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NITROGEN CYCLING IN TROPICAL PLANTATION FORESTS: POTENTIAL CONTROLS ON NITROGEN RETENTION

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Abstract. The establishment and management of tropical plantations has the potential to significantly alter patterns in nitrogen (N) cycling relative to old-growth tropical forests, which are generally characterized by high N availability and large fluxes of nitrous oxide (N_2O), an important greenhouse gas. We used ^{15}N tracer additions to examine the effects of plantation establishment and management on gross N-cycling rates, N retention via microbial assimilation and dissimilatory nitrate (NO_3^-) reduction to ammonium (NH_4^+) (DNRA), and N losses via N_2O emissions. In general, plantations had lower rates of N cycling and increased potential for N losses compared to old-growth forests, but there were few differences between very short (one-year) rotation and 10-yr-old uncut plantations. Gross N mineralization declined by almost 50% in the plantations compared to the old-growth forests, and much of the mineralized N was nitrified at all sites. Gross nitrification rates were more variable and did not differ between old-growth forests and unfertilized plantations; however, fertilization increased gross nitrification by a factor of 6 in short-rotation forests, signaling a potential mechanism for increased N losses via leaching and gaseous emissions. Old-growth forests had significantly higher microbial biomass N and NH_4^+ assimilation rates. No microbial N assimilation was measured in the plantation soils, nor was there evidence of gross NH_4^+ immobilization from estimates of NH_4^+ consumption and nitrification. Plantations and old-growth forests had similar DNRA rates (0.23 $\mu g \cdot g^{-1} \cdot d^{-1}$), which retains N in the ecosystem, and plantations had lower N_2O emissions. Nitrous oxide fluxes from plantations were highly sensitive to reducing conditions, highlighting the potential for high rates of N_2O losses. Our results show that plantation establishment can decrease rates of N cycling, but once forests are converted to plantations, internal N-cycling pathways and N_2O fluxes are relatively resistant to disturbance associated with short rotation length.

Key words: Cordia alliodora *plantations; dissimilatory nitrate reduction to ammonium; field experiment; gross nitrification; gross nitrogen mineralization; land-use change; La Selva Biological Station, Costa Rica; ^{15}N; nitrogen fertilization; nitrous oxide; tropical forests; tropical plantations cf. old-growth forests.*

INTRODUCTION

Lowland humid tropical forests are often characterized by large mineral-N pools, high mineralization and nitrification rates, and the lack of strong N limitation to plants and microbes (Vitousek and Sanford 1986, Vitousek and Matson 1988, Tanner et al. 1992). Ample N availability and rapid N-cycling create the potential for high N losses from tropical soils, particularly from the NO_3^- pool (Vitousek and Howarth 1991, Vitousek and Matson 1992, McDowell 2002). Effective N-conservation mechanisms help to limit N losses through plant and microbial uptake, and may also include internal N-cycling processes such as dissimilatory NO_3^- reduction to NH_4^+ (Silver et al. 2001) and abiotic NO_3^- sorption (Dail et al. 2001) that decrease the size of NO_3^- pool.

Rates of N cycling, retention, and loss are likely to change when tropical forests are converted to other land uses. Between the decades of the 1980s and 1990s tropical deforestation rates grew by 3 to 10% (DeFries et al. 2002, Houghten 2003). Tropical plantation establishment grew by 42% during the same period, accounting for approximately one quarter of the deforested land area (Houghten 2003). Forest clearing and burning initially increase rates of net N cycling and N losses (Ewel et al. 1981, Matson et al. 1987, Robertson and Tiedje 1988). Subsequent plantation establishment may further modify N transformations by altering soil temperature, soil moisture (Malmer 1996), C pools (Bashkin and Binkley 1998, Binkley and Resh 1999),

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PLATE 1. Plantations of *Cordia alliodora* ages 1 (foreground), 3 (middle), and 11 years (background) at La Selva Biological Station, Costa Rica. This fast-growing Neotropical tree takes up large quantities of nitrogen, frequently accumulating concentrations >4% in its foliage. Photo credit: J. J. Ewel.

organic-N inputs (Lugo 1992), and decomposition rates (Butterfield 1999). Management strategies such as fertilization and rotation length should be major determinants of the type and magnitude of change in N cycling. Fast-growing tropical trees are often harvested on short rotations, sometimes as frequently as every few years (Brown et al. 1997). Repeated short rotation lengths can lead to accelerated N and cation leaching (Bigelow et al. 2004) and depleted soil C stocks (Russell et al. 2004).

The effects of plantation establishment and management on N trace-gas emissions are not well established, but have important implications for both ecosystem N cycling and global atmospheric chemistry. Tropical forests are the largest natural source of nitrous oxide (N_2O) globally, an important greenhouse gas (Lashof and Ahuja 1990) and a catalyst for stratospheric ozone depletion (Cicerone 1987). Nitrous oxide production represents a permanent loss of N from the ecosystem and is controlled by soil redox conditions, nitrification and denitrification rates, NO_3^- availability, and labile C pools (Tiedje et al. 1982). In humid environments, denitrification is thought to be the dominant source of N_2O production (Davidson et al. 1986), with losses via nitrification playing a secondary, but potentially important, role. Denitrification is an anaerobic process while nitrification occurs only in the presence of oxygen. Humid tropical-forest soils commonly fluctuate between aerobic and anaerobic conditions (Silver et al. 1999) facilitating both the production and reduction of NO_3^- in space and time.

Dissimilatory nitrate reduction to ammonium (DNRA) may compete with denitrification for available NO_3^-. DNRA is an anaerobic microbial process that rapidly converts NO_3^- to NH_4^+ without the incorporation of NO_3^- into microbial tissues (Tiedje 1988). DNRA can increase rates of N retention in ecosystems by providing additional NH_4^+ for uptake and assimilation, and by decreasing the size of the NO_3^- pool. The relative balance between NO_3^- reduction to NH_4^+ via DNRA and losses via N_2O emissions is likely to be sensitive to a variety of ecosystem properties, particularly soil redox status and soil C and NO_3^- pools. Denitrification to N_2 and N_2O provides more potential energy per electron donor, but DNRA is more favorable when considering energy available per unit of NO_3^- consumed, and has a greater capacity for accepting electrons (8 electrons) than does denitrification (5 electrons). Thus, the constraints on microbial energetics suggest that denitrification should be favored in the presence of a low C-to-NO_3^- ratio, while the inverse should be true for DNRA (Tiedje et al. 1982). Several factors can influence the ratio of C to NO_3^- including soil chemical or physical properties, plant community

TABLE 1. Soil mineral N pools, total soil N and C, the total C-to-NO_3^- ratio, and soil bulk density in plantations and forests at La Selva Biological Station, Costa Rica.

