Oecologia (2002) 130:297–308
DOI 10.1007/s004420100801

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Former land-use and tree species affect nitrogen oxide emissions from a tropical dry forest

Received: 19 January 2001 / Accepted: 1 August 2001 / Published online: 28 September 2001

Abstract Species composition in successional dry forests in the tropics varies widely, but the effect of this variation on biogeochemical processes is not well known. We examined fluxes of N oxides (nitrous and nitric oxide), soil N cycling, and litter chemistry (C/N ratio) in four successional dry forests on similar soils in western Puerto Rico with differing species compositions and land-use histories. Forests patch-cut for charcoal 60 years ago had few legumes, high litter C/N ratios, low soil nitrate and low N oxide fluxes. In contrast, successional forests from pastures abandoned several decades ago had high legume densities, low litter C/N ratios, high mean soil nitrate concentrations and high N oxide fluxes. These post-pasture forests were dominated by the naturalized legume *Leuceana leucocephala*, which was likely responsible for the rapid N cycling in those forests. We conclude that agriculturally induced successional pathways leading to dominance by a legume serve as a mechanism for increasing N oxide emissions from tropical regions. As expected for dry regions, nitric oxide dominated total N oxide emissions. Nitric oxide emissions increased with increasing soil moisture up to about 30% water-filled pore space then stabilized, while nitrous oxide emissions, albeit low, continued to increase with increasing soil wetness. Inorganic N pools and net N mineralization were greatest during peak rainfalls and at the post-agricultural site with the highest fluxes. Soil nitrate and the nitrate/ammonium ratio correlated positively with average N oxide fluxes. N oxide fluxes were negatively and exponentially related to litter C/N ratio for these dry forests and the relationship was upheld with the addition of data from seven wet forests in northeastern Puerto Rico. This finding suggests that species determination of litter C/N ratio may partly determine N oxide fluxes across widely differing tropical environments.

Keywords Dry tropical forest · Nitrogen mineralization · Nitric oxide · Nitrous oxide · Tropical legumes

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Introduction

Ecosystem ecologists have long known that plant species can have different effects on soils and soil processes (Zinke 1962). Recently, specific effects of different plant species on ecosystem processes, especially those involving the cycling of nitrogen (N) have been explored in detail (e.g., Pastor et al. 1984; Wedin and Tilman 1990; Finzi et al. 1998; García-Montiel and Binkley 1998). One of the key ways plants modify their soil environment is through litterfall and its subsequent effects on soil processes (Pastor et al. 1984; Wedin and Pastor 1993; Prescott et al. 2000). Litter high in N is associated with fast rates of decomposition (Melillo et al. 1982; Taylor et al. 1989) and high soil N turnover (Pastor et al. 1984; Hobbie 1992; Reich et al. 1997).

High rates of soil N cycling, particularly in tropical soils, result in increased emission of the globally important N oxide gases, nitric (NO) and nitrous (N_2O) oxide (Matson and Vitousek 1990; Davidson et al. 2000; Erickson et al. 2001). NO reacts in the atmosphere to form nitric acid, an important component of acid deposition; NO is also central in the photochemical production of ozone in the lower atmosphere (Williams et al. 1992). N_2O is a greenhouse gas with about 200 times the warming potential as CO_2 and destroys ozone in the stratosphere (Prather et al. 1995). However the exact sources of these gases are still largely unknown (Bouwman et al. 1995; Davidson and Kingerlee 1997), and large variations in N oxide emissions often exist within similar soil types.

Variation in soil N availability may explain some of the wide variations in emissions (Matson and Vitousek 1990; Davidson et al. 2000; Erickson et al. 2001). Leguminous tree species are often common in tropical forests; the Leguminosae may be the most prevalent plant family in continental tropical dry forests (Gentry 1995). Tropical legumes typically produce litter with high N (Sprent et al. 1996), leading to high soil N availability and/or rates of soil N cycling (García-Montiel and Binkley 1998; Erickson et al. 2001). Thus legumes may be important drivers of soil N dynamics. Despite this general understanding, few studies of N oxide fluxes have considered taxonomic structure of the plant community as a possible cause for the variation.

Tropical and subtropical dry forests were globally once quite extensive (~24 million km^2) (Murphy and Lugo 1990). Due to clearing and conversion to agriculture, pastures and post-agricultural forests now cover most of the area formerly in dry forest (Murphy and Lugo 1995). Successional forests likely differ in tree composition from original forests, yet because floristic studies are much less common in successional than in undisturbed dry forest (Murphy and Lugo 1986a) this is largely undocumented. If post-agricultural changes in forest species, particularly increased dominance by legumes, lead to increases in soil N availability, N oxide emissions may also increase. For example, among several tropical ecosystems in Africa, successional *Acacia* forests with a history of anthropogenic disturbance had the highest NO fluxes (Serça et al. 1998).

We report results of a study examining relationships among tree species, previous land-use, litterfall C/N ratios, soil N cycling and N oxide gas emissions in a dry tropical forest region of southwest Puerto Rico. We ask whether two post-agricultural forests differ compositionally from two forests not previously under agriculture within the same area (Guánica Commonwealth Forest). We then examine how NO and N_2O emissions contrast among the forests and relate to litter chemistry, soil moisture, and soil N cycling.

Materials and methods

Study sites

Four tropical dry forest stands located 3–8 km from the Caribbean Ocean within the 4,000 ha Guánica Commonwealth Forest (17°47′N, 65°52′W) in southwestern Puerto Rico were used for this study. The climate is hot (MAT=25°C); a dry season typically occurs between January and May. Annual precipitation averages 860 mm (Murphy and Lugo 1986b), with high intra-annual variability. Soils are typic Calciustolls in the Aquilita series (Lugo-López and Rivera 1976). Nearly 25% of the ground surface is exposed limestone. Approximately one-third of the tree species within Guánica are deciduous or semi-deciduous, the remainder being broad-leaved evergreens (Murphy and Lugo 1995). The Guánica Forest has been protected from human disturbance since the 1950s. Prior to the 1940s, tree-sized patches were commonly cut (herein patch-cut) for charcoal. This is evident in the historical aerial photos (1936) of the forest showing many dispersed small canopy openings covering nearly 5% of the total area, and by the high degree of coppicing currently in the forest (Murphy and Lugo 1986b). Several larger-sized fragments were entirely cleared in the late 1940s primarily for pasturing (Vélez 1996).

