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NITROGEN TRANSFORMATIONS FOLLOWING TROPICAL FOREST FELLING AND BURNING ON A VOLCANIC SOIL[1]

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Abstract. We measured nitrogen transformations and loss following forest clearing in a relatively fertile tropical forest site. Nitrogen mineralization, nitrification, and amounts of ammonium and nitrate increased substantially in surface soils during the 6 mo following burning, then returned to background levels. The nitrogen content of microbial biomass declined to half its original value 6 mo after clearing and remained low in the cleared sites. Plant uptake of nitrogen was substantial on cleared plots (50 g/m^2), but it accounted for only 18% of ^{15}N label added to field plots. Microbial immobilization of ^{15}N was small relative to that in a cleared temperate site, and measurements of denitrification potentials suggested that relatively little mineralized nitrogen was lost to the atmosphere. Substantial amounts of nitrogen (40–70 g/m^2) were retained as exchangeably bound nitrate deep in the soils of a cleared plot on which revegetation was prevented; this process accounted for 12% of the ^{15}N label added to field plots.

Key words: anion exchange; Costa Rica; disturbance; nitrification; nitrogen mineralization; nutrient cycling; nutrient retention; slash and burn; tropical deforestation.

INTRODUCTION

A number of studies have demonstrated that large amounts of organic carbon and nitrogen are lost from surface soils during and after land clearing in the tropics. Fires associated with land clearing volatilize 300–700 kg/ha of N from vegetation and surface litter (Nye and Greenland 1964, Ewel et al. 1981), and another 500–2000 kg/ha of N disappear from surface soils in the year or two following clearing and burning (Nye and Greenland 1960, Laudelot 1962, Brinkmann and de Nascimento 1973, Bartholomew 1977, Chijicke 1980, Sanchez et al. 1982, 1985, Allen 1985, Robertson and Rosswall 1986). If overall losses average 1000 kg/ha, then 20–25 × 10^9 kg of N are mobilized annually from the 20–25 × 10^6 ha cleared in shifting cultivation or permanent forest conversion (Lanly 1982, Melillo et al. 1985). This amount is equivalent to more than half of industrial nitrogen fixation globally and is greater than the total amount of nitrogen delivered by rivers to the oceans (Söderlund and Rosswall 1982). If much of this mobilized nitrogen is lost to the atmosphere or to aquatic systems, it could represent a drain on the potential productivity of tropical ecosystems as well as a source of water and air pollution (Magee 1977, Crutzen 1983).

Despite these large changes and their potential large-scale consequences, relatively little information is available concerning the effects of tropical forest clearing on soil nitrogen transformations, on the pathways of nitrogen loss following clearing, or on the regulation of nitrogen retention or loss in disturbed forests. In the temperate zone, forest cutting generally increases rates of nitrogen mineralization and nitrification and decreases plant uptake of nitrogen (Matson and Vitousek 1981, Vitousek and Matson 1985). Greater amounts of ammonium and/or nitrate accumulate in the soil (Romell 1935, Krause 1982), and losses of nitrate to streamwater, groundwater, and perhaps the atmosphere increase (Bormann and Likens 1979, Vitousek

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and Melillo 1979, Robertson and Tiedje 1984). However, such losses often account for only a small fraction of the nitrogen mineralized in cleared sites due to uptake by regrowing vegetation and immobilization by forest floor and soil microorganisms (Marks and Bormann 1972, Vitousek and Matson 1984, 1985).

While these same processes can be expected to change in the same directions following clearing of tropical forests, their overall effects on nitrogen losses could differ. Rates of litter decomposition and soil nitrogen mineralization are generally rapid in lowland tropical forests (Bernhard-Reversat 1977, Anderson and Swift 1983, Robertson 1984, Vitousek and Denslow 1986), and consequently a large flush of inorganic nitrogen could follow disturbance. Very high concentrations of soil nitrate have in fact been observed in cleared tropical sites (Nye and Greenland 1960, Berish 1983). With the exception of montane and white-sand sites, more nitrogen circulates through vegetation annually in most tropical forests than in most temperate forests (Vitousek 1984, Vitousek and Sanford 1986). Nitrogen concentrations in litterfall are also higher, suggesting that microbial immobilization is less likely to retain nitrogen in disturbed tropical sites than in temperate sites. Finally, vegetation regrows rapidly following cutting in many lowland tropical sites (Nye and Greenland 1964, Harcombe 1977*b*, Brown 1982, Uhl, *in press*) and nitrogen concentrations in regrowing vegetation are high. Consequently, plant nitrogen uptake could be more important in retaining nitrogen within recently disturbed tropical sites than it is in many temperate forests (Vitousek and Matson 1984).

We measured nitrogen transformations, retention, and loss in a Tropical Premontane Wet Forest site (sensu Holdridge et al. 1971) near Turrialba, Costa Rica (9°53′ N, 83°40′ W). Previous work on the site indicated that large amounts of nitrogen disappeared from surface soil during and after clearing and burning (Ewel et al. 1981, Berish 1983); we focused on the magnitude of changes in nitrogen mineralization, nitrification, and immobilization in a cleared site, and on the relative importance of plant uptake vs. microbial immobilization in retaining mineralized nitrogen. Comparable measurements had been carried out in a cleared loblolly pine forest near Henderson, North Carolina (Vitousek and Matson 1984, 1985, Vitousek and Andariese 1986).

Study Site

This study was carried out at the Florencia Norte Forest on the property of the Centro Agronómico Tropical de Investigación y Enseñanza (CATIE) near Turrialba, Costa Rica. The site is at 650 m elevation; mean annual temperature is 22°C, and mean annual precipitation is 2700 mm with a distinct January to April dry season. The soil is derived from a Pliocene lava flow overlain by volcanic ash, and is classified as a Typic Dystrandept of the Colorado series. Horizonation in this soil is weak; a detailed description is given by Alvarado et al. (1981).

Tropical andepts generally accumulate large amounts of organic carbon and nitrogen, which form complexes with allophane (Bornemisza and Pineda 1969). These soils cover only a small fraction (<1%) of the lowland tropics (Sanchez et al. 1982) but they are more widespread at higher elevations where they are intensively cleared and utilized.