Site	NH_4-N (μg/g)	NO_3-N (μg/g)	Total carbon (%)	Total nitrogen (%)	Total C:NO_3^-	Bulk density (g/cm^3)
Plantations						
1-yr-old	1.07 (0.64)	1.55[a] (0.22)	2.20[a] (0.19)	0.32[a] (0.01)	1.44[a] (0.10)	0.81[a] (0.03)
1-yr-old + N	0.32 (0.03)	1.69[a] (0.38)	2.24[a] (0.40)	NA	1.49[a] (0.41)	0.92[a] (0.03)
10-yr-old	0.93 (0.33)	0.79[b] (0.02)	2.32[a] (0.12)	0.32[a] (0.01)	2.94[b] (0.14)	0.87[a] (0.03)
Old-growth forest						
Alluvial soils	0.90 (0.48)	2.19[a] (0.30)	4.81[b] (0.37)	0.53[b] (0.06)	2.35[ab] (0.56)	0.58[b] (0.03)
Residual soils	0.44 (0.14)	1.68[a] (0.29)	6.40[b] (0.47)	0.52[b] (0.03)	3.24[b] (0.28)	0.55[b] (0.05)

Notes: Total C and N data for plantations are from J. J. Ewel et al., *unpublished data*; total C and N data for old-growth forests are from D. B. Clark (*personal communication*). Sample size is three plots per forest or plantation type. Data are means with SE in parentheses; NA = not available. Means with the same lowercase letter are not significantly different within variables and across sites at $P < 0.05$.

composition, and land-use history. In the tropics, forest conversion is likely to initially increase NO_3^- concentrations (Silver and Vogt 1993) and then decrease the size of the soil NO_3^- pool as a result of increased leaching, trace-gas losses, and uptake by recovering plants (Keller et al. 1993, Silver and Vogt 1993, Bigelow et al. 2004). Tropical land-use change can either increase or decrease soil C pools depending upon the type, duration, and intensity of land use (Silver et al. 2000).

In this study we used young plantations and old-growth tropical forests to determine the effects of plantation establishment and management (rotation length, N fertilization) on patterns in gross N cycling, microbial N assimilation, DNRA rates, and nitrous oxide fluxes. We also conducted a laboratory experiment using plantation soils to explore the effects of redox conditions on N fluxes. Redox conditions of humid tropical soils have rarely been explicitly considered in estimating rate processes, but are likely to significantly impact redox-sensitive rate processes such as nitrification, DNRA, and denitrification.

METHODS

Site description

The field research was conducted at the La Selva Biological Station (10°26′ N, 83°59′ W, elevation 40 m), Costa Rica (see Plate 1). Mean annual temperature is 25.8°C and mean annual precipitation is ~4000 mm, with weak seasonality throughout the year (Sanford et al. 1994). We used experimental plantations and unmanipulated old-growth forest for our experiments. The plantations were part of an ongoing study to examine the effects of life-form diversity and rotation frequency on soil fertility, plant–pest interactions, and productivity (Haggar and Ewel 1994). Sites included 10-yr-old *Cordia alliodora* R. & P. Cham. (Boraginaceae) plantations and fertilized and unfertilized 1-yr-old *C. alliodora* plantations. The 1-yr-old plantations had been cleared annually and replanted each year for 10 years (see Plate 1). Fertilized 1-yr-old plantations received a liquid formulation of urea plus NO_3^- (31% N volume:volume) at a rate of 320 kg·ha^{-1}·yr^{-1} every two weeks; the fertilizer was applied uniformly across the soil surface, and an equal volume of water was sprayed concomitantly on control plots. The plantations were located on alluvial terraces 41 m above sea level and surface soils are well-drained sandy loams (Andisols) (Hiremath and Ewel 2001). The old-growth forest sites were part of a landscape-scale study designed to quantify C storage and fluxes in tropical forest and were located on alluvial terraces and volcanically derived upland residual soils (Clark and Clark 2000). Forest sites on alluvial soils were similar in soil texture, topography, and drainage to the plantation sites. Although the alluvial soils have not been aged, they may have been older than the plantation terraces and were younger than the residual soils (Veldkamp et al. 2003). We included the sites on the residual soils to compare N cycling between two common tropical-forest soil types and to expand the range of C-to-NO_3^- ratios sampled. The residual soils (Ultisols) have high clay content and are well drained due to good aggregation. There was significantly more soil C and N in the old-growth forest, and significantly lower bulk density of the surface soil (0-10 cm depth) than in the plantations (Table 1).

Field experiment

A field experiment was conducted using ^{15}N tracers to examine patterns in gross N cycling, microbial N assimilation, DNRA (dissimilatory nitrate reduction to ammonium), and nitrous oxide fluxes. The field study was conducted at the height of the rainy season (late June) when soils experience periods of saturation. We used three replicate plots of each treatment in the plantations, and three plots each on alluvial and residual soils in the old-growth forest. In the plantations and old-growth forest on alluvial soils we installed 28 uncapped, 6-cm-diameter × 12-cm-long PVC cores into the top 10 cm of soil in each plot, yielding a sample size of four cores per ^{15}N label per time period per plot, plus a set of four natural-abundance samples per plot. In the old-growth forest on residual soils, we used 42 cores per plot, giving a sample size of six cores per

label and time point per plot, plus six natural-abundance cores per plot. Cores were randomly selected for natural-abundance measurements and removed from the field for extraction. Additional randomly selected cores were injected with ^{15}N label and incubated in situ prior to being sampled at ~30 min (approximating an initial period), at 3 h, and at 24 h after label addition. We focus our results on the 3-h incubation because N cycling and associated label transformations were rapid, indicating significant potential for label recycling by 24 h. Label addition can impact rates of N cycling by increasing soil moisture. In this study there was no significant pattern in soil moisture between natural-abundance cores and those with label added. We use the 24-h data as conservative estimates of microbial N pools, rates of microbial N assimilation, and the mean residence time of the NH_4^+ pool.

The concentrations of label solution were determined following measurement of background concentrations of NH_4^+ and NO_3^- in the soils with the goal of establishing a target enrichment of 15 atom % in all sites. We injected all labeled cores with six 1-mL aliquots of solution distributed throughout the core volume. The plantation soils were injected with either 0.21 μg ^{15}N-NH_4^+/g or 0.60 μg ^{15}N- NO_3^-/g. The old-growth forest sites received 1.36 μg ^{15}N- NH_4^+/g or 1.15 μg ^{15}N-NO_3^-/g. All label solutions were 99 atom % ^{15}N. Gas fluxes were measured for the 1-h period before cores were removed from the field at 3 h. For gas sampling we collected 30 mL of headspace gas from 450-mL PVC chambers four times over 1 h from half the labeled cores from each plot (sample size, $n = 6$ samples per label per sampling period for all alluvial soils; $n = 9$ samples for residual soils). Following gas sampling, cores were harvested, extruded into plastic bags, well mixed, transported to La Selva's laboratory, and immediately extracted. A 30-g oven-dry equivalent (ODE) sample was then measured into 150 mL of 2 mol/L KCl. For microbial biomass N and ^{15}N determinations, we divided additional subsamples into two aliquots: one was extracted immediately in 0.5 mol/L K_2SO_4 and the other was fumigated with ethanol-free chloroform for four days before extraction. Additional subsamples were used to determine soil moisture after drying soils at 105°C to a constant mass. Extracts were shipped frozen to the University of California, Berkeley, California USA (UC Berkeley), for analysis.

