpublished manuscript*; Table 1). This increase was associated with a threefold increase in summer NO emissions beyond those of the second highest managed field site (Fig. 1A). This increase could not be attributed to soil pH, texture, or other abiotic factors (Fig. 1C, D). We conclude that the unchecked expansion of *Prosopis* following establishment may alter the soil organic C and N stocks as well as dissolved organic C and N pools, resulting in increased internal N cycling and subsequent N gas fluxes from soils.

CONCLUSIONS

The dominant controls over N oxide emissions from temperate savanna soils in Northern Texas are spatial, topo-edaphic variations governing aboveground biomass and soil physical properties, both of which exert control on the supply and cycling of N in soils. Temporal fluctuations in temperature and precipitation, which control the dynamic cycling of N within the system, affect the timing and magnitude of soil N oxide fluxes. In this study, soil N trace gas emissions were dominated by NO emissions. In addition, our laboratory assays showed that nitrification rates equaled net mineralization rates in the savanna soils. This finding, coupled with high nitrification potentials correlated with high NO emissions, supports the hypothesis that nitrification and associated NO production is the dominant pathway for N trace gas loss from this semiarid ecosystem. While *Prosopis* aboveground biomass was

found to be the best spatial predictor of NO emissions, the microsite position, under or between canopies, did not greatly affect NO emissions and correlations remained significant only within the shallow clay soils. Soil pH and clay content covaried with AG *Prosopis* biomass and NO emissions indicating the interrelated controls of the physical environment on both plant production and nutrient cycling.

Temporally, measured NO fluxes were correlated with temperature; N oxide pulses following rain events had the potential to double the predicted summer NO emissions from these soils and produce small amounts of N_2O. Our measurements of soil N availability were often correlated with NO emissions both spatially and temporally. However, they did not significantly aid in determining the proximal controls over N gas fluxes beyond what was linked to AG biomass and soil type (spatial) and temperature (temporal).

Average annual NO emissions were 0.9 kg NO-N·ha^{-1}·yr^{-1}, with a range of 0.1–1.7 kg NO-N·ha^{-1}·yr^{-1}. This is equivalent to ~2% of the estimated nitrification rate, supporting a long-established fractional index for modeling N trace gas emissions from soils (Potter et al. 1996, Parton et al. 2001). These data show that mesquite encroachment in temperate grasslands increases NO emissions in a spatially explicit manner determined by AG biomass and soil type.

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Literature Cited

Ansley, R. J., X. B. Wu, and B. A. Kramp. 2001. Observation: long-term increases in mesquite canopy covering North Texas. Journal of Range Management **54**:171–176.

Archer, S. 1994. Woody plant encroachment into southwestern grasslands and savannas: rates, patterns, and proximate causes. Pages 13–68 *in* M. Vavra, W. A. Laycock, and R. D. Pieper, editors. Ecological implications of livestock herbivory in the West. Society for Range Management, Denver, Colorado, USA.

Archer, S. 1995. Tree–grass dynamics in a *Prosopis*–thornscrub savanna parkland: reconstructing the past and predicting the future. Ecoscience **2**:83–99.

Archer, S., T. W. Boutton, and K. A. Hibbard. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. Pages 115–137 *in* E.-D. Shultze, S. P. Harrison, M. Meimann, E. A. Holland, J. Lloyd, I. C. Prentice, and D. S. Schimel, editors. Global biogeochemical cycles in the climate system. Academic Press, San Diego, California, USA.

Archer, S., C. Scifres, and C. R. Bassham. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. Ecological Monographs **58**:111–127.

Asner, G. P., S. Archer, R. F. Hughes, R. J. Ansley, and C. A. Wessman. 2003. Net changes in regional woody vegetation cover and carbon storage in Texas rangelands, 1937–1999. Global Change Biology. **9**:316–335.

Asner, G. P., C. A. Wessman, and D. S. Schimel. 1998. Heterogeneity of savanna canopy structure and function from imaging spectrometry and inverse modeling. Ecological Applications **8**:1022–1036.

