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Nitrogen transformations and nitrous oxide flux in a tropical deciduous forest in México

Georgina García-Méndez[1], J. Manuel Maass[1], Pamela A. Matson[2], and Peter M. Vitousek[3]

[1] Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70–275, México, D.F. 04510, México
[2] Earth Systems Science Division, NASA-Ames Research Center, Moffett Field, CA 94305 USA
[3] Department of Biological Sciences, Stanford University, Stanford, CA 94305 USA

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Summary. Emissions of nitrous oxide and soil nitrogen pools and transformations were measured over an annual cycle in two forests and one pasture in tropical deciduous forest near Chamela, México. Nitrous oxide flux was moderately high (0.5–2.5 ng cm^{-2} h^{-1}) during the wet season and low (<0.3 ng cm^{-2} h^{-1}) during the dry season. Annual emissions of nitrogen as nitrous oxide were calculated to be 0.5–0.7 kg ha^{-1} y^{-1}, with no substantial difference between the forests and pasture. Wetting of dry soil caused a large but short-lived pulse of N_2O flux that accounted for $<2\%$ of annual flux. Variation in soil water through the season was the primary controlling factor for pool sizes of ammonium and nitrate, nitrogen transformations, and N_2O flux.

Key words: Tropical deciduous forest – Tropical pasture – Land clearing – Nitrogen loss – Nitrous oxide

Tropical forest soils are a significant natural source of the radiatively active gas nitrous oxide. Measured fluxes of nitrous oxide are substantially greater from most tropical than most temperate or boreal forests (Keller et al. 1986; Matson and Vitousek 1990), and these field flux estimates are supported by determinations of the latitudinal distribution of sources based on concentration profiles in the atmosphere (Cicerone 1989; Prinn et al. 1990). There is also some evidence that recent anthropogenic increases in nitrous oxide could be driven in part by land use change in the tropics (Keller et al. 1986; Luizão et al. 1989), but contradictory evidence exists (cf Goreau and de Mello 1988; Vitousek et al. 1989), and that possibility remains uncertain.

The large nitrous oxide fluxes observed in the tropics are associated with relatively high rates of nitrogen cycling in tropical forests, most of which circulate more nitrogen at higher concentrations than most temperate or boreal forests (Vitousek and Sanford 1986). Rates of net nitrogen mineralization are often higher and rates of nitrogen immobilization lower in tropical as compared to other forest soils (Vitousek and Matson 1988). However, most information on tropical nitrogen cycling has been obtained in moist to wet tropical forests; less is known about savannas (Hao et al. 1988; Johansson and Sanhueza 1988; Sanhueza et al. 1990), and there is very little information on drought-deciduous tropical forests. This dearth of information on dry tropical forests is unfortunate, because drought-deciduous forests once covered 6–10 million km^2 of the tropics, and they have been cleared and converted to other uses much more extensively than moist or wet forests (Murphy and Lugo 1986). The limited information on nitrogen cycling in such forests suggest that they are similar to moist to wet forests in circulating relatively large amounts of nitrogen at high concentrations (Raman 1975; Gessel et al. 1980; Lugo et al. 1988).

We determined nitrous oxide fluxes over an annual cycle in a drought-deciduous forest at Chamela, Jalisco, Mexico. The site is part of the remaining 2% of a 500000 km^2 dry tropical forest that once stretched along the Pacific coast from Mexico to Colombia (Janzen 1988). Ongoing watershed-level nutrient cycling studies at Chamela demonstrate that nitrogen is relatively abundant and labile there (Esteban 1986; Patiño 1990), although phosphorus is in short supply, and survey measurements of nitrous oxide during the wet season yielded moderately high flux (Vitousek et al. 1989). In this study, we determined: 1) fluxes of nitrous oxide through an annual cycle; 2) the relationships among fluxes, soil moisture, and soil nitrogen pools and transformations; and 3) the consequences of land conversion from forest to pasture.

Methods

Study sites

Flux measurements were carried out on or near the Estación de Biología "Chamela" of the Universidad Nacional Autónoma de

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Offprint requests to: G. García-Méndez

México. Chamela is at 19°30′ N, 105°03′ W in the state of Jalisco on the Pacific coast. The area receives 748 mm of precipitation annually, more than 80% of which falls in July through October (Bullock 1986). Mean annual temperature is 24.9° C. The soils are rocky, infertile entisols derived from rhyolite; the upland forests are short-statured (6–10 m) and drought-deciduous (Bullock and Solís-Magallanes 1990), dominated by small-diameter trees (Lott et al. 1987)

Three sites were sampled through an annual cycle from September 1989 to September 1990, and several others were sampled occasionally. The three regularly sampled sites included two intact forests (WS 1 and WS 4). Both were located on gentle slopes in upland positions within gaged experimental watersheds (Sarukhán and Maass 1990). A nearby site was located in a similar slope position in a 12-yr old pasture dominated by Panicum maximum; the pasture had been burned annually, grazed seasonally, and never fertilized. Less frequently sampled sites included other forests at different slope positions within the experimental watersheds, two recently-cleared fields planted to maize and two longer-term (> 15 y) sorghum fields, and a range of pasture sites including one intensively managed and fertilized lowland pasture.