Laboratory experiment

We conducted the laboratory experiment in the drier season (February) to determine the potential effects of redox conditions on N cycling. Four composite soils bags were collected per plot from each of three plots of 10-yr-old *Cordia alliodora* monocultures and 10-yr-old polyculture plantations planted with *C. alliodora* and two monocots, *Heliconia imbricata* A (Kunze) Baker and *Euterpe oleracea*. Mart, yielding a total of 24 replicates (12 replicates per cover type). Each soil bag was a composite of multiple samples (approximately 320 g ODE soil each) collected from randomly selected locations from the 0–10 cm depth using a 2.5-cm-diameter corer. Soils were delivered to UC Berkeley within 48 h of collection. Soil bags were split upon arrival into a set held under ambient conditions and a set that was held in an N_2 atmosphere for 12 h (overnight) to impose short-term anaerobic conditions. Half of each group of samples (ambient and N_2 incubations) received $(^{15}NH_4)_2SO_4$ at a soil concentration of 0.31 μg/g (final soil enrichment of 15.6 atom % $^{15}NH_4^+$), and the other half received $^{15}KNO_3$ added at a soil concentration of 0.42 μg/g (final soil enrichment of 15.4 atom % $^{15}NO_3^-$). We incubated 30 g ODE samples from each set of labeled soils in 450-mL jars under ambient conditions and under an N_2 headspace for 15 min and 3 h, all at 25°C. Two 30-mL gas samples were taken from each jar at the end of the incubation for N_2O and $^{15}N_2O$ analyses. The soils receiving a $^{15}NO_3^-$ label were split into three aliquots after gas sampling. One was extracted with 150-mL of 2 mol/L KCl for determination of mineral N and ^{15}N pools. Another was extracted immediately with 80 mL of 0.5 mol/L K_2SO_4. The third was fumigated with ethanol-free chloroform for five days and then extracted with 80 mL of 0.5 mol/L K_2SO_4. The latter two were used for microbial biomass N and ^{15}N analyses.

Analytical and statistical procedures

We determined NH_4^+ and $NO_3^- + NO_2^-$ concentrations colorimetrically (Lachat Quik Chem flow injection analyzer; Lachat Zellweger Instruments, Milwaukee, Wisconsin, USA). Extracts were prepared for isotope analysis by diffusion (Herman et al. 1995), and N-isotope ratios were measured using an automated nitrogen–carbon analyzer coupled to an isotope-ratio mass spectrometer (ANCA-IRMS; PDZ Europa Limited, Crewe, UK). We determined N_2O concentrations by gas chromatography using an electron capture -^{63}Ni detector (GC 8610c; SRI Instruments, Torrance, California, USA), and determined N-gas isotope ratios using a trace-gas module coupled to the IRMS. Total N in K_2SO_4 extracts was measured by Kjeldahl digestion and colorimetry. Isotope ratios were measured by diffusion and ANCA-IRMS. Microbial N was calculated as the difference in extractable Kjeldahl N between the fumigated and unfumigated soils with no correction for efficiency.

We calculated rates of DNRA, using the $^{15}NO_3$-labeled samples, as the difference in the $^{15}NH_4^+$ atom % over the incubation interval (3 h), multiplied by the mean NH_4^+ pool size during the interval, and corrected for changes in the isotopic composition of the $^{15}NO_3^-$ source pool over the incubation interval (Silver et al. 2001). We also corrected for any NH_4^+ transported out of the NH_4^+ pool (i.e., mean residence time [MRT] of NH_4^+) over the interval. For the field experiment we estimated the MRT of the $^{15}NH_4^+$ pool by dividing the

initial NH_4^+ pool (in micrograms per gram) by the rate of gross consumption, estimated from the 24-h assay of the $^{15}NH_4^+$-labeled incubations. The MRT value from the 0-24 h interval was chosen because it reduced the short-term impact of soil disturbance, and as it was the longest MRT value measured, its use in the DNRA calculation provided the most conservative estimates of DNRA. For the laboratory experiment we used individual MRT values generated from each treatment.

Gross mineralization, nitrification, and NH_4^+ and NO_3^- consumption were calculated according to Kirkham and Bartholomew (1954) and Hart et al. (1994). We determined the rates of $^{15}N_2O$ fluxes after correction for changes in the $^{15}NO_3^-$ source pool over time (similar to the DNRA calculation) and report the data in the standard units ($ng \cdot cm^{-2} \cdot h^{-1}$) and as $\mu g \cdot g^{-1} \cdot d^{-1}$ for comparison with other N fluxes. Soil moisture was determined gravimetrically after drying subsamples at 105°C to a constant mass. Natural-abundance ^{15}N was measured as above after extracting 30 g ODE soils with 150 mL of 2 mol/L KCl.

Statistical analyses were performed using SYSTAT (Wilkinson 1990). We used one-way analysis of variance (ANOVA) to determine if treatments differed in pool sizes or rates. All analyses were conducted using plot mean values calculated from the multiple cores in each plot. There were three replicate plots per treatment, and five treatments (unfertilized 1-yr-old plantations, fertilized 1-yr-old plantations, 10-yr-old plantations, old-growth forest on alluvial soil, and old-growth forest on residual soil) yielding a total sample size of 15 plots. We compared mineral-N pools, gross N transformations, N_2O fluxes, DNRA, and microbial biomass N pools among all five treatments. Soil microbial-biomass N values were pooled across labels for analyses (sample size, $n = 15$ plots); we analyzed microbial biomass ^{15}N separately for $^{15}NO_3^-$ and $^{15}NH_4^+$ labels. We also tested the hypothesis that N pools and transformations differed fundamentally by cover type, comparing plantations ($n = 9$ plots) with old-growth forest ($n = 6$ plots), omitting plantation treatment and soil type. For the laboratory experiment, we had 12 replicates per cover type and two cover types (monoculture and polyculture). Data were log-transformed when necessary to meet assumptions for ANOVA. Significant differences were determined as $P < 0.05$ unless otherwise noted.

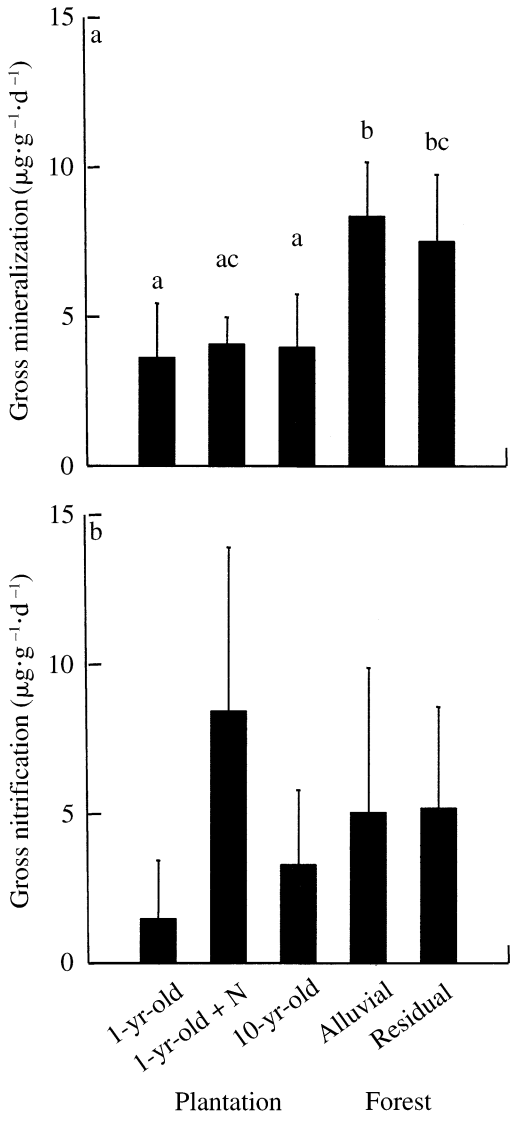

FIG. 1. (a) Gross N mineralization and (b) nitrification rates in plantations and old-growth forests in Costa Rica. Sites were either 1-yr-old (N fertilized or unfertilized) or 10-yr-old plantations, or old-growth forests on alluvial or residual soils. Rates were determined following 3 h of incubation. Data are means and standard errors. There were three replicate plots per treatment. In panel (a), bars with the same lowercase letter are not significantly different among treatments at $P < 0.09$; there are no significant differences among treatments in panel (b).