Bailey, R. G. 1996. Ecosystem biogeography. Springer, New York, New York, USA.

Bakwin, P. S., S. C. Wofsy, S. Fan, M. Keller, S. E. Trumbore, and J. M. Da Costa. 1990. Emission of nitric oxide (NO) from tropical forest soils and exchange of NO between the forest canopy and atmospheric boundary layers. Journal of Geophysical Research **95**:16,755–16,764.

Baumgartner, M., and R. Conrad. 1992. Effects of soil variables and season on the production and consumption of nitric oxide in oxic soils. Biology and Fertility of Soils **14**: 166–174.

Bernhard-Reversat, F. 1982. Biogeochemical cycle of nitrogen in a semi-arid savanna. Oikos **38**:321–332.

Blackmer, A. M., and M. E. Cerrato. 1986. Soil properties affecting formation of nitric oxide by chemical reactions of nitrite. Soil Science Society of America Journal **50**: 1215–1218.

Boutton, T. W., S. R. Archer, and A. J. Midwood. 1999. Stable isotopes in ecosystem science: structure, function and dynamics of subtropical savanna. Rapid Communications in Mass Spectrometry **13**:1263–1277.

Bouwman, A. F., K. W. V. d. Hoek, and J. G. J. Olivier. 1995. Uncertainties in the global source distribution of nitrous oxide. Journal of Geophysical Research **100**:2785–2800.

Burke, I. C. 1989. Control of nitrogen mineralization in a sagebrush ecosystem. Ecology **70**:1115–1126.

Burke, I. C., W. A. Reiners, and D. S. Schimel. 1989. Organic matter turnover in a sagebrush landscape. Biogeochemistry **7**:11–31.

Cole, J. K., R. E. Martin, E. A. Holland, S. R. Archer, H. K. Hibbard, and M. Scholes. 1996. Nitric oxide fluxes from a subtropical savanna. Texas Agricultural Experiment Station, La Copita Research Area 1996 Consolidated Progress Report **CPR-5047**.

Connin, S. L., R. A. Virginia, and C. P. Chamberlain. 1997. Carbon isotopes reveal soil organic matter dynamics following arid shrub expansion. Oecologia **110**:374–386.

Conrad, R. 1996. Metabolism of nitric oxide in soil and soil microorganisms and regulation of flux into the atmosphere. Pages 167–204 *in* J. C. Murrell and D. P. Kelly, editors. Microbiology of atmospheric trace gases: sources, sinks and global change processes. Springer-Verlag, Berlin, Germany.

Davidson, E. A. 1993. Soil water content and the ratio of nitrous oxide to nitric oxide emitted from soil. Pages 369–386 *in* R. S. Oremland, editor. Biogeochemistry of global change: radiatively active trace gases. Chapman and Hall, New York, New York, USA.

Davidson, E. A., M. K. Keller, H. E. Erickson, L. V. Verchot, and E. Veldkamp. 2000. Testing a conceptual model of soil emissions of nitrous and nitric oxides. BioScience **50**:667–680.

Davidson, E. A., and W. Kingerlee. 1997. A global inventory of nitric oxide emissions from soils. Nutrient Cycling in Agroecosystems **48**:37–50.

Davidson, E. A., P. M. Matson, P. M. Vitousek, R. Riley, K. Dunkin, G. Garcia-Mendez, and J. M. Maass. 1993. Processes regulating soil emissions of NO and N_2O in a seasonally dry tropical forest. Ecology **74**:130–139.

Davidson, E. A., and L. V. Verchot. 2000. Testing the hole-in-the pipe model of nitric and nitrous oxide emissions from soils using TRAGNET database. Global Biogeochemical Cycles **14**:1035–1043.

Davidson, E. A., P. M. Vitousek, P. A. Matson, R. Riley, G. Garcia-Mendez, and J. M. Maass. 1991. Soil emissions of nitric oxide in a seasonally dry tropical forest of Mexico. Journal of Geophysical Research **96**:15,439–15,445.