Substantial previous work has been carried out on and around this site, notably Harcombe's studies of vegetation–nutrient interactions (Harcombe 1977*a*, *b*) and Ewel and coworkers' studies of disturbance, succession, and ecosystem properties, including productivity and biomass (Berish 1982, Brown 1982), herbivory (Ewel et al. 1982, Blanton and Ewel 1985, Brown and Ewel 1987), soil nutrients (Berish 1983), precipitation chemistry (Hendry et al. 1984), and nutrient leaching through macropores and the soil matrix (Berish 1983, Russell and Ewel 1985).

The results and some of the experimental plots from Ewel's study were used in the design of this study. Vegetation on those plots was felled in January 1979 and burned in March 1979. The plots were then subjected to a variety of treatments, including six that underwent succession with no further modification and one that was maintained entirely free of vegetation. Nutrient losses during and immediately after clearing and burning were measured on these and other plots (Ewel et al. 1981); nearly 900 kg/ha of N had been lost by early April 1979. Large amounts of organic nitrogen (1800–2500 kg/ha) then disappeared from surface soils in the following 18 mo (Berish 1983). While leaching losses of nitrate-nitrogen were substantial (35 kg/ha for 18 mo from successional plots, 260 kg/ha from the vegetation-free plot), it accounted for only a small fraction of the total loss. Our study was designed to investigate alternative processes that could account for the missing nitrogen.

We measured nitrogen transformations on five types of plots. Two of these were derived from a 22 × 22 m plot established when we clear-felled 75-yr-old secondary forest in January 1984. Slash was burned on the plot in March 1984, and this plot was then split into two 11 × 22 m plots. Natural vegetation regrowth was permitted on one (1984 successional plot) and prevented by hand weeding on the other (1984 bare plot). The other three types of plots were (1) two of Ewel's 5-yr-old successional plots (1979 successional); (2) a plot that had been maintained free of vegetation for 5 yr (1979 bare plot); and (3) a patch of 75-yr-old secondary forest adjacent to the newly cleared plots (secondary forest plot). Measurements began <1 wk after burning the 1984 cleared plots and continued for 1 yr.

Methods

Nitrogen availability

We estimated nitrogen availability in newly cleared and successional plots by measuring ammonium and nitrate, rates of ammonium and nitrate formation, and the nitrogen content of soil microbial biomass. Sampling was based on monthly in situ incubations (Pastor et al. 1984, Vitousek and Matson 1985) from March 1984 (beginning 4 d after the burn) through March 1985. This procedure provided an estimate of net ammonium and nitrate release in intact soil cores under field temperature conditions and the soil moisture content at the time of sampling.

Each month, two adjacent soil cores were collected at each of eight randomly placed points within each plot. Litter (where present) was removed from the surface, and mineral soil was collected to a depth of 15 cm using a corer 5.5 cm in diameter. One of the cores in each pair was placed intact into a 0.02 mm thick polyethylene bag, sealed within another polyethylene bag, replaced in the corer hole, and cover with ≈ 1 cm of soil. After 28 d these bags were recovered, and soil from those that had remained intact was mixed and extracted for ammonium and nitrate analyses as described below.

The other core in each pair was returned to the laboratory within 3 h of collection, where the soil was mixed and roots and other inclusions >0.5 cm in diameter were removed. Three subsamples were then removed: a 50–100 g sample for soil water content, a 10-g sample for ammonium and nitrate concentrations, and a 50-g sample for microbial biomass nitrogen determinations.

The 10-g subsample from each soil core was extracted in 100 mL of 2 mol/L KCl, and extracts were transported to California for chemical analysis. Ammonium and nitrate concentrations were determined colorimetrically using a Technicon AutoAnalyzer II. The nitrogen content of microbial biomass was estimated on the 50-g subsample using a modification of the chloroform fumigation-incubation (CFI) technique (Jenkinson and Powlson 1976). One mL of chloroform was added directly to each 50-g sample (Vitousek and Matson 1985), and soils were incubated for 10 d at 22°C after chloroform was removed. Microbial biomass nitrogen was calculated as the amount of ammonium released by CFI divided by a recovery coefficient (assumed to have a constant value of 0.33).

Denitrification

We used the acetylene-inhibition technique to estimate denitrification. This procedure is based on the observation that acetylene inhibits the reduction of N_2O to N_2, so that N_2O production in acetylene-amended soils can be used as an estimate of denitrification (Tiedje 1982, Robertson and Tiedje 1984).

Eighteen 2.3 cm diameter by 20 cm deep intact soil cores were collected in each treatment in March (2 d after burning), July, and November 1984. Cores were obtained using a slide-hammer punch auger, returned to the laboratory within 3 h, flushed with 50 mL of air, and half were injected with 5 mL of acetylene (Robertson et al. 1987). Gas samples were collected in evacuated 3-mL vacuum vials (Venoject TM) at 2, 6, and 18 h. These samples were then overpressured with 2 mL of an internal standard (He) and transported to Michigan State University for N_2O analyses.

Nitrous oxide was determined by autoinjection gas chromatography (Robertson and Tiedje 1985) using a Varian 3700 gas chromatograph with Poropak-Q columns and ^{63}Ni electron capture detectors. Concentrations were corrected for the volume of helium added. The pore plus headspace volume of each core was determined with a pressure transducer (Parkin et al. 1984), and the dry mass of soil in each core determined. Nitrous oxide concentrations were converted to fluxes/cm^2 of soil surface; denitrification was defined as the N_2O flux in the acetylene-amended cores. In addition, we measured N_2O fluxes in the field in July 1984. Ten chambers, 12 cm in diameter, were inserted into the soil, and 3-mL samples were collected into evacuated containers after 0, 10, and 20 min.

Laboratory experiments

Several laboratory measurements and experiments were carried out to aid in the interpretation of the field measurements. Surface soils (0–15 cm) collected in March, July, and November 1984 were incubated in the laboratory at field capacity and 22 $\pm$ 2° using procedures described by Vitousek and Matson (1985). Water content was monitored gravimetrically and adjusted weekly with distilled water. After 28 d, the incubated soils were extracted in 2 M KCl and analyzed as described above. This technique allowed the identification of differences among treatments that were caused by variations in substrate quality as opposed to those that were caused by field temperature and moisture conditions (Matson and Vitousek 1981). Soils from a wider range of depths (0–5 cm, 5–15 cm, 0–25 cm, 25–45 cm, and 45–85 cm) were incubated in the laboratory in January 1985; these samples were collected as part of the ^{15}N-retention experiment described below.

