

Nitrification and nitrogen mineralization in a lowland rainforest succession in Costa Rica, Central America

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Summary. Nitrogen availability is a critical component of productivity in successional lowland rainforests, and nitrogen losses from a given system may largely depend on rates of nitrification in soils of the system. Two hypotheses were tested in a study of a 6-point secondary rainforest sere in the coastal lowlands of Costa Rica: that nitrification and N mineralization change in a directed fashion in lowland rainforest successions, and that nitrification is regulated by ammonium availability at all points along the sere. Nitrate and mineral N production were measured in short-term laboratory incubations of soils from different stages of secondary succession corresponding to 0, 3, 8, 16, 31 and 60+ years following disturbance. Results indicate that nitrification increases through the first 4 successional stages and then declines somewhat before leveling off. In soils from all sites, most of the N mineralized was nitrified, and added NH_4Cl strikingly stimulated net nitrate production. Added NaH_2PO_4 , CaCO_3 , and CaSO_4 did not stimulate net nitrate production or did not result in a greater proportion of nitrate than in controls. These results suggest that nitrification and N mineralization may tend to increase through secondary rainforest succession and that ammonium availability along the sere regulates rates of nitrification.

Introduction

Nutrient availability is a critical component of productivity in lowland tropical rainforests, and is indirectly an important determinant of current rates of tropical deforestation: rainforest sites that have been converted to agriculture and in which productivity rapidly declines are sites which are soon abandoned for different, not recently cleared sites (Myers 1979; NAS 1980).

Successful cultivation in the humid tropics has for centuries depended principally on adequate time for the recovery of abandoned cropland before it once again is cleared for cultivation. In recent times, population pressures have increasingly foreshortened this fallow period to a matter of years rather than decades (FAO/SIDA 1974; Myers

1979; Sanchez et al. 1982), yet we know little about the effects of these shorter fallows on long-term site productivity in these lowland systems, and even less about the underlying mechanisms that affect the rates at which fertility is reestablished during secondary succession.

There is indirect evidence that phosphorus most commonly limits productivity in late-successional tropical forests (Vitousek 1983), but losses of nitrogen rather than phosphorus availability may more persistently affect productivity in many cleared and early successional systems (FAO 1974; Brady 1982; Sanchez et al. 1982). Nitrogen is lost from wet tropical systems primarily via leaching, denitrification, volatilization upon burning, and harvest, although other processes such as erosion and NH_3 volatilization may be locally important. Of these, only leaching and denitrification are likely to be important in regenerating rainforests on non-sloping land.

Losses of nitrogen through leaching and denitrification are largely dependent on soil nitrate production – unlike mineral nitrogen in the ammonium form, in most soils nitrate is both extremely mobile in the soil solution and readily available to denitrifiers for conversion to N gases. Consequently, nitrogen losses from regenerating rainforests may be partly regulated by the activity of nitrifiers, soil bacteria that transform mineral nitrogen from the tightly-held ammonium form to the mobile, nitrate phase. Because rates of nitrification vary widely among both temperate and tropical forests (Robertson 1982a), and because the fertility of regenerating rainforests may depend in part on how quickly this process occurs, it becomes important to understand both patterns of nitrification in secondary rainforest successions and the factors that regulate these patterns.

A number of studies have addressed questions related to nitrification in temperate region successions (see, e.g., Skujins and Klubek 1982; Robertson and Vitousek 1981; Montes and Christensen 1979; Rice and Pancholey 1972), and others have examined patterns in subtropical forest successions (Lamb 1980) and tropical montane successions (Vitousek et al. 1983). I am aware of no substantive studies of nitrification or nitrogen mineralization in wet tropical successions, however, and undertook the study described here to test the hypotheses that 1) rates of nitrification and N mineralization change in a directed fashion in the course of secondary succession in wet tropical forests, and 2) ammonium availability regulates nitrification in these seres.

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Study sites

Sites examined in this study were located at the La Selva Biological Field Station in the coastal lowlands of Costa Rica (10° 26' N, 83° 00' W, 35–150 m elevation). The station is maintained as a biological reserve by the Organization for Tropical Studies, and includes several hundred hectares of old-growth rainforest and adjacent tracts in different stages of secondary succession. Annual precipitation at La Selva averages 3,800 mm yr⁻¹ (± 800 mm s.d.). On average, ca. 80% falls during the June to December wet season. Mean daily temperature is 24° C; diurnal variation (± ca. 5°) is usually greater than seasonal.