Diggs, G. M., B. L. Lipscomb, and R. J. O'Kennon. 1999. Shinner and Mahler's illustrated flora of north central Texas. Botanical Research Institute of Texas and Austin College, Ft. Worth, Texas, USA.

Donahue, R. L. 1990. Soils; an introduction to soils and plant growth. Fourth edition. Prentice Hall, Englewood, New Jersey, USA.

Erickson, H., M. K. Keller, and E. A. Davidson. 2001. Nitrogen oxide fluxes and nitrogen cycling during post agricultural succession and forest fertilization in the humid Tropics. Ecosystems **4**:67–84.

Firestone, M. K., and E. A. Davidson. 1989. Microbiological basis of NO and N2O production and consumption in soil. Pages 7–21 *in* M. O. Andrea and D. S. Schimel, editors. Exchange of trace gases between terrestrial ecosystems and the atmosphere. John Wiley and Sons, New York, New York, USA.

Fisher, C. E., C. H. Meadors, R. Behrens, E. D. Robinson, P. T. Marion, and H. L. Morton. 1959. Control of mesquite on grazing lands. Texas Agricultural Experiment Station Bulletin **935**.

Geesing, D., P. Felker, and R. L. Bingham. 2000. Influence of mesquite (*Prosopis glandulosa*) on soil nitrogen and carbon development: implications for global carbon sequestration. Journal of Arid Environments **46**:157–180.

Godde, M., and R. Conrad. 2000. Influence of soil properties on the turnover of nitric oxide and nitrous oxide by nitrification and denitrification at constant temperature and moisture. Biology and Fertility of Soils **32**:120–128.

Goldberg, D. E., and R. M. Turner. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. Ecology **67**:695–712.

Hart, S. C., J. M. Stark, E. A. Davidson, and M. K. Firestone. 1994. Nitrogen mineralization, immobilization and nitrification. Pages 985–1018 *in* R. W. Weaver, C. Angle, and P. Bottomly, editors. Methods of soil analysis. Part 2: Microbial and biochemical properties. Soil Science Society of America, Madison, Wisconsin, USA.

Hartley, A. E., and W. H. Schlesinger. 2000. Environmental controls on nitric oxide emissions from northern Chihuahuan desert soils. Biogeochemistry **50**:279–300.

Hibbard, K. A., S. Archer, D. S. Schimel, and D. V. Valentine. 2001. Herbaceous biomass dynamics and net primary production accompanying woody plant encroachment in a subtropical savanna. Ecology **82**:1999–2001.

Hutchinson, G. L., and G. P. Livingston. 2002. Soil–atmosphere gas exchange. Pages 1159–1182 *in* J. H. Dane and G. C. Topp, editors. Methods of soil analysis. Part 4: Physical methods. Soil Science Society of America, Madison, Wisconsin, USA.

Hutchinson, G. L., G. P. Livingston, and E. A. Brams. 1993. Nitric and nitrous oxide evolution from managed subtropical grassland. Pages 290–316 *in* R. E. Oremland, editor. Biochemistry of global change: radiatively active trace gases. Chapman and Hall, New York, New York, USA.

Hutchinson, G. L., W. X. Yang, and C. E. Andre. 1999. Overcoming humidity dependence of the chromium trioxide converter used in luminol-based nitric oxide detection. Atmospheric Environment **33**:141–145.

Johansson, C., H. Rodhe, and E. Sanhueza. 1988. Emission of NO in a tropical savanna and a cloud forest during the dry season. Journal of Geophysical Research **93**:7180–7192.

Johansson, C., and E. Sanhueza. 1988. Emission from savanna soils during the rainy season. Journal of Geophysical Research **93**:14193–14198.

Johnson, H. B., and H. S. Mayeux. 1990. *Prosopis glandulosa* and the nitrogen balance of rangelands: extent and occurrence of nodulation. Oecologia **84**:176–185.

Kieft, T. L., C. S. White, S. R. Loftin, R. Aguilar, J. A. Craig, and D. A. Skaar. 1998. Temporal dynamics in soil carbon and nitrogen resources at a grassland–shrubland ecotone. Ecology **79**:671–683.