In addition, we estimated microbial immobilization of nitrogen by adding ^{15}N-labelled ammonium and nitrate to soils prior to laboratory incubations (Vitousek and Andariese 1986). Large composite soil samples were collected and mixed from each plot in November 1984, and duplicate samples for water content, initial ammonium and nitrate concentrations, and the nitro-

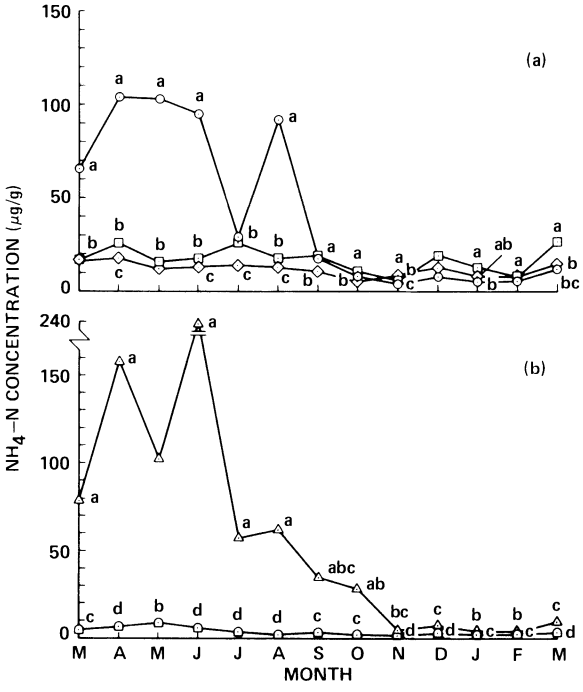

FIG. 1. Ammonium-N concentrations (μg/g dry soil) in the 0–15 cm depth interval each month from March 1984 to March 1985. Fig. 1a includes □ secondary forest, ○ 1984 successional plot, and ◇ 1979 successional plot. 1b includes △ 1984 bare plot and ▢ 1979 bare plot. Different letters indicate significant differences in pairwise comparisons of the five treatments shown in 1a and 1b for each month ($P < .05$; Student's t test). Significance values for comparisons among months are not shown. Values are means of eight samples.

gen content of microbial biomass were taken as described above. Eight additional 50-g subsamples of each composite were then established; four received 2 mL of a 150 mg/L solution of 97.2% ^{15}N-labelled nitrogen as ammonium sulfate, while the other four received 2 mL of 150 mg/L 99% ^{15}N-labelled nitrogen as sodium nitrate. All of the subsamples were adjusted to a constant water content and incubated in the laboratory as described above.

After 30 d, two subsamples in each set were extracted in KCl for ammonium and nitrate analyses and for determination of ^{15}N. The other two subsamples were treated with chloroform, and the amount and ^{15}N content of the ammonium released was determined. Samples were prepared for ^{15}N analyses by converting ammonium to ammonia at high pH, diffusing the ammonia to HCl in a closed flask at 70°, and evaporating the HCl to ammonium chloride at 90° (Vitousek and Matson 1985). Nitrate was reduced to ammonium with Devarda's alloy. Samples for ^{15}N analyses were shipped to Isotope Services, in Los Alamos, New Mexico, for isotope-ratio mass spectrometer analyses.

Finally, we investigated the controls of denitrification using a series of laboratory experiments. Fifty intact soil cores were collected in the 1984 successional plot in July 1984. Of these, 10 were not treated, 10 received 5 mL of distilled water (equivalent to a 1.2-cm rain), 10 received 5 mL of a 100 mg/L solution of ammonium-nitrogen, 10 received 5 mL of 100 mg/L nitrate-nitrogen, and the final 10 received 5 mL of 1000 mg/L glucose. Half the cores were incubated with 5 mL of acetylene, and gas samples for N_2O analyses were collected as described above. These measurements were repeated in November 1984, except that all the cores were amended with acetylene, no ammonium was added, and succinate (which is nonfermentable) rather than glucose was used as an energy source. Similar measurements were done in January 1985, at which time an additional 10 cores were purged with N_2 prior to incubation.

^{15}N retention in field plots

We used ^{15}N in isolated field plots to identify the mechanisms by which nitrogen was retained within the cleared sites (Vitousek and Matson 1984). During March and April 1984, trenches were dug to a depth of 1 m around three 1 × 1 m plots in the 1984 successional, 1984 bare, and 1979 bare plots. The trenches were lined with plastic and backfilled, and 1.3 g of 65.2% ^{15}N-labelled ammonium-nitrogen as ammonium sulfate were added in solution to the surface of each plot in May 1984, after the rainy season had started.

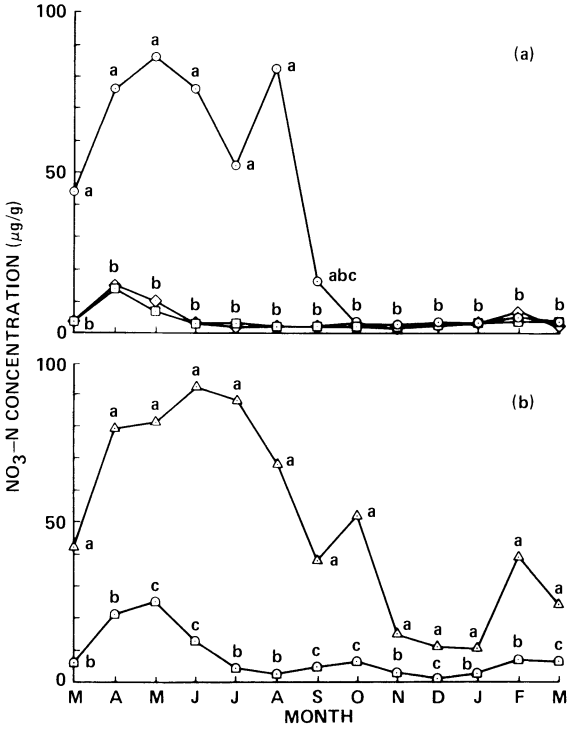

FIG. 2. Nitrate-N concentrations (μg/g dry soil) each month. Values and symbols as in Fig. 1.