Nitrous oxide flux measurements

Nitrous oxide flux from the soil surface was determined by measuring changes in concentration over time in closed chambers. The 25 cm diameter chamber system consisted of a molded acrylonitrile-butadiene-styrene plastic cap with septum and pressure relief ports, fitted to a 10-cm-high polyvinyl chloride (PVC) ring. The sharpened ring was driven approximately 2 cm into the soil, left for 10 or more min, and tightly capped with the chamber top. At each site and on each sampling date, a total of eight chambers were placed randomly along two 30 m transects. Gas samples were withdrawn through the injection port at 0, 6, 12, 20, and 30 min, sealed in nylon syringes, and returned to the laboratory at the Chamela station for analysis.

Nitrous oxide concentrations were determined using a Shimadzu Mini-2 gas chromatograph equipped with a ^{63}Ni electron capture detector at 340° C. A 95% argon/5% methane carrier gas was used; CO_2 peaks were clearly separated from N_2O, but were not quantified. Gas samples were injected through a 0.5 ml sample loop, a precolumn, and a backflush valve onto a Poropak Q separation column at 80° C. Peak areas were quantified using a Hewlett-Packard 3390 integrator; standards (513 ppb in N_2; Scott Research Laboratory, Inc., Plumsteadville, Pennsylvania) bracketed every 10 samples. Nitrous oxide fluxes were calculated by regressing N_2O concentration within each chamber against sampling time, and correcting for temperature and the ratio of chamber volume to soil surface area covered.

Soil measurements

A soil sample was collected within each of the eight chambers per site after nitrous oxide flux measurements were completed. Soil was sorted to remove roots and debris, and each sample was divided into 3 subsamples in the laboratory. One 10 g subsample was placed in 50 ml of 2 N KCl the day of collection and shaken throughly. After 18–24 h the supernatant was removed, stored under refrigeration, and returned to the Laboratorio de Análisis Químicos of the Centro de Ecología (LAQ–CE) in Mexico City for ammonium- and nitrate-nitrogen analyses using a Technicon AutoAnalyzer II (Technicon Instrument System 1973, 1977). Another 10 g subsample was placed in 150 ml plastic cups, incubated at 20° C in the dark for 7 days, and then extracted in 2 N KCl to determine potential net nitrogen mineralization. Finally, a 50–100 g subsample was dried for 3 d at 70° C to determine soil water content.

Potential net nitrogen mineralization was calculated as final ammonium- plus nitrate-nitrogen (at the end of incubation) minus the sum of initial ammonium- and nitrate-nitrogen. Potential nitrate production was calculated as the final nitrate-nitrogen concentration (after incubations) minus the initial value.

Soil wetting

In May 1990, the effect of wetting soils near the end of the long dry season was evaluated experimentally in two of the repeatedly sampled sites (WS 1 and pasture) and another forest site. A liter of water was added to each of 4 rings in each site, simulating a 2 cm rain, and N_2O fluxes were measured at approximately 0.6, 2, 4, 6, 8, and 24 h post-wetting. Similar measurements were made during the wet season in September 1990.

Results

The annual variation in soil moisture and nitrogen pools and transformations is summarized in Table 1. Ammonium and nitrate concentrations were lowest in the middle and late wet season, and increased slowly through the dry season. The June samples were collected several days after the first rains of 1990; by then, soil ammonium concentrations had declined relative to those in the dry season. Wetting experiments late in the dry season yielded a similar response in less than 24 h following wetting. Results for net nitrogen mineralization and nitrification were more variable, especially during the dry season, but there was a trend towards elevated rates of net nitrogen mineralization and especially nitrification during the wet season.

Nitrous oxide fluxes also varied seasonally, with very low and even negative fluxes during the dry season and variable but substantial fluxes in the wet season (Fig. 1). Artificial wetting of soil late in the dry season increased N_2O fluxes rapidly and substantially, with the greatest flux occurring 2–6 h after wetting (Fig. 2). Very similar results were observed in the dry season of 1989 in a single set of measurements in WS 1 (Vitousek et al. 1989).

