

Nitrogen Oxide Fluxes and Nitrogen Cycling during Postagricultural Succession and Forest Fertilization in the Humid Tropics

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ABSTRACT

The effects of changes in tropical land use on soil emissions of nitrous oxide (N₂O) and nitric oxide (NO) are not well understood. We examined emissions of N₂O and NO and their relationships to land use and forest composition, litterfall, soil nitrogen (N) pools and turnover, soil moisture, and patterns of carbon (C) cycling in a lower montane, subtropical wet region of Puerto Rico. Fluxes of N₂O and NO were measured monthly for over 1 year in old (more than 60 years old) pastures, early- and mid-successional forests previously in pasture, and late-successional forests not known to have been in pasture within the tabonuco (*Dacryodes excelsa*) forest zone. Additional, though less frequent, measures were also made in an experimentally fertilized tabonuco forest. N₂O fluxes exceeded NO fluxes at all sites, reflecting the consistently wet environment. The fertilized forest had the highest N oxide emissions (22.0 kg N · ha⁻¹ · y⁻¹). Among the unfertilized sites, the expected pattern of increasing emissions with stand age did not occur in all cases. The mid-successional forest most dominated by leguminous trees had the highest emissions (9.0 kg N · ha⁻¹ · y⁻¹), whereas the mid-successional forest

lacking legumes had the lowest emissions (0.09 kg N · ha⁻¹ · y⁻¹). N oxide fluxes from late-successional forests were higher than fluxes from pastures. Annual N oxide fluxes correlated positively to leaf litter N, net nitrification, potential nitrification, soil nitrate, and net N mineralization and negatively to leaf litter C:N ratio. Soil ammonium was not related to N oxide emissions. Forests with lower fluxes of N oxides had higher rates of C mineralization than sites with higher N oxide emissions. We conclude that (a) N oxide fluxes were substantial where the availability of inorganic N exceeded the requirements of competing biota; (b) species composition resulting from historical land use or varying successional dynamics played an important role in determining N availability; and (c) the established ecosystem models that predict N oxide loss from positive relationships with soil ammonium may need to be modified.

Key words: nitrous oxide; nitric oxide; soil N availability; litterfall C:N ratio; tropical forests; net nitrogen mineralization; legumes; secondary succession; land-use change; forest fertilization.

INTRODUCTION

Tropical regions often exhibit high soil emissions of the greenhouse gas nitrous oxide (N₂O) and the

tropospheric-ozone precursor nitric oxide (NO) (Davidson and Kinglerlee 1997; Matson and Vitousek 1990). Although atmospheric N₂O concentrations have been increasing in recent decades, the estimates of the terrestrial sources for N₂O have large uncertainties (Bouwman and others 1995). Fluxes of N₂O and NO from the tropics vary according to land use, land-use history, and soil fertility (Davidson 1991; Firestone and Davidson 1989;

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Keller and others 1993; Keller and Reiners 1994; Luizão and others 1989; Matson and Vitousek 1987; Riley and Vitousek 1995; Verchot and others 1999). Notably high fluxes of N_2O , NO, or both gases have been found in both newly deforested areas (Luizão and others 1989; Keller and others 1993) and fertilized agricultural fields (Matson and others 1996; Veldkamp and Keller 1997), whereas relatively low fluxes have been found in both old pastures (Keller and others 1993; Verchot and others 1999; Veldkamp and others 1999) and successional forests (Keller and Reiners 1994; Verchot and others 1999).

Low N oxide fluxes are presumably due to reduced rates of N cycling and lower N availability. Net N mineralization and net nitrification are often reduced in old tropical pastures relative to forests (Neill and others 1997b; Reiners and others 1994; Rhoades and Coleman 1999), and rates of soil N transformations may recover gradually in successional forests (Rhoades and Coleman 1999; Reiners and others 1994; Verchot and others 1999). Robertson and Tiedje (1988) have suggested that global denitrification losses of N_2O and N_2 from humid tropical regions might currently be lower than those occurring in precolonial times, when fewer sites were in mid-successional growth phases. Nearly one-third of original tropical closed forest is now in secondary forest (Brown and Lugo 1990a). Given that successional forest cover is expected to increase as additional old growth forest is temporarily converted to agriculture, more studies are needed in successional forests to confirm the generality of the Robertson and Tiedje (1988) prediction.

Rates of soil N transformations are high in many tropical ecosystems relative to higher latitude ecosystems (Vitousek 1984; Vitousek and Sanford 1986; Vitousek and Matson 1988; Neill and others 1997b; Reiners and others 1994). This may be partially due to the common presence of leguminous trees in many tropical forests (Brown and Lugo 1990b; Vitousek 1984). Legumes and other N-fixing plant species often have high litter N contents, which, in turn, affect rates of N cycling (Binkley and others 1992; García-Montiel and Binkley 1998; Vitousek 1982; Vitousek and others 1987; Wedin and Tilman 1990). Despite this general understanding, the relationships among successional dynamics, plant species composition, soil N cycling, and N oxide gas emissions have seldom been studied. Previous land use may influence current forest species composition (Brown and Lugo 1990a; García-Montiel and Scatena 1994), with effects on soil proper-

ties potentially lasting for decades (Compton and others 1998; Compton and Boone 2000).

Our research focused on the specific relationships among forest age and composition, litter quality (C:N ratio), soil N pools and transformations, carbon mineralization, and N oxide emissions in a humid tropical setting. We also examined similar relationships under experimental forest fertilization. We measured monthly fluxes of N_2O and NO and soil N cycling for 1 year in duplicated chronosequences of pasture-forest succession and less frequently in an experimentally fertilized successional forest in northeastern Puerto Rico. We expected that soil N availability and N oxide fluxes would be low in old pastures, that they would increase with succession and possibly be related to species composition, and that they would be high in fertilized vs unfertilized forest. Finally, we expected that fluxes of N_2O , the more reduced N oxide gas, would exceed those of NO in the wet subtropical region of northeast Puerto Rico.

METHODS

Study Areas

Over the last 60 years, land use in Puerto Rico has changed from predominantly agricultural to urban and industrial uses. This shift has decreased the land area in agriculture and pasture and increased the area in forest (Thomlinson and others 1996). In the mid-1980s, forests covered almost 40% of the island, an increase from a low of less than 10% in the 1930s (Birdsey and Weaver 1987). The increase in mid-successional forest cover on Puerto Rico presents an opportunity to examine the effects of agricultural (including pasture) abandonment and forest recovery on N oxide gas fluxes and rates of N cycling.

The research was conducted in three areas—Mameyes, Sabana, and El Verde—located within or near the Luquillo Experimental Forest (LEF) in northeastern Puerto Rico (18°18'N, 65°50'W) (Figure 1). Native vegetation is subtropical wet forest. All areas lie within the tabonuco zone dominated by *Dacryodes excelsa* Vahl. (tabonuco, Burceraceae) and are characterized by steep mountainous terrain. Two of the areas, Mameyes and Sabana, contain pasture-abandonment chronosequences. The third area, El Verde, contains an experimentally fertilized late-successional forest.

Average monthly temperatures at the LEF are high and vary little, ranging from 23.5 to 27.0°C (Brown and others 1983). The sites at Mameyes and Sabana range between 125 and 200 m above

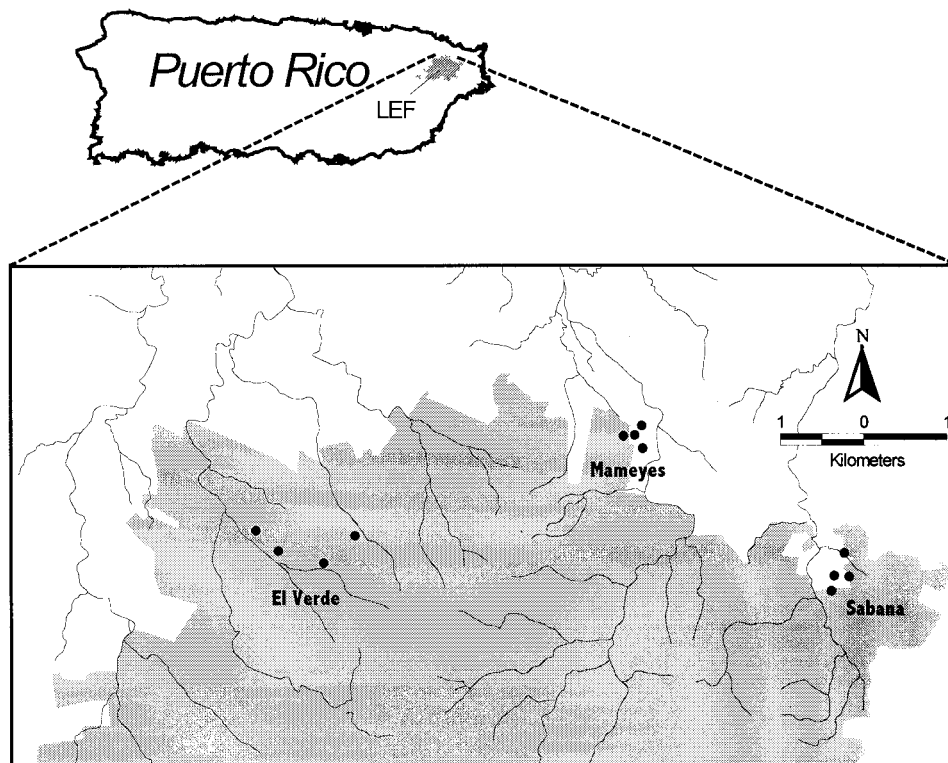


Figure 1. Location of the three study areas—Mameyes, Sabana, and El Verde—and the Luquillo Experimental Forest in northeastern Puerto Rico. At Mameyes and Sabana, points represent pasture, early-, mid-, and late-successional forest. At El Verde, points represent experimental blocks, each containing a fertilized and an unfertilized plot.

sea level, whereas the sites at El Verde are around 350 m. Annual precipitation is approximately 2900 mm for Sabana, 3200 mm for the Mameyes sites (Scatena 1989), and 3500 mm for El Verde (García-Martínó and others 1996). The season is slightly drier from December to April, with a mean monthly precipitation that is two-thirds the amount seen from May to November.