Weekly harvests of senescing leaves on the ^{15}N-amended 1984 successional subplots were begun in November 1984; all the plots were harvested in late January 1985. Plants rooted in the ^{15}N subplots of the 1984 successional plot (some of which were nearly 5 m tall) were clipped at ground level, and all organic debris on the soil surface was collected. Five soil cores each were collected from the 0–5 cm, 5–15 cm, 0–25 cm, 25–45 cm, and 45–85 cm depth increments. The first two were collected with a 5.5 cm diameter corer, the last three with a 5.25 cm diameter slide-hammer driven punch tube. Finally, large roots were excavated from the 1984 successional plot.

Soils were passed through a 2-mm sieve, and all fine roots and recognizable organic particles were removed, dried, and weighed. Subsamples of the mineral soil fraction were extracted with KCl for ammonium and nitrate (and their ^{15}N content), extracted with deionized water to distinguish exchangeably bound from free nitrate, and treated with chloroform for microbial biomass nitrogen and its ^{15}N. Subsamples were also incubated for nitrogen mineralization as described above.

All of the solid fractions (plants, litter, and soil) were oven dried at 70°, weighed, ground, digested using persulfate/peroxide, analyzed for total nitrogen, and diffused and analyzed for ^{15}N. The label retained in each pool was calculated by subtracting the natural abundance of ^{15}N (0.366%) from the measured value and multiplying by the total amount of nitrogen contained in that fraction.

Results

Nitrogen availability in surface soils

Ammonium and nitrate pools.—The concentrations of ammonium-N and nitrate-N increased to very high levels (>80 μg/g dry soil) in the surface soils of the 1984 plots shortly after clearing and burning (Figs. 1 and 2). These elevated ammonium and nitrate concentrations persisted in the 1984 successional plot for ≈6 mo following burning and were equivalent to ≈130 kg/ha of ammonium-N and >100 kg/ha nitrate-N in the top 15 cm. In contrast, ammonium-N in the secondary forest never exceeded 40 kg/ha, and the amount of nitrate was always <5 kg/ha except during the dry season.

Nitrogen mineralization and nitrification.—The high initial ammonium and nitrate concentrations in the 1984 successional and bare plots contributed to highly variable estimates of net nitrogen mineralization during the 1st 5 mo. It is clear, however, that field estimates of nitrogen mineralization were elevated in the 1984 sites shortly after burning, and that they returned to levels close to those in the secondary forest within 6 mo in both treatments (Fig. 3). Nitrogen mineralization was generally greater in the secondary forest than in the 1979 successional plot and lowest in the 1979 bare plot. Almost all of the mineralized nitrogen was oxidized to nitrate during the incubations.

TABLE 1. Net annual nitrogen mineralization estimated by in situ incubations.

Plot	Mineralization ($kg \cdot ha^{-1} \cdot yr^{-1}$)
1984 bare	1040
successional	1140
1979 bare	217
successional	588
Secondary forest	759

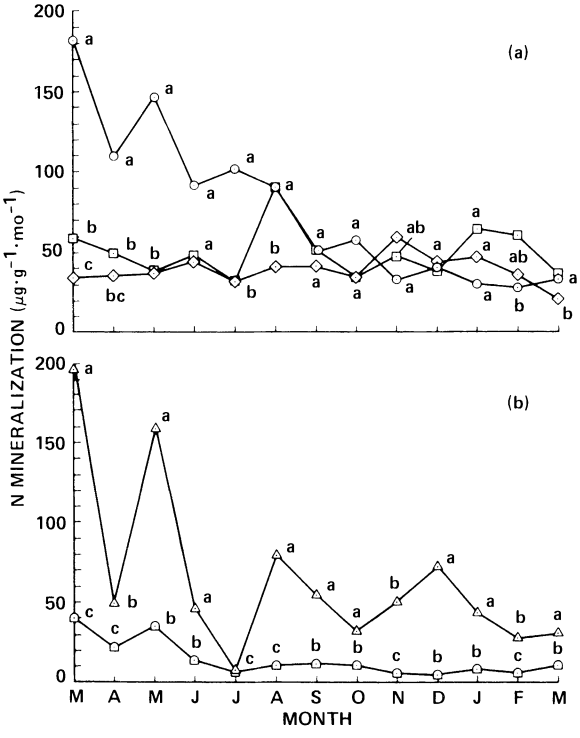

FIG. 3. Total production of inorganic nitrogen ($\mu g \cdot g^{-1} \cdot mo^{-1}$) over month-long in situ incubations. Values and symbols as in Fig. 1.

The amount of nitrogen mineralized during in situ incubations was converted to an areal basis and summed over the year (Table 1). By this estimate, net annual mineralization increased ≈50% in the 1984 cleared plots relative to the secondary forest; all of the increase occurred during the 1st 5 mo (Fig. 3).

Microbial biomass nitrogen.—Amounts of nitrogen in microbial biomass shortly after burning were similar in both of the 1984 cleared plots and in the secondary forest (Fig. 4). Thereafter, they declined steadily in cleared plots to approximately half of their original value by September. The amount of nitrogen that disappeared from microbial biomass during this decline, 450 kg/ha, was similar to the concurrent increase in net nitrogen mineralization (Table 1). Overall, the largest quantities of nitrogen in microbial biomass were found in the secondary forest, while the 1979 succes-

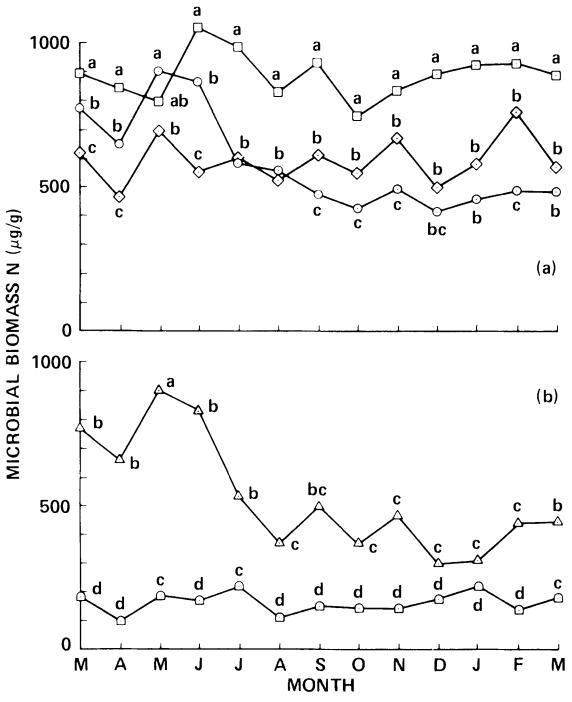

FIG. 4. Nitrogen in microbial biomass (μg/g dry soil) each month. Values and symbols as in Fig. 1.

sional plot was intermediate and very low levels were found in the 1979 bare plot (Fig. 4).