We chose two stands that were "closed forest" in 1936 aerial photos and two younger stands that had been cleared for agriculture by 1950. The two older stands were never cleared enough in 1936 or on subsequent photos (1950, 1963, 1971, 1983, 1989) to be designated open forest, although they were among the areas that were patch-cut for charcoal. These sites were at least 70 years old by the time our study began in 1995, assuming 10 years for canopy closure if they had been completely cut prior to 1936. The younger sites were closed forests by 1963, making them approximately 45 years old at the time of sampling. Interviews with a surviving member of a family who farmed one of the cleared areas indicated that subsistence crops, primarily corn, squash and peas were grown and fertilizer was never used (Miguel Canals, personal communication, biologist, Puerto Rico Department of Natural Resources and the Environment). We designate the older forests OF1 and OF2, and the younger, post-agricultural successional forests, SF1 and SF2, cognizant that all sites had seen previous human activity. OF1 was contained within a larger area that has been sampled extensively for ecosystem studies of dry forest (Lugo and Murphy 1986; Murphy and Lugo 1986a, b). A ground fire burned through SF2 as late as 1980 (Miguel Canals, personal communication).

N oxide emission and ancillary measures

Additional details for the methods summarized below are found in Erickson et al. (2001). Within each site, eight chamber points were located as follows. A 30-m transect was run in the direction of maximum slope; at four equidistant intervals a sampling point was randomly located on each side and not exceeding 7.5 m of the main line. PVC chamber bases (25 cm diameter) were permanently installed at each of the points.

Gas fluxes were measured four times at each site over a 10-month period from December 1995 to October 1996. Air samples for N_2O analyses were removed from the vented covered chambers immediately, and at 10, 20 and 30 min after chamber closure. Gases were analyzed using electron capture detection gas chromatography (Schimadzu GC-14A) within 24 h. N_2O fluxes were calculated from the linear regression of concentration versus time using the four data points from each chamber. NO was measured in the field using flow-through chambers and a portable LMA3 Scintrex nitrogen oxide analyzer. Briefly, NO is converted to NO_2 and detected by chemiluminescence. NO flux was calculated from at least a 3-min linear increase in concentration, obtained within the first 8 min of sampling. Using our system, NO_2 was not differentiated from NO. NO_2 emissions from soils are usually negligible (Conrad et al. 1990; Davidson et al. 1991). Due to time constraints, 4–6 of the 8 chambers were sampled each time at a site; all sites were sampled over a 2-day period.

Air temperature, soil temperature (to 2 cm depth), and soils (see below) were sampled within 1 m of the chambers simultaneously with gas sampling. Rainfall data were obtained from a station within the Guánica Forest located approximately mid-way between the sites. Hurricane Hortense passed through the area in September 1996, causing moderate damage to the canopy.

Soil moisture, pH and bulk density

Soils were sampled adjacent to each chamber to 10 cm depth with an 8-cm-diameter corer. Gravimetric moisture was determined after drying a subsample at 105°C for at least 48 h. Soil pH (water) was measured on samples collected in July 1996.

Bulk density was measured once at each sampling station by excavating soil from rectangular holes (approximately 10×10×10 cm) located within 1 m of the chambers. Removed soil was sieved to 2 mm, dried and weighed. Hole volumes were measured by filling the plastic-lined hole with water to a known volume, and

corrected for removed rock volume. Water-filled pore space (WFPS) was then calculated as the proportion of gravimetrically determined water volume to total pore volume (Hillel 1980).

Soil N transformations

On three of the four sampling dates (December 1995, March 1996 and October 1996), we measured inorganic N, net N mineralization and net nitrification on soils. Nitrification potential was measured on one date, December 1995. Inorganic N was extracted with 2 M KCl. We used a 7-day aerobic laboratory incubation to determine net N mineralization, following Hart et al. (1994) with modifications detailed in Erickson et al. (2001). Nitrification potential was estimated from the change in NO_3^--N concentration over a 24-h period (2, 4, 18 and 24 h) in a shaken soil-slurry with excess NH_4^+-N, NO_3^--N and NH_4^+-N were determined colorimetrically on an Alpkem Rapid Flow Analyzer.

Total C and N were measured by combustion on a LECO CNS-2000 on a subsample of soils collected in July 1996. Air-dried soils were ground to pass a 20-mesh sieve. The sample for total C was rinsed with sufficient HCl prior to analysis to remove all carbonates; N was analyzed on untreated samples. An additional subsample was dried at 105°C to correct results for soil moisture content.

Overstory vegetation and litterfall

A nested circular plot technique was used to sample forest vegetation. We recorded diameter at breast height (dbh) and species identification for all trees equal to or greater than 1 cm dbh within a 500- m^2 circular plot encompassing our gas sampling chambers. Within a concentric 1,000-m^2 circular plot all trees larger than 10 cm dbh were recorded. Nomenclature follows Liogier and Martorell (2000).

We collected litterfall from March 1996 to March 1997. Nine litterfall traps (0.25 m^2) were spaced 40 m apart in an 80×80 m grid encompassing the gas sampling areas. Litter was collected monthly, oven-dried at 60°C, sorted into leaves and other classes of litter and weighed to the nearest 0.01 g. For each site/date combination, leaves from the nine baskets were pooled into a single sample. Subsamples were removed, ground to pass a 20-mesh sieve, and analyzed for total C and N by combustion on a LECO CNS-2000. For all analyses, results are expressed on an oven-dry (soil or litter) basis.

Statistical analyses

A repeated measures ANOVA was used to compare the effects of site, sampling date and their interactions on N_2O flux and soils data. Differences in NO flux due to the same effects were assessed with a two-way, rather than a repeated measures ANOVA because different chambers were sampled for NO on different dates. We used a univariate approach for the repeated measures analysis (SAS 1987). Gas flux and most soil variables were log-transformed prior to analysis to meet the assumptions of ANOVA, except for percentage data, which were arcsin-transformed (Sokal and Rohlf 1995). We assessed differences among sites within a date using a one-way ANOVA followed by a Tukey's multiple comparison. Where a parameter was measured only once (e.g., soil pH and nitrification potential) only differences among sites were evaluated. Linear and exponential models were used to examine relationships between total N oxide fluxes and N availability indices; in each case, the model with the higher R^2 value is reported.