Nitrification and nitrogen mineralization potentials were measured in soils from six sites at various stages of secondary succession within the Station boundaries. Ages of the sites varied from 3 months since clearing to undisturbed rainforest. All sites were ≥ 1 ha, within 500 m of one another, and underlain by soils (probably hydric dystandepts) derived from volcanic parent materials deposited by alluvial action (Holdridge et al. 1971; Bourgeois et al. 1972; Johnson et al. 1977). Table 1 presents soil characteristics of the sites; with one exception, sites were identical to those studied by Werner (1983), and a more thorough soil characterization is available there.

Vegetation in the undisturbed forest has been described by Hartshorn (1972) and Holdridge et al. (1971). Hartshorn (1978) estimated that the undisturbed forest turns over via gap formation on the order of every 120 years. Chief among the dominants in the old-growth forest is *Pentaclethra macroloba*; canopy height is ca. 40 m, understory vegetation is sparse except in recent gaps, and there is no well-defined litter layer except during protracted dry periods.

Preclearing histories of the successional sites (Werner 1983) varied somewhat, although all were undisturbed rainforest within several years previous to clearing, and all successional sites had been planted to upland rice (31 yr site) or used as pasture (0, 3, 8, and 16 yr sites) for 2–4 yrs following the original forest cutting. Superimposed on the first part of the sere was a disturbance gradient: the 0 yr site had been cut three times since the original 1965 clearing, each time at 5 yr intervals (1971, 1976, 1981), and the 3 yr site had been cut twice since the same 1965 clearcut (1973, 1978).

The 3 yr site, not included in Werner's (1983) study, included as dominants *Heliocarpus appendiculatus*, *Goethalia meiantha* and *Ochroma lagopus*. The 8 yr site was similar in vegetation to the 16 yr site, which was dominated by *G. meiantha*, *Rollinia microsepala* and *Casearia arborea*. The 16 yr site was also dominated by *G. meiantha*.

Methods

Six subsites randomly located within each of the 6 study sites were sampled in March 1981. At each subsite, three 6 cm diameter by 12 cm deep soil cores were taken within 1 m of each other, transported to the field station laboratory, and composited by site. After mixing and removal of infrequent stones and roots > 4 mm diameter, subsets of soils from all 6 sites were determined for percent moisture, pH, and mineral nitrogen determinations as described below. Except as indicated, all soil incubations, extractions, and analyses were carried out at the Station.

Table 1. Soil properties (to 10 cm) of a lowland tropical rainforest in Costa Rica at various stages of secondary succession. Data (except pH) are from Werner (1983). na = not available

Site	Bulk Density	Clay (%)	PO ₄ -P (mg/kg)	Ca ⁺² K ⁺		CEC	pH	C:N
				(meq/100 g)				
0 yr	0.62	50	2.7	1.75	0.38	27	5.4	7.7
3 yr	na	na	na	na	na	na	5.4	na
8 yr	0.54	49	4.7	0.98	0.21	32	5.4	8.3
16 yr	0.64	51	2.4	0.39	0.16	27	5.3	8.3
31 yr	0.57	52	4.1	0.46	0.23	26	5.4	7.8
60+ yr	0.58	53	2.4	0.60	0.18	25	5.3	8.6

Table 2. Experimental nutrient additions made to incubated soils from the secondary sere described in text

Treatment	Application, Rate (kg wet soil ⁻¹)
NH ₄ ⁺	100 mg N as NH ₄ Cl
PO ₄ ³⁻	5 mg P as NaH ₂ PO ₄
CaCO ₃	5% CaCO ₃ , or 20 g Ca ⁺² as CaCO ₃
CaSO ₄	20 g Ca ⁺² as CaSO ₄
Control	H ₂ O

Incubation procedures for nitrification and N mineralization potentials were similar to those used by Ellenberg (1974), Robertson and Vitousek (1981) and others. Soils were incubated in polyethylene containers that allowed free gas exchange between container headspace and the atmosphere. 300 g subsets of soil from each site were mixed with 6 ml of either filtered precipitation or nutrient solution at rates indicated in Table 2, and then incubated for 9 days at ambient air temperatures (24° ± 4°) inside an opaque box with a loose-fitting lid. At 2 d intervals subsets were checked for water loss; replenishment to keep weights within 2% of initial levels was not necessary over the course of the incubation period. Control soils (amended with H₂O only) were sampled at intervals of 3, 6, and (with 1 exception) 9 days; all other treatments (with 1 exception) were sampled only on day 9. The exception was 0-yr soils, which were sampled on day 7.5 rather than day 9. Six replicate extractions were made of each sampled incubation on each sample date; additionally, on the initial and final sample dates both control and CaCO₃ amended soils were analyzed for soil pH as described below.