RESULTS

Nitrogen pools and internal fluxes

The background NH_4^+ pool averaged 0.73 ± 0.17 μg/g (mean ± SE) and did not differ significantly among treatments (Table 1). Soil NO_3^- averaged 1.58 ± 0.16 μg/g; there was significantly less soil NO_3^- in the 10-yr-old plantations than in the 1-year-old plantations or the old-growth forests. The ratio of soil C (in percentage) to NO_3^- (in micrograms per gram) ranged from 1.44 ± 0.10 in the unfertilized young plantation to 3.24 ± 0.28 in the old-growth forest on residual soils, and was significantly lower in the young plantations than in the older plantations and old-growth forests (Table 1). Background soil NO_3^- pools were positively correlated with soil C ($r^2 = 0.60$, $P < 0.01$).

There were large and statistically significant differences in gross N mineralization rates among sites (Fig. 1, Table 2). Gross mineralization rates were signifi-

TABLE 2. Rates of gross N cycling, dissimilatory nitrate reduction to ammonium (DNRA), and the ratio of DNRA to gross N-cycling rates in fertilized and unfertilized plantations and old-growth forests at La Selva Biological Station, Costa Rica.

Measurement	Plantations		Forests	
	Mean	SE	Mean	SE
Gross N mineralization ($\mu g \cdot g^{-1} \cdot d^{-1}$)	3.88[a]	0.60	7.94[b]	0.99
Gross NH_4^+ consumption ($\mu g \cdot g^{-1} \cdot d^{-1}$)	3.24[a]	0.69	11.45[b]	2.87
Gross nitrification ($\mu g \cdot g^{-1} \cdot d^{-1}$)	4.40	1.73	5.09	2.02
Gross NO_3^- consumption ($\mu g \cdot g^{-1} \cdot d^{-1}$)	2.27	0.85	5.22	2.61
DNRA ($\mu g \cdot g^{-1} \cdot d^{-1}$)	0.23	0.12	0.24	0.08
DNRA : gross mineralization (%)	5.34	2.24	3.43	1.27
DNRA : gross nitrification (%)	9.88	8.32	2.82	0.75

Notes: Sample size: for plantations, $n = 9$ plots; for forests, $n = 6$ plots. Means with the same lowercase letter are not significantly different between cover types at $P < 0.05$.

cantly higher in the old-growth forests than in the plantations. Fertilized 1-yr-old plantations tended to have higher gross N mineralization rates than did controls (Fig. 1), but the differences were not significant at the 95% level, and were not as large as differences between plantations and old-growth forests. Gross mineralization rates did not differ between 1-yr-old and 10-yr-old plantations, but 10-yr-old plantations had significantly lower rates of gross N mineralization than the old-growth forest on the same soil type. There was no effect of soil type on gross N mineralization in the old-growth forests. Gross mineralization rates were similar to rates of gross NH_4^+ consumption (Table 2), and the two were significantly positively correlated ($r^2 = 0.60$, $P < 0.01$). Gross nitrification rates averaged 63–64% of gross mineralization in the absence of fertilization. In the fertilized plots gross nitrification rates were similar to gross mineralization. Fertilization led to a fivefold increase in rates of gross nitrification in 1-yr-old plantations relative to controls ($P = 0.1$) (Fig. 1b). Gross nitrification rates were more variable than gross mineralization rates, and there were no significant differences among unfertilized plantations or old-growth forests. Gross nitrification rates averaged 4.7 ± 1.3 $\mu g \cdot g^{-1} \cdot d^{-1}$, and the mean gross NO_3^- consumption rate was 3.4 ± 1.2 $\mu g \cdot g^{-1} \cdot d^{-1}$. Total gross N consumption (gross NH_4^+ consumption plus gross NO_3^- consumption) was significantly and positively correlated with gross N mineralization ($r^2 = 0.52$, $P < 0.01$).

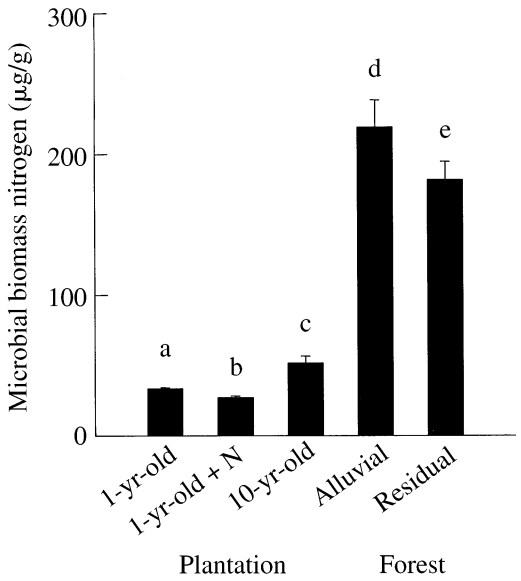

FIG. 2. Microbial-biomass N in plantations and old-growth forests in Costa Rica. Data are means and standard errors. There were three replicate plots per treatment; there were no statistically significant differences between labels so data were pooled. See Fig. 1 legend for site information. Bars with different lowercase letters are significantly different among treatments at $P < 0.01$.

Microbial-biomass N varied greatly among treatments (Fig. 2). Values were lowest in the fertilized 1-yr-old plantations (27 ± 0.8 μg/g [mean ± SE]) and highest in the old-growth forests on alluvial soils (219 ± 15 μg/g). On average, microbial biomass was 5 times greater in the old-growth forests than in plantations. Microbial biomass N was significantly and positively correlated with gross mineralization rates ($r^2 = 0.47$, $P < 0.01$). The microbial-biomass ^{15}N was slightly enriched (0.402 ± 0.017 atom %; $P = 0.09$) relative to mineral-N natural-abundance values (0.365 ± 0.001 atom %) in the old-growth forests, amounting to an uptake of approximately 5% of the added label. It is important to note that we did not correct the microbial-biomass estimates for the efficiency of extraction. If we use a standard conversion value of K_n (the proportion of N mineralized during the procedure) = 0.54 (Horwath and Paul 1994) the amount of $^{15}NH_4^+$ uptake by the microbial biomass was ~0.11 $\mu g \cdot g^{-1} \cdot d^{-1}$ or 8% of the added label. Following $^{15}NO_3^-$ addition there was no significant enrichment in microbial biomass ^{15}N compared to natural-abundance values, indicating little or no microbial assimilation of the $^{15}NO_3^-$ label.

