

Nitrification and denitrification in humid tropical ecosystems: potential controls on nitrogen retention

G. P. ROBERTSON

W. K. Kellogg Biological Station and Department of Crop and Soil Sciences, Michigan State University, Hickory Corners, MI 49060-9516, USA

SUMMARY

1 Nitrification is an important microbial process in humid tropical ecosystems because of its effects on potentials for nitrogen loss via nitrate leaching and denitrification and on the hydrogen ion cycle. Nitrification rates in humid tropical soils vary markedly among different forest types but in general appear to increase following disturbance. Proximal controls on nitrifiers include ammonium and oxygen; other major controls (water, temperature, net nitrogen mineralization, plant uptake, cation exchange capacity (CEC), respiration rates and aggregate structure) operate chiefly through their effects on the availability of ammonium and oxygen. There are a number of more distal controls, particularly plant community structure (the composition and physical stature of the plant community), which can be greatly influenced by human activity.

2 Denitrification has been less extensively studied in the humid tropics. A priori predictions suggest that denitrification rates ought to be high in the humid tropics as long as nitrate is available: soils tend to be highly aggregated and are often moist, resulting in low O₂ diffusion potentials, and carbon inputs from primary producers tend to be high. Recent results from *in situ* studies suggest that denitrification trends among rain forest sites may be similar to those for nitrification: high where nitrogen mineralization is high and low where nitrogen mineralization is low. Thus denitrification tends to be lowest in mid-successional sites where nitrate availability limits denitrifier activity.

3 Nitrification and denitrification can both lead to high nitrogen losses after vegetation clearing: denitrification directly and nitrification via its effects on nitrate leaching and denitrification potentials. Additionally, both processes may play an important role in the maintenance of soil exchange properties following disturbance. Nitrification, by producing hydrogen ions, will tend to force the soil exchange system to a net positive charge (to a net anion exchange capacity) and denitrification, by consuming some of the H⁺ ions produced by nitrifiers, will tend to restore negative charges. Feedbacks in the system following disturbance may tend to make soil pH equilibrate near the soil's point of zero charge, a pH at which exchangeable ions are held only loosely against leaching from the rooting zone.

INTRODUCTION

Nitrification and denitrification are two of the potentially most important regulators of nitrogen retention in tropical rain forests. In temperate forests, nitrification can play a central role with respect to nitrogen loss from these systems (Fig. 1). When nitrification is low, mineral nitrogen stays in the ammonium form which tends to be conserved by cation exchange processes and by plant and microbial uptake. When nitrification is high, however, mineral nitrogen becomes more susceptible to loss because nitrate ions are not preferentially utilized and thereby immobilized by most microbial heterotrophs, are not held against leaching on cation exchange sites, and are available for gaseous loss via denitrification. Denitrification, the microbial reduction of nitrate to nitrogen gas in oxygen-depleted microsites in soil, can be a major pathway for nitrogen loss in some temperate zone forests (Melillo *et al.* 1983; Robertson & Tiedje 1984).

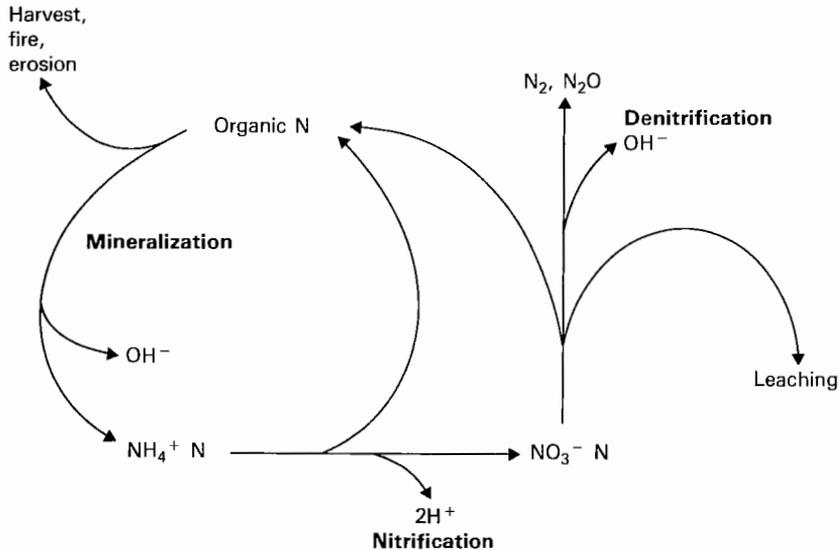


FIG. 1. Major potential pathways of nitrogen loss in a hypothetical terrestrial ecosystem.