Results

Forest composition

The legume *Leuceana leucocephala* had the greatest basal area and stem density of any tree species in SF1 and SF2, the two post-agricultural successional forests (Table 1). Legume basal areas, including *Acacia* at SF2, represented 29% and 66% of the total basal areas and 50% and 58% of the individual stems for SF1 and SF2, respectively. In contrast, in the more floristically diverse and dense older forests, legumes were either much less dominant (OF2) or not present (OF1) (Table 1). Cactaceae genera *Cereus* and *Pilosocereus* are also among the dominants in the successional forests, but were absent from our plots in the older forests. The OF sites had a greater number of stems, most with diameters less than 10 cm (data not shown), when compared to the post-agricultural successional forests and this is most likely due to stump sprouting from trees cut for charcoal production (Murphy and Lugo 1995).

Aboveground litterfall inputs and chemistry

Daily rates of litterfall ranged from 0.5 to 3.0 g m^{-2} (data not shown) during most months except immediately after Hurricane Hortense, when daily rates at all sites exceeded 7.0 g m^{-2}. On average, aboveground total litterfall was 30% greater in the older forests (OF1 and OF2) than in the post-agricultural successional forests (SF1 and SF2), although due to high within-site variation, differences among sites were not statistically significant (Table 2, $P>0.05$). Leaf litterfall was also 30% lower in the younger compared with older forests (Table 2), but here, differences were significant.

Leaf litter C/N ratio differed significantly among all four sites (Table 2), ranging from a low of 22.8 at SF1 to a high of 49.0 at OF1. Leaf litter N concentrations differed in a like manner among the sites, ranging from a high of 2.23% at SF1 to a low of 1.05% at OF1. The concentration at OF1 compares favorably with a 1.01% leaf litter N reported from the well-studied area encompassing our plot (Lugo and Murphy 1986). Total leaf litter N inputs were, on average, greater for successional (mean=4.97 g N m^{-2} $year^{-1}$) than for older forests (mean=4.23 g N m^{-2} $year^{-1}$) though N inputs from OF2 could not be statistically distinguished from either successional forest (Table 2).

Soil characteristics

Soil pH values for the upper 10 cm of mineral soil were lowest at SF1 (mean=6.6) compared to the other three sites where means ranged from 7.7 to 7.9 (Table 3). Soil temperature ranged from 25°C to 32°C (data not shown) but showed no consistent pattern of differences among the sites. Bulk density was higher in the successional

Table 1 Tree species ranked by basal area (*BA*, m^2 ha^{-1}) in the two post-agricultural successional forests (*SF1* and *SF2*) and the two older forests (*OF1* and *OF2*) within the Guánica Forest Preserve, PR. *D* Density of individuals (no. ha^{-1}), within the 500 m^2 plots only. Legumes are indicated in boldface

SF1			SF2			OF1			OF2		
Species	BA	D	Species	BA	D	Species	BA	D	Species	BA	D
Leucaena leucocephala (Lam.) Dewit	4.82	1966	*Leucaena leucocephala* (Lam.) Dewit	5.27	3571	*Exostema caribaeum* (Jacq.) R. & S.	2.50	2427	*Pisonia albida* (Heimerl) Britt. & Stand.	2.14	782
Cereus hexagonus (L.) P. Miller	4.62	160	*Guaiacum officionale L.*	2.81	2106	*Gymnanthes lucida* Sw.	1.98	2809	*Thouinia striata var. portoricensis* (Radlk.) Votava & Alain	2.04	1304
Pilosocereus royenii (L.) Byles & Rowley	3.73	401	*Acacia tortuosa* (L.) Willd.	1.90	722	*Bourreria succulenta* Jacq.	1.09	903	*Coccoloba diversifolia* Jacq.	1.00	1164
Opuntia spp.	1.44	120	*Cereus hexagonus* (L.) P. Miller	0.44	60	*Bucida buceras* L.	0.93	140	*Antirhea lucida* (Sw.) Hook.	0.83	562
Bucida buceras L.	0.78	60	*Machoania porto-ricensis* Baill.	0.15	241	*Coccoloba krugii* Lindau	0.71	1685	*Eugenia axillaris* (Sw.) Willd.	0.78	1144
Machoania portoricensis Baill.	0.27	120	*Pithecellobium unguiscati* (L.) Mart.	0.12	181	*Crossopetalum rhacoma* Crantz	0.54	622	*Exostema caribaeum* (Jacq.) R. & S.	0.74	160
Capparis indica (L.) Fawc. & Rendle	0.15	341	*Schaefferia frutescens* Jacquin	0.06	120	*Bursera simaruba* (L.) Sarg.	0.52	140	*Pithecellobium unguiscati* (L.) Mart.	0.71	722
Unknown	0.07	60	*Rauvolfia nitida* Jacq.	0.05	40	*Erithalis fruticosa* L.	0.35	682	*Bunchosia glandulosa* (Cav.) L.C. Rich	0.71	662
Pithecellobium unguis-cati (L.) Mart.	0.06	120	*Trichilia hirta* L.	0.04	20	*Comocladia dodoanea* (L.) Urban.	0.26	461	*Exostema caribaeum* (Jacq.) R. & S.	0.70	361
Unknown	0.04	20	*Croton astroites* Dryand.	0.04	261	*Eugenia foetida* Pers.	0.21	762	*Celtis trinervia*	0.47	140
Bourreria succulenta Jacq.	0.03	100	*Senna atomaria* (L.) Irwin and Barnaby	0.01	20	*Cassine xylocarpa* Ventenat	0.21	381	*Leucaena leucocephala* (Lam.) Dewit	0.45	221
Trichilia hirta L.	0.03	40	*Thouinia striata var. portoricensis* (Radlk.) Votava & Alain	0.01	40	*Thouinia striata var. portoricensis* (Radlk.) Votava & Alain	0.19	562	*Bucida buceras* L.	0.41	80
Capparis hastata Jacq.	0.03	60	*Bourreria succulenta* Jacq.	<0.01	20	Unkown	0.17	140	*Guaiacum officionale* L.	0.41	742
Eugenia monticola (Sw.) DC	0.01	20	Total	10.9	7403	*Gyminda latifolia (Sw.) Urban*	0.13	321	*Eugenia foetida* Pers.	0.38	120
Eugenia axillaris (Sw.) Willd.	0.01	60				*Coccoloba pyrifolia* Desf.	0.12	60	*Hypelate trifoliata* Sw.	0.32	341
Total	16.8	3651				*Pictetia aculeata* (Vahl) Urban	0.11	120	*Schaefferia frutescens* Jacquin	0.29	60
						Unknown	0.10	160	*Bursera simaruba* (L.) Sarg.	0.29	80
						Amyris balsamifera L.	0.09	140	*Guettarda elliptica* Sw.	0.27	80
						Unknown cactus	0.08	20	*Comocladia dodoanea* (L.) Urban.	0.23	160
						Reynosia krugii Urban	0.06	221	*Coccoloba costata* C. Wr.	0.19	160
						Eugenia axillaris (Sw.) Willd.	0.05	140	*Erythroxylum areolatum* L.	0.18	261