The soils at Mameyes and Sabana are clayey (Tropohumults), formed from fine-textured residuum from weathered volcanic rock, and have moderate shrink-swell potential (Bocceciamp 1977). The soils at El Verde are fine kaolinitic Oxisols (Kandiudox), part of the Zarzal-Cristal complex (Soil Survey Staff 1995).

In each chronosequence, we selected an “old” pasture (more than 60 years old), an early-successional forest (around 10 years old), a mid-successional forest (25–45 years old), and a late-successional forest (more than 60 years old). Land-use histories were determined primarily by aerial photography. The late-successional forests were under forest cover in 1936, the date of the earliest photographs, and every year thereafter for which photographs were available (1951, 1964, 1971, 1977, 1983, 1991, and 1993). Active pastures had been in pasture since 1936 and at the time of our study, were intensively grazed and dominated by grasses

(for example, *Axonopus compressus*) and herbs (for example, *Commelina* sp.) (Aide and others 1995). The early-successional forests had been abandoned for about 10 years and were dominated by tall shrubs, primarily of the genus *Miconia* (Melastomataceae). Occasional trees were present, suggesting that the sites had not been cleared entirely in the recent past. The mid-successional forest at Sabana had been in pasture up to 1971 and was forested by 1977. Land-use history for the mid-successional forest at Mameyes, where the photo record never indicated complete deforestation, is less certain. In 1951, the area had a sparse canopy, indicating that some clearing had been done. Buried barbed wire at the site also suggested previous human activity, possibly pasture use. Based on current tree species composition, the site was probably used for growing coffee (Zimmerman and others 1995a; D. García-Montiel personal communication), a common practice in the area during the early 20th century. We lost access to the early-successional forest at Mameyes midway through the study when it was cleared by the owners.

At El Verde, experimental manipulations altering nutrient inputs to 20 m × 20 m forest plots were begun in 1989 (Zimmerman and others 1995b; Walker and others 1996). During that same year, a hurricane damaged the forest at El Verde. By 1994,

litterfall had returned to prehurricane levels (J. Zimmerman personal communication). We worked at four experimental blocks, each containing two plots, one fertilized and one a control. The fertilized plots have had ammonium nitrate and urea added at a rate of $300 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$ in four applications per year (Zimmerman and others 1995b; Walker and others 1996).

N Oxide Sampling

We sampled N oxide gases using chamber techniques, generally following the methods of Keller and Reiners (1994) and Veldkamp and Keller (1997). Eight chamber bases, consisting of thin-walled PVC pipe (25 cm diameter $\times$ 12 cm height), were inserted into the soil at the chronosequence sites. We permanently located bases in the forests, but to avoid damage by cattle and minimize new soil disturbance we reinserted bases at the same place each time in the pastures. The eight points were randomly located within four slope positions (strata), covering a maximum area of $30 \text{ m} \times 15 \text{ m}$. At El Verde, four permanent sampling locations were randomly located along a diagonal across each plot.

For sampling N_2O , all chamber bases were covered with vented (compare Hutchinson and Mosier 1981) removable acrylonitrile-butadiene-styrene caps. Air samples were removed with 20 mL nylon syringes immediately and at 10, 20, and 30 min after chamber closure and analyzed for N_2O using electron capture detection (ECD) gas chromatography (Schimadzu GC-14A) within 24 h. Fluxes were calculated from the linear regression of concentration vs time using the four data points from each chamber (Keller and Reiners 1994).

NO was measured using a portable Scintrex LMA-3 NO_2 detector, as described by Keller and Reiners (1984). We added 1 ppm NO at a rate of approximately 3 mL min^{-1} to the sample stream to raise the concentrations of NO_2 (NO is converted to NO_2) to within the linear range of the detector. We calibrated the detector before and after sampling at each site by using a larger standard addition. NO flux was calculated from at least a 3-min linear increase in concentration, obtained within the first 8 min of sampling. On a given date, from four to six chambers were sampled at a site.

At Mameyes and Sabana, N_2O measurements began in February 1995; NO measurements began in March 1995 and continued monthly through February 1996 (except December 1995). N_2O measurements at El Verde began in March 1995 and were continued in May 1995, June 1995, November 1995, April 1996, and June 1996; NO was mea-

sured at El Verde in April and June of 1996. At El Verde, we always sampled at least 1 month after the quarterly fertilizer application.

Air temperature, soil temperature (to a depth of 2 cm), and soil moisture (to a depth of 10 cm, measured gravimetrically) were sampled within 1 m of the chambers simultaneously with gas sampling.

Inorganic N, Net N Mineralization, Net Nitrification, and Nitrification Potential

Soils were sampled four times (May 1995, August 1995, November 1995, and February 1996) from Sabana and Mameyes and once (April 1996) from El Verde to determine inorganic N pool sizes and dynamics of soil N turnover. We collected a single replicate core (8 cm $\times$ 10 cm deep) from within 1 m of each chamber base, yielding eight cores for each of the chronosequence sites and four cores for each El Verde plot with each sampling. Soils were refrigerated until processing, which was done within 1 week. A pilot study had shown that soil storage of up to 7 days had no effect on either inorganic N concentrations or transformation rates (H. Erickson unpublished) ($P < 0.05$, paired t -test). Each sample was homogenized by hand; after removing the roots and other plant parts, we subsampled for inorganic N, net N mineralization, and nitrification potentials.

Inorganic N (NH_4^+ plus NO_3^-) pool sizes were measured by extracting approximately 15 g moist soil in 100 mL 2M KCl. Net N mineralization and net nitrification were measured during 7-day aerobic laboratory incubations (Hart and others 1994b). Filtered extracts were analyzed colorimetrically on an Alpkem Rapid Flow Analyzer. Because NO_3^- was converted to NO_2^- during analysis, all reported NO_3^- values also include NO_2^- .

We used a shaken soil-slurry method (Hart and others 1994b) to assess nitrification potentials. In brief, soils were shaken for 24 h in a solution containing excess NH_4^+ (1.5 mM), with subsamples removed at 2, 4, 18 (or 20), and 24 h and analyzed for NO_3^- . Nitrification potential was calculated as the slope in the linear regression of NO_3^- concentration over 24 h (average Pearson $r = 0.98$). NH_4^+ concentrations were measured on a subset of samples to ensure that NH_4^+ did not become limiting.

Soil CO_2 Production

To test the effect of postagricultural succession on soil CO_2 production (microbial respiration) (compare Hart and others 1994a), we measured CO_2 fluxes on incubating soil samples from two dates for the Mameyes and Sabana sites. Polyethylene bottles

containing soils were placed into 957-mL glass Mason jars with rubber septa inserted into lids. After 3 and 6 days, a 20 mL sample of headspace gas was collected. We chose day 3 to avoid possibly high and variable pulses of CO₂ associated with initial disturbance. To maintain atmospheric pressure, the removed air was replaced with an equal volume of air taken from the outdoors (where CO₂ concentrations were generally 20 times lower than in the samples). CO₂ concentrations were measured using ECD gas chromatography and never exceeded 1.5%. Production was calculated as the change in CO₂ concentration between days 3 and 6. From each site, we used five and eight soil samples from August 1995 and February 1996, respectively; we report the means from the two dates.

Additional Soil Methods

Total C and N were measured on the May 1995 and November 1995 soil samples from Mameyes and Sabana and on the April 1996 samples from El Verde. A 0.2-g air-dried subsample was ground to pass through a 20 mesh (0.85 mm) screen and analyzed by combustion with a LECO CNS-2000 analyzer. Results for total C and N and all other chemical parameters are reported on an oven dry mass basis.

Soil pH was measured once using moist soils (August 1995 at Mameyes and Sabana and April 1996 at El Verde). Soils were mixed with deionized water to a 1:1 ratio, and pH was measured within 5 min.

We measured soil bulk density to 10 cm at Mameyes and Sabana by excavating soil from rectangular holes (approximately 10 cm × 10 cm) for drying and weighing. Hole volumes were measured either with a ruler or by filling with water in a plastic-lined hole. Water-filled pore space (WFPS) was calculated as the proportion of gravimetrically determined water volume to total pore volume (Hillel 1980). The values of WFPS over 100% may have been caused by inadvertently sampling ponded water in microsites or by ignoring possible temporal variation in bulk density with our single estimate.

Estimates of Pasture Production, Aboveground Leaf Litterfall Mass, and N Quality

We assessed annual aboveground (AG) net primary production in the pastures from 13 April 1995 until 15 April 1996 using a modification of a moveable enclosure harvest technique (McNaughton and others 1996). Four 0.25 m × 1 m (compare Long and others 1989) sampling areas were clipped of AG

biomass, covered with a cage, then reclipped after 30 days. Sampling areas were newly located each period. Aboveground net production was calculated as the sum of the mean regrowth per sampling date, corrected for length of the growing period.