In the humid tropics the influence of nitrification and denitrification on nitrogen loss may differ in at least three ways from that in temperate regions. First, because soils in humid tropical systems are often highly weathered with variable-charge clays predominant (Uehara & Gillman 1981; Sollins, Robertson & Uehara 1988), the soil charge system may under certain circumstances effectively switch polarity so that nitrate rather than ammonium is conserved on exchange sites. Thus nitrifiers in such soils may help to conserve mineral nitrogen as nitrate, particularly at depth (Matson *et al.* 1987).

Second, denitrification may be an especially important sink for available nitrogen in the humid tropics. As discussed later, soil O_2 potential is a major proximal control on denitrification in soil. Because soil moisture in the humid tropics is often high and because primary productivity and consequently decomposition also tend to be high in rain forests, soil oxygen diffusion can be inhibited at the same time that oxygen demands are great. This means that a large proportion of microsites in these soils may be anaerobic and hence favourable sites for denitrification. In addition, where the availability of nitrate is enhanced, as it may be in soils with a net anion exchange capacity, denitrification rates may be further elevated.

Third, and perhaps specific to humid tropical forests, nitrifiers and denitrifiers may regulate the charge status of these soils through their net effect on the H^+ ion cycle. In soils dominated by variable-charge clays, charge capacities are driven by the protonation and deprotonation of variable-charge surfaces (Uehara & Gillman 1981); because variable-charge soils typically are only weakly buffered, biological processes which (like nitrification) produce H^+ ions may reduce cation exchange capacity (CEC) and enhance anion exchange capacity (AEC). On the other hand, biological processes such as denitrification which consume H^+ ions may increase CEC at the expense of AEC. These changes may have important implications for overall ion retention.

In the sections that follow, I give an overview of nitrification and denitrification in humid tropical ecosystems, with a particular emphasis on the factors controlling these processes. In addition, I present a discussion of how these processes fit into the larger ecosystem, and the consequent potentials for system-wide effects.

NITRIFICATION

Nitrification in humid tropical soils has been studied extensively since early surveys of nitrifier numbers in West African forest soils (e.g. Laudelout & DuBois 1951; Dommergues 1952; Berlier, Dabin & Leneuf 1956; Jacquemin & Berlier 1956). Together with studies of soil nitrate concentrations under different vegetation types following clearing (e.g. Diamond 1937; Greenland 1958), results suggested that nitrification rates differed substantially among forest types and tended to increase temporarily after vegetation clearing. As early as 1950, for example, Vine (1953) had documented enhanced concentrations of soil nitrate following primary forest clearing and had noted that these concentrations tended to fall off after 8–10 years of cultivation.

Results from recent work using more direct measures of nitrification in tropical forest soils do not contradict these early findings. Using soil incubation and ^{15}N techniques Matson *et al.* (1987) found that nitrification rates in a premontane (650 m elevation) secondary rain forest in Central America were substantially increased for the first 6 months following secondary forest clearing, after which rates returned to levels close to those in uncut plots. Robertson &

Sollins (1987) documented nitrification increases following the clearing of 20-year-old secondary lowland vegetation on a Costa Rican Oxic Dystropept soil (Fig. 2). In this experiment cleared plots were kept vegetation-free throughout the 1-year experiment and nitrification rates remained high for the entire period.