Table 1 (cotinued)

SF1			SF2			OF1			OF2		
Species	BA	D	Species	BA	D	Species	BA	D	Species	BA	D
						Colubrina elliptica (Sw.) Briz. & Stern	0.02	80	*Krugiodendron ferreum* (Vahl) Urban	0.17	60
						Randia aculeata L.	0.02	40	*Capparis indica* (L.) Fawc. & Rendle	0.14	140
						Unknown	0.01	40	*Colubrina arborescens* (Mill.) Sarg.	0.14	100
						Total	10.5	13060	*Amyris balsamifera* L.	0.13	60
									Tabebuia heterophylla (DC.) Britt.	0.12	662
									Eugenia pseudopsidium Jacq.	0.11	100
									Trichilia triacantha Urban	0.10	261
									Eugenia ligustrina (Sw.) Willd.	0.07	60
									Colubrina elliptica (Sw.) Briz. & Stern	0.06	20
									Eugenia confusa DC.	0.05	100
									Coccoloba michrostachya Willd.	0.05	40
									Ardisia obovata Desc.	0.04	40
									Albizia procera (Roxb.) Benth.	0.04	20
									Randia aculeata L.	0.03	100
									Eugenia monticola (Sw.) DC	0.01	20
									Erythroxylon rotun-difolium Lunan	0.01	20
									Capparis hastata Jacq.	<0.01	
									Total	14.8	11114

Table 2 Annual means (SE in parentheses) for total aboveground (*AG*) litterfall, total leaf litterfall, and leaf litter N chemistry for two mid-successional and two older tropical dry forests in Guánica Forest, P.R. Means for litterfall are based on annual estimates calculated for each basket at a site (n=9). Means for C/N ratio and N (%) are based on 14 different collections (n=14). Different superscripts within columns indicate significant differences (P< 0.05) determined by an a posteriori Tukey multiple comparisons test after ANOVA

Site	Total AG litterfall (g m^{-2} year^{-1})	Leaf litterfall (g m^{-2} year^{-1})	Leaf litter C/NRatio	Leaf litter N(%)	Leaf litterfall N (g m^{-2} year^{-1})
SF1	367^{a} (43.6)	258^{b} (23.0)	22.8^{d} (0.61)	2.23^{a} (0.06)	5.74^{a} (0.50)
SF2	388 ^{a} (55.3)	250 ^{b} (23.4)	30.2 ^{c} (0.97)	1.72 ^{b} (0.05)	4.19 ^{b} (0.37)
OF1	488^{a} (54.4)	342^{ab} (36.3)	49.0^{a} (1.63)	1.04^{d} (0.04)	3.59^{b} (0.38)
OF2	498 ^{a} (33.3)	380 ^{a} (23.3)	39.4 ^{b} (2.04)	1.33^{c} (0.06)	4.88^{ab} (0.28)

Table 3 Selected site and soil (0–10 cm) characteristics for the four study areas within the Guánica Forest Preserve. Values are means (SE in parentheses, n=8) except for porosity, which is calculated as 1–(bulk density/2.65). Different superscripts within columns indicate significant differences (P<0.05) determined by an a posteriori Tukey multiple comparisons test after ANOVA

Site	Most recent disturbance	Bulk density (g cm^{-3})	Soil porosity	pH	Total C		Total N	
					(%)	(kg m^{-2})	(%)	(kg m^{-2})
SF1	Pasture until 1950s	0.99^{a} (0.04)	0.63	6.64 ^{a} (0.30)	7.25^{a} (0.61)	7.19^{a} (0.60)	0.72^{a} (0.05)	0.72 ^{a} (0.05)
SF2	Pasture until 1950s, ground fire in 1970s	1.01^{a} (0.05)	0.62	7.66 ^{b} (0.12)	5.07^{a} (0.53)	5.10^{a} (0.49)	0.49^{a} (0.02)	0.50 ^{a} (0.02)
OF1	Patch cut – 1930s	0.79^{b} (0.04)	0.70	7.86^{b} (0.04)	7.79^{a} (1.88)	6.17^{a} (1.49)	0.75^{a} (0.13)	0.59 ^{a} (0.11)
OF2	Patch cut – 1930s	0.89^{ab} (0.03)	0.66	7.88^{b} (0.03)	7.88^{a} (1.04)	7.02^{a} (0.93)	0.80^{a} (0.12)	0.72 ^{a} (0.11)

forests (mean=1.00 g cm^{-3}) versus the older forests (0.85 g cm^{-3}). Although SF2, the successional forest that burned 16 years earlier, had nearly 25% lower total soil C and N in the upper 10 cm than the other three sites (Table 3), the difference was not significant (P>0.05). Soil C/N ratios ranged from 10.0 to 10.2 and did not vary among the sites (P>0.05).

Inorganic N pools and soil N transformations

For soil extractable NO_3^--N and NH_4^+-N and net nitrification, the effects of sampling date, site and date × site interactions were statistically significant (Table 4). Soil NO_3^--N ranged widely, from ~7 to 48 µg N g soil^{-1}, with the largest concentrations measured in March 1996 (Fig. 1, Table 4). Similarly, extractable NH_4^+-N showed large variation, ranging from ~4 to 52 µg N g soil^{-1}, with the largest pools also measured in March 1996 (Fig. 1). Soil NO_3^--N pools at SF1 were 1.7–4 times greater than at the other sites. NH_4^+-N pools tended to be similar among the sites, except during March 1996 when pools were high at all sites (Fig. 1). Then, NH_4^+-N pools at OF1 were twice those of the other sites (Fig. 1). Net nitrification was highest for all sites in March 1996 (Fig. 1c), and was greatest at OF1.

The effect of sampling date on net N mineralization depended on site (interaction P=0.0017, Table 4). Net N mineralization, ranging from about 3.5 to 8.8 µg N g soil^{-1} 7 day^{-1}, was usually similar among the sites (Fig. 1d). The one exception was during March 1996 when the highest rate measured for any site (~21 µg N g soil^{-1} 7 day^{-1}) was measured for SF1. Nitrification potential was greatest at SF1 (2.77 mg N kg^{-1} h^{-1}) but overlapped with rates from SF2 and OF2 (Table 5).