Recent precipitation filtered through glass wool was used for all on-site solutions and analyses; subsequent analyses of blanks preserved with Hg₂Cl₂ showed mineral-N content of this water to be < 15 µeq N l⁻¹, always < 20% and usually < 2% of extraction N-concentrations for both NO₃⁻ and NH₄⁺. pH was determined in 1:1 soil slurries (20 g wet soil: 20 ml H₂O) following ≥ 30 minutes of equilibration and using pH paper electrometrically calibrated to 0.1 pH units. Percent moisture subsets were dried at 105° for 48 hrs. All extractions were made in 1.5 N KCl at a wet soil to extractant ratio of 5 : 1 (10 g wet soil : 50 ml extractant); the extraction solution also contained 1 mg Hg₂Cl₂ l⁻¹ to retard microbial growth. Extractions were shaken well, allowed to equilibrate overnight, and then filtered into sample vials which were flown to Sweden and refrigerated before subsequent analyses for mineral N. Ni-

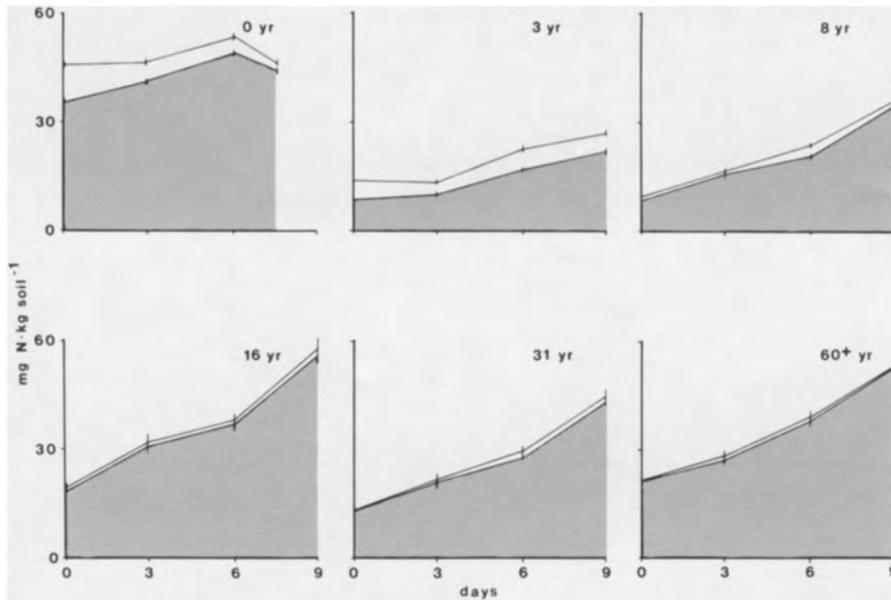


Fig. 1. Nitrate (shaded portion of each sketch) and total mineral nitrogen (nitrate + ammonium N, upper line) accumulation during a 9 d laboratory incubation of soils from 6 sites along a Central American lowland rainforest succession. Vertical bars at sampling points represent standard errors ($n=6$)

trate, nitrite, and ammonium analyses were performed via flow injection analysis.

Statistical analyses were performed on ln-transformed data. Net mineralization was defined as final (day 9) mineral N ($\text{NH}_4^+ - \text{N} + \text{NO}_3^- - \text{N}$) less initial (day 0) mineral N; net nitrification was defined as final less initial $\text{NO}_3^- - \text{N}$ (Robertson and Vitousek 1981).

Results

Data for initial mineral nitrogen levels and nitrogen accumulation in incubated soils amended with H_2O are summarized in Fig. 1. At the time of initial sampling (day 0) there was no apparent pattern among sites for amounts of NO_3^- or NH_4^+ in the soil except higher levels of both mineral N forms in the 0 yr site. Over the course of the incubation period both nitrate and ammonium appeared to accumulate monotonically in most sites; with the possible exceptions of the first (0–3 d) sample period in both the 0-yr and 3-yr sites, there was little evidence for a lag in either nitrification or N mineralization in any incubations. At any sample point in the incubation period nitrate always made up at least 75% of total mineral N; by the time of final sampling this proportion was greater than 95% in all sites but the 3-yr, in which 84% of the total mineral N was NO_3^- .