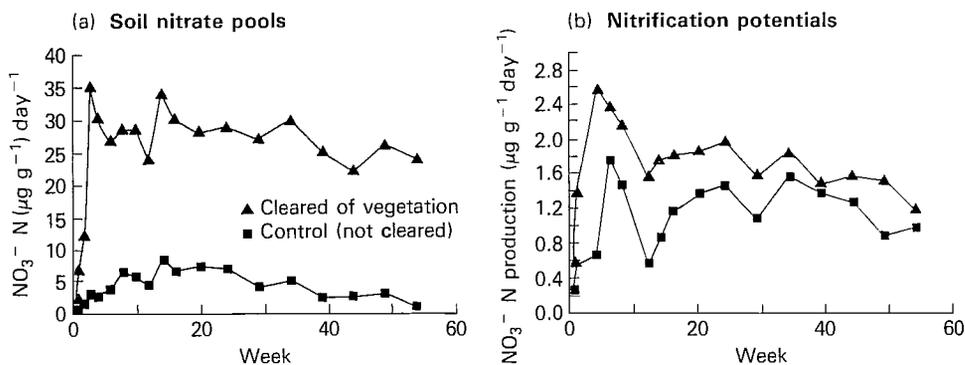


FIG. 2. Nitrate accumulation (a) and nitrification potentials (b) in a site cleared of secondary vegetation at a lowland rain forest site in Central America (from Robertson & Sollins (1987)).

Higher nitrification rates early in rain forest successions are typically followed by rates lower than those in either early or old-growth forest. Working in a subtropical rain forest sere in Australia, Lamb (1980) found lower nitrification rates in a 10-year-old site than in four older sites. Robertson (1984) found lower nitrification in the three early sites along a five-site sere in Costa Rica (Fig. 3).

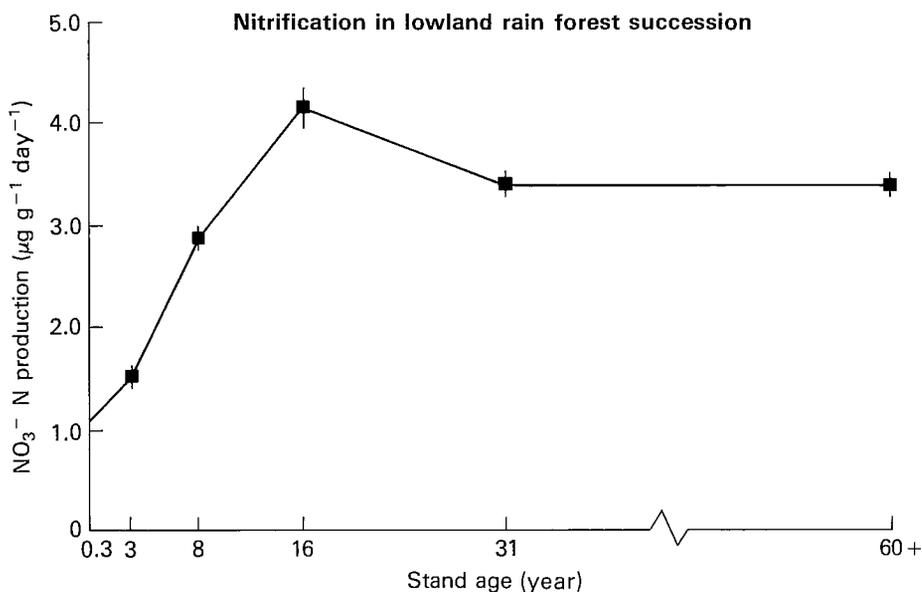


FIG. 3. Nitrification rates along a lowland tropical rain forest sere (from Robertson (1984)).

Such patterns of nitrification in succession are consistent with the hypothesis (Gorham, Vitousek & Reiners 1979) that in many types of seres soil nitrogen turnover should be high mainly very early and relatively late in succession when plant biomass accumulation, and therefore net plant nitrogen immobilization, is low. As discussed below, such trends have important implications for the effects of tropical deforestation on global nitrogen cycle processes such as nitrous oxide accumulation in the upper atmosphere.