N oxide emissions

Site, sampling date and their interaction influenced the fluxes of NO (P<0.001). The effect of site depended on date. SF1 had the highest NO fluxes on all four dates, though its fluxes could not be distinguished from SF2's in December 1995 (Fig. 2). The two highest mean NO fluxes (>23.0 ng N cm^{-2} h^{-1}) were measured in March 1996 and June 1996. Mean NO fluxes from the OF sites were generally low (<2 ng N cm^{-2} h^{-1}), and differed from the SF sites most dates.

SF1 had higher N_2O fluxes in March 1996 (P<0.05) and June 1996 (P=0.07) than the other sites (Fig. 2, Table 4). Fluxes from the other sites did not differ during any of the four sampling dates. Only two mean N_2O fluxes were greater than 0.50 ng N cm^{-2} h^{-1} (3.25 and 0.57, measured during March 1996 for SF1 and SF2 respectively). While average fluxes of N_2O (n=8) were negative at three of the sites, indicating N_2O up-

Table 4 Repeated measures ANOVA results for soil NO_3^--N, NH_4^+-N, net N mineralization, net nitrification and N_2O emissions

	NO_3^--N			NH_4^+-N			Net N mineralization			Net nitrification			N_2O flux		
	df	*F* ratio	*P*	*df*	*F* ratio	*P*	*df*	*F* ratio	*P*	*df*	*F* ratio	*P*	*df*	*F* ratio	*P*
Between chambers															
Site	3	12.8	<0.001	3	3.57	0.027	3	0.83	NS	3	5.24	0.005	3	10.84	<0.001
Error	28			27			27			28			28		
Within chambers															
Date	2	88.1	<0.001	2	146.0	<0.001	2	7.19	0.002	2	92.3	<0.001	3	18.1	<0.001
Site×Date	6	4.3	0.001	6	5.92	<0.001	6	4.34	0.001	6	5.29	<0.001	9	8.64	<0.001
Error	56			54			54			56			84		

Table 5 Mean inorganic N, soil N cycling rates and N oxide fluxes (SE in parentheses) for the four study areas within the Guánica Forest Preserve. Means are based on means over time for each sampling point (*n*=8), except for nitrification potential which was only measured once

Site	Nitrification potential (μg N g soil^{-1} h^{-1})	Net N mineralization	Net nitrification	NH_4^+-N	NO_3^--N	NO_3^--N/ NH_4^+-N	N_2O	NO
		(μg N g soil^{-1} 7 days^{-1})		(μg N g soil^{-1})			(ng N cm^{-2} h^{-1})	
SF1	2.77 (0.50)^{a}	10.45 (1.5)^{a}	16.0 (2.8)^{ab}	15.0 (5.7)^{ab}	34.0 (4.0)^{a}	3.6^{a}	0.88 (0.29)^{a}	13.7
SF2	1.65 (0.17)^{ab}	5.3 (0.8)^{b}	8.0 (1.2)^{b}	7.5 (0.8)^{b}	14.7 (1.0)^{b}	2.1^{b}	0.05 (0.10)^{b}	2.82
OF1	1.09 (0.14)^{b}	6.19 (1.0)^{ab}	20.8 (2.8)^{a}	21.4 (3.5)^{a}	10.2 (2.7)^{b}	0.5^{c}	–0.04 (0.02)^{b}	0.90
OF2	2.09 (0.52)^{ab}	7.67 (1.7)^{ab}	12.7 (2.3)^{ab}	12.0 (2.9)^{ab}	14.5 (2.5)^{b}	1.2^{bc}	0.03 (0.05)^{b}	0.55

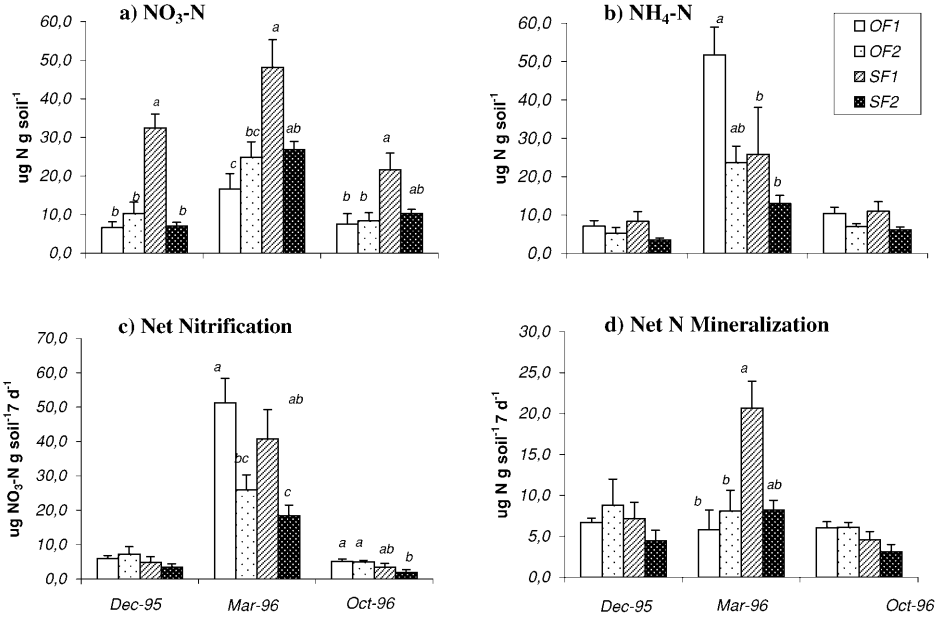

Fig. 1 KCl (2 M) extractable NO_3^--N (**a**) and NH_4^+-N (**b**) and net rates of nitrification (**c**) and N mineralization (**d**) for the four sites at Guánica. *OF* "Older forest", *SF* "post-agricultural successional forest". Data are means (*n*=8) and standard errors. For each variable, different lower-case letters within a given sampling date indicate significantly different means ($P< 0.05$) using a Tukey multiple comparisons test after one-way ANOVA. Statistical analyses were done on log-transformed data; means and standard errors are based on non-transformed data to facilitate comparison with other studies

take, these means were not significantly different from zero.

Rainfall, soil moisture and N oxide emissions

We sampled N oxide gases during both wet and dry periods (Fig. 3). WFPS ranged from a low of just over 16% to a high of 55%, varying by site and date of sampling (ANOVA, $P<0.05$ for the main effects; the effect for interaction was NS). March 1996 was the wettest month; during which time WFPS nearly doubled compared to the other months (Fig. 2C). Overall, WFPS was about 25% lower at OF1 compared to the other sites (Fig. 2C).