We collected litterfall at the six forested sites in the chronosequences from 3 April 1995 to 2 April 1996. Nine litterfall traps (0.25 m²) were equally spaced in either a 50 m × 50 m or a 40 m × 40 m grid in the mid- and late- or early-successional forests, respectively. Litter was collected every 2 weeks, dried at 65°C, sorted by class (leaves and other groupings), and weighed. To measure mass of leaf litterfall N and C:N ratio, leaf litter samples were composited monthly, yielding 13 time samples per site. Subsamples were ground to pass a 20 mesh sieve and analyzed for total C and N with a LECO CNS-2000.

Litterfall from the El Verde plots had been collected approximately every 2 weeks (compare Zimmerman and others 1995b). Leaf litter samples from 8 September 1994 to 29 August 1995 were composited monthly by block and treatment for chemical analyses.

Overstory Vegetation

We used a nested circular plot technique to sample vegetation at the forested sites at Mameyes and Sabana. Diameter at breast height (dbh) and species identification were recorded for all trees greater than 1 cm dbh within a 500-m² circular plot encompassing our gas sampling chambers. Within a concentric 1000-m² circular plot, all trees larger than 10 cm dbh were recorded. Plant nomenclature follows Liogier (1985).

Statistical Analyses

Mean N oxide fluxes for a site were calculated from means over time from each chamber and used to estimate annual fluxes. Therefore, within-site variance is spatially, rather than temporally, derived. NO means were based on estimated annual fluxes from any chamber that was sampled on at least three occasions; most chambers included in the analysis were sampled nine or more times. An estimate of annual leaf litterfall was computed from the nine baskets at each site. At El Verde, annual N oxide fluxes and leaf litterfall were calculated for each plot, yielding four annual estimates per treatment. We recognize that because NO fluxes were only measured twice at El Verde, these annual estimates are highly uncertain. We nonetheless make the calculations to facilitate intersite comparisons. Flux, soil, and litterfall data were log-transformed if necessary to homogenize variances.

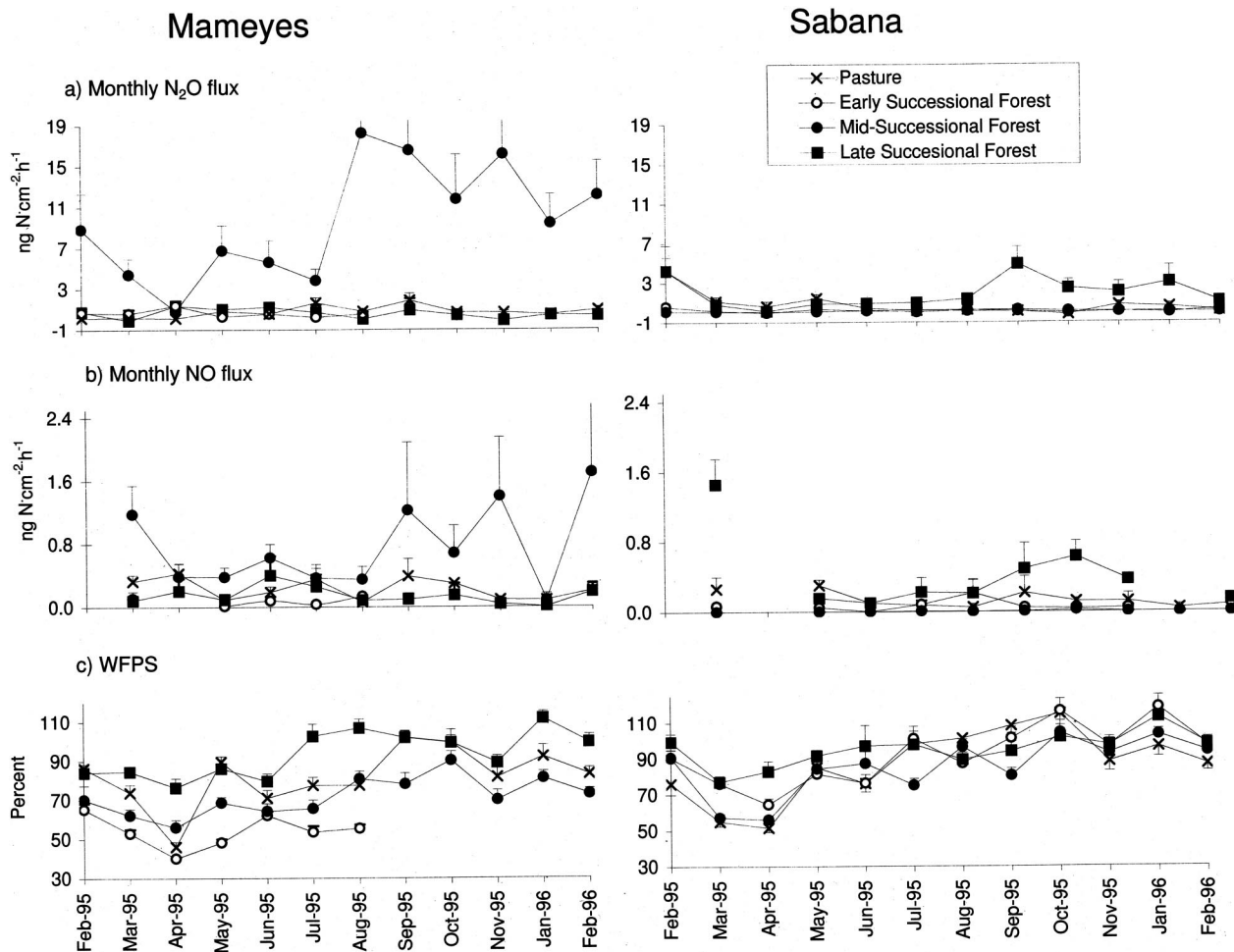


Figure 2. Monthly N_2O (a) and NO (b) fluxes and water-filled pore space (WFPS) (c) for the two pasture abandonment sequences, Mameyes and Sabana. Values are means plus standard error; $n = 8$ for N_2O and WFPS, and $n = 4\text{--}6$ for NO .

We analyzed data from the chronosequences using a one-way ANOVA followed by a Tukey multiple comparisons test. A two-way ANOVA was used to examine the effect of date and site on selected parameters; PROC GLM (SAS) was used to handle the unbalanced design due to missing dates from the Mameyes early-successional forest and to handle the unequal sample sizes with NO measurements. At El Verde, effects of fertilizer addition on N oxide fluxes, litter, and soil characteristics were assessed with ANOVA using a randomized complete block design.

We examined several relationships, including those between N oxide fluxes and indices of N cycling, among indices of soil N transformations, between N and C mineralization and leaf litter $\text{C}:\text{N}$ ratio, and between N_2O flux and soil moisture by using correlation analysis and model fitting. When relationships appeared curvilinear, exponential models were fit to the data, and R^2 values were

used to compare linear vs exponential models. All statistical analyses were conducted using PC SAS (SAS 1987).

RESULTS

Temporal Patterns of N Oxide Emissions, Soil Moisture, and Indices of Soil N Cycling

Monthly emissions of N_2O and NO (Figure 2a and b) from the unfertilized sites were consistently low (less than 2.0 and less than $0.4 \text{ ng N} \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$, respectively). The mid-successional forest at Mameyes was the exception, with N_2O fluxes ranging from 1 to $18 \text{ ng N} \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ (Figure 2a). Monthly emissions of N_2O and NO from the unfertilized El Verde forest also were very low (Figure 3) in contrast to the fertilized plots, where N_2O ranged from 14 to $36 \text{ ng N} \cdot \text{cm}^{-2} \cdot \text{h}^{-1}$ (Figure 3).

Water-filled pore space (WFPS) ranged from a

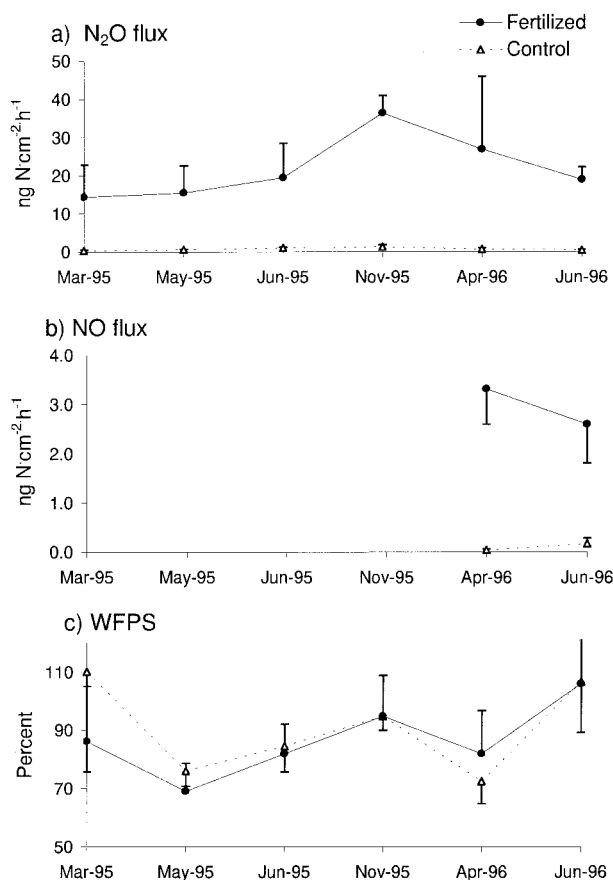


Figure 3. Monthly N₂O (a) and NO (b) fluxes and water-filled pore space (WFPS) (c) for a fertilized and a nonfertilized tabonuco forest at El Verde, Puerto Rico. Values are means plus standard error; $n = 4$ for each variable/treatment combination.

low of 40% to over 100% and was greater than 70% most of the time (Figures 2c and 3c). Although monthly changes in WFPS were noted, the effect on N oxide flux was minimal. WFPS significantly explained variation in N₂O flux only at the sites with the highest fluxes—the mid-successional forest at Mameyes and the fertilized forest ($P < 0.05$), (Figure 4).