Although nitrification trends in tropical rain forest succession appear to be consistent across a wide variety of forest types, undisturbed forests nevertheless differ widely in their extent of nitrification. Reports of nitrification in soils from intact primary rain forest range from <0.1 to $>6 \mu\text{g g}^{-1} \text{day}^{-1} \text{NO}_3^- \text{-N}$ (deRham 1970; Tanner 1977; Lamb 1980; Vitousek *et al.* 1983; Chandler 1985; Robertson 1984). Although this wide range may to some extent be an artefact of different incubation techniques, both Montagnini & Buschbacher (1988) and Vitousek & Matson (1988) reported equally wide ranges in two surveys in which identical techniques were employed across a broad range of sites. Vitousek & Matson (1988) in a survey of nitrogen turnover in nine old-growth tropical forests in several different geographic regions documented rates that showed a more than fivefold difference between sites (Table 1), and Montagnini & Buschbacher (1988) documented rates among three Amazonian and Costa Rican sites that differed more than tenfold (Table 2).

TABLE 1. Net nitrification and nitrogen mineralization in nine old-growth tropical rain forest sites sampled on a single date within each site; values (\pm S.E.) based on 10-day incubations of fresh soil (from Vitousek & Matson (1988)) (na = no S.E. available)

Site	Nitrification ($\mu\text{g g}^{-1} \text{day}^{-1} \text{N}$)	N mineralization ($\mu\text{g g}^{-1} \text{day}^{-1} \text{N}$)
Costa Rica (lowland forest)		
Residual soil	2.5 (0.3)	3.9 (0.5)
Old alluvial soil	1.8 (0.8)	2.7 (0.03)
Panama (semi-deciduous forest)		
Basalt	1.2 (0.1)	1.2 (0.2)
Sedimentary	1.6 (0.1)	1.6 (0.2)
Brazil (lowland forest)		
Oxisol	2.2 (0.3)	1.9 (0.3)
Oxisol/Ultisol	1.5 (0.1)	1.4 (0.2)
Psamment	0.6 (0.1)	0.8 (0.1)
Hawaii (montane forest)		
>1000-year-old Andept	0.0 (0.05)	0.1 (0.04)
>4000-year-old Andept	0.5 (na)	0.5 (na)

TABLE 2. Comparison of nitrogen mineralization and nitrification rates in soils from old-growth forests of San Carlos de Rio Negro, south-west Venezuela, and La Selva, north-east Costa Rica (from Montagnini & Buschbacher (1988))

	pH	Nitrification ($\mu\text{g g}^{-1} \text{day}^{-1}$)	N mineralization ($\mu\text{g g}^{-1} \text{day}^{-1}$)
San Carlos, Oxisol	3.3	0.50	0.47
San Carlos, Ultisol	3.5	0.12	0.06
La Selva, Inceptisol	5.3	3.43	3.43

Understanding the mechanisms underlying these differences in nitrification rates requires an understanding of the potential controls on nitrification in rain forest soils. As shown in Fig. 4, two main factors regulate nitrification at a fundamental, cellular level in most soils: ammonium ions and oxygen. All other important factors exert their influence mainly by affecting the ways in which ammonium and oxygen interact with individual cells. Soil moisture, for example, influences nitrification chiefly by controlling the diffusion of ammonium ions and oxygen through water films to the individual nitrifiers. Temperature (climate) influences nitrification mainly by its direct effects on processes affecting ammonium availability (mineralization/immobilization and ammonium ion diffusion), by its direct effects on the availability of O_2 (respiration and O_2 diffusion), and by its longer term effects on plant community structure and soil type.

Figure 4 shows the five major scales at which nitrification can be regulated in rain forest soils, ranging from the most proximal (ammonium and oxygen availability) to the most distal (climate, soil type and disturbance). This approach emphasizes indirect effects and explicitly identifies those factors operating at several different levels. A major secondary factor controlling nitrification through its influence on ammonium ions, for example, is the balance between nitrogen mineralization and immobilization. Nitrifiers are well-known to be poor competitors for ammonium in soil (Jones & Richards 1977; Schmidt 1982): where the available soil organic matter fraction has a high C : N ratio, microbial heterotrophs will readily immobilize NH_4^+ ions in solution, leaving little for nitrifiers. In temperate zone forests this immobilization can account for significant nitrogen retention in the system following clearcutting (Vitousek & Matson 1984); it may partly explain the low nitrification early on in some rain forest seres in which woody slash does not completely burn or is left on site (e.g. Robertson 1984). A more important mechanism retaining ammonium in many rain forest soils following clearing is plant uptake, however. Robertson & Rosswall (1986) estimated from literature reviews that early successional rain forest (0–20 years old) in West Africa removed an average $229 \text{ kg ha}^{-1} \text{ year}^{-1}$ N from the soil solution; of this around $114 \text{ kg N year}^{-1}$ was incorporated into standing biomass. Although mature forests were estimated to take up an equivalent amount of nitrogen — $211 \text{ kg ha}^{-1} \text{ year}^{-1}$ — less than $1 \text{ kg ha}^{-1} \text{ year}^{-1}$ appeared to be retained via biomass accretion. This implies that in primary rain forests a much higher proportion of the system's nitrogen is circulating through the soil solution and available to nitrifiers, and partly explains the enhanced rates of nitrification late in many rain forest successions.