The highest fluxes of NO for three of the sites (OF1, OF2 and SF2) coincided with the high March WFPS values (Fig. 4a). For SF1, the highest fluxes (22–25 ng N cm^{-2} h^{-1}) occurred during the relatively wet months of

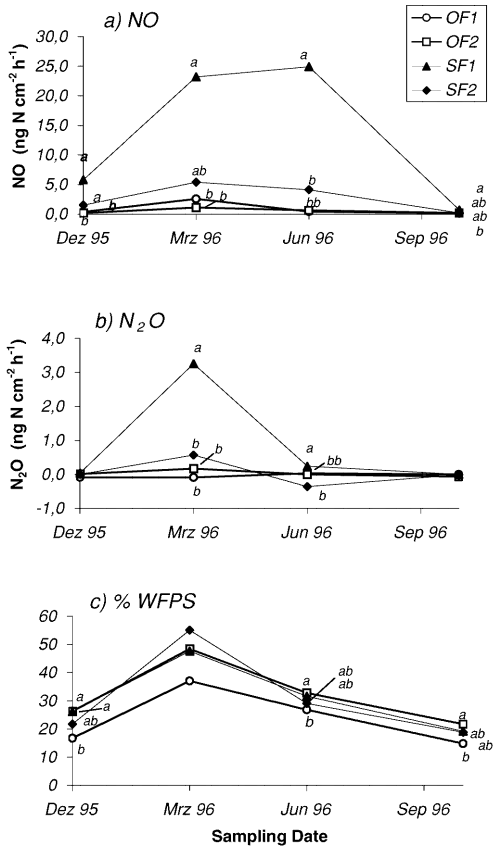

Fig. 2 Fluxes of NO (**a**), N_2O (**b**), and percent WFPS measured from the four sites at Guánica. Within a given date, different lower-case letters indicate significantly different means ($P < 0.05$) using a Tukey multiple comparisons test after one-way ANOVA. Note differences in scales in all three panels. Site codes are explained in Fig. 1

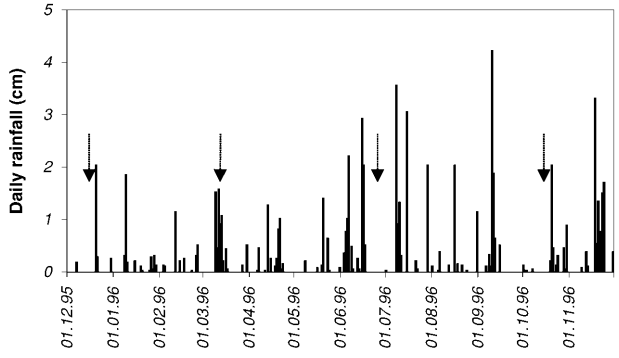

Fig. 3 Daily rainfall and dates of N oxide sampling (*arrows*) at Guánica from 12 January 1995 to 12 January 1996

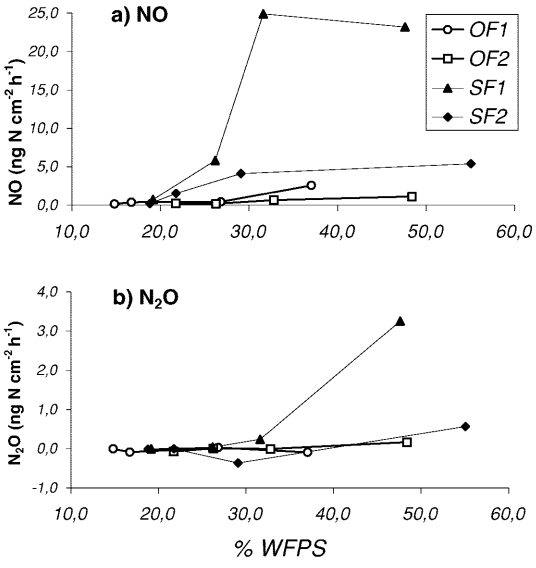

Fig. 4 Fluxes of NO (**a**) and N_2O (**b**) versus % WFPS for each of the four sites at the Guánica Forest, P.R. Note differences in scales between the two panels. Site codes are explained in Fig. 1

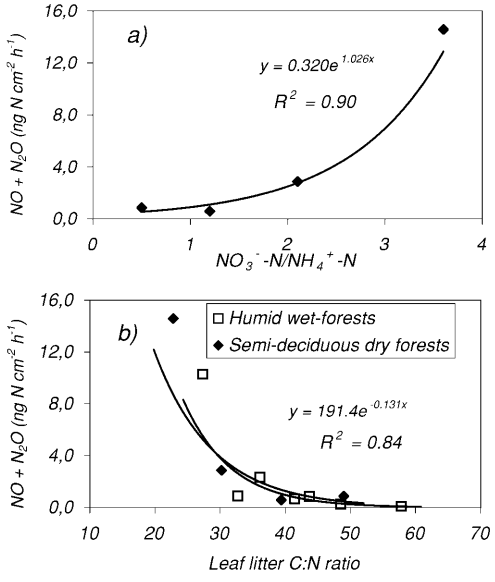

Fig. 5 The sum of N oxide fluxes (N_2O + NO) versus **a** the ratio of NO_3^--N/NH_4^+-N and **b** leaf litter C/N ratio. For **b**, two separate curves are plotted for the humid and dry forests; the equation and model R^2 value are from the combined data sets. For fluxes and inorganic N pools, each data point is the mean of the 8 sampling points for a site: fluxes were measured 4 times in the dry forest and 12 times in the humid forest sites; inorganic N pools were measured 3 times in the dry forest. Litterfall C/N ratios are based on means of 14 collections made at each site

March and June when WFPS was 25–55%. For the two sites with the highest fluxes, SF1 and SF2, NO fluxes showed no significant increase with WFPS values beyond 30% (Fig. 4a).

The fluxes of N_2O for three of the sites (SF1, SF2, and OF2) peaked when WFPS was greatest for each site (>40%; Fig. 4b). N_2O:NO ratios, calculated only if mean N_2O fluxes were significantly different from zero, ranged from 0.105 to 0.140, indicating the predominance of NO emissions over N_2O (Fig. 4).