Kirkman, G. A., W. X. Yang, and F. X. Meixner. 2001. Biogenic nitric oxide emissions upscaling: an approach for Zimbabwe. Global Biogeochemical Cycles **15**:1005–1020.

Levine, J. S., E. L. Winstead, D. A. B. Parsons, M. C. Scholes, R. J. Scholes, W. R. Cofer III, D. R. Cahoon Jr., and D. I. Sebacher. 1996. Biogenic soil emissions of nitric oxide (NO) and nitrous oxide (N_2O) from savannahs in South Africa: the impact of wetting and burning. Journal of Geophysical Research **101**:23689–23697.

Martin, R. E., M. C. Scholes, A. R. Mosier, D. S. Ojima, E. A. Holland, and W. J. Parton. 1998. Controls on annual emissions on nitric oxide from soils of the Colorado shortgrass steppe. Global Biogeochemical Cycles **12**:81–91.

Midwood, A. J., T. W. Boutton, S. R. Archer, and S. E. Watts. 1998. Water use by woody plants on contrasting soils in a savanna parkland: assessment with δ2H and δ18O. Plant and Soil **205**:13–24.

Nagele, W., and R. Conrad. 1990. Influence of pH on the release of NO and N_2O from fertilized and unfertilized soil. Biology and Fertility of Soils **10**:139–144.

Otter, L. B., L. Marufu, and M. C. Scholes. 2001. Biogenic, biomass and biofuel sources of trace gases in southern Africa. South African Journal of Science **97**:131–138.

Otter, L. B., W. X. Yang, M. C. Scholes, and F. X. Meixner. 1999. Nitric oxide emissions from a southern African savanna. Journal of Geophysical Research **104**:18471–18485.

Parent, L. E., and J. Coran. 1993. Physical properties of organic soils. Pages 441–458 *in* M. R. Carter, editor. Methods of soil analysis. Soil Science Society of America, Madison, Wisconsin, USA.

Parsons, D. A. B., M. C. Scholes, R. J. Scholes, and J. S. Levine. 1996. Biogenic NO emissions from savanna soils as a function of fire regime, soil type, soil nitrogen, and water status. Journal of Geophysical Research **101**:23,683–23,688.

Parton, W. J., E. A. Holland, S. J. Del Grosso, M. D. Hartman, R. E. Martin, A. R. Mosier, D. S. Ojima, and D. S. Schimel. 2001. Generalized model for NO_x and N_2O emissions from soils. Journal of Geophysical Research **106**:17,403–17,419.

Peech, M. 1965. Hydrogen ion activity. Pages 914–926 *in* C. A. Black, editor. Methods of soil analysis. Part 2: Chemical and microbiological properties. Soil Science Society of America, Madison, Wisconsin, USA.

Potter, C. S., P. A. Matson, P. M. Vitousek, and E. A. Davidson. 1996. Process modeling of controls on nitrogen trace gas emissions from soils worldwide. Journal of Geophysical Research **101**:1361–1377.

Prather, M. J., R. Derwent, D. Ehhalt, P. Fraser, E. Sanhueza, and X. Zhou. 1995. Other trace gases and atmospheric chemistry. Pages 73–126 *in* J. T. Houghton et al., editors. Climate change 1994, radiative forcing of climate change and an evaluation of the IPCC IS92 emission scenarios. Cambridge University Press, New York, New York, USA.

Remde, A., F. Slemr, and R. Conrad. 1989. Microbial production and uptake of nitric oxide in soil. Federation of Europeon Microbiological Societies Microbiology Ecology **62**:221–230.

Reuss, R. W., and S. W. Seagle. 1994. Landscape patterns in soil microbial processes in the Serengeti National Park, Tanzania. Ecology **75**:892–904.

Robertson, G. P., M. O. Andrea, H. G. Bingemer, P. J. Crutzen, R. A. Delmas, J. H. Duyzer, I. Fung, R. C. Harris, M. Kanakidou, M. keller, J. M. Mellilo, and G. A. Zavarzin.