A fourth secondary control on nitrification via effects on ammonium availability in rain forest soils (Fig. 4) is the cation exchange capacity (CEC) of the soil. Those soils with a higher CEC will tend to retain NH_4^+ ions against leaching, thereby enhancing their availability to nitrifiers provided that there is little competition from plants and microbial heterotrophs and that sufficient moisture is available for the ions to diffuse.

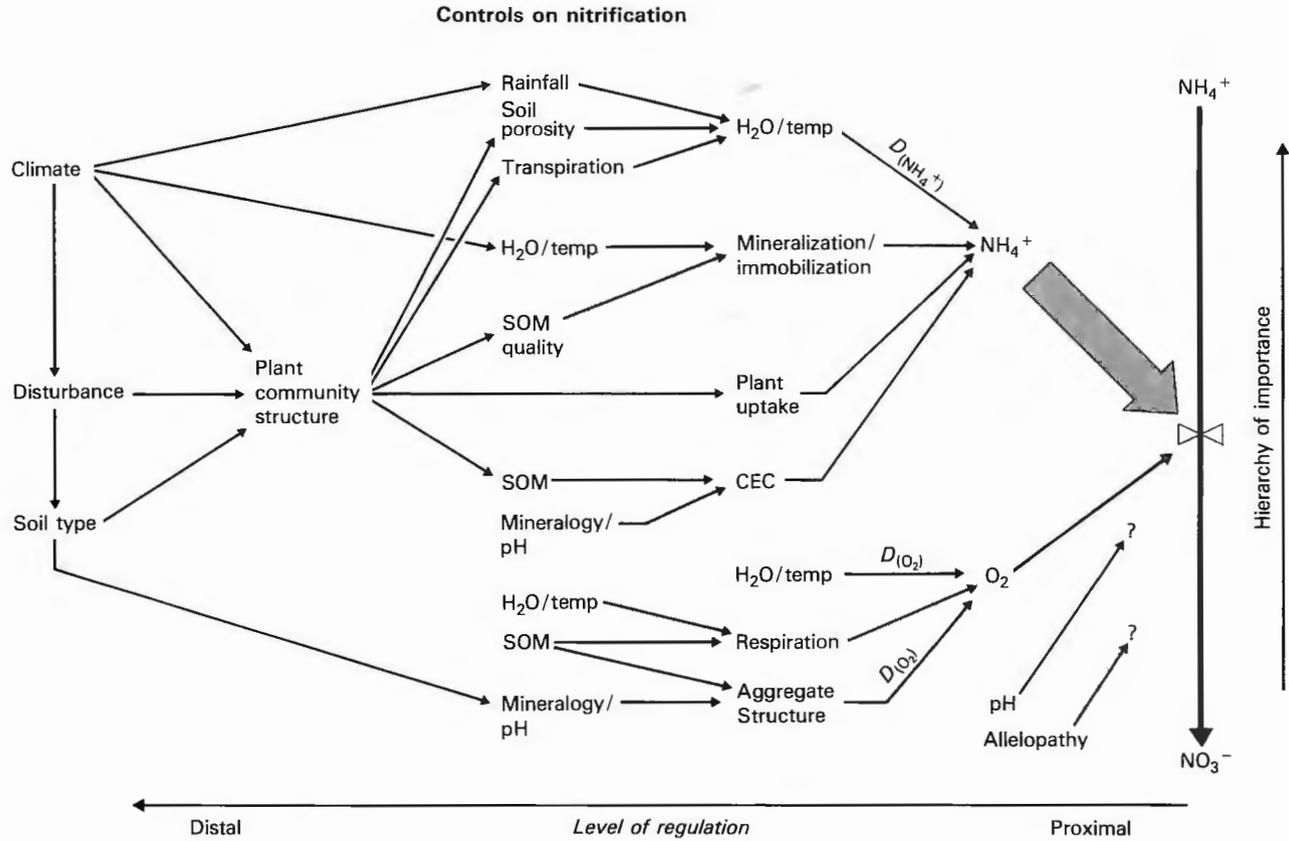


FIG. 4. A schematic diagram of the major factors regulating nitrification in rain forest soils (adapted from Tiedje (1987)). $D_{(\text{NH}_4^+)}$ and $D_{(\text{O}_2)}$ refer to the diffusion of NH_4^+ ions and O_2 to the nitrifiers.

At the tertiary level, factors that affect ammonium availability through their effects on water flow include rainfall, soil porosity, and transpiration, each in turn affected mainly by the composition and structure of the plant community. The chief factors that affect ammonium availability through effects on net nitrogen mineralization include water and soil organic matter (SOM) quality, which are also directly affected by plant community structure, as is plant uptake and the effect of SOM on soil CEC. Soil mineralogy and, in variable-charge soils, soil pH, interact with SOM to control soil CEC.

Secondary controls on nitrification via effects on oxygen availability include soil moisture (as mentioned above), respiration, and soil aggregate structure. Respiration in many soils can be high; Singh & Gupta (1977) reported oxygen consumption rates of more than $70 \text{ mmol O}_2 \text{ cm}^{-2} \text{ h}^{-1}$ as a result of root and microbial respiration, rates that can exceed oxygen supply especially where soil moisture impedes diffusion. Soil aggregation can further impede oxygen availability by providing an additional diffusion barrier for microbes within aggregates. Tertiary level controls on oxygen availability include the effects of water and soil organic matter on respiration and of soil organic matter and mineralogy/pH interactions on aggregate structure.