Total fluxes vs N availability indices

Across all sites the sum of the N oxide fluxes was positively related to mean soil NO_3^--N, and the ratio of NO_3^--N/NH_4^+-N and negatively related to leaf litter C/N ratio ($P<0.05$; Fig. 5). Average N oxide fluxes were not related to averages of net N mineralization, net nitrification, nitrification potential or to NH_4^+-N. Exponential model fits had higher R^2 values than linear models for NO_3^--N/NH_4^+-N and to leaf litter C/N ratio (Fig. 5). The relationship between N oxide fluxes and leaf litter C/N ratio for the four Guánica sites was remarkably similar to that obtained for seven forests in the humid NE (Fig. 5 and Erickson et al. 2001).

Discussion

Forest species, feedback and N oxide fluxes

Land-use and land-use history are known to affect fluxes of important N oxide gases from the tropics. Despite this understanding, estimates of terrestrial sources of these gases remain uncertain (Bouwman et al. 1995; Davidson and Kingerlee 1997). Forest clearing (Luizão et al. 1989; Keller et al. 1993), burning (Levine et al. 1988; Neff et al. 1995; Serça et al. 1998) and fertilization of agricultural lands (Matson et al. 1996; Mosier and Delgado 1997; Veldkamp and Keller 1997) have been identified as causes of increasing N_2O or NO emissions from tropical regions. In the dry forests of Guánica, total N oxide fluxes were greater from legume- (mostly *Leuceana leucocephala*) dominated post-agricultural successional forests than from the nearly legume-free non-agricultural older forests (Table 5). These findings indicate that agricultural abandonment leading to successional trajectories favoring legumes can significantly affect N oxide fluxes.

The low level of canopy removal and subsequent stump sprouting at the OF sites likely maintained the original species complement (Murphy and Lugo 1995). Nearly complete canopy removal and fewer sprouts in the former agricultural sites suggest that invasion by new species was the mechanism for forest recovery. *L. leucocephala*, the dominant species at the successional sites, is known to invade pastures and recently disturbed areas elsewhere in Guánica (Farnsworth 1993; Molina and Lugo, unpublished data). Our floristic data show that *L. leucocephala* is minimally present in the less disturbed forests, and likely became dominant in the post-agricultural successional forests after agricultural abandonment. *L. leucocephala* has been naturalized in Puerto Rico and the Caribbean (F. Wadsworth, personal communication) and is considered relatively short-lived. Moreover, it is widely distributed elsewhere in the neotropics, where it may also be important in post-agricultural succession. If abandonment of additional agricultural lands leads to forests dominated by *L. leucocephala*, N oxide emissions would be expected to increase.

Lower N oxide fluxes from successional versus primary forests had been widely reported (Robertson and Tiedje 1988; Keller and Reiners 1994; Verchot et al. 1999), but without detailed information on species composition. In humid northeastern Puerto Rico, the greatest N oxide fluxes (primarily N_2O) were from a successional forest that had more legumes than other nearby successional and old growth forests (Erickson et al. 2001). Similarly, successional *Acacia* forests had greater NO fluxes compared with other non-legume forests in Africa (Serça et al. 1998). These findings, together with our Guánica results, suggest that some successional forests may contribute more N oxides to the atmosphere than previously thought (cf., Robertson and Tiedje 1988). While rarely documented, species composition, especially the abundance of N-fixing genera, may help explain the variation in N oxide fluxes among tropical forests.

Despite lower leaf litterfall, the *L. leucocephala* successional forests at Guánica had, on average, greater inputs of leaf litter N than the older forests due to greater leaf litter N concentrations. High foliar N in N-fixing species is common, and N in legume foliage may be high in both nodulated and non-nodulated genera (Sprent et al. 1996). Nonetheless, symbiotic N fixation by *L. leucocephala* appears to be widespread (Högberg and Kvarnström 1982; Parrotta et al. 1994, 1996; Sprent et al. 1996). One of the successional forests, SF1, had greater N oxide fluxes and foliar N concentrations than the previously burned successional forest, SF2, though both forests had similar densities (50% and 58% respectively) of legumes. Ground fire can increase inorganic N pools (cf., Ellingson et al. 2000) which, in turn, may decrease N fixation (Marschner 1995), providing a possible explanation for the discrepancy in N oxide fluxes between the two successional sites.

Litterfall C/N ratios often relate negatively to decomposition rates (Mellilo et al. 1982) and to net N mineralization (Pastor et al. 1984; García-Montiel and Binkley 1998; Erickson et al. 2001). SF1 had the lowest leaf litter C/N ratio, the highest rates of net N mineralization, and the highest combined N oxide fluxes. Although one of the older forests, OF2, had high total inputs of litterfall N (this forest also had minimal representation by legumes), the litter was, on average, of higher C/N and N oxide fluxes were low. Thus for the Guánica sites litter chemistry, or C/N ratio, relates more directly to soil processes than does the quantity of N from litterfall.

Despite greater inputs of N in the successional forests, total pools of soil N did not differ among the sites. While not statistically significant, the most recently burned successional site tended to have less soil C and N than the other sites.

The high bulk density in the post-agricultural sites is most likely due to compaction by cattle (Rhoades et al. 1999). High bulk density leads to increased WFPS, which may affect N oxide fluxes, although among these sites N availability appears to be a more important driver (see below).

N oxide emissions in drought-deciduous forests: magnitudes and controls

The positive relationship between N oxide fluxes and various measures of soil N availability is well documented (Matson and Vitousek 1987, 1990; Keller and Reiners 1994; Verchot et al. 1999; Davidson et al. 2000; Erickson et al. 2001). Many indices of N availability (e.g., soil nitrate, net N mineralization and net nitrification) have been evaluated, and the strength and character of their relationships to N oxide fluxes vary somewhat among sites. For example we found positive relationships with soil nitrate, the NO_3^--N/NH_4^+-N ratio and leaf litter C/N ratio (Fig. 5). High soil nitrate relative to ammonium indicates excess N availability relative to plant demand (Keller and Reiners 1994; Neill et al. 1997; Davidson et al. 2000; Erickson et al. 2001). Erickson et al. (2001) reported an exponential decline in N oxide fluxes with increasing leaf litter C/N for forests in humid eastern Puerto Rico; adding the results from this study resulted in a remarkably similar relationship (Fig. 5). Erickson et al. (2001) also suggested that as plant and aerobic heterotrophic microbial sinks for N became satisfied, the proportion of inorganic N available for nitrification and denitrification, the two processes responsible for N oxide production, would increase, resulting in the non-linear relationship. Although an exponential relationship described the relationship between total N oxide flux and the ratio of NO_3^--N/NH_4^+-N for the dry forest sites (Fig. 5a), a linear model better described the relationship for the wet forest sites (data not shown). Leaf litter C/N ratio appears to be a more consistent predictor of total N oxide fluxes than soil inorganic-N in the wet and dry tropical environments encompassed in these studies.