Dissimilatory NO_3^- reduction to NH_4^+ occurred in all plantation and old-growth forest soils (Table 2). Rates of DNRA averaged 0.23 ± 0.08 $\mu g \cdot g^{-1} \cdot d^{-1}$ and did not differ among treatments. DNRA accounted for only a small proportion of gross mineralization (5 ±

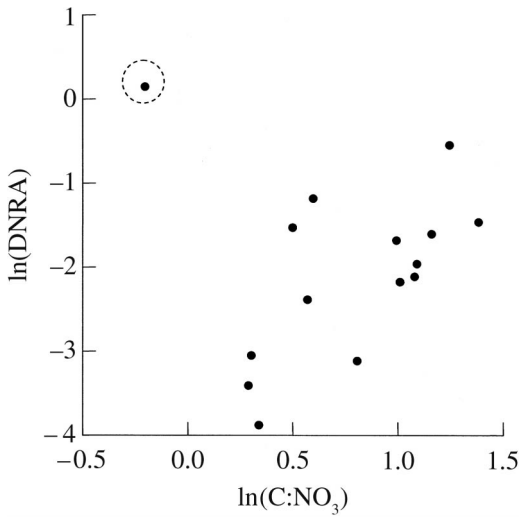

FIG. 3. The C-to-NO_3^- ratio plotted against DNRA rates (dissimilatory nitrate reduction to ammonium, in micrograms per gram per day) for plantations and old-growth forests in Costa Rica. One data point from the fertilized young plantation (circle with dashed line) was excluded as an outlier from the analyses. There were three replicate plots per treatment.

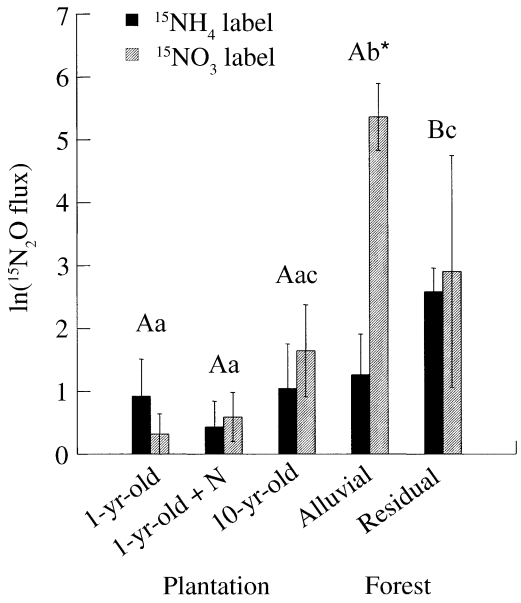

FIG. 4. $^{15}N_2O$ fluxes (in nanograms per square centimeter per hour) following NO_3^- and NH_4^+ label additions in plantations and old-growth forests in Costa Rica. Rates were determined following 3 h of incubation. Data are means and standard errors. There were three replicate plots per treatment. Bars with the same lowercase letters are not significantly different among NO_3^- label treatments at $P < 0.05$. Bars with the same uppercase letter are not significantly different among NH_4^+ label treatments at $P \leq 0.05$. The asterisk identifies a significant difference between NO_3^- and NH_4^+ labels at $P < 0.05$.

1%) and nitrification (7 ± 5%). Across all plantation and old-growth forest sites the ratio of soil C to NO_3^- explained 44% of the variability in DNRA rates ($P < 0.01$, outlier removed; Fig. 3).

Nitrous oxide fluxes

Nitrous oxide losses also occurred from all treatments. There were few differences between the $^{15}NH_4$ and $^{15}NO_3$ labels in the $^{15}N_2O$ fluxes (Fig. 4); only in the old-growth forest on alluvial soils did we see greater $^{15}N_2O$ effluxes following $^{15}NO_3^-$ addition than from $^{15}NH_4^+$ additions ($P < 0.05$). The highest $^{15}N_2O$ fluxes occurred from alluvial soils in old-growth forest after $^{15}NO_3^-$ addition (251 ± 104 ng·cm^{-2}·h^{-1}), which were significantly higher than at all other sites. The plantations all averaged < 7 ng $^{15}N_2O$·cm^{-2}·h^{-1} and did not vary significantly by age, fertilization, or label added. When converted to the same unit as DNRA "(μg·g^{-1}·d^{-1})," $^{15}N_2O$ emissions were significantly lower than DNRA rates in the plantations, driven primarily by differences in the 10-yr-old site, and similar to DNRA rates in the old-growth forests. The flux of $^{15}N_2O$ (NO_3^- label) was not correlated with soil C, NO_3^-, or the C:NO_3^- ratio (data not shown).

The effects of reducing conditions

There were no statistically significant differences in rates of N cycling between the monoculture and polyculture plantations, so data were pooled for analyses. Laboratory gross N-cycling rates under ambient atmospheres were within the same range of values reported in the field experiment (Tables 2 and 3). Gross

TABLE 3. Rates of gross N cycling, dissimilatory nitrate reduction to ammonium (DNRA), and the ratio of DNRA to gross N-cycling rates in 10-yr-old plantations at La Selva Biological Station, Costa Rica.

Measurement	Ambient headspace		N_2 headspace	
	Mean	SE	Mean	SE
Gross N mineralization (μg·g^{-1}·d^{-1})	5.18[a]	1.17	2.19[b]	0.47
Gross nitrification (μg·g^{-1}·d^{-1})	7.45[a]	0.86	5.03[b]	1.16
Microbial biomass N (μg/g)	51.13	2.26	53.59	2.52
DNRA (μg·g^{-1}·d^{-1})	0.33	0.12	0.34	0.08
DNRA : gross mineralization	8.28[a]	3.17	25.01[b]	11.67
DNRA : gross nitrification	5.06[a]	2.13	9.27[b]	3.66

Notes: $N = 24$ replicates. Different means with the same lowercase letter are not significantly different between ambient and N_2 headspaces at $P < 0.05$.

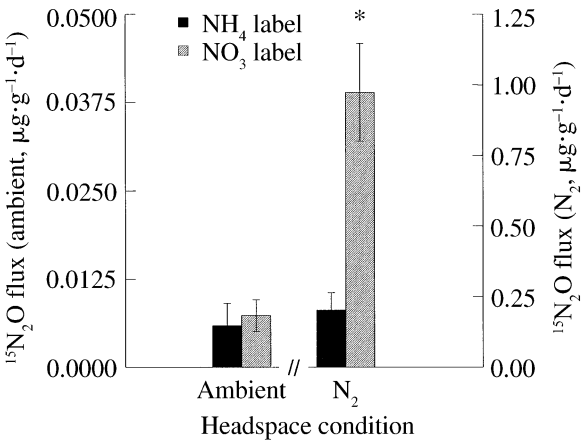

FIG. 5. $^{15}N_2O$ fluxes following NO_3^- and NH_4^+ label additions under ambient and N_2 headspace conditions in tropical plantation soils from Costa Rica. Data are means ± SE. There were 24 replicates per treatment. The asterisk identifies a significant difference between $^{15}N_2O$ fluxes from the NH_4^+ and NO_3^- labels ($P < 0.05$).

mineralization and nitrification rates both decreased significantly under an N_2 headspace (Table 3). Microbial biomass N was measured following $^{15}NO_3^-$ addition and averaged 52 ± 2 μg/g (Table 3), and there was no ^{15}N enrichment, indicating no uptake of the label (data not shown). DNRA averaged 0.33 ± 0.10 $\mu g \cdot g^{-1} \cdot d^{-1}$ and was not affected by the composition of the headspace atmosphere. DNRA averaged 8 ± 3% of gross mineralization and 5 ± 2% of gross nitrification under ambient headspace. Under an N_2 headspace, the ratio of DNRA to gross mineralization increased significantly to 25 ± 11% and 9 ± 4% of gross nitrification due to the decline in gross mineralization and nitrification rates (Table 3).