Variation in NO₃⁻ and NH₄⁺ pools, net N mineralization, net nitrification, and potential nitrification were greater among sites than among the four sampling dates. Relative rankings of the sites for each of the parameters changed little from date to date, and in most cases the effect of date was not significant ($P > 0.05$). For example, there was a significant effect of site ($F_{7,210} = 16.27$, $P < 0.001$) but not date ($F_{3,210} = 2.27$, $P = 0.081$) on net nitrification. In this study, these indexes of soil N cycling exhibited a high temporal stability.

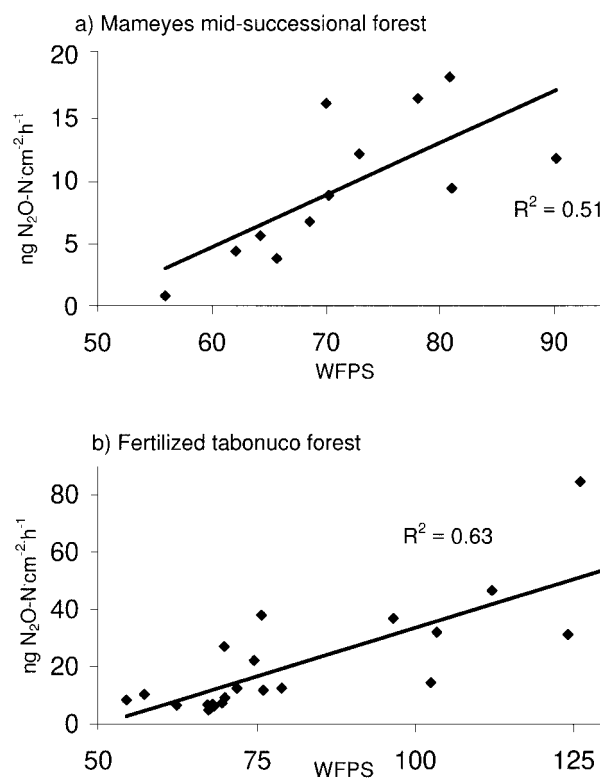


Figure 4. N₂O flux vs WFPS for the two sites with the highest annual N₂O emissions—(a) Mameyes mid-successional forest and (b) El Verde fertilized forest. For b, one data point with an unexplainably high %WFPS value was left out of the regression.

N Oxides, Soil Properties, and Land Use: Mameyes and Sabana

N oxide fluxes varied significantly among the sites; but contrary to our expectations, successional stage did not have consistent effects within the Sabana and Mameyes sequences (Table 1). The Mameyes mid-successional forest had the highest annual emissions of N₂O and NO, whereas the Sabana mid-successional forest had the lowest emissions. Active pastures and early-successional forest sites had low to moderately low annual N oxide fluxes. The late-successional forest at Sabana ranked second for N oxide emissions, but the late-successional forest at Mameyes had low emissions similar to the pastures.

Some soil properties varied according to successional stage (Table 2). Soil temperatures were higher in pastures than all other sites, and soil pH was lowest in pastures and increased with forest age. However, bulk density varied little with land use. As was the case for N oxide fluxes, the N availability indexes were not consistently related to successional stage. Soil NO₃⁻ pools were lowest in the pastures relative to other sites in each area,

Table 1. Average N_2O and NO Emissions for Sites at Mameyes and Sabana and El Verde, Puerto Rico

	Mameyes				Sabana				El Verde Forest	
	Active Pasture	Early-successional Forest	Mid-successional Forest	Late-successional Forest	Active Pasture	Early-successional Forest	Mid-successional Forest	Late-successional Forest	Control	Fertilized
N ₂ O (ng N · cm ⁻² · h ⁻¹)	0.58 ^c (0.21, 8)	0.59 ^{bc} (0.18, 8)	9.53 ^a (2.23, 8)	0.73 ^{bc} (0.23, 8)	0.79 ^{bc} (0.29, 8)	0.18 ^c (0.07, 8)	0.09 ^c (0.04, 8)	1.90 ^b (0.30, 8)	0.78 ^{**} (0.12, 4)	21.94 (7.9, 4)
NO (ng N · cm ⁻² · h ⁻¹)	0.23 ^{bc} (0.03, 4)	0.07 ^{bc} (0.03, 4)	0.72 ^a (0.20, 6)	0.15 ^{bc} (0.05, 4)	0.13 ^{bc} (0.06, 4)	0.06 ^{bc} (0.02, 5)	0.002 ^c (0.002, 4)	0.40 ^{ab} (0.07, 4)	0.11 [*] (0.06, 4)	2.95 (0.76, 4)

Data are means (standard error; n).
Values at Mameyes and Sabana are based on means of monthly fluxes over a 1-year period for separate chambers; n = number of chambers; means at El Verde are based on mean fluxes over the sampling period for replicate plots within a treatment; n = number of plots.
Within rows at Mameyes and Sabana, different superscripts indicate means are significantly different ($P < 0.05$) determined by one-way ANOVA and Tukey a-posteriori comparisons.
Asterisks at values for the Control at El Verde indicate significant differences between treatments determined by randomized complete block ANOVA.
* $P < 0.05$
** $P < 0.01$

except for the Sabana mid-successional forest, where NO_3^- was often below detection. Similarly, net N mineralization, net nitrification, and nitrification potential were also low in the pastures. Early-successional forests had larger soil NO_3^- pools and higher rates of net nitrification than pastures, yet the effect was significant only at Mameyes. Late-successional forests had three times the soil NO_3^- and greater rates of net N mineralization and net nitrification than their pasture counterparts.

The two mid-successional forests span the ranges in rates of soil N turnover. The mid-successional forest at Mameyes had the highest rates of soil N turnover (net N mineralization, net nitrification, and nitrification potential) and the largest soil NO_3^- pools compared with the other unfertilized forests (Table 2), whereas soil NH_4^+ pools were lowest. Furthermore, this was the only unfertilized site where NO_3^- pools exceeded those of NH_4^+ . Soil organic matter quality, indicated by a very low soil C:N ratio of 10.1, was relatively high. In contrast, the Sabana mid-successional forest had the lowest rates of soil N turnover, the lowest NO_3^- pools, and the highest soil C:N ratio (15.5), indicating relatively poor-quality organic matter. In fact, net N mineralization was negative at the Sabana mid-successional forest, indicating net microbial immobilization of available N over the 7-day incubation period.

Aboveground leaf litterfall N and litter quality (C:N ratio) followed the same pattern as N oxide fluxes and soil N cycling (Table 2). The mid-successional forest at Mameyes with the highest fluxes of N oxides had the highest input of leaf litter N and the highest-quality litter, whereas the mid-successional forest at Sabana had the lowest input of leaf litter N and the lowest quality litter.

The highest and lowest rates of CO₂ production during laboratory incubations were found in the soils from the Sabana and Mameyes mid-successional forests, respectively (Table 2). For the six nonpasture sites, microbial respiration was directly related to litterfall C:N ratio ($r = 0.843$, $P < 0.05$), (Figure 5A), whereas net N mineralization was inversely related to C:N ratio ($r = -0.902$, $P < 0.01$), (Figure 5B).

Pasture Production and Forest Structure: Mameyes and Sabana

Aboveground net primary production was equal for the two pastures (Table 2). Canopy height, number of species, and basal area (Appendix) increased along a series from early- through mid-successional to late-successional forest in each area. (Canopy heights for the early successional forests are based

Table 2. Site Characteristics, Soil Properties, and Indexes of Soil N Cycling for Sites at Mameyes, Sabana, and El Verde, Puerto Rico