The central role of plant community structure (the composition and physical stature of the plant community) in controlling nitrification at a distal level can be seen from its position in Fig. 4. Through effects on soil porosity, on the amount of water extracted from the soil, on soil organic matter inputs and quality, and on ammonium uptake, community structure exerts a major indirect influence on nitrification rates. Changes in plant community structure brought about by long-term changes in climate or soil type or by direct human influence in the short term may greatly alter nitrification rates, mainly through effects on factors which influence the supply of NH_4^+ ions and oxygen to nitrifiers. Knowledge about these factors and their interactions should allow us to predict and to some extent to manage many aspects of the response of nitrifiers to disturbance and to major differences in plant community types.

Both soil pH and allelopathy are included in Fig. 4 as potential proximal regulators of nitrification in the humid tropics. However, neither have been shown to influence nitrification directly in unamended soils. Active nitrification is known to occur in a variety of soils at pH values of less than 4.0 (Robertson 1982; Schmidt 1982), and recent attempts to document allelochemical inhibition of nitrifiers *in situ* in rain forest soils have met with little success (Chandler 1985).

DENITRIFICATION

Less is known about denitrification than about any other major part of the nitrogen cycle in humid tropical ecosystems. This is largely due to the difficulty of measuring nitrogen gas fluxes in soil: available methods are technically difficult, laborious, provide results that can be difficult to interpret, and require instru-

mentation which is not easily transported or maintained in rain forest environments.

Controls on denitrification in tropical rain forests (Fig. 5) are similar to controls in temperate region ecosystems (Groffman *et al.* 1988). Oxygen, carbon, and NO_3^- ions regulate denitrification at the most proximal, cellular level. Of these, oxygen dominates. Denitrification is an anaerobic process that occurs only in the absence of oxygen (Tiedje 1988); in soils this appears to occur mainly in soil organic matter particles and soil aggregates, microenvironments where high respiratory demand can exceed the supply of oxygen slowly diffusing through the surrounding water film.