An N_2 headspace stimulated $^{15}N_2O$ fluxes following both $^{15}NH_4^+$ and $^{15}NO_3^-$ additions (Fig. 5). There were no statistically significant differences in $^{15}N_2O$ fluxes between labels under ambient conditions, but $^{15}N_2O$ fluxes were much greater following $^{15}NO_3^-$ addition under a N_2 headspace. DNRA rates were significantly greater than $^{15}N_2O$ fluxes following both label additions under an ambient headspace. Under an N_2 headspace and following the $^{15}NO_3^-$ addition, average N fluxes were almost 3 times greater via $^{15}N_2O$ production (0.97 ± 0.17 $\mu g \cdot g^{-1} \cdot d^{-1}$) than DNRA (0.34 ± 0.08 $\mu g \cdot g^{-1} \cdot d^{-1}$) (Fig. 6).

DISCUSSION

Gross nitrogen cycling rates in plantations and natural forests

Our results indicate that plantation establishment in tropical forests can result in a decline in the rate of N cycling, although the effect varied among N-cycling pathways. Plantations had significantly lower rates of gross N mineralization and NH_4^+ consumption. Gross nitrification averaged over 60% of gross mineralization in unfertilized plantations and old-growth forests in the absence of root uptake. If we estimate the rate of gross NH_4^+ immobilization as NH_4^+ consumption minus gross nitrification (Davidson et al. 1991), then there was no gross NH_4^+ immobilization for the plantations, while the old-growth forests immobilized approximately 6.4 ± 4.5 $\mu g \cdot g^{-1} \cdot d^{-1}$ (mean ± SE). This pattern is consistent with trends in N mineralization, coupled with the dramatic decline in soil microbial-biomass N in the plantations. Ammonium immobilization serves to retain N in ecosystems. The loss of immobilization capacity in the plantations signals a loss of an important N conservation mechanism.

Gross N-cycling rates have not been measured in many tropical forests or plantations. Gross N-mineralization rates in our 10-yr-old plantations were lower than rates reported for 12-yr-old *Albizia* and *Eucalyptus* plantations growing under similar mean annual rainfall and temperature, but on younger soils in Hawaii. However, gross nitrification rates in Hawaii were generally lower than those in the Costa Rican plantations (Garcia-Montiel and Binkley 1998). Gross N-cycling rates in the Costa Rican old-growth forest sites were higher than those in seasonally dry forests in Brazil (Neill et al. 1999) and wet forests in Puerto Rico (Silver et al. 2001). The comparison with Puerto Rico is particularly striking for gross nitrification rates (5 ± 1 $\mu g \cdot g^{-1} \cdot d^{-1}$ in Costa Rica and 0.6 ± 0.1 $\mu g \cdot g^{-1} \cdot d^{-1}$ in Puerto Rico [means ± SE]), and is likely a result of the stronger reducing conditions in the Puerto Rican soils limiting nitrifier activity (Silver et al. 2001).

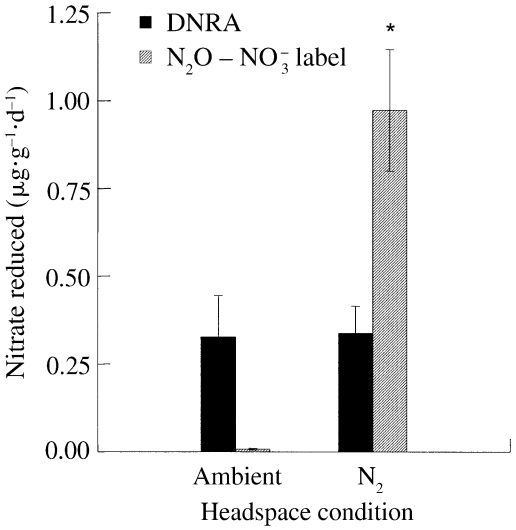

FIG. 6. Comparison of NO_3^- reduced via DNRA and denitrification to N_2O under ambient and N_2 headspace conditions in tropical plantation soils from Costa Rica. Samples were taken 3 h after $^{15}NO_3$ label addition. Data are means and standard errors. There were 24 replicates per treatment. The asterisk identifies a significant difference between ambient and N_2 headspaces ($P < 0.01$).

The very short rotation length in the 1-yr-old plantations had few obvious effects on gross N cycling relative to 10-yr-old plantations. This is somewhat surprising given high rates of NO_3^- leaching reported for these sites (Bigelow et al. 2004). Fertilization did not increase rates of gross N mineralization, but it more than tripled gross nitrification, suggesting that fertilization may be stimulating nitrifier activity (Tietema 1998). Long-term fertilization in Hawaiian forests significantly increased rates of gross mineralization relative to controls where net primary production (NPP) was limited by N, but had no effect in forests that showed no N limitation to NPP (Hall and Matson 2003). The relatively large N pools (particularly in the forests) and high rates of cycling measured in this study might suggest that these soils have sufficient N available to plants and microbes. While this is expected in the old-growth forests (Vitousek and Sanford 1986), it is surprising in the short-rotation plantation forests. Sufficient N availability for plant growth is only sustainable if high leaching and N exports in harvests are balanced by N deposition and N fixation.

The role of DNRA and N_2O fluxes in nitrogen cycling

Dissimilatory nitrate reduction to ammonium (DNRA) has the potential to reduce N losses via leaching and gaseous emissions by decreasing the size of the NO_3^- pool. Bigelow et al. (2004) measured high NO_3^- leaching losses from the 1-year-old plantations amounting to ~62 $kg \cdot ha^{-1} \cdot yr^{-1}$. We can roughly determine the relative importance of N retention via DNRA and N losses via leaching and N_2O fluxes by converting their data to a daily leaching rate and adding this to the N_2O fluxes measured here. The rate of N loss via these pathways is ~18 mg $N \cdot m^{-2} \cdot d^{-1}$, more than double the amount of N conserved via DNRA (8 mg $N \cdot m^{-2} \cdot d^{-1}$). In the 10-yr-old plantations, N retention via DNRA was 3 times greater (15 mg $N \cdot m^{-2} \cdot d^{-1}$) than the combined losses via leaching and N_2O emissions (5 mg $N \cdot m^{-2} \cdot d^{-1}$). This coupled with relatively high N uptake rates by plants in the 10-yr-old plantations (~40 mg $N \cdot m^{-2} \cdot d^{-1}$, Hiremath and Ewel 2001) suggests that the older, less disturbed plantations are cycling N much more efficiently. It is important to note that we did not report N lost via nitric oxide (NO) or di-nitrogen (N_2). We would not expect to see high NO fluxes from these very humid soils, but N_2 fluxes during denitrification could be a significant N-loss pathway, particularly at low levels of NO_3^- availability.