Nitrous oxide fluxes were significantly positively correlated with soil moisture across the annual cycle. The pattern of this relationship (Fig. 3) suggests a threshold near 11% soil moisture below which N_2O flux is negligible. Also, variation among chambers in N_2O flux was positively correlated with variation in soil moisture early in the wet season (Fig. 4). Most of the chambers exceeded 11% soil moisture at that time, and there was a suggestion of an additional threshold near 15% moisture content above which fluxes were elevated substantially. At that same time, variation in soil nitrate concentrations among chambers also was correlated with both soil moisture and N_2O, but no other monotonic relationships between N_2O flux and soil nitrate or any other soil nitrogen pools or transformations were observed.

There was no difference in N_2O fluxes among the 3 repeatedly-sampled site through the annual cycle (Fig. 1). For the less-frequently-sampled sites, N_2O fluxes were relatively low during the dry season in all sites. During the wet season, the 2 maize fields and the intensively-managed lowland pasture had greater N_2O fluxes than any of the other sites, but fluxes from a number of other

Table 1. Available nitrogen pools and transformations and soil water content through an annual cycle in forest and pasture sites near Chamela, Jalisco, Mexico. All values for nitrogen in µg/g, with standard errors in parentheses; % water on a wet-soil basis. TMin is net nitrogen mineralization potential, Nitr is potential net nitrate production during laboratory incubation, and "–" represents sample sets that were not collected or were lost in transport or analysis

	NO_3^--N	NH_4^+-N	TMin	Nitr	Moisture%
Pasture					
Sept '89[a]	2.48	4.53	4.62	5.48	15.8
Nov	1.58(±0.27)	9.02(±1.17)	16.94(±0.95)	0.54(±0.11)	7.45(±0.25)
Dec	3.59(±0.78)	14.39(±1.82)	24.37(±2.34)	2.55(±0.55)	9.8 (±1.07)
Jan '90	4.07(±1.07)	13.52(±1.59)	14.01(±1.03)	0.38(±0.17)	4.94(±0.25)
March	–	–	–	–	6.25(±0.70)
May	8.61(±2.04)	12.20(±2.37)	1.29(±3.71)	0.78(±1.19)	4.12(±0.12)
June	24.92(±8.62)	5.64(±1.93)	13.09(±5.13)	8.64(±1.83)	14.98(±0.48)
Sept	4.9 (±0.43)	3.10(±0.31)	–	12.66(±2.04)	10.08(±0.55)
Watershed 1					
Sept '89[a]	4.53	5.79	2.36	4.84	10.8
Nov	9.86(±0.64)	10.85(±1.43)	12.85(±0.75)	− 0.45(±0.43)	5.33(±0.85)
Dec	3.99(±0.31)	6.13(±0.63)	21.44(±2.03)	2.8 (±0.63)	7.04(±0.23)
Jan '90	10.59(±1.29)	20.6 (±2.11)	2.76(±1.25)	− 0.70(±0.48)	4.45(±0.35)
March	–	–	–	–	5.21(±0.84)
May	15.25(±1.77)	22.75(±1.96)	2.98(±5.25)	0.10(±1.34)	2.02(±0.09)
June	14.63(±2.19)	12.74(±1.63)	20.55(±7.26)	7.42(±2.03)	13.27(±0.63)
Sept	4.57(±0.40)	3.15(±0.53)	23.54(±2.61)	10.77(±2.94)	9.82(±0.34)
Watershed 4					
Sept '89[a]	3.85	7.29	–	–	13.5
Nov	6.41(±0.85)	5.48(±1.11)	13.88(±1.20)	− 0.96(±0.26)	5.57(±0.49)
Dec	5.30(±1.33)	12.30(±2.21)	15.58(±1.32)	3.06(±0.51)	10.08(±0.53)
Jan '90	6.90(±0.41)	16.15(±2.11)	5.94(±0.65)	− 0.45(±0.10)	2.98(±0.18)
March	–	–	–	–	3.26(±0.20)
May	10.21(±0.85)	22.48(±1.94)	− 2.07(±3.0)	0.77(±0.8)	2.09(±0.22)
June	10.82(±1.81)	15.70(±2.28)	21.32(±2.77)	22.38(±3.64)	13.22(±0.31)
Sept	4.78(±0.72)	3.26(±2.29)	28.86(±7.12)	16.76(±3.92)	7.93(±0.48)