The production of both nitrate and total mineral N were lowest in soils from the 0-yr site, and production appeared to increase through the 8-yr successional stage (Fig. 2). After the 8 yr stage, production decreased somewhat and appeared to level off.

In all sites, NH_4^+ additions stimulated nitrate production over the course of the incubation period to a greater extent than did any other treatment (Fig. 3, Table 3). CaCO_3 also stimulated nitrate production in soils from the first three sites, but because it stimulated nitrogen mineralization as well, it is likely that the increased nitrification was due to increased ammonium availability. CaCO_3 stimulated N mineralization in the older three sites, also. That the CaCO_3 effects were greater than those for CaSO_4 in soils from all sites indicates that the pH change rather than the Ca^{+2} was likely responsible for the increased produc-

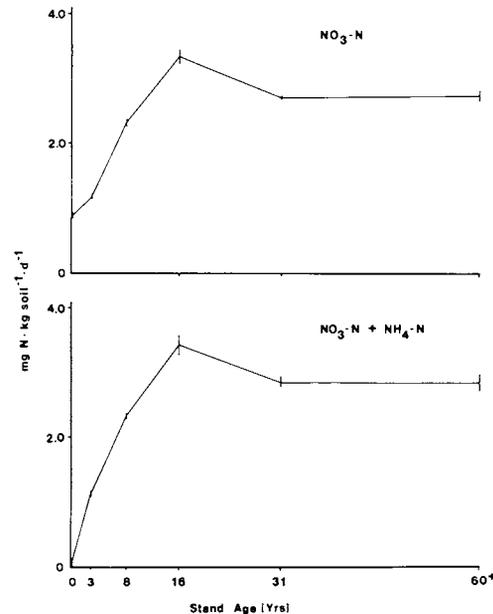


Fig. 2. Nitrate (upper graph) and total mineral N (lower graph) production in soils from 6 sites along a Central American rainforest sere incubated for 7.5 (site 0 yr) or 9 d (all others). Vertical bars represent standard errors ($n=6$). All sites were sampled simultaneously; see text for pre-sampling histories

tion. CaCO_3 additions resulted in bulk soil pH's of 6.5–6.6 for all sites, while the pH's of H_2O -treated soils varied between 5.1 and 5.5 throughout the incubation period (Table 4). Throughout the sere, an increasingly lower proportion of mineral nitrogen was found as nitrate in the soils amended with CaCO_3 .

Phosphorus treatments did not stimulate nitrification or nitrogen mineralization in soils from any of the sites, but appeared to have inhibited net mineral N production in the 8, 16, and 31 yr old sites. In the undisturbed rainforest, phosphorus additions had no apparent effect on mineral N transformations.