There are few reported values for DNRA in upland ecosystems. The values reported here are lower than those for humid tropical old-growth forests in Puerto Rico where DNRA rates averaged ~0.9 $\mu g \cdot g^{-1} \cdot d^{-1}$ following 2.5 h of incubation and exceeded $^{15}N_2O$ losses by a factor of 3 (Silver et al. 2001). Unlike the Puerto Rico study, DNRA in these soils did not appear to be sensitive to the range of available NO_3 and nitrification rates, nor to the size of the C pool. Tiedje et al. (1982) predicted that DNRA rates would increase as the ratio of available C to available NO_3^- increased. Here we had no measure of labile C, but DNRA increased proportionally with the ratio of total C to NO_3^-. We expect that a significant proportion of the C in surface soils of tropical forests and plantations is relatively labile (Trumbore et al. 1995), explaining the relationship we report here.

Average DNRA rates were strikingly similar in plantations and forests, suggesting that plantation establishment, repeated disturbance, and disturbance coupled with fertilization did not affect the rate of N retention via this pathway, even though rates of gross N mineralization declined in the plantations. Patterns of N loss via $^{15}N_2O$ emissions were sensitive to cover type. Plantations lost significantly less $^{15}N_2O$ than the old-growth forests, and there was no effect of plantation age or fertilization on $^{15}N_2O$ fluxes. The lower rates of $^{15}N_2O$ emissions from the plantations relative to the old-growth forests may result from other fates of $^{15}NO_3^-$ such as leaching or denitrification to N_2. The amount of $^{15}N_2O$ produced following a $^{15}NO_3^-$ label, presumably dominated by denitrification, exceeded the amount emitted following a $^{15}NH_4^+$ label in the alluvial old-growth forest soils, but not in the plantations. In the plantations, high nitrification rates undoubtedly contributed to N_2O losses; low overall N_2O fluxes and relatively high variability may have also contributed to the lack of statistically significant differences between labels.

The effects of reducing conditions on nitrogen cycling

Our laboratory experiment was designed to estimate the sensitivity of N-cycling pathways to periodic reducing conditions common in humid tropical-forest soils. We collected samples from two plantation types, a monoculture and a three-species polyculture, but found that community structure had no impact on N pools or cycling rates. Laboratory rates of gross N mineralization under an ambient atmosphere were similar to those in the field and decreased in an N_2 headspace. Although the process of N mineralization does not require oxygen, a decrease in activity of aerobic microorganisms with declining oxygen could result in an overall decrease in rates of gross mineralization. Gross nitrification rates also decreased under an N_2 headspace, which is expected for an aerobically mediated process. DNRA rates were insensitive to headspace conditions. Similar results were reported in Puerto Rican forests, and were attributed to NO_3^- limitation of DNRA under ambient and reducing conditions. In that study, soil NO_3^- pools were small and DNRA rates were similar to rates of gross nitrification (Silver et al. 2001). In our present study, DNRA rates were ~5–9% of gross nitrification and the initial NO_3^- pools were relatively large (3–4 $\mu g/g$). Clearly, other factors limit

DNRA in the 10-year old plantations, where NO_3^- does not appear to be in short supply, even under an N_2 headspace.

Reducing conditions had a large and significant impact on N_2O emissions via denitrification. Under an N_2 atmosphere $^{15}N_2O$ fluxes increased by more than two orders of magnitude and were greater than DNRA. These data highlight the greater relative sensitivity of N_2O production than DNRA to low redox conditions in these soils. These data also highlight the potential for significant N trace-gas losses from these soils if redox declines.

Conclusions

This study was designed to examine the effects of plantation establishment and management on gross N cycling, potential N retention via DNRA, and N losses via N_2O emissions. We also determined the effects of common humid tropical soil conditions (redox, soil type) on N dynamics. Our results show that gross N mineralization can decline in young plantations, decreasing the supply of available N, and that much of the mineralized N is nitrified, becoming susceptible to loss via leaching and gaseous emissions. Repeated annual harvesting and replanting, without fertilization, had few additional impacts on N cycling relative to longer-term rotations, despite high leaching losses from the short-rotation systems (Bigelow et al. 2004) and decreased C pools (Russell et al. 2004). This is unlikely to be sustainable, and implies that N removal with harvesting is low and/or that N inputs via N fixation are relatively high. Fertilization of the short-rotation plantations increased rates of gross nitrification, but did not significantly affect N_2O fluxes or DNRA. In this study, young plantations exhibited much lower N_2O emissions did than did old-growth forests, but had similar rates of N retention via DNRA. DNRA rates were positively correlated with the ratio of soil C to NO_3^-, while denitrification N_2O fluxes were most sensitive to changes in redox conditions. Our results highlight the potential for changes in N cycling following the replacement of old-growth forests with plantations, but also identify mechanisms that increase the resilience of these systems to intensive management. As plantations become an increasingly important component of the tropical landscape, more information will be needed to better manage these ecosystems for sustainable growth and yield, C sequestration, and lowered greenhouse-gas emissions.

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Literature Cited

Bashkin, M. A., and D. Binkley. 1998. Changes in soil carbon following afforestation in Hawaii. Ecology **79**:828–833.

Bigelow, S. W., J. J. Ewel, and J. P. Haggar. 2004. Enhancing nutrient retention in tropical tree plantations: no short cuts. Ecological Applications **14**:28–46.

Binkley, D., and S. C. Resh. 1999. Rapid changes in soils following eucalyptus afforestation in Hawaii. Soil Science Society of America Journal **63**:222–225.

Brown, A. G., E. K. S. Nambiar, and C. Cossalter. 1997. Plantations for the tropics: their role, extent and nature. Pages 1–23 *in* E. K. S. Nambiar and A. Brown, editors. Management of soil, water, and nutrients in tropical plantation forests. Monograph 43. Australian Centre for International Agricultural Research (ACIAR), Canberra, Australia.

Butterfield, J. 1999. Changes in decomposition rates and Collembola densities during the forestry cycle in conifer plantations. Journal of Applied Ecology **36**:92–100.

Cicerone, R. J. 1987. Changes in stratospheric ozone. Science **237**:35–42.

Clark, D. B., and D. A. Clark. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. Forest Ecology and Management **137**:185–198.

Dail, D. B., E. A. Davidson, and J. Chorover. 2001. Rapid abiotic transformation of nitrate in an acid forest soil. Biogeochemistry **54**:131–146.

Davidson, E. A., S. C. Hart, C. A. Shanks, and M. K. Firestone. 1991. Measuring gross nitrogen mineralization, immobilization, and nitrification by N-15 isotopic pool dilution in intact soil cores. Journal of Soil Science **42**:335–349.

Davidson, E. A., W. T. Swank, and T. O. Perry. 1986. Distinguishing between nitrification and denitrification as sources of gaseous nitrogen production in soil. Applied Environmental Microbiology **12**:1280–1286.