[a] Original data lost in transit; standard errors cannot be calculated

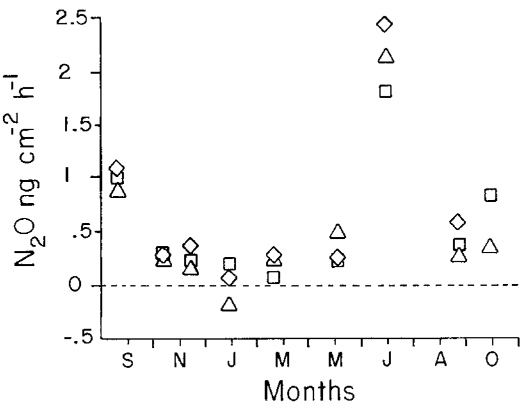

Fig. 1. Annual variation during 1989–90 in N_2O-N flux from 3 seasonally-dry sites near Chamela, Mexico. The symbols are: □ – intact drought-deciduous forest on watershed 1 (WS 1); ◇ – intact drought-deciduous forest on watershed 4 (WS 4); △ – 12 yr old pasture

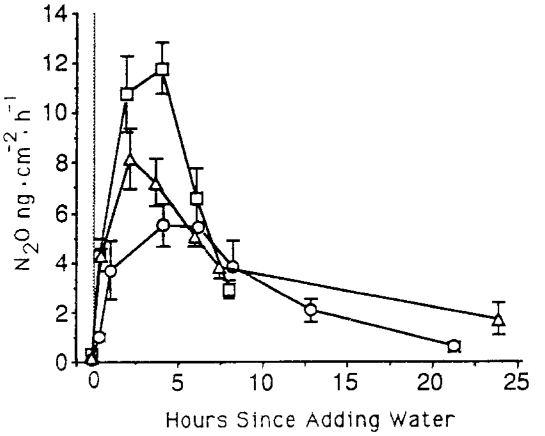

Fig. 2. The effect of a simulated 2 cm rain on N_2O-N fluxes at the end of the dry season in seasonally dry sites near Chamela, Mexico. The symbols are: □ – WS 1 forest; △ – 12 yr old pasture; ○ – an intact drought-deciduous forest on the Verdin trail near Chamela Biological Station

pastures and from the sorghum fields were relatively low (Vitousek et al. 1989; Table 2). N_2O flux from the intensively-managed pasture decreased substantially from the wet season of 1989 to the wet season of 1990, coincident with disking of that site.

Discussion

Flux measurements were carried out 9 times in a little more than 1 year in the 3 repeatedly sampled sites. This is rather sparse, but it still represents a more extensive (temporally) set of measurements than any published set from the moist or wet tropics, excepting Luizão et al. (1989). We estimated the annual flux of N_2O by averaging results across the wet (4 times) and the dry (5 times) seasons, and multiplying the result by the length of each season. We assumed an average 168-day wet season (June 15–November 30) and a 196-day dry season. The significance of the very high fluxes caused by the first wet-season rain was estimated by calculating the area under the curves in Fig. 2 (based on the midpoint of each increment of time between samples), and assuming that such fluxes occur only one day each year. The results of wet-season watering experiments and a single test of repeated watering late in the dry season suggest that this is a reasonable assumption; the elevated fluxes only occur at the end of a long antecedent dry period.

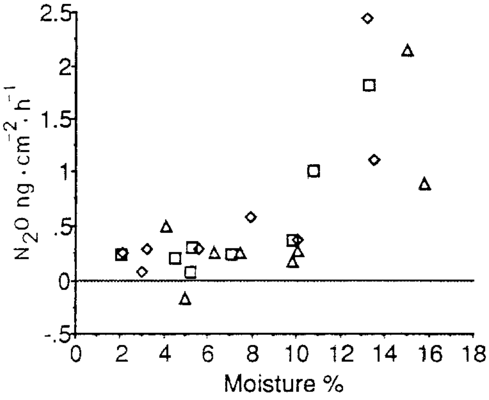

Fig. 3. The relationship between mean soil moisture in a site and mean N_2O flux from that site for 3 sites through an annual cycle at Chamela. $r^2 = 0.54, p < 0.01$. Symbols are: □ – WS 1 forest; ◇ – WS 4 forest; △ – 12 yr old pasture

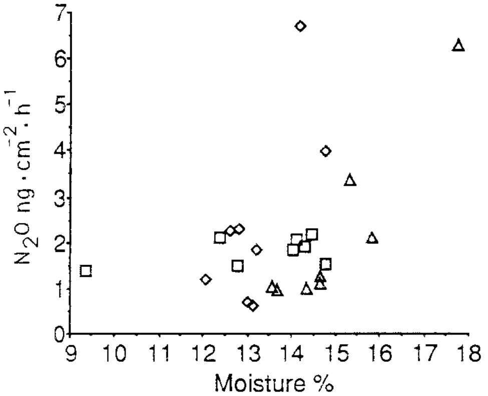

Fig. 4. The relationship between soil moisture content within a chamber and N_2O flux from that chamber for 3 sites early in the wet season at Chamela. $r^2 = 0.23$, $P < 0.05$. Symbols are: □ – WS 1 forest; ◇ – WS 4 forest; △ – 12 yr old pasture