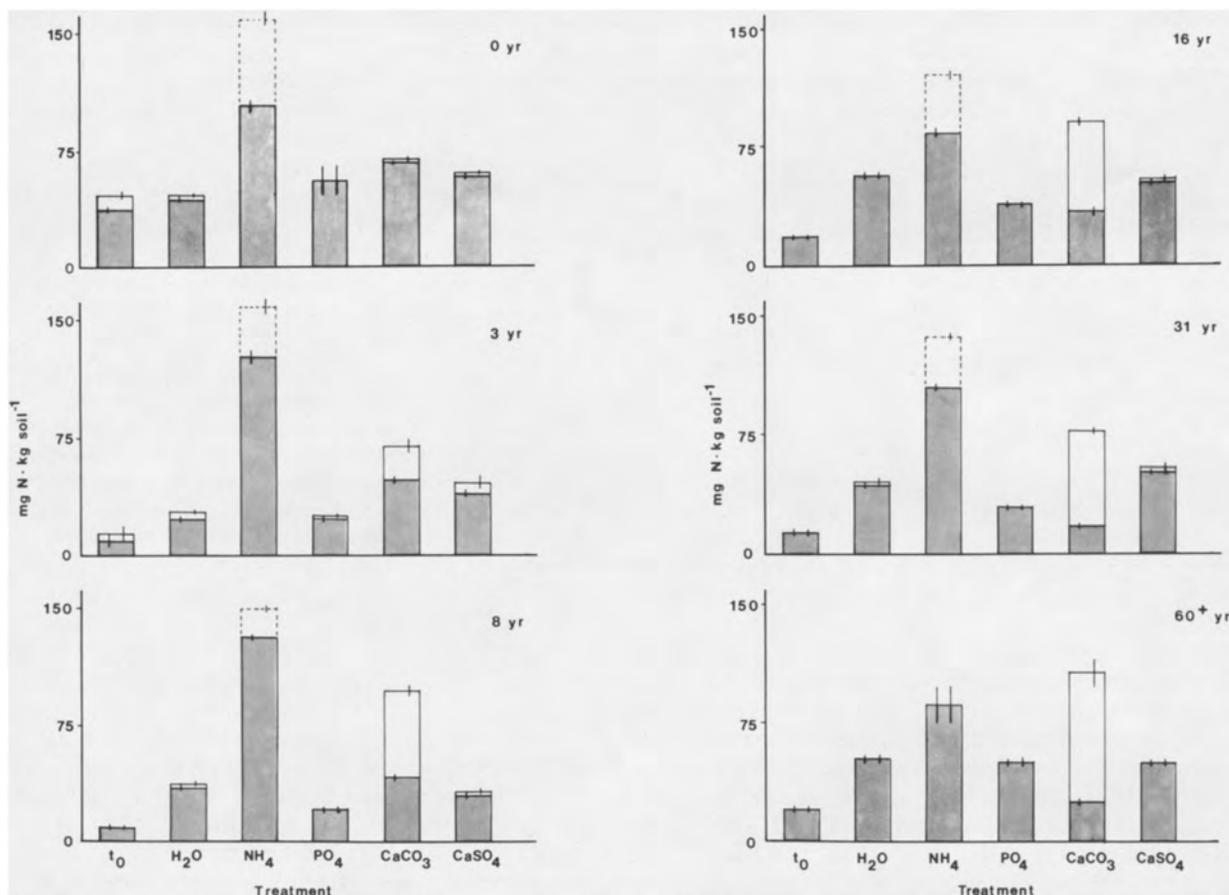


Fig. 3. Nitrate (shaded portion of each bar) and total mineral nitrogen (nitrate + ammonium N) accumulation in soils from along a rainforest sere incubated with and without the indicated ammdments. t_0 = initial N concentrations, H_2O = control. Vertical lines at the top of each bar segment indicate standard errors: for analysis of variance results see Table 3

Table 3. Nitrate production (not nitrate accumulation as in Fig. 1) in soils collected from along a lowland rainforest sere and incubated for 8–9 d with and without the indicated nutrients added at day 0. Values are $mg\ N \cdot kg\ dry\ soil^{-1} \cdot d^{-1}$ (\pm standard error, $n=6$). Data were analyzed by 2-way analysis of variance; different superscripts within rows (but not within columns) indicate significant differences among means at $P < 0.05$

Site	Control	NH_4^+	PO_4^{+3}	$CaCO_3$	$CaSO_4$
0 yr	1.08 (0.07) ^a	8.8 (0.70) ^b	2.53 (1.25) ^{cd1)}	4.13 (0.15) ^c	2.98 (0.09) ^d
3 yr	1.50 (0.07) ^a	12.9 (0.48) ^b	1.59 (0.02) ^a	4.29 (0.21) ^c	3.37 (0.17) ^d
8 yr	2.86 (0.04) ^a	13.4 (0.15) ^b	1.37 (0.03) ^c	3.48 (0.06) ^d	2.27 (0.10) ^e
16 yr	4.18 (0.24) ^a	7.2 (0.20) ^b	2.26 (0.09) ^c	1.65 (0.04) ^d	3.84 (0.13) ^a
31 yr	3.39 (0.11) ^a	10.3 (0.20) ^b	1.85 (0.05) ^c	0.63 (0.04) ^d	4.35 (0.08) ^e
60+ yr	3.46 (0.15) ^a	7.3 (1.3) ^b	3.15 (0.15) ^a	0.49 (0.06) ^c	3.15 (0.27) ^a

1) $n=2$

Table 4. pH of soils (\pm standard errors, $n=3$) from along the sere described in text before and after incubation with and without $CaCO_3$