	Mameyes				Sabana				El Verde Forest			
	Active Pasture	Early-successional Forest	Mid-successional Forest	Late-successional Forest	Active Pasture	Early-successional Forest	Mid-successional Forest	Late-successional Forest	Control	Fertilized		
Time in current land use (y)	>60	~10	45 (?)	>60	>60	~10	~25	>60	>60	>60		
Canopy height (m)	ND	4	13	30	ND	5	8	22	ND	ND		
Soil temperature ^c	29.6	26.4	24.8	25.0	28.1	24.7	24.5	24.2	22.8	22.6		
Soil pH	4.3 ^c (0.1)	ND	4.7 ^{ad} (0.1)	5.7 ^a (0.2)	4.4 ^{de} (0.1)	4.8 ^{bc} (0.1)	4.7 ^{ad} (0.04)	5.1 ^b (0.1)	4.6 (0.1)**	4.0 (0.1)		
Bulk density (g/cm ³) ^f	.89 ^a	.69 ^b	.84 ^{ab}	.89 ^a	.78 ^{ab}	.78 ^{ab}	.83 ^{ab}	.83 ^{ab}	.73	.64		
NO ₃ -N (μg N/g soil)	4.3 ^{cd} (1.0)	13.6 ^b (1.6)	21.5 ^a (1.7)	14.7 ^b (2.1)	2.1 ^{cd} (0.6)	4.2 ^{cd} (0.8)	0.2 ^d (0.1)	7.7 ^c (1.2)	2.4 (0.9)*	22.5 (4.1)		
NH ₄ -N (μg N/g soil)	19.3 ^b (3.0)	17.8 ^b (3.1)	8.1 ^b (1.8)	22.2 ^b (4.9)	19.7 ^b (2.4)	39.3 ^a (5.0)	20.1 ^b (1.6)	40.6 ^c (3.4)	31.2 (3.2)**	8.7 (2.0)		
Net N mineralization (μg N · g soil ⁻¹ · d ⁻¹)	-8.5 ^d (2.1)	4.6 ^{bc} (4.6)	19.5 ^a (2.6)	3.1 ^{bcd} (2.0)	-3.8 ^d (2.5)	-3.1 ^{cd} (2.5)	-7.7 ^d (2.1)	9.4 ^{ab} (2.1)	18.9 (6.4)	25.0 (5.0)		
Net nitrification (μg N · g soil ⁻¹ · 7 d ⁻¹)	8.5 ^{cd} (2.3)	16.4 ^{abc} (4.7)	23.8 ^a (2.5)	21.8 ^{ab} (2.6)	9.5 ^{bcd} (3.0)	15.5 ^{abc} (2.8)	1.9 ^d (0.6)	19.7 ^{abc} (3.6)	17.8 (5.4)	31.9 (4.5)		
Nitrification potential (μg N · g soil ⁻¹ · h ⁻¹)	0.24 ^c (0.03)	0.57 ^b (0.03)	1.16 ^a (0.14)	0.62 ^b (0.08)	0.20 ^c (0.03)	0.17 ^c (0.03)	0.11 ^c (0.01)	0.15 ^c (0.03)	0.39 (0.03)*	.30 (0.23)		
Litterfall or foliar production (g · m ⁻² · y ⁻¹) ^g	1215	620 ^b	1039 ^a	820 ^{ab}	1217	588 ^b	666 ^b	798 ^{ab}	511	556		
Leaf litterfall N (g N · m ⁻² · y ⁻¹)	ND	7.4 ^b	19.5 ^a	11.1 ^{ab}	ND	6.2 ^b	6.2 ^b	11.9 ^b	6.0	8.2		
Leaf litter C:N	ND	41.5 ^c	27.4 ^c	32.2 ^{cd}	ND	48.8 ^b	57.7 ^a	35.8 ^{de}	43.7*	34.7		
CO ₂ production (μg C · g soil ⁻¹ · d ⁻¹)	39.2 ^{ab}	33.6 ^{ab}	19.3 ^b	28.6 ^{ab}	43.4 ^{ab}	31.8 ^{ab}	50.3 ^a	38.0 ^{ab}	ND	ND		
Soil % C	4.6 ^{ab} (0.5)	6.0 ^{ab} (0.2)	4.5 ^{ab} (0.4)	5.3 ^{ab} (0.4)	4.3 ^b (0.3)	5.2 ^{ab} (0.3)	6.2 ^c (0.2)	6.4 ^c (1.0)	10.4 (1.9)	11.0 (1.1)		
Soil % N	0.45 ^{ab} (0.04)	0.51 ^a (0.01)	0.44 ^{ab} (0.03)	0.45 ^{ab} (0.02)	0.36 ^b (0.02)	0.41 ^{ab} (0.01)	0.40 ^{ab} (0.01)	0.50 ^a (0.05)	0.65 (0.08)	0.70 (0.03)		
Soil C:N	10.2 ^c (0.2)	11.7 ^{bc} (0.4)	10.1 ^c (0.4)	11.8 ^{bc} (0.5)	12.3 ^b (0.2)	12.8 ^b (0.3)	15.5 ^a (0.3)	12.5 ^b (0.7)	15.6 (0.9)	15.3 (0.8)		

ND, no data available

Data are means (standard error).

For Mameyes and Sabana, $n = 8$ for most variables; exceptions occur for leaf litterfall and associated chemical variables, where $n = 9$, CO₂ production, where $n = 2$, and bulk density, where n ranges from 4 to 12. At El Verde, $n = 4$.Within rows at Mameyes and Sabana, different superscripts indicate means are significantly different ($P < 0.05$), determined by one-way ANOVA and Tukey a -posterior comparisons.Asterisks at values for the Control at El Verde indicate significant differences between treatments determined by randomized complete block ANOVA. * $P < 0.05$ ** $P < 0.01$ ^cSoil temperatures measured between 1000 and 1500^fBulk density data for El Verde provided courtesy of X. Zou^gFor pastures, foliar production estimated from monthly clipping of live biomass; for forests, leaf litterfall is from biweekly collections.

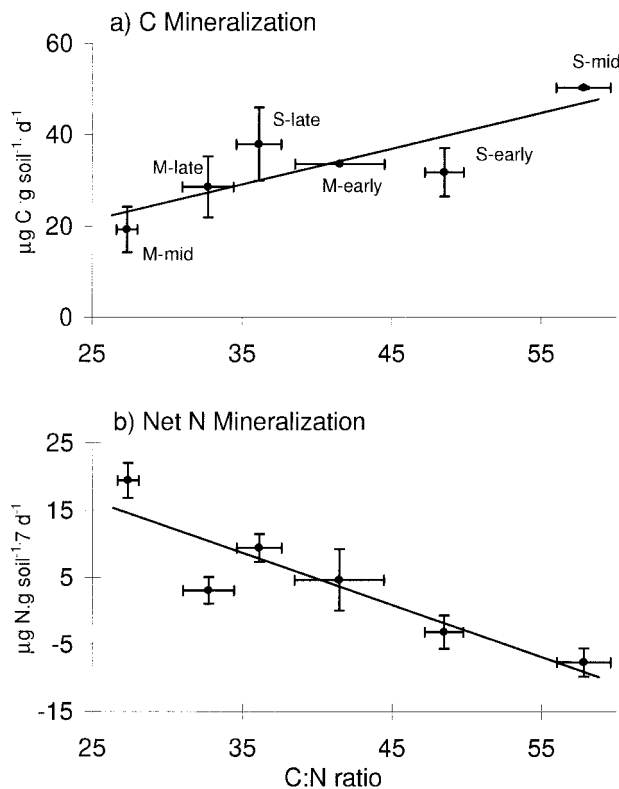


Figure 5. Relationships between (a) net C mineralization and leaf litterfall C:N ratio ($r = 0.843$, $P = 0.035$) and (b) net N mineralization and litterfall C:N ratio ($r = -0.902$, $P < 0.01$) for the six forested sites at Mameyes and Sabana. In a, C mineralization rates were determined from laboratory incubations and are the means (plus standard error) of two different dates, except for the early-successional forest at Mameyes that could only be sampled once. In b, N mineralization rates are the means (plus standard error) from four dates ($n = 4$).

on the heights of *Miconia*, a pasture-colonizing shrub, not the remnant trees.)

Species composition in the two early-successional forests was very similar, with the shrub *Miconia prasina* and two tree species, *Tabebuia heterophylla* and *Schefflera morototoni*, ranked as the top dominants in each site (Appendix). Species composition differed among the older forests. *Cecropia schreberiana*, *Guarea guidonia*, and *Andira inermis*, a legume, were among the top dominants at the Mameyes mid-successional forest, whereas *T. heterophylla*, *Syzigium jambo*, and *Myrcia deflexa* were among the top dominants at the Sabana mid-successional forest. Within the late-successional forests, 85% of the basal area at Mameyes was dominated by *S. macrophylla*, whereas 83% of the basal area at Sabana was dominated by *T. heterophylla*, *C. schreberiana*, and *Prestoea montana*.

N Oxides, Soil Properties, and Fertilization: El Verde

As expected, N oxide emissions from the fertilized forest exceeded those from the nonfertilized forest (Table 1). N_2O and NO fluxes from the fertilized forest were two and four times greater, respectively, than the highest mean fluxes from the high-fertility mid-successional site at Mameyes. The fertilized plots also had significantly higher soil NO_3^- pools and nitrification potentials and lower soil NH_4^+ pools and pH than unfertilized plots (Table 2). Based on our single soil sampling at El Verde, both net N mineralization and net nitrification appeared to increase with fertilization, although the differences were not statistically significant. Forest fertilization decreased leaf litter C:N ratios by over 20%, yet it increased leaf litterfall by a nonsignificant 10% ($P > 0.05$). Of all the mid- to late-successional forest sites, leaf litterfall was lowest at the El Verde control plots. Soil C:N ratios at El Verde were as high (15.6 and 15.3 for control and fertilized treatments, respectively) as C:N ratios at the mid-successional forest at Sabana, suggesting relatively low-quality soil organic matter in the forest at El Verde.

Relationships among N cycling indices and N oxide emissions

If we combine the data from all sites, we see that soil NO_3^- pools were positively and linearly related to net N mineralization, net nitrification, and nitrification potential (Figure 6). Soil NH_4^+ was not related to net N mineralization or net nitrification, and it was negatively related to nitrification potential. Nitrification potential was high when soil NO_3^- exceeded $10 \mu\text{g N/g soil}$ and when soil NH_4^+ was less than $20 \mu\text{g N/g soil}$ (Figure 6).

Annual fluxes of N_2O plus NO were related positively to soil NO_3^- , net N mineralization and net nitrification, and nitrification potentials (Figure 7). When the fertilized forest was omitted from the analysis, fluxes were also positively related to leaf litter N inputs and C:N ratios (Figure 7f and g); the fertilized forest had higher fluxes than would be predicted based on leaf litter N or C:N ratio alone (Tables 1 and 2). Exponential models ($y = ae^{bx}$) were fitted to the data relating the sum of N_2O plus NO to the various measurements of N cycling and resulted in either higher (four cases) or equal R^2 's (two cases) when compared to linear models (Figure 7). The two sites with the greatest fluxes—the mid-successional forest at Mameyes and the fertilized forest at El Verde—tend to drive the pattern of the relationships.