1989. Group report. Trace gas exchange and the chemical and physical climate: critical interactions. Pages 303–320 *in* M. O. Andreae and D. S. Schimel, editors. Exchange of trace gases between terrestrial Ecosystems and the atmosphere. John Wiley and Sons, Chichester, UK.

Sanhueza, E., W. M. Hao, D. Scharffe, L. Donoso, and P. J. Crutzen. 1990. N_2O and NO emissions from soils in the northern part of the Guayana Shield. Journal of Geophysical Research **95**:22481–22488.

Schimel, D. S., and W. J. Parton. 1986. Microclimatic controls of nitrogen mineralization and nitrification in shortgrass steppe soils. Plant and Soil **93**:347–357.

Schlesinger, W. H., and A. M. Pilmanis. 1998. Plant–soil interactions in deserts. Biogeochemistry **42**:169–187.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of nutrients in desert ecosystems. Ecology **77**:364–374.

Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. Science **247**:1043–1048.

Scholes, M. C., R. Martin, R. J. Scholes, D. Parsons, and E. Winstead. 1997. NO and N_2O emission from savanna soils following the first simulated rains of the season. Nutrient Cycling in Agroecosystems **48**:115–122.

Scholes, R. J., and S. R. Archer. 1997. Tree–grass interactions in savannas. Annual Review of Ecology and Systematics **28**:517–544.

Scholes, R. J., and B. H. Walker. 1993. An African savanna: synthesis of the Nylsvley Study. Cambridge University Press, New York, New York, USA.

SCS. 1962. Soil survey of Wilbarger County, Texas, 18. United States Department of Agriculture/Soil Conservation Service, Fort Worth, Texas, USA.

Shearer, G., and D. H. Kohl. 1989. Estimates of nitrogen fixation in ecosystems. The need for and basis of the nitrogen-15 natural abundance method. Pages 342–374 *in* P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, editors. Stable isotopes in ecological research. Academic Press, San Diego, California, USA.

Teague, R., R. Borchardt, J. Ansley, B. Pinchak, J. Cox, J. K. Fox, and J. McGrann. 1997. Sustainable management strategies for mesquite rangeland: the Waggnor Kite Project. Rangelands **19**:4–8.

USACE (U.S. Army Corps of Engineers). 1994. Engineering and design—management of water control data systems. ER-1110-2-249. U.S. Army Corps of Engineers, Department of the Army, Washington, D.C., USA.

Van Cleemput, O., and L. Baert. 1984. Nitrite: a key compound in N loss processes under acid conditions? Plant and Soil **76**:233–241.

Venterea, R. T., and D. E. Rolston. 2000. Mechanisms and kinetics of nitric and nitrous oxide production during nitrification in agricultural soil. Global Change Biology **6**: 303–316.

Verchot, L. V., E. A. Davidson, J. H. Cattonio, I. L. Ackerman, H. E. Erickson, and M. K. Keller. 1999. Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia. Global Biogeochemical Cycles **13**:31–46.

Villagra, G. M. L., and P. Felker. 1997. Influence of understory removal, thinning and P fertilization on N_2 fixation in a mature mesquite (*Prosopis glandulosa* var. *glandulosa*) stand. Journal of Arid Environments **36**:591–610.

Virginia, R. A., L. M. Baird, J. S. La Favre, W. M. Jarrell, B. A. Bryan, and G. Shearer. 1984. Nitrogen fixation efficiency, natural ^{15}N abundance, and morphology of mesquite (*Prosopis glandulosa*) root nodules. Plant and Soil **79**:273–284.

Virginia, R. A., W. M. Jarrel, W. G. Whitford, and D. W. Freckman. 1992. Soil biota and soil properties in the surface rooting zone of mesquite (*Prosopis glandulosa*) in historical and recently desertified Chihuahuan Desert habitats. Biology and Fertility of Soils **13**:90–98.

Williams, E. J., G. L. Hutchinson, and F. C. Fehsenfeld. 1992. NO_x and N_2O emissions from soil. Global Biogeochemical Cycles **6**:351–388.