DeFries, R. S., R. A. Houghton, M. C. Hansen, C. B. Field, D. Skole, and J. Townshend. 2002. Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. Proceedings of the National Academy of Sciences (USA) **99**:14256–14261.

Ewel, J., C. Berish, B. Brown, N. Price, and J. Raich. 1981. Slash and burn impacts on a Costa Rican wet forest site. Ecology **62**:816–829.

Garcia-Montiel, D. C., and D. Binkley. 1998. Effect of *Eucalyptus saligna* and *Albizia falcataria* on soil processes and nitrogen supply in Hawaii. Oecologia **113**:547–556.

Haggar, J. P., and J. J. Ewel. 1994. Experiments on the ecological basis of sustainability: early findings on nitrogen, phosphorus, and root systems. Interciencia **19**:347–51.

Hall, S. J., and P. A. Matson. 2003. Nutrient status of tropical rain forests influences soil N dynamics after N additions. Ecological Monographs **73**:107–129.

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

Herman, D. J., P. D. Brooks, M. Ashraf, F. Azam, and R. L. Mulvaney. 1995. Evaluation of methods for nitrogen-15 analysis of inorganic nitrogen in soil extracts. II. Diffusion methods. Communications in Soil Science and Plant Analysis **26**:1675–1685.

Hiremath, A. J., and J. J. Ewel. 2001. Ecosystem nutrient use efficiency, productivity, and nutrient accrual in model tropical communities. Ecosystems **4**:669–682.

Horwath, W. R., and E. A. Paul. 1994. Microbial biomass. Pages 753–774 *in* R. W. Weaver, J. S. Angle, P. N. Bottomley, D. F. Bezdicek, M. S. Smith, M. A. Tabatabai, and A. G. Wollum, editors. Methods of Soil analysis, Part 2. Microbiological and biochemical properties. Soil Science Society of America, Madison, Wisconsin, USA.

Houghton, R. A. 2003. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000. Tellus Series B—Chemical and Physical Meteorology **55**:378–390.

Keller, M., E. Veldkamp, A. M. Weitz, and W. A. Reiners. 1993. Effect of pasture age on soil trace-gas emissions from a deforested area of Costa Rica. Nature **365**:244–246.

Kirkham, D., and W. V. Bartholomew. 1954. Equations for following nutrient transformations in soil, utilizing tracer data. Soil Science Society of America Proceedings **18**:33–34.

Lashof, D. A., and D. R. Ahuja. 1990. Relative contributions of greenhouse gas emissions to global warming. Nature **344**:529–531.

Lugo, A. E. 1992. Comparison of tropical tree plantations with secondary forests of similar age. Ecological Monographs **62**:1–41.

Malmer, A. 1996. Hydrological effects and nutrient losses of forest plantation establishment on tropical rainforest land in Sabah, Malaysia. Journal of Hydrology **174**:129–148.

Matson, P. A., P. M. Vitousek, J. J. Ewel, M. J. Mazzarino, and G. P. Robertson. 1987. Nitrogen transformations following tropical forest felling and burning on a volcanic soil. Ecology **68**:491–502.

McDowell, W. H. 2002. Nutrient flux from tropical rain forests. Pages 149–163 *in* R. S. Ambasht and N. K. Ambasht, editors. Modern trends in applied terrestrial ecology. Kluwer Academic Press, New York, New York, USA.

Neill, C., M. C. Piccolo, J. M. Melillo, P. A. Steudler, and C. C. Cerri. 1999. Nitrogen dynamics in Amazon forest and pasture soils measured by ^{15}N pool dilution. Soil Biology & Biochemistry **31**:567–572.

Robertson, G. P., and J. M. Tiejde. 1988. Deforestation alters denitrification in a lowland tropical forest. Nature **336**:756–759.

Russell, A. E., C. A. Cambardella, J. J. Ewel, and T. B. Parkin. 2004. Species, rotation, and life-form diversity effects on soil carbon in experimental tropical ecosystems. Ecological Applications **14**:47–60.

Sanford, R. L., Jr., P. Paaby, J. C. Luvall, and E. Phillips. 1994. Climate, geomorphology, and aquatic systems. Pages 19–33 *in* L. A. McDade, K. S. Bawa, H. A. Hespenheide, and G. S. Hartshorn, editors. La Selva: ecology and natural history of a neotropical rain forest. University of Chicago Press, Chicago, Illinois, USA.

Silver, W. L., D. J. Herman, and M. K. Firestone. 2001. Dissimilatory nitrate reduction to ammonium in upland tropical forest soils. Ecology **82**:2410–2416.

Silver, W. L., M. Keller, and A. E. Lugo. 1999. Soil oxygen availability and biogeochemical cycling along elevation and topographic gradients in Puerto Rico. Biogeochemistry **44**:301–328.

Silver, W. L., R. Ostertag, and A. E. Lugo. 2000. The potential for carbon sequestration through reforestation of tropical agricultural and pasture lands. Restoration Ecology **8**:394–407.

Silver, W. L., and K. A. Vogt. 1993. Fine root dynamics following single and multiple disturbances in a subtropical wet forest ecosystem. Journal of Ecology **8**:729–738.

Tanner, E. V. J., V. Kapos, and W. Franco. 1992. Nitrogen and phosphorus fertilization effects on Venezuelan montane forest trunk growth and litterfall. Ecology **73**:78–86.

Tiedje, J. M. 1988. Ecology of denitrification and dissimilatory nitrate reduction to ammonium. Pages 179–244 *in* A. J. B. Zehnder, editor. Biology of anaerobic microorganisms. John Wiley and Sons, New York, New York, USA.

Tiedje, J. M., A. J. Sexton, D. D. Myrold, and J. A. Robinson. 1982. Denitrification: ecological niches, competition, and survival. Antonie van Leeuwenhock **48**:569–583.

Tietema, A. 1998. Microbial carbon and nitrogen dynamics in coniferous forest floor material collected along a European nitrogen-deposition gradient. Forest Ecology & Management **101**:29–36.

Trumbore, S. E., E. A. Davidson, P. Barbosa de Camargo, D. C. Nepstad, and L. A. Martinelli. 1995. Belowground cycling of carbon in forests and pastures of Eastern Amazonia. Global Biogeochemical Cycles **9**:515–528.

Veldkamp, E., A. Becker, L. Schwendenmann, D. A. Clark, and H. Schulte-Bisping. 2003. Substantial labile carbon stocks and microbial activity in deeply weathered soils below a tropical wet forest. Global Change Biology **9**:1171–1184.

Vitousek, P. M., and R. W. Howarth. 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry **13**:87–115.

Vitousek, P. M., and P. A. Matson. 1988. Nitrogen transformations in a range of tropical forest soils. Soil Biology and Biochemistry **20**:361–367.

Vitousek, P. M., and P. A. Matson. 1992. Tropical forests and trace gases: potential interactions between tropical biology and the atmospheric sciences. Biotropica **24**:233–239.

Vitousek, P., and R. Sanford. 1986. Nutrient cycling in moist tropical forest. Annual Review of Ecology and Systematics **17**:137–167.

Wilkinson, L. 1990. SYSTAT. The system for statistics. SYSTAT, Evanston, Illinois, USA.