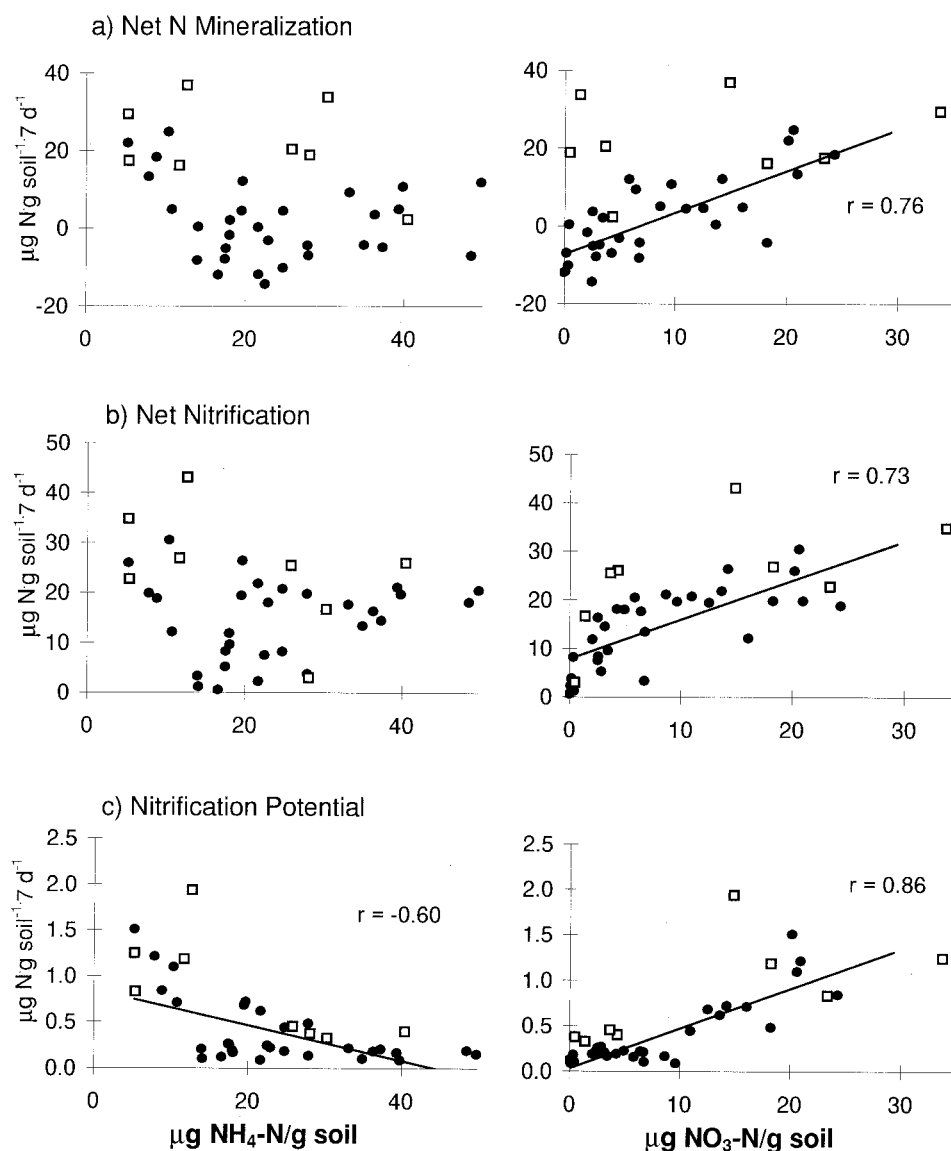


Figure 6. Soil NH_4^+ (left) and NO_3^- (right) vs net N mineralization (a), net nitrification (b), and nitrification potential (c). Solid circles are quarterly sampled soils from Mameyes and Sabana; empty squares are from a single sampling at El Verde and represent values from the individual plots. Fitted lines ($P < 0.001$) are based on data from Mameyes and Sabana only.

DISCUSSION

Differences in Forest Recovery at Mameyes and Sabana

The extremes in N oxide fluxes from the two mid-successional forests were a surprising result. Successional forests typically accumulate nutrients and mass and tend to be nutrient-conserving (Vitousek and Reiners 1975). Under these circumstances, we expected low N oxide fluxes during forest recovery. The low fluxes from the early-successional forests and the mid-successional forest at Sabana are consistent with this view and have been observed in mid-successional forests elsewhere (Keller and Reiners 1994; Robertson and Tiedje 1988; Verchot and others 1999). In contrast, however, the annual flux from the mid-successional forest at Mameyes

($9.0 \text{ kg N} \cdot \text{ha}^{-1} \cdot \text{y}^{-1}$) is among the highest measured for any (unfertilized) tropical forest.

These fluxes from the mid-successional forests appear to reflect species differences and associated effects on ecosystem N cycling. Species compositions at Mameyes and Sabana suggest different successional trajectories and/or land-use histories between the two sets of sites. At Sabana, *Tabebuia heterophylla* was the dominant tree species in the mid- and late-successional forests, but it was absent from these forests at Mameyes. *T. heterophylla* naturally invades pastures at this elevation (Zimmerman and others 1995a) and was widely planted by the United States Forest Service during the 1950s to reclaim previously forested areas. Likewise, *Myrcia deflexa*, which is common in former pastures in the Luquillo Mountains (Zimmerman and others

Annual N Oxide Fluxes

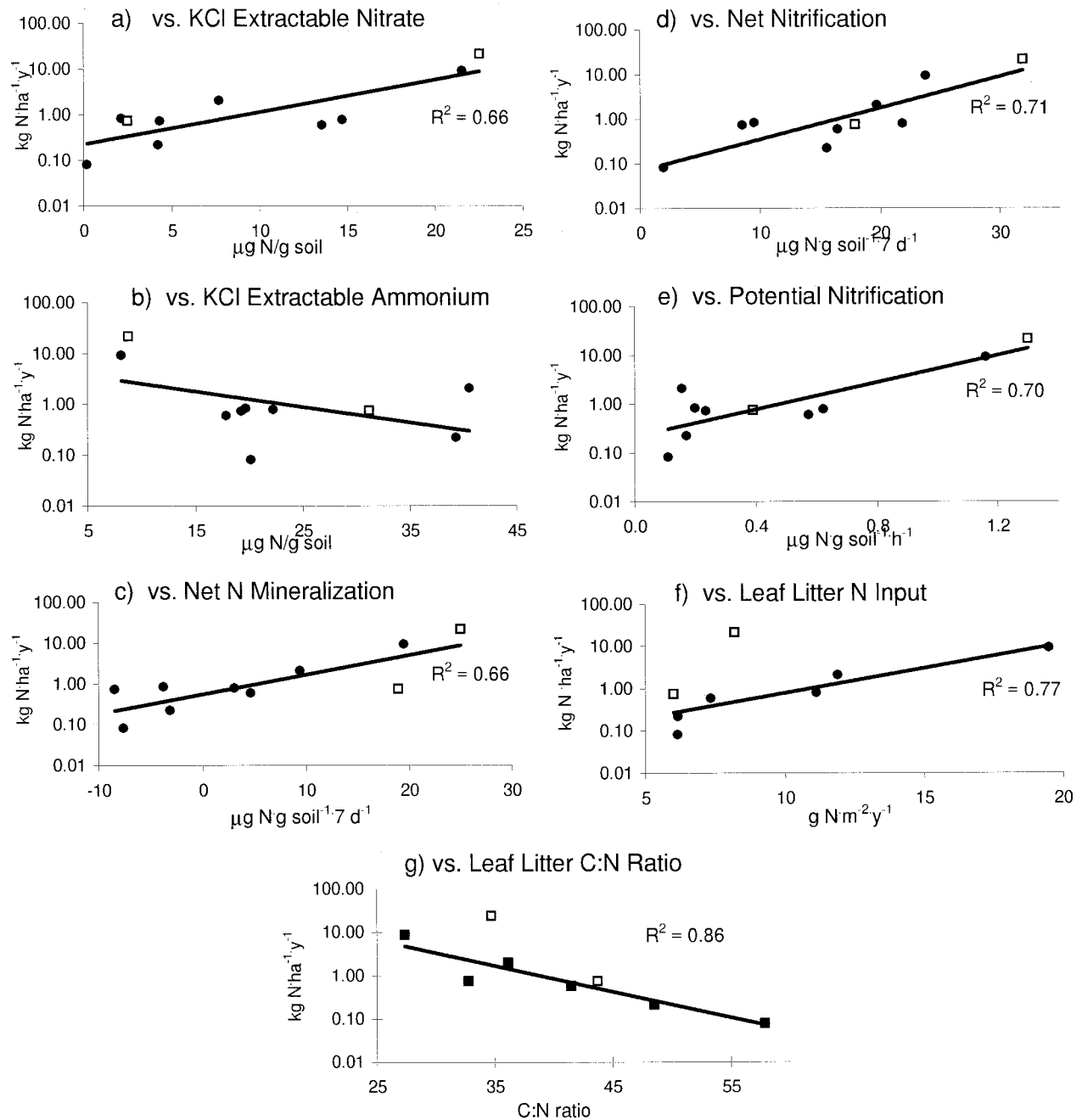


Figure 7. Sum of N₂O plus NO vs (a) soil NO₃⁻, (b) soil NH₄⁺, (c) net N mineralization, (d) net nitrification, (e) potential nitrification, (f) leaf litter N input, and (g) leaf litter C:N ratio. Solid circles are annual averages for Mameyes and Sabana; empty squares are averages from El Verde. Fluxes are annual estimates based on mean fluxes from each chamber for the Mameyes and Sabana sites and based on the means from the four plots within each treatment at El Verde. Note the logarithmic scale on the y axis. Printed R^2 's are from exponential model fits; a linear model fit equally well in panel e. In panels f and g, data from the fertilized forest at El Verde were omitted from the regression analyses; when the fertilized forest was included, neither model was significant ($P < 0.05$). On the remaining data points in f, a linear model ($y = 0.599x - 3.917$, $R^2 = 0.86$) fit slightly better than an exponential model ($y = 0.0531e^{0.2685x}$, $R^2 = 0.77$); but because the linear model indicated negative fluxes within the range of the data, we preferred the exponential model.