NO_3^- ions are an important proximal control on denitrification where the demand for them by plants is high or where their production via nitrification is low. Available carbon, too, can be limiting because most denitrifiers are heterotrophs that rely on organic carbon for the donor electron. Although the effect of carbon on denitrifiers is more likely to be indirect via the effects of carbon on oxygen availability, direct effects are potentially important in soils with high concentrations of NO_3^- ions such as fertilized agricultural sites and very recently cleared or perhaps late successional rain forest.

Although denitrification has rarely been measured in humid tropical ecosystems, one might predict that rates should be high in uncut forests (Greenland 1956): variable-charge soils tend to exhibit strong aggregate structure, soils in these regions are rarely dry, and they tend to have high carbon inputs from high primary productivity. This suggests that oxygen-stressed microsites with adequate carbon may be relatively plentiful in many rain forest soils, and in those where nitrification is high, nitrate will be available and denitrification high.

This has been shown in at least one lowland rain forest region in Central America. Robertson & Tiedje (1988) measured denitrification in four primary forest sites in Costa Rica using the acetylene inhibition technique on intact soil cores. Over a 14-month period, average rates extrapolated to an annual flux of 7.6–21 $\text{kg ha}^{-1} \text{ year}^{-1}$ N gas in the primary forest site, up to four times greater than rates in nearby mid-successional sites (*c.* 15 years from primary forest cutting and 5 years since last grazed; Fig. 6). Rates of denitrification in early successional sites cleared several weeks prior to first measurements were even higher than rates in the most active primary forest site (Fig. 6), although these high rates did not persist for more than a few months.

It was suggested from the results of a nitrate amendment experiment (Table 2) that low rates in mid-successional sites were the result of low nitrate availability. Nitrate added as sodium nitrate to soil cores from the primary forest sites had no appreciable effect on denitrification in these cores, whereas nitrate added to cores from the two mid-successional sites significantly stimulated denitrification. Such results suggest that denitrification rates in humid tropical forests will parallel nitrification trends fairly closely; however, until denitrification rates are measured elsewhere it will be difficult to generalize. At only one additional site has

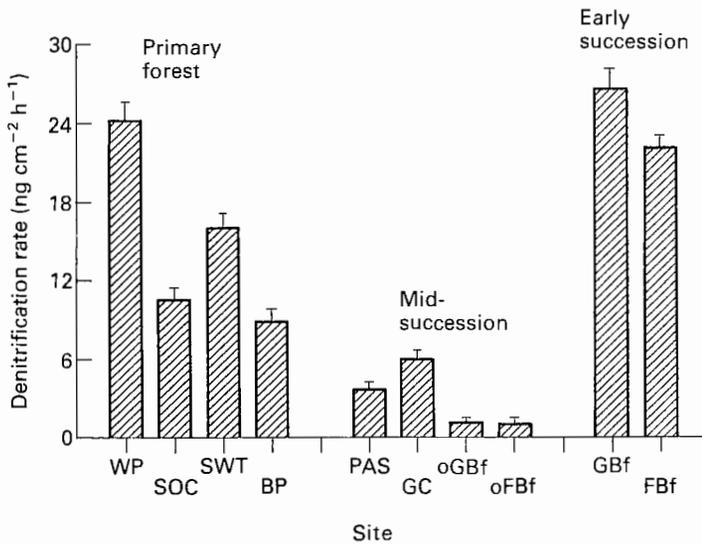


FIG. 6. Mean denitrification rates ($N_2 + N_2O$ production) in lowland rain forest sites at La Selva, north-east Costa Rica, at different stages of secondary succession. Primary forest sites have never been cut; early succession sites were recently cleared of mid-successional growth. Two mid-successional sites (oGBf and oFBf) had been cut over a year earlier and maintained vegetation-free. Vertical bars show the S.E. (from Robertson & Tiedje (1988)).

denitrification been measured *in situ*. Matson *et al.* (1987) quantified rates of denitrification in a premontane (650 m elevation) rain forest cleared of secondary vegetation and also found that rates immediately following clearing were high; later trends, however, were masked by high within-site variability.