Site	Initial		Final	
	Control	+ $CaCO_3$	Control	+ $CaCO_3$
0 yr	5.4 (0.01)	6.6 (0.01)	5.4 (0.01)	6.5 (0.02)
3 yr	5.4 (0.03)	6.6 (0.01)	5.4 (0.03)	6.5 (0.06)
8 yr	5.4 (0.06)	6.7 (0.01)	5.4 (0.03)	6.5 (0.06)
16 yr	5.3 (0.03)	6.7 (0.01)	5.2 (0.01)	6.5 (0.08)
31 yr	5.4 (0.03)	6.6 (0.01)	5.2 (0.01)	6.6 (0.05)
60+ yr	5.3 (0.01)	6.6 (0.01)	5.1 (0.01)	6.5 (0.03)

Discussion

Nitrification in this sere appears to increase monotonically through the first 8 yrs of the succession, after which it appears to decrease slightly but remain at about the 8-yr level. A similar pattern was reported by Lamb (1980) for a subtropical rainforest sere in Australia ($28^\circ 14' S$, 900 m elevation, 1400 mm annual precipitation); although the first of Lamb's 5 sites was 10 years old at the time of sampling, he too found that the earliest sites produced the least nitrate in laboratory incubations. This pattern differs from those reported for many temperate seres, and contradicts the generalization that nitrification decreases in the course of secondary succession (Rice and Panacholy 1972). Measure-

ments of nitrification potentials from along temperate region seres suggest that there is no consistent pattern for nitrification in temperate secondary succession (Coile 1940; Montes and Christensen 1979; Robertson and Vitousek 1981), although the oldest sites of some seres may have a greater capacity than younger sites for nitrate production (Robertson and Vitousek 1981).

Nitrate production in all control soils from the rainforest sere closely and consistently reflected total mineral-N production, and this observation together with the observation that added NH_4^+ -N stimulated nitrate production in all soils, suggests that nitrification is ammonium limited at all stages of this succession. The absence of pronounced lags over the short-term incubation period suggests that allelochemical inhibitors of nitrification (Rice and Pancholy 1974; Jordan et al. 1979; Rice 1979) are not likely to be present in these sites (Robertson 1982b). Lamb (1980) also found that NH_4^+ stimulated nitrate production in soils from both of the rainforest sites that he tested.

The low rates of N mineralization and consequently of nitrification in soils from the very early sites of this sere seem somewhat anomalous: one might expect that N mineralization and nitrification potentials would be high in soils which were recently subjected to a substantial pulse of biomass N. Numerous temperate studies, for example, have documented or inferred increased nitrification following clearcutting or vegetation suppression (e.g. Hesselman 1926; Romell 1935; Dominski 1971; Bormann et al. 1974; Glavac and Koenies 1978; Stone et al. 1978; Matson and Vitousek 1981), and in many cases the increase could be related to increased rates of N mineralization.

One explanation for the low rates in the earliest site may be that the site supported successional rather than old-growth forest at the time that it was cleared, and so there was less biomass N available for mineralization than if the cleared vegetation had been older. However, even if mineral N transformation rates in the early sites were low at the time they were cleared, potential rates should still have increased upon the addition of oxidizable biomass N. The 3 yr site was also in successional forests prior to clearing, and the fact that N mineralization rates were lower at 3 months following abandonment than at 3 yrs suggests that the explanation above cannot alone account for the lower rates early in the sere.

A more complete explanation might include climatic and substrate quality factors. High soil temperatures and adequate moisture following clearcutting can lead to very rapid mineralization and nitrification rates in situ (Moureaux 1967; Myers 1975; Focht and Verstraete 1977; Matson and Vitousek 1981), and it is likely that microclimatic differences between intact and recently cutover forest at the soil surface are much greater in tropical regions than in temperate. Cunningham (1963), for example, found soil temperature differences between bare fallow and shaded plots in southern Ghana to approach 11°C , whereas Dominski (1971) and Matson and Vitousek (1981) found differences in intact vs. recently cutover temperate sites at mid-summer to be no greater than 5°C and usually $<2^\circ$. Together with plentiful rainfall in the humid tropics, highly elevated temperatures in rainforest clearcuts may lead to extremely rapid N mineralization, immobilization, and nitrification rates that may, in the clearcuts examined in this study, have led to a rapid depletion of mineralizable N by the 3-month sample date. Thus, had the experimental

design included sites at earlier stages of succession, high rates of mineral N transformations early in secondary succession may have been observed. The high initial levels of soil nitrate found in incubations of soil from the 3 month site (Fig. 1) is consistent with this explanation.