1995a), including the Sabana mid-successional forest, was also absent from Mameyes. *Andira inermis* (Leguminosae) was among the top five dominants at the Mameyes mid-successional forest and is an important indicator of forests with prior pasture use (Aide and others 1996). The two dominant tree species at the Mameyes mid-successional forest, *G. guidonia* and *C. schreberiana*, are often found at abandoned coffee plantations (Zimmerman and others 1995a), suggesting that this forest may have also been used previously for coffee cultivation. Regardless of the exact history, previous land use for the sites in the two recovery sequences appears to have differed.

Legumes and other N-fixing tree species often have greater amounts of foliar N, litterfall N, and higher-quality litter (that is, lower C:N ratio) than non-N-fixing species (Binkley and others 1992; García-Montiel and Binkley 1998). N concentrations of 1.95% have been recorded for fresh leaves of *A. inermis* (Sánchez and others 1997). Because litter quality may directly influence soil N transformations (Pastor and others 1984; Vitousek 1984), it indicates the potential effects of plant species and communities on soil ecosystems. The high-quality litter at the Mameyes mid-successional site compared with the low-quality litter from the Sabana mid-successional site suggests that this is a major mechanism whereby the plant communities influence the different soil processes at the two sites.

Non-N-fixing tree species may have similarly notable effects on soil N transformations, especially if litter quality varies. At the Mameyes mid-successional forest, where N oxide fluxes were highest, *G. guidonia* is also relatively abundant and has high amounts of foliar N and P (Scatena and others 1993); mean leaf litterfall N concentration at that site was the highest at 1.8% (data not shown). *T. heterophylla*, the dominant species at the Sabana mid- and late-successional forest sites, has a relatively low N concentration (approximately 1.1%) in leaf litterfall (E. Cuevas unpublished). Mean leaf litterfall N concentrations were 0.9% and 1.4%, respectively, for these forests. Clearly, incorporating information on tree species composition and historical land use could strengthen future biogeochemical studies of N cycling processes, including N oxide emissions, in tropical forests.

Robertson and Tiedje (1988) contend that denitrification losses from humid tropical regions are currently lower because the number of mid-successional forests has increased since precolonial times. Our study shows that there may be important exceptions to that generalization at sites where leguminous trees dominate.

Differences in Soil Properties and N Transformations among Land Uses

When forest is converted to pasture in the tropics, soil acidity typically decreases—most likely because of inputs of ash from burning (Neill and others 1995, 1997a; Reiners and others 1994; Verchot and others 1999). Soil bulk density also increases (Verchot and others 1999; Keller and others 1993; Neill and others 1997a), presumably due to compaction by cattle. We found lower pH in pastures than in forests and—surprisingly—no significant changes in bulk density in either abandonment sequence. Several factors may account for these contrary findings. In northeastern Puerto Rico, burning is not a common practice because of high moisture (J. Zimmerman personal communication). As pastures age, soil pH may decline as base cations are leached (Neill and others 1997a; Moraes and others 1996) or as base-rich biomass is removed by grazing. Zou and Gonzales (1997) found significantly greater earthworm densities in the Mameyes and Sabana pastures than in the adjacent forests. Because earthworms are known to decrease soil bulk density, we believe that their activities may act to counter the compaction caused by cattle.

In tropical pastures, NH_4^+ is often the dominant form of inorganic N, whereas in many tropical forests NO_3^- is equal to or exceeds NH_4^+ (Piccolo and others 1994; Neill and others 1995, 1997b; Reiners and others 1994; Keller and Reiners 1994; Rhoades and Coleman 1999; Verchot and others 1999). Results from the late-successional forests at Mameyes and Sabana support this apparently widespread pattern (Table 2), providing growing evidence for distinguishing a “nitrate economy” in late-successional forests from an “ammonium economy” in old pastures.

Reduced rates of net N transformations when forest is converted to pasture have also been found elsewhere in the tropics (Piccolo and others 1994; Reiners and others 1994; Neill and others 1995, 1997b; Verchot and others 1999). Our two old pastures and the early- and mid-successional forests at Sabana showed substantial net immobilization during laboratory incubations. Presumably, competition by heterotrophic microbes limits the availability of N for nitrification and denitrification at these sites. As observed in other studies (Keller and others 1993; Veldkamp and others 1999; Verchot and others 1999), the old pastures had low N oxide fluxes and are not contributing to increases in atmospheric N_2O .

We also found large differences in rates of soil N transformations among the mid- and late-succes-

sional forests; the highest and lowest rates were measured in these forests. Previously, either no difference in N turnover in secondary vs primary forests (Robertson 1984; Reiners and others 1994; Rhoades and Coleman 1999) or rates intermediate to pastures and primary forest (Verchot and others 1999) were reported. Robertson (1984) found that the production of nitrate and total mineral N increased early in succession and remained high. These contradictory results suggest that the recovery of N cycling processes in neotropical forests is site-specific and that successional dynamics and land use strongly influence rates of recovery.

Our data show a connection between C and N mineralization and litterfall C:N ratio (Figure 5) that appears to be related to stoichiometry. Inverse relationships between litter quality and net N mineralization have been documented elsewhere (Vitousek 1982; Wedin and Tilman 1990; Pastor and others 1984; Scott and Binkley 1997) and were confirmed in this study. We also show an increase in C mineralization with increasing C:N ratio. Hence, as the C:N ratio increases, CO₂ production increases and net N mineralization decreases, suggesting a switch from C to N limitation of microbial activity as substrate quality decreases. Schimel (1986) and Rhoades and Coleman (1999) found a similar inverse relationship between C and N mineralization. Furthermore, under N-limited conditions, the availability of NH₄⁺ to nitrifiers is presumably reduced (Figure 6), a conclusion also supported by the inverse relationship between C mineralization and soil NO₃⁻ ($r = -0.90$, $P < 0.01$, $n = 8$).

Controls on N Oxide Fluxes

In our study areas, where precipitation is abundant and relatively evenly distributed throughout the year, N₂O fluxes exceeded NO fluxes 97.5% of the time, with an average N₂O:NO ratio of 9.4 (Figures 2 and 3). In contrast, where precipitation is more variable, N₂O and NO emissions shift in importance, with N₂O flux dominating in wet months and NO in dry months (Keller and Reiners 1994; Verchot and others 1999; Davidson and others 1993).

Our results (Figure 7) are consistent with those of other investigators who have found a direct relationship between N₂O fluxes (or N₂O plus NO) and soil N turnover (Matson and Vitousek 1987; Riley and Vitousek 1995; Verchot and others 1999) or soil NO₃⁻ (Keller and Reiners 1994; Verchot and others 1999). Collectively, these findings serve to confirm the "hole in the pipe" model (Davidson 1991; Firestone and Davidson 1989), which predicts that an increase in N availability will result in

an increase in N trace gas production. Our results also indicate that several measures of N availability relate equally well to N oxide emissions, including leaf litter N and C:N ratio. However, leaf litter N and C:N ratios shift only slightly following fertilization (Figure 7f–g). Apparently, when the supply of N exceeds the ability of the vegetation to take it up, indices of leaf litter quality are not good predictors of N oxide emissions.

One or more competing sinks for N (plants or heterotrophic microbes) must saturate before N is available to "leak" from the ecosystem via nitrification and denitrification. Aber and others (1989) have suggested that ecosystem responses to elevated N inputs would be nonlinear with critical threshold points. Above the threshold points, nitrification and ecosystem N losses increase. Thresholds are suggested in our data (Figure 7), yet we note that either an exponential or a threshold response would be consistent with this idea.

High rates of nitrification and N₂O loss are symptoms associated with ecosystem N saturation (Aber and others 1989, 1998; Fenn and others 1998). We found that nitrification was stimulated by the N fertilizer additions at El Verde, evidenced by the increase in potential nitrification and the shift in dominance of the inorganic N pools from NH₄⁺ to NO₃⁻ (Table 2). This suggests that the fertilized El Verde forest may be N-saturated after 6 years of N addition at 300 kg · ha⁻¹ · y⁻¹. Recently, Hall and Matson (1999) showed that the addition of 50 kg N ha⁻¹ to P-limited but N-rich forest soils in Hawaii led to high losses of N as gaseous N oxides shortly after fertilization. Similar losses did not occur from an N-limited soil. They contend that the N-rich forest acted as if it was "naturally 'N-saturated'." Similarly, the high N oxide fluxes from the Mam-eyes mid-successional forest and the N-rich characteristics of its N cycle suggest that here too, an excess of N may be present relative to plant demand. In contrast, at the Sabana mid-successional forest and the unfertilized forest at El Verde, where soil C:N is high and soil NO₃⁻, nitrification potentials, leaf litterfall returns, and nitrogen oxide fluxes are all low, the cycling of N may be relatively "efficient" (compare Vitousek 1982, 1984).