Denitrification.—Estimates of denitrification and nitrous oxide using the intact-core method were highly variable. Immediately after burning, rates in the newly cleared plots were significantly higher than in other plots (Table 2). By July, however, these rates were greatly reduced and the secondary forest had the highest denitrification. If the nitrogen flux remained constant from March until July, roughly 3.3 kg of N/ha would have been lost through denitrification and nitrous oxide flux from the newly disturbed plots in the 4 mo following the burn. After that, rates in the 1984 successional plot dropped to <0.04 kg·ha^{-1}·mo^{-1}, and rates in the 1984 bare plot were <0.2 kg·ha^{-1}·mo^{-1}.

Nitrous oxide fluxes measured with chambers and with the intact core method (with no acetylene added) were also highest in the secondary forest in July. Fluxes into chambers ranged from 2.6 ng·cm^{-2}·h^{-1} in secondary forest to $\approx$2.0 in the 1984 plots and the 1979 successional plot, to <1 in the 1979 vegetation-free plot. Values from intact cores were similar in pattern and magnitude.

Laboratory experiments

Nitrogen mineralization potentials.—Results of the laboratory incubations of surface soils demonstrated that differences in substrate quality affected the patterns of nitrogen mineralization observed in situ. Even under constant conditions, soil from the 1984 plots had high rates of potential nitrogen mineralization shortly after burning, but then rapidly dropped to below secondary forest levels (Table 3). Mineralization in the 1979 vegetation-free plot soils was very low, as was observed in the field.

Soils collected from a range of depths in the 1984 successional and vegetation-free plots and the 1979 vegetation-free plot were also incubated under controlled conditions in the laboratory. The highest rates of mineralization were observed in surface soils, but measurable nitrogen release occurred down to the 45–85 cm depth interval, the deepest studied (Fig. 5).

Immobilization.—Regardless of whether ^{15}N was added as ammonium or nitrate, most of the added label was recovered in nitrate after 30 d (Table 4). Relatively small amounts of ^{15}N were recovered in microbial biomass, and very little was present as ammonium. Immobilization by microbes was greater in soil from all of the vegetated plots than from either bare plot, and the amount of nitrogen immobilized increased with vegetation age. Finally, less ^{15}N label was recovered as inorganic nitrogen and more as microbial biomass when ^{15}N was added as ammonium than as nitrate (Table 4).

Denitrification experiments.—Despite the extremely large amounts of nitrate in the soil of the newly cleared plots, rates of denitrification were low. Results from the laboratory experiments designed to examine controls on denitrification indicated no significant response to nitrogen addition, but greater than an order of magnitude response to carbon additions (Fig. 6). Purging the soils with nitrogen gas during the experiment caused increased denitrification compared to controls, but significantly less than in carbon-amended

TABLE 2. Denitrification-N plus nitrous oxide-N flux rates from intact acetylene-inhibited cores incubated under constant conditions for 18 h. Values are means (±SE) of 4 to 10 cores. Common superscripts within a column indicate no significant differences ($P < .05$; Student's t test) between treatments in each month.

Plot	N flux rates (ng·cm^{-2}·h^{-1})		
	March	July	November
1984 bare	14 ± 4.8^{b}	1.5 ± 0.37^{b}	2.2 ± 1.2^{a}
successional	8.5 ± 3.3^{b}	0.39 ± 0.12^{c}	0.50 ± 0.29^{a,b}
1979 bare	0.24 ± 0.08^{c}	0.99 ± 0.93^{b,c}	0.11 ± 0.02^{b}
successional	0.61 ± 0.18^{c}	2.8 ± 1.9^{b}	0.54 ± 0.28^{a,b}
Secondary forest	1.1 ± 0.30^{a}	12.6 ± 4.5^{a}	2.4 ± 1.1^{a}

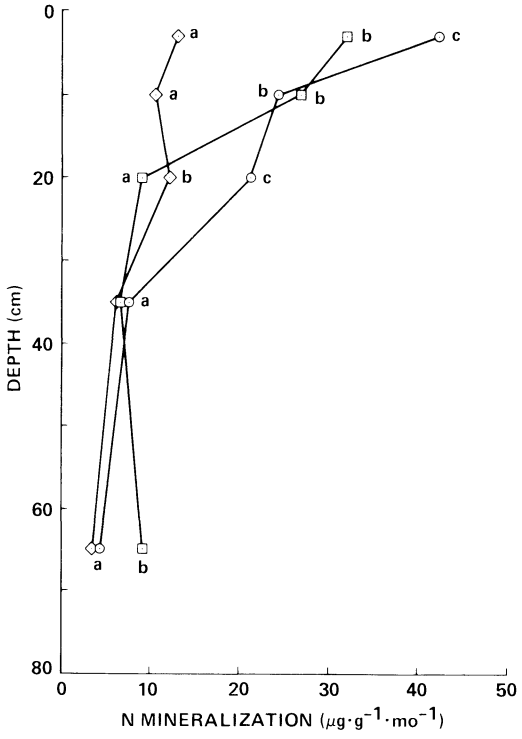

FIG. 5. Production of inorganic nitrogen ($\mu g \cdot g^{-1} \cdot mo^{-1}$) at five depth intervals during month-long laboratory incubations under controlled conditions, comparing ○ 1984 successional, □ 1984 bare, and ◇ 1979 bare plots. Different letters indicate significant differences in pairwise comparisons of the three treatments at each depth. Values are means of three isolated subplots per plot.