Substrate quality may also play a role in the pattern of mineralization observed in this sere. If the vegetation in the rainforest when it was cut were of low quality (e.g. high C:N ratio or high lignin content), then little biomass N would likely be available for mineralization early in the succession and significant amounts of mineralized nitrogen might be immobilized into microbial biomass rather than be nitrified. Data are not at hand to evaluate directly whether low substrate quality could have led to the observed pattern of low net mineralization early in the sere.

It is difficult to compare absolute rates of N mineralization and nitrification found in this study with rates found for other systems because of differences in incubation conditions, but in general it appears that mineralization in intact rainforest at La Selva occurs almost as rapidly as has yet been measured. Most temperate forest soil incubations produce mineral N at rates of around $1\text{--}2\ \mu\text{g N}\cdot\text{g dry soil}^{-1}\cdot\text{d}^{-1}$ (Robertson 1982a); typical rates for tropical forest soils thus far examined range from <0.1 to $>6\ \mu\text{g N}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ (de Rham 1970; Lamb 1980; Tanner 1977; Vitousek et al. 1983). Rates for the older La Selva sites are towards the high end of the spectrum, ca. $4\ \mu\text{g N}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$. This may indicate that in the old-growth La Selva forest nitrogen is plentiful and not likely to be limiting productivity. Consistent with this interpretation, phosphorus amendments of soils from older successional sites led in 3 of 4 cases to apparent N-immobilization, which may indicate that microbial growth in these sites is phosphorus-limited. Taken together, these observations suggest that primary productivity may be limited more by phosphorus in the older sites than by nitrogen, as has been suggested by Vitousek (1983) for humid tropical forests in general.

Conclusions

1. Nitrogen mineralization and nitrification potentials of soils from 6 stages of a lowland rainforest sere suggest that both nitrification and N mineralization increase through the 8-yr stage of succession and then level off.
2. Experimental nutrient additions to soils from this sere suggest that ammonium availability limits nitrification at all successional stages. During incubations there was no clear evidence for a lag in nitrate production that might indicate the presence of allelochemical inhibitors.

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References

- Bormann, FH, Likens GE, Siccama TG, Pierce RS, Eaton JS (1974) The export of nutrients and recovery of stable conditions