ECOSYSTEM-LEVEL INTEGRATION

At the ecosystem level, both nitrification and denitrification can have important consequences for overall site fertility and for the recovery of fertility following disturbance. Indirect evidence suggests that phosphorus rather than nitrogen most commonly limits productivity in late successional tropical rain forests (Vitousek 1984; Vitousek & Sanford 1986); however, loss of nitrogen rather than phosphorus availability may more persistently affect productivity in many cleared and early successional systems, including agricultural ones (Brady 1982; Sanchez *et al.* 1982; FAO 1974). Consequently, the effects of nitrification and denitrification on nitrogen availability at a rain forest site may be particularly important in early to mid-successional stages.

In addition to effects on nitrogen availability early in secondary succession, nitrification and denitrification may play a critical role in maintaining the

availability of other nutrients in the rooting zone during this period. As noted earlier, in variable-charge soils cation exchange capacity is largely dependent on the protonation and deprotonation of soil mineral surfaces. Because nitrification can play a large role in the H^+ budget of a site, and because nitrification generally increases following rain forest clearing (see above), it has the potential to alter the soil charge system significantly following disturbance. Specifically, nitrification following clearing may produce sufficient H^+ to drive soil pH close to or below the point of zero charge (PZC), the pH at which the soil has very little capacity to hold exchangeable ions in the rooting zone. Denitrification will tend to counteract this tendency, especially if it is also stimulated by disturbance: denitrifiers effectively consume the H^+ produced by nitrifiers when they denitrify NO_3^- ions to an uncharged nitrogen gas species. Thus if nitrification and denitrification are in balance following disturbance, soil pH will remain unchanged as long as other parts of the H^+ cycle remain unchanged.

Recent evidence suggests that at least under some circumstances the system does not stay in balance and soil pH can decline sharply following clearing with nitrifiers largely responsible for this decline. Robertson & Sollins (1987), in a field experiment on an Oxic humitropept soil in Costa Rica, found a soil pH drop of *c.* 0.5 units in the 2 weeks following vegetation removal on their site. The resulting pH, around pH 3.9, was almost 0.2 pH units below the soil's PZC and was lower than soil pH measured in a weak KCl solution for months following clearing (Sollins *this volume*), implying a correspondingly large drop in CEC in this soil for the period (Uehara & Gillman 1981). Subsequent laboratory experiments with similar soils strongly suggested that nitrification was the principal cause of the pH drop: in incubations in which nitrifiers were experimentally inhibited with 10 Pa acetylene (Berg, Klemetsson & Rosswall 1982), soil pH did not drop (Fig. 7). Such results indicate the presence of a charge system in these soils that can be under biological control, and implicate nitrifiers as the principal agents of this control.

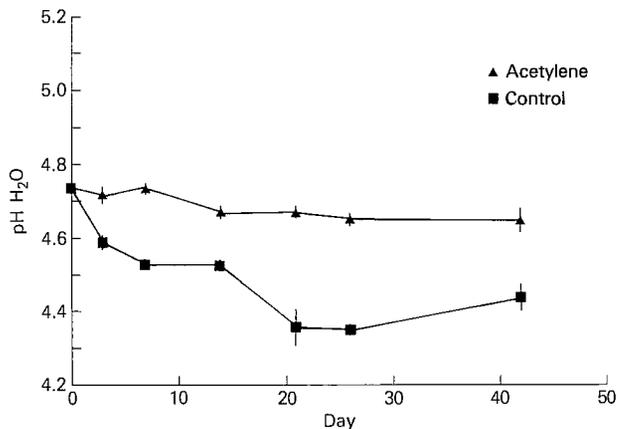


FIG. 7. Changes in soil pH in an Oxic Humitropept soil incubated with and without nitrification inhibited by 10 Pa acetylene. Vertical bars show the S.E. ($n = 5$) (from Robertson & Sollins (1987)).

If denitrifiers are stimulated by added nitrate in soils from disturbed systems (Table 3), and if nitrate pools increase on disturbance due to both increased nitrification and the development of significant anion exchange, then denitrifiers could help to keep soil pH from dropping below the soil's PZC. Specifically, as pH drops below PZC and greater quantities of NO_3^- ions are held in the upper soil horizons because of increasing anion exchange capacity, denitrifiers may respond to this increased nitrate pool by reducing additional quantities of NO_3^- and concomitantly consuming H^+ ; this could have the effect