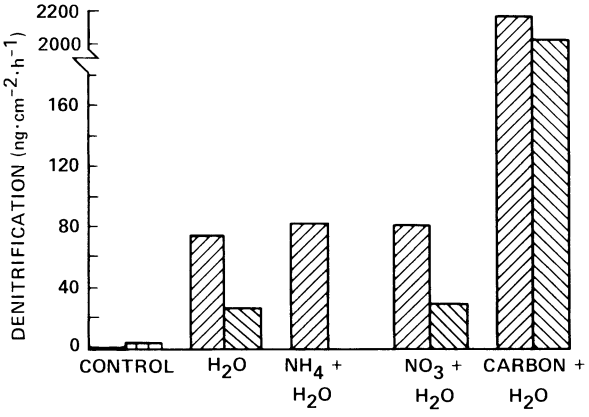

FIG. 6. Denitrification ($ng \cdot cm^{-2} \cdot h^{-1}$) from acetylene-amended cores from the 1984 successional plot. The bar on the left in each pair represents July 1984 samples, the bar on the right represents November 1984 samples. Cores were incubated under five different treatments for 18 h in the laboratory. Values are means of 10 replicates.

soils. In these high-nitrogen soils, it appears that denitrification is not limited by nitrate concentration, as is the case for some cleared temperate forests (Robertson et al. 1987), but rather by carbon availability.

^{15}N retention in field plots

Nitrogen distribution.—Subplots that had been labelled with ^{15}N were sampled to a depth of 85 cm. Differences in amounts of soil organic nitrogen among these disturbed plots were relatively small, but large differences in the amounts and vertical distributions of other forms of nitrogen were observed (Table 5). The most striking result was the large amount of nitrate-nitrogen at depth in the 1984 vegetation-free plot (Fig. 7). Less than half of this nitrate was extractable in distilled water (Table 5); the remainder was held by anion exchange. These results led us to undertake additional sampling down to 150 cm depth 6 wk later, in March 1985. The highest nitrate concentrations were still located in the 45–85 cm depth increment, but elevated concentrations of nitrate were found at least down to 110–150 cm (Fig. 7).

Nitrogen uptake by regrowing vegetation in the 1984 successional plot was substantial; nitrogen in plants plus senesced leaves (above- and belowground) amounted to 50 g/m^2 10 mo after burning (Table 6). Most nitrogen was in the form of soil organic nitrogen in all the treatment plots, and there were no significant differences among treatments in the total amount of nitrogen to a depth of 85 cm (Fig. 8). However, the amount of labile nitrogen (which we define as plant + particulate organic + soil inorganic + microbial nitrogen) differed significantly both in total quantity and in distribution among treatments. The 1984 successional plot had 50 g/m^2 of nitrogen in plants and <4 g/m^2 in inorganic forms, while the 1984 vegetation-free plot had <1 g/m^2 in vegetation and 43 g/m^2 of nitrogen in inorganic nitrogen (mostly nitrate) to a depth of 85 cm.

TABLE 3. Net nitrogen mineralization ($\mu g \cdot g^{-1} \cdot mo^{-1}$) under constant conditions in the laboratory. Values are means (±SE) of three replicates in July and November and two in March and January. Common superscripts indicate no significant difference ($P < .05$; Student's t test) among treatments for a given month.

Plot	March	July	November	January
1984 bare	123.5 ± 5.6[a]	59.9 ± 2.8[a]	48.3 ± 1.9[a]	57.0 ± 0.53
1984 successional		30.7 ± 13.2[a,b,c]	45.0 ± 0.12[a]	43.7 ± 4.4[a]
1979 bare	38.2 ± 3.3[b]	14.2 ± 0.99[b]	22.0 ± 3.7[b]	19.2 ± 1.2[b]
1979 successional	69.4 ± 15.2[c]	26.9 ± 10.3[b,c]	62.0 ± 3.9[c]	72.4 ± 3.5[c]
Secondary forest	77.4 ± 8.8[c]	42.9 ± 3.7[c]	82.0 ± 10.6[c]	74.5 ± 5.5[c]

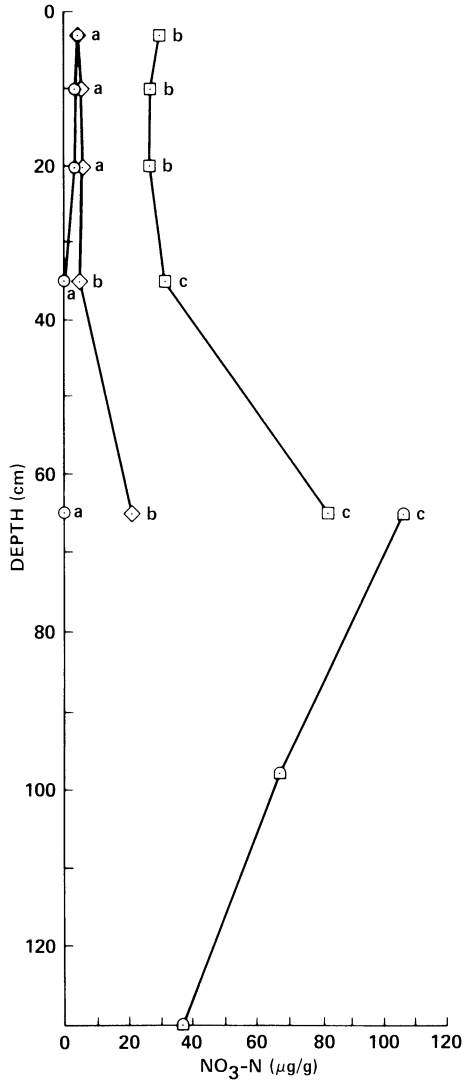

FIG. 7. Nitrate-N concentrations (μg/g dry soil) at seven depth intervals in the isolated plots. Different letters indicate significant differences in pairwise comparisons of the treatments ($P < .05$; Student's t test). ○ 1984 successional, □ 1984 bare, and ◇ 1979 bare plots were sampled in January 1985 and ⌂ 1984 bare plots were sampled again in March 1985. Values are means of three isolated plots per treatment.

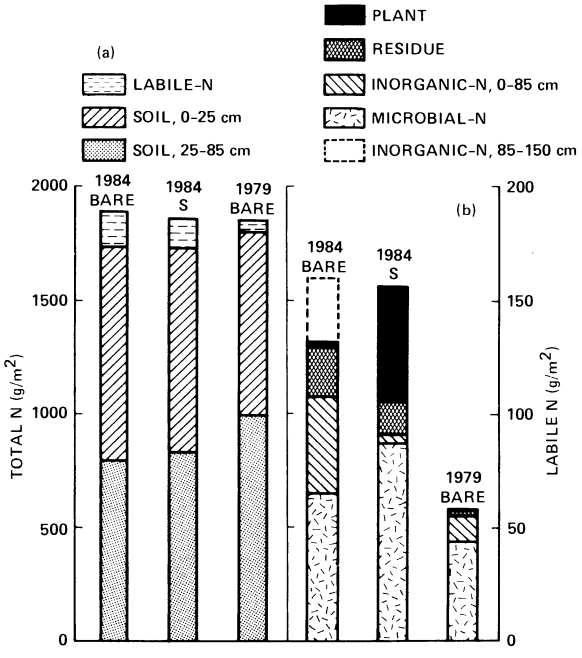

FIG. 8. (a) Total nitrogen distribution (g/m^2) in components of the isolated plots. (b) An enlargement of the labile N component from 8a, with separation into inorganic, plant, microbial, and residue organic pools. Values are means of three replicates per treatment.

^{15}N distribution.—A relatively small fraction of the added ^{15}N (18%) was recovered within vegetation in subplots of the 1984 successional plot (Table 7). Microbial biomass accounted for an additional 5–6% of the label in all the treatments, and 12% was recovered from inorganic nitrogen (mostly as nitrate at the 45–85 cm depth increment) in the 1984 vegetation-free plot. Soil organic nitrogen represented the largest single pool of ^{15}N label, with the 0–25 cm layer accounting for 24% of the applied label in the 1984 bare plot and 22% in the 1984 successional plot.

The low concentrations of nitrogen in deeper soils (>25 cm) made determination of ^{15}N recovery from those soils difficult, but the determinations suggest that an additional 15–25% of the label was recovered there, raising total recovery to 64% in the 1984 successional

TABLE 4. Recovery of ^{15}N label in inorganic N and microbial biomass following 30 d incubation under constant conditions in the laboratory. Label was added as $^{15}NH_4Cl$ or $Na^{15}NO_3$; values are the mean of two subsamples (±SE).

Plot	$^{15}NH_4$ added			$^{15}NO_3$ added		
	NH_4^+	NO_3^-	Microbial biomass	NH_4^+	NO_3^-	Microbial biomass
	Percent of added ^{15}N					
1984 bare	0.1 ± 0.01	74 ± 1.0	6.2 ± 1.5	0.1 ± 0.002	79 ± 2.3	2.5 ± 0.5
successional	0.3 ± 0.02	63 ± 0.6	11 ± 1.0	0.1 ± 0.005	71 ± 0.7	5.2 ± 0.1
1979 bare	3.6*	54*	5.0*	0.1 ± 0.001	77 ± 3.7	4.0 ± 0.2
successional	0.5 ± 0.05	54 ± 0.2	14 ± 1.7	0.3 ± 0.03	74*	11 ± 0.7
Secondary forest	0.4 ± 0.02	52 ± 4.7	17 ± 0.08	0.2 ± 0.001	90 ± 0.4	11 ± 0.3

* $n = 1$.

TABLE 5. Amounts of nitrogen in various forms in soil from the field ^{15}N retention plots. Values are means (±SE) of three replicates.

Plot depth	Distilled-water–extractable nitrate-N (μg/g)	KCl-extractable		Microbial biomass-N (μg/g)	Total N (μg/g)
		Nitrate-N (μg/g)	Ammonium-N (μg/g)		
1984 bare					
0–25 cm	22.3 ± 1.3	29.3 ± 3.6	4.0 ± 0.52	279 ± 19.4	4200 ± 190
25–45 cm	21.5 ± 3.3	30.8 ± 3.6	1.7 ± 0.14	28.4 ± 9.1	2100 ± 80
45–85 cm	35.8 ± 3.2	81.9 ± 9.3	1.1 ± 0.08	3.5 ± 0.94	1400 ± 50
1984 successional					
0–25 cm	3.0 ± 0.1	3.9 ± 0.5	6.5 ± 0.62	387 ± 22.6	4600 ± 580
25–45 cm	1.3 ± 0.4	1.0 ± 0.5	2.0 ± 0.26	22.1 ± 4.8	1900 ± 40
45–85 cm	0.4 ± 0.2	0.7 ± 0.4	1.4 ± 0.18	3.8 ± 0.25	1300 ± 80
1979 bare					
0–25 cm	5.1 ± 0.7	5.2 ± 1.3	2.5 ± 0.48	159 ± 7.8	4600 ± 170
25–45 cm	4.2 ± 0.8	4.8 ± 1.5	1.5 ± 0.14	39 ± 6.9	2600 ± 230
45–85 cm	9.6 ± 2.5	21.4 ± 7.8	1.4 ± 0.05	12 ± 5.2	1500 ± 20

plot, 70% in the 1984 bare plot, and 58% in the 1979 bare plot (Table 7).

DISCUSSION

Forest felling and burning in this relatively nutrient-rich tropical site leads to rapid and major changes in nitrogen transformations. In situ estimates of annual nitrogen mineralization in the secondary forest were higher than those in most tropical and all temperate forests that have been studied to date (Vitousek and Denslow 1986). With disturbance, rates of nitrogen mineralization further increased to two to three times greater than those in secondary forest, then decreased to comparable levels within 6 mo. Return to near-background levels was much more rapid than that observed in comparable studies in the temperate zone (Matson and Vitousek 1981, Gordon and Van Cleve 1983, Matson and Boone 1984, Vitousek and Matson 1985). Although short-lived, the increased nitrogen mineralization represented an additional 300 to 400 kg/ha of N released in the cleared site (Table 1).

Increased nitrogen mineralization was reflected in very large amounts of inorganic nitrogen in the cleared plots (Figs. 1 and 2), as has been observed elsewhere (Nye and Greenland 1960, Jordan 1985). However, ammonium and nitrate concentrations in both successional and bare plots returned to levels close to those of the secondary forest within 6 mo, except that nitrate remained somewhat elevated in the surface soils of the 1984 bare plot throughout the year.

In contrast, nitrogen in microbial biomass did not return to predisturbance levels within the period of the study. After 1 yr, microbial biomass nitrogen was 50% of its initial value in both the 1984 successional and bare plots. If the 6-yr-old successional plots were identical to the secondary forest at the time they were cleared (which cannot be determined), then microbial biomass nitrogen remained low for several years following land clearing, and continued to decline for several years in the 1979 bare plot.

Nitrogen in plants, organic residue, microbes, and exchange sites should represent the major forms in which mineralized nitrogen is retained within a disturbed site. Ten months after clearing, plants on the 1984 successional plot contained 50 g/m^2 of nitrogen. In contrast, the 1984 bare plot had 43 g/m^2 of nitrate-N at a soil depth of 45–85 cm, the majority of it exchangeably bound (Table 5). An additional 28 g/m^2 of nitrate-N were held between 85 and 150 cm. Nitrate adsorption is neither a familiar nor an important process in the nitrogen cycle of temperate forest ecosystems, but it can be substantial on variable-charge clays

TABLE 6. Biomass and nitrogen content of plants and organic residue on the ^{15}N retention plots in January 1985. Values are means (±SE) of three plots, expressed as g/m^2.

	1984 bare		1984 successional		1979 bare	
	Biomass	Nitrogen	Biomass	Nitrogen	Biomass	Nitrogen
Plants						
Shoots	0	0	2683 ± 490	41.5 ± 13	0	0
Roots (coarse and fine)	60.6 ± 9	0.8 ± 0.2	734 ± 160	8.9 ± 0.6	18.6 ± 5.9	0.3 ± 0.01
Organic debris						
Forest floor	713 ± 109	9.3 ± 1.6	464 ± 64	6.0 ± 0.34	0	0
Soil organic material	1120 ± 600	13.1 ± 6	585 ± 84	8.6 ± 1.7	22 ± 63	1.4 ± 0.8

TABLE 7. ^{15}N recovery in components of the field plots. Values are means (±SE) of three replicates, expressed as percent of the added ^{15}N label. OM = organic matter.

	1984 bare	1984 successional	1979 bare
	Percent of added ^{15}N		
Vegetation	<1	18 ± 1	<1
Particulate OM	4 ± 1	3 ± 1	<1
Inorganic N			
0–85 cm depth	12 ± 2	<1	15 ± 6
Microbial N	5 ± 1	5 ± 1	5 ± 1
Soil organic N			
0–25 cm depth	24 ± 3	22 ± 2	18 ± 2
25–85 cm depth	25 ± 4	15 ± 5	18 ± 6

in the tropics (Uehara and Gillman 1981), especially in volcanic ash-derived soils (Singh and Kanehiro 1969, Kinjo and Pratt 1971).

The potential importance of plant uptake, immobilization, and nitrate adsorption in retaining nitrogen on-site was confirmed using subplots amended with ^{15}N. Plants retained 18% of the applied label in the 1984 successional subplots, while inorganic adsorption at depth accounted for 12–15% of the label in the bare subplots. Another 25–30% of label was recovered in microbial biomass or soil organic nitrogen above 25 cm depth in all plots, but a large fraction of label was not recovered. Very little nitrate was recovered at depth in the successional plot; it may have been taken up before leaching to that depth, or it may have been recovered by roots of successional vegetation, some of which reached that deep.

Overall, Berish (1983) reported that 180–250 g/m^2 of N disappeared from surface soils (0 to 25 cm) at the site in the 18 mo following land clearing and estimated that ≈3.5 g/m^2 and 26 g/m^2 of nitrate-N leached past 25 cm in successional and bare plots respectively. We measured denitrification rates in intact cores and N_2O fluxes from the soils and found that losses by these pathways were small, probably <1 g/m^2 in the year following clearing. We also found substantial amounts of nitrate (≈70 g/m^2) and some ^{15}N label below 45 cm depth in the bare plot. We suggest that this site loses less nitrogen following disturbance than would appear from measurements of total nitrogen pool sizes in the upper horizons, and that anion exchange in the subsoil can retain much of the mobilized nitrogen on-site. Leaching appears to be the most important vehicle of nitrogen removal from surface soil; it is possible that Berish (1983) underestimated an early pulse of nitrate leaching. His measurements began in July 1979, 4 mo after his plots were burned.

The mechanisms retaining nitrogen within this cleared site differed sharply from those in a harvested pine plantation on the North Carolina Piedmont (Vitousek and Matson 1984, 1985, Vitousek and Andariese 1986). This comparison is not intended to exemplify the differences between tropical and temperate forest ecosystems; rather it represents the only two cleared forest sites for which this kind of information is available. Rates of nitrogen mineralization in North Carolina were 3–4 times greater in cleared than in uncut reference plots, but they remained an order of magnitude lower than those at Turrialba (Vitousek and Matson 1985). Nitrogen losses were much lower in North Carolina; leaching losses and denitrification were small, and 94% of added ^{15}N was recovered in cleared subplots that had been subjected to minimum intensity management (Vitousek and Matson 1984, Robertson et al. 1987). Finally, microbial immobilization of nitrogen, which we defined as the sum of label recovered in microbial biomass, soil organic matter, and particulate organic matter, was more important in the North Carolina than the Turrialba site. Immobilization in the top 15 cm accounted for 83% of the applied ^{15}N in field plots in North Carolina compared to 30% in the top 25 cm at Turrialba, and <10% of ^{15}N added to laboratory incubations remained in inorganic forms after 29 d compared to >70% in Costa Rica. Lower rates of immobilization at Turrialba are associated with lower C/N ratios in plant residue, the absence of a distinct forest floor, and smaller amounts of structural organic material remaining on site after disturbance.

Anion exchange of nitrate-nitrogen at depth was an important process in the tropical site; it was not observed in the temperate site. This translocation of nitrogen to deeper in the soil profile, presumably followed by uptake once plant roots reach that depth, may be an important mechanism maintaining the fertility of cleared tropical sites (Bartholomew 1977). Uptake and cycling of this nitrogen by vegetation in the fallow phase of shifting cultivation could help to account for the extraordinarily rapid rates of nitrogen accretion that are observed under successional vegetation. Moreover, these results suggest that nitrogen lost from surface soils after clearing and burning of some tropical forests may not enter either atmospheric or hydrologic cycles.

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