The mean NO flux for SF1 (11.9 kg N ha^{-1} $year^{-1}$) represents, to our knowledge, the largest mean soil-atmosphere NO flux measured for a tropical forest. In their review, Davidson and Kingerlee (1997) list the highest mean or median NO flux as 4.3 kg ha^{-1} $year^{-1}$ from an Amazonian tropical evergreen forest (Kaplan et al. 1988) and 0.7 kg ha^{-1} $year^{-1}$ from a tropical deciduous forest of Mexico (Davidson et al. 1991). (The mean flux from the Guánica old forest sites – 0.62 kg ha^{-1} $year^{-1}$ – is remarkably similar to the Mexican dry forest estimate.) We averaged the four time measurements of NO fluxes for comparative purposes but recognize the limitation in extrapolating to annual fluxes. The March 1996 measurements were made immediately after a rainfall event, and likely represent extremely high fluxes. Experimental wetting has been shown to stimulate NO fluxes (Davidson 1991. 1993; Poth et al. 1995; Levine et al. 1996), especially after long periods of drought. June fluxes, however, made 8 days after measurable precipitation, were also high. We also measured the fluxes from areas not covered by rock. Reducing the mean fluxes from SF1 and SF2 by 25% to reflect the proportion of the ground covered by rock, we still estimate a relatively high mean NO flux of 5.4 kg N ha^{-1} $year^{-1}$ for these legume-dominated forests. Furthermore, if leaf N proves to adequately predict N oxide fluxes, the 2.23% N for SF1 is among the highest reported for any tropical forest (Jaramillo and Sanford 1995), suggesting our flux estimates are reasonable.

NO is absorbed by forest canopies. Therefore, NO emissions from soils may be particularly important from drought deciduous forests because absorption is presumably less during periods of low leaf mass (Matson and Vitousek 1995). Even the relatively low mean NO flux from the OF sites at Guánica (0.62 kg ha^{-1} $year^{-1}$) was from 2 to 100 times greater than annual NO fluxes from sites in humid northeastern Puerto Rico (Erickson et al. 2001). Only the site most dominated by legumes from that study (a successional forest) matched the mean NO flux from the OF sites at Guánica.

Because the relative proportion of N_2O versus NO fluxes is related to soil moisture (Davidson 1991), higher fluxes of NO would be expected in seasonally dry climates. Rainfall in northeastern Puerto Rico is nearly five times the average rainfall at Guánica. N_2O:NO ratios were >1 from the sites in northeastern Puerto Rico (Erickson et al. 2001) and <1 from the sites at Guánica. Based on published annual fluxes (Davidson et al. 1991; García-Méndez et al. 1991) the ratios for a dry forest at Chamela, Mexico, were also generally at or below 1. These data support the idea that regional differences in relative N oxide emissions may be accounted for by variation in precipitation and effects on soil moisture (Davidson 1991; Davidson et al. 2000). Davidson (1991) also proposed a unimodal relationship between soil moisture and N oxide gas emissions, in which the optimal water content for maximum emissions occurs at intermediate values and emissions decline as moisture increases or decreases. Thus, at dry sites, higher NO fluxes are often found during the wet season (this study, Davidson et al. 1991; Serça et al. 1998) whereas, at more humid sites, higher fluxes are found during the dry season (e.g., Verchot et al. 1999). At Guánica, NO increases at lower percent WFPS, while at higher WFPS, NO levels out, and N_2O clearly increases (Fig. 4), suggesting the optimal water content for NO emissions had been reached.

The exact effect of moisture on N oxide fluxes appears constrained primarily by N availability. The highest N oxide fluxes occurred in March 1996 when soils were the wettest (Fig. 2), inorganic N pools and net nitrification highest (Fig. 1), and coincided with a rainfall event that had been preceded by a long dry period (Fig. 3). Generally higher rates of net N mineralization during wet seasons have been documented for other tropical dry or seasonal forests (García-Méndez 1991; Babbar and Zak 1994; Rhoades et al. 1999). Yet despite WFPS above 35% at all of the sites in March 1996 (see also Fig. 4), fluxes from the two older forests, with lower soil NO_3^- pools, were not nearly as high as fluxes from the successional forests, with greater soil NO_3^- pools.

Conclusions

In our study, a legume capable of high rates of symbiotic N fixation (*L. leucocephala*) dominated the post-agricultural successional forests after nearly 25 years or more since the last known disturbance. These successional forests showed substantially greater fluxes of N oxides (primarily NO) than two nearby older forests that had never been cleared for agriculture. The former land-use and dominance of *L. leucocephala* in the post-pasture successional forests suggests that when agricultural abandonment leads to dominance by legumes, fluxes of NO may also increase. Thus dry tropical forest clearing and succession leading to legumes is identified as a previously unrecognized source of N oxides.

The high N oxide fluxes were directly related to low leaf litter C/N and high soil NO_3^--N/NH_4^+-N ratios. In fact, the exponential relationship between total N oxide fluxes and leaf litter C/N ratio for all sites was nearly identical to one obtained for seven forest sites of varying ages in a wet region of northeastern Puerto Rico (Erickson et al. 2001). This argues for coupling measures of litter chemistry and N oxide gases where possible. Litter C/N ratio appears to be a robust predictor of N oxide fluxes across very different tropical environments.

In all cases in Guánica, NO emission surpassed those of N_2O. Rainfall increased N oxide emissions at all sites, but not nearly as much in the older forests. This suggests that N availability is the primary control of N oxide emission, and moisture a secondary control.

Acknowledgements We thank María Rivera, Carlos Ortiz, Brynne Bryan, Carmen Marrero, Mary Jean Sánchez and Edwin López for top-notch assistance in the field and laboratory. Sandra Molina and Miguel Canals are thanked for assisting with field sites and M.C. also for logistical support, rainfall data and contacting the Gutteriez family for oral history. Jill Thompson, John Pastor and Fred Scatena provided insightful reviews of earlier drafts. This research was supported by the NASA Terrestrial Ecology Program under NASA grants NAGW-3772 and NAG5–6277. We acknowledge support from the NASA-IRA program to the University of Puerto Rico, and from the National Science Foundation's Model Institutions for Excellence program.

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