Implications for Simulation Models

Biogeochemical models that predict NO and N₂O emissions from soils, such as CASA (Potter and others 1996), NGAS (Parton and others 1996), and DNDC (Li and others 1992), may need to be revised if the relationships between N cycling and N oxide production suggested in this study are confirmed. The CASA ecosystem process model (Potter and

others 1996) estimates production of N oxides as a fixed percentage of gross mineralized N, which, in turn, is derived from litterfall N. Our results indicate either that a threshold of litterfall N must be exceeded before significant N oxide production occurs, or that the relationship between N mineralized from litter N and N oxide production is exponential (Figure 7f). In NGAS and DNDC, the size of the NH_4^+ pool is used as a driver for N_2O production directly (NGAS) or for nitrification (DNDC). However, our findings show a negative (or no) relationship between N oxide fluxes and soil NH_4^+ (Figure 7a); thus, NGAS and DNDC would overpredict N_2O fluxes from the NH_4^+ -rich pasture soils we studied. Our results indicate that soil NH_4^+ is drawn down where nitrification potential is high (Figure 6). Hence, high NH_4^+ concentrations are more likely to be the *effect* of low population sizes or low activities of nitrifiers than the *cause* of high rates of nitrification and N oxide production.

Moreover, an important limitation of nearly all biogeochemical models of terrestrial ecosystems is their limited ability to address species composition during secondary succession. We have shown that land-use histories and resulting species composition of increasingly important secondary forests can have important influences on N cycling processes, including regulation of the availability of N and the emissions of N_2O and NO from soils.

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Appendix Tree Species Ranked by Basal Area (BA) in the Forests at Mameyes and Sabana

Mameyes	BA (m ² /ha)	Sabana	BA (m ² /ha)
Early-successional Forest			
<i>Miconia prasina</i> (Sw.) DC.	5.010	<i>Miconia prasina</i> (Sw.) DC.	4.889
<i>Tabebuia heterophylla</i> (DC.) Britton	3.531	<i>Tabebuia heterophylla</i> (DC.) Britton	1.410
<i>Schefflera morototoni</i> (Aubl.) Maguire.	0.422	<i>Schefflera morototoni</i> (Aubl.) Maguire.	0.782
<i>Miconia</i> sp.	0.018	Unknown	0.388
Unknown	0.008	<i>Inga laurina</i> (Sw.) Willd.	0.235
<i>Philodendron angustatum</i>	0.005	<i>Andira inermis</i> (W. Wright) DC.	0.138
Total	9.0	<i>Casearia silvestres</i> Sw.	0.137
		<i>Genipa americana</i> L.	0.111
		<i>Cyathea arborea</i> (L.) J.E. Smith	0.095
		<i>Psidium guajava</i> L.	0.038
		<i>Psychotria brachata</i>	0.010
		<i>Palicourea croceoides</i> W. Ham.	0.005
		<i>Inga vera</i> Willd.	0.005
		<i>Myrcia deflexa</i> (Poir.) DC.	0.003
		Total	8.2
Mid-successional Forest			
<i>Cecropia schreberiana</i> (L.) Miq.	11.715	<i>Tabebuia heterophylla</i> (DC.) Britton	10.205
<i>Guarea guidonia</i> (L.) Schleumer	9.300	<i>Syzigium jambos</i> L.	7.014
<i>Ficus</i> sp.	6.208	<i>Myrcia deflexa</i> (Poir.) DC.	1.492
<i>Andira inermis</i> (W. Wright) DC.	2.357	<i>Byrsonima spicata</i> (Cav.) H.B.K.	0.648
<i>Alchornea latifolia</i> Sw.	1.564	<i>Schefflera morototoni</i> (Aubl.) Maguire	0.351
<i>Schefflera morototoni</i> (Aubl.) Maguire.	1.176	<i>Homalium racemosum</i> Jacq.	0.178
<i>Psychotria brachiata</i> Sw.	0.636	<i>Casearia guianensis</i> (Aubl.) Urban	0.127
<i>Ocotea leucoxylon</i> (Sw.) Mez	0.455	<i>Miconia prasina</i> (Sw.) DC.	0.066
<i>Artocarpus heterophyllus</i> Lam.	0.136	<i>Miconia mirabilis</i> (Aubl.) L.O. Wms.	0.060
<i>Casearia arborea</i> (L.C. Rich) Urban	0.101	<i>Casearia domingensis</i>	0.055
<i>Miconia impetiolaris</i> (Sw.) D. Don	0.058	<i>Dacryodes excelsa</i> Vahl	0.051
<i>Casearia silvestres</i> Sw.	0.055	<i>Myrcia splendens</i> (Sw.) DC.	0.050
<i>Inga vera</i> Willd.	0.049	<i>Casearia silvestres</i> Sw.	0.039
<i>Miconia serrulata</i> (DC.) Naud.	0.040	<i>Palicourea croceoides</i> W. Ham.	0.037
<i>Manilkara bidentata</i> (A. DC.) Chev.	0.037	<i>Calophyllum calaba</i> L.	0.034

Appendix (Continued)

Mameyes	BA (m ² /ha)	Sabana	BA (m ² /ha)
<i>Palicourea croceoides</i> W. Ham.	0.026	Unknown	0.028
<i>Swietenia macrophylla</i> King.	0.024	<i>Miconia tetrandra</i> (Sw.) D. Don	0.026
<i>Piper glabrescens</i> (Miq.) C. DC.	0.010	<i>Faramea occidentalis</i> (L.) A. Rich.	0.022
<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	0.005	<i>Ixora ferrea</i> (Jacq.) Benth.	0.017
<i>Tabebuia donnell-smithii</i> (Rose) Miranda	0.004	<i>Manilkara bidentata</i> (A. DC.) Chev.	0.015
<i>Myrcia splendens</i> (Sw.) DC.	0.004	<i>Matayba domingensis</i> (DC.) Radlk.	0.013
<i>Miconia prasina</i> (Sw.) DC.	0.003	<i>Ocotea leucoxylon</i> (Sw.) Mez	0.012
<i>Faramea occidentalis</i> (L.) A. Rich.	0.003	<i>Chrysobalanus icaco</i> L.	0.008
Total	34.0	Total	20.5
Late-successional Forest			
<i>Swietenia macrophylla</i> King.	45.045	<i>Tabebuia heterophylla</i> (DC.) Britton	12.493
<i>Mangifera indica</i> L.	2.984	<i>Cecropia schreberiana</i> (L.) Miq.	10.729
		<i>Prestoea montana</i> (R. Grah.)	
<i>Guarea guidonia</i> (L.) Schleumer	1.421	Nichols	6.708
		<i>Schefflera morototoni</i> (Aubl.)	
<i>Erythrina poeppigiana</i> (Walp.) O.F. Cook	1.188	Maguire.	1.134
<i>Cecropia schreberiana</i> (L.) Miq.	0.526	<i>Swietenia macrophylla</i> King.	0.977
		<i>Dendropanax arboreus</i> (L.) Decne.	
<i>Casearia silvestres</i> Sw.	0.494	& Planch.	0.752
<i>Ocotea leucoxylon</i> (Sw.) Mez	0.392	<i>Andira inermis</i> (W. Wright) DC.	0.618
<i>Cordia sulcata</i> DC.	0.316	<i>Alchornea latifolia</i> Sw.	0.495
		<i>Tetragastris balsamifera</i> (Sw.)	
<i>Dendropanax arboreus</i> (L.) Decne. & Planch.	0.314	Kuntze	0.341
<i>Inga vera</i> Willd.	0.282	<i>Hymenaea courbaril</i> L.	0.319
<i>Psychotria brachiata</i> Sw.	0.146	<i>Ocotea leucoxylon</i> (Sw.) Mez	0.256
<i>Nectandra sintenissii</i> Mez.	0.053	<i>Psychotria berteriana</i> DC.	0.215
<i>Myrcia splendens</i> (Sw.) DC.	0.024	<i>Palicourea croceoides</i> W. Ham.	0.194
<i>Nectandra coriacea</i> (Sw.) Griseb.	0.023	<i>Inga laurina</i> (Sw.) Willd.	0.259
<i>Nectandra membranacea</i> (Sw.) Griseb.	0.018	<i>Cyathea arborea</i> (L.) J.E. Smith	0.123
<i>Palicourea croceoides</i> W. Ham.	0.013	<i>Trichilia pallida</i> Sw.	0.101
<i>Miconia impetiolaris</i> (Sw.) D. Don	0.011	<i>Sapium lauserasus</i> Desf.	0.067
<i>Alchornea latifolia</i> Sw.	0.006	<i>Psychotria brachiata</i> Sw.	0.060
<i>Samyda dodecandra</i> Jacq.	0.005	<i>Casearia arborea</i> (L.C. Rich) Urban	0.046
<i>Urera baccifera</i> (L.) Gaud.	0.004	<i>Syzigium jambos</i> L.	0.044
<i>Ocotea floribunda</i> (Sw.) Mez.	0.003	<i>Cordia borinquensis</i> Urban	0.033
<i>Zanthoxylum martinicense</i> (Lam.) DC.	0.003	<i>Ocotea floribunda</i> (Sw.) Mez.	0.033
<i>Piper glabrescens</i> (Miq.) C. DC.	0.002	<i>Manilkara bidentata</i> (A. DC.) Chev.	0.023
Total	53.3	<i>Myrcia deflexa</i> (Poir.) DC.	0.017
		<i>Guarea guidonia</i> (L.) Schleumer	0.017
		<i>Cestrum</i> sp.	0.009
		<i>Miconia prasina</i> (Sw.) DC.	0.007
		Unknown	0.006
		<i>Miconia impetiolaris</i> (Sw.) D. Don	0.005
		<i>Piper jacquimontianum</i> Kunth.	0.002
		<i>Myrcia splendens</i> (Sw.) DC.	0.002
		Total	36.1

Taxa in the Leguminosae are given in boldface type.