Results of these calculations are summarized in Table 3. The spectacular increase in flux upon wetting dry soils (Fig. 2) is so short-lived as to be insignificant (< 2%) in the annual emission of N_2O from these sites. In contrast, the effect of such wetting on NO flux in these sites is much more substantial (Davidson et al. in press).

By the calculations in Table 3, annual emissions of N_2O from the Chamela sites are low in comparison with most moist to wet tropical forests (Matson and Vitousek 1990); although they are greater than those from most temperate forests. In part, these emissions reflect very low flux during the extended dry season (Fig. 1), but flux during the wet season also is lower than that in the majority of moist to wet tropical forests examined to date. However, variation in flux among moist to wet tropical forests is highly correlated with overall soil fertility (Matson and Vitousek 1987), and the soils at Chamela are infertile. Sanhueza et al (1990) reported substantially higher wet season N_2O fluxes in a short-term study of a semideciduous forest island in Venezuelan savanna, supporting the possibility that N_2O fluxes at Chamela may be low relative to most tropical deciduous forests. If rates at Chamela are typical, tropical dry forests could emit 0.5–0.7 Tg of N_2O–N annually (assuming an annual flux of 0.5–0.7 kg N ha^{-1} y^{-1} and 10 million km^{-2} areal extent); if wet-season fluxes are more often similar to those in fertile moist to wet forest soils, dry tropical forests could emit as much as 1.5 Tg. These compare to 2.4 Tg y^{-1} from intact moist to wet tropical forest (Mat-

Table 3. Calculated seasonal and annual flux of N_2O from the repeatedly-sampled sites at Chamela. All values in mg m^{-2} y^{-1}. No experimental wet-up was carried out in WS 4; we used the result from WS 1

Site	Wet Season	Dry Season	Wet-up	Total
WS 1	40.3	9.9	0.9	51.1
WS 4	55.6	11.8	0.9	68.3
Pasture	36.7	9.9	0.8	47.4

Table 2. Nitrous oxide flux (ng cm^{-2} h^{-1}) from occasionally-sampled sites near Chamela, Mexico. Several additional sites which were sampled only in September 1989 are reported in Vitousek et al (1989). Means (± standard errors) based on 8 chambers/site unless otherwise noted

Site	September 1989 wet		May 1990 dry		Oct 1990 wet	
Upland forest-Verdin	0.46	(0.06)(N = 24)	0.17	(0.08)	0.73	(0.18)
Arroyo forest			0.30	(0.05)	1.54	(0.46)
Improved pasture	9.95	(1.73)(N = 20)	0.54	(0.09)	1.05	(0.06)[a]
Maize	2.90	(0.50)	0.85	(0.17)		
Sorghum					0.39	(0.10)(N = 14)

[a] This site was disked prior to sampling in the wet season of 1990. When we compacted the soil in small plots, there was a nearly 40-fold increase in flux

son and Vitousek 1990) and 1.4 Tg y^{-1} from tropical savanna (Sanhueza et al. 1990).

A comparison of fluxes between intact forests and human-altered sites suggests that there is no regionally-important effect of land transformation on N_2O fluxes. The repeatedly sampled pasture did not differ from either of the repeatedly-sampled forests, and all of the occasionally-sampled upland pastures had similar fluxes. These pastures represent the most extensive human land use in the area (de Ita-Martinez 1983). Maize fields that recently had been cleared from forest and burned (<1 yr) did have significantly elevated N_2O fluxes, but in this area maize is a short-term land use and accounts for little land area at any one time. Two sorghum fields that had been cultivated for a much longer period had low fluxes. An intensively managed and fertilized pasture – the only one of the sites to have been fertilized – was the only site to have very high N_2O flux (Table 3). Such pastures are uncommon in the Chamela region, and so is land that could support them. If they are more common elsewhere, they could represent a regionally significant source of N_2O. Overall, these results demonstrate that the elevated N_2O fluxes from tropical pasture observed by Luizão et al. (1989) are not generalizable to all tropical pastures. We suggest that the potential global magnitude of increased N_2O flux that they estimated (~ 0.7 Tg y^{-1}) should therefore be considered an upper bound.

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