- following deforestation at Hubbard Brook. *Ecol Monogr* 44:255–277
- Bourgeois WW, Cole DW, Reikerk H, Gessel SP (1972) Geology and soils of comparative ecosystem study areas, Costa Rica. Contrib No 11, Inst For Prod, Coll For Res, Univ Wash, Seattle
- Brady NC (1982) Chemistry and the world food supply. *Science* 218:847–853
- Cole TS (1940) Soil changes associated with loblolly pine succession on abandoned agricultural land of the Piedmont Plateau. *Duke Univ Sch For Bull* 5:1–85
- Cunningham RK (1963) The effect of clearing a tropical forest soil. *J Soil Sci* 14:334–345
- Dominski AS (1971) Nitrogen transformations in a northern hardwood podzol on cutover and forested sites. PhD Thesis, Yale Univ, New Haven, CT
- Ellenberg H (1974) Stickstoff als Standortsfaktor, insbesondere für mitteleuropäische Pflanzengesellschaften. *Oecol Plant* 12:1–22
- FAO (1974) Fertilizers, the first decade: A summary of results achieved between 1961 and 1971. FAO, Rome
- FAO/SIDA (1974) Shifting cultivation and soil conservation in Africa. Summaries and recommendations. *Soils Bull No 24*. FAO, Rome
- Focht DD, Verstraete W (1977) Biochemical ecology of nitrification and denitrification. In: Alexander M (ed) *Advances in Microbial Ecology*, Vol 1. Plenum Press, NY, p 135–214
- Glavac V, Koenies H (1978) Mineralstickstoff-Gehalte und N-Nettomineralisation im Boden eines Fichtenforstes und seines Kahlschlagel während der Vegetationsperiode. *Oecol Plant* 13:207–218
- Greenland DJ (1980) The nitrogen cycle in West Africa – agronomic considerations. In: Rosswall T (ed) *Nitrogen Cycling in West African Ecosystems*. Roy Swed Acad Sci, Stockholm, pp 73–81
- Hartshorn GS (1972) The ecological life history and population dynamics of *Pentaclethra maculosa*, a tropical wet forest dominant and *Stryphnodendron excelsum*, an occasional associate. PhD Thesis, Univ Wash, Seattle
- Hartshorn GS (1978) Three falls and tropical forest dynamics. In: Tomlinson PB, Zimmermann MH (eds) *Tropical Trees as Living Systems* Cambr Univ Press, London, pp 617–638
- Hesselman H (1926) Studier over barrskogens humustacke dess egenskaper och beroende skogsvarden. *Medd f Skogsforstanst* 22:169–522
- Holdridge LR, Grenke WC, Hatheway WH, Liang T, Tosi JA (1971) Forest environments in tropical life zones: a pilot study. Pergamon Press, NY
- Johnson DW, Cole DW, Gessel SP, Singer MJ, Minden RV (1977) Carbonic acid leaching in a tropical, temperate, subalpine, and northern forest soil. *Arctic Alpine Res* 9:329–343
- Jordan CF, Todd RL, Escalante G (1979) Nitrogen conservation in a tropical rainforest. *Oecol* 39:123–128
- Lamb D (1980) Soil nitrogen mineralisation in a secondary rainforest succession. *Oecol* 47:257–263
- Matson PA, Vitousek PM (1981) Nitrogen mineralization and nitrification potentials following clearcutting in the Hoosier National Forest, Indiana. *For Sci* 27:781–791
- Montes RA, Christensen NL (1979) Nitrification and succession in the Piedmont of North Carolina. *For Sci* 25:287–297
- Moureaux C (1967) Influence de la temperature et de l'humidité sur les activités biologique de quelques solo Ouest-Africaine. *Cah ORSTOM, Ser Pedol* 5:393–420
- Myers N (1979) *The sinking ark*. Pergamon Press, New York
- Myers RJK (1975) Temperature effects on ammonification and nitrification in a tropical soil. *Soil Biol Biochem* 7:83–86
- NAS (1980) *Research Priorities in Tropical Biology*. NRC, Washington, DC
- de Rham P (1970) L'azote dans quelques forêts, savanes et terrains de culture d'Afrique tropicale humide. *Veroff Geobot Inst Zurich* 45:1–125
- Rice EL (1979) Allelopathy – an update. *Bot Rev* 45:15–109
- Rice EL, Pancholy SK (1972) Inhibition of nitrification by climax vegetation. *Am J Bot* 59:1033–1040
- Rice EL, Pancholy SK (1974) Inhibition of nitrification by climax ecosystems. III. Inhibitors other than tannins. *Am J Bot* 61:1095–1103
- Robertson GP (1982a) Nitrification in forested ecosystems. *Phil Trans R Soc Lond B* 296:445–457
- Robertson GP (1982b) Factors regulating nitrification in primary and secondary succession. *Ecology* 63:1561–1573
- Robertson GP, Vitousek PM (1981) Nitrification potentials in primary and secondary succession. *Ecology* 62:376–386
- Romell LG (1935) Ecological problems of the humus layer in the forest. *Cornell Univ Agric Exp Sta Mem* 170:1–28
- Sanchez PA, Bandy DE, Villachica JH, Nicholaides JJ (1982) Amazon basin soils: management for continuous crop production. *Science* 216:821–827
- Skujins J, Klubek B (1982) Soil biological properties of a montane forest sere: corroboration of Odum's postulates. *Soil Biol Biochem* 14:505–513
- Stone EL, Swank WT, Hornbeck JW (1978) Impacts of timber harvest and regeneration on stream flow and soils in the eastern deciduous region. In: Youngberg CT (ed) *Forest Soils and Land Use*. Colorado St Univ, Ft Collins, CO, p 516–535
- Tanner EVJ (1977) Four montane rainforests of Jamaica: a quantitative characterization of the floristics, the soils and the foliar mineral levels, and a discussion of the interrelations. *J Ecol* 65:883–918
- Vitousek P (1983) Nutrient cycling and the control of litter production in tropical forests. *Ecology* (in press)
- Vitousek PM, Van Cleve K, Balakrishnan N, Mueller-Dombois D (1983) Soil development and nitrogen turnover in montane rainforest soils on Hawaii. *Biotropica* (in press)
- Werner P (1983) The variation in soil properties under tropical rainforest succession in Costa Rica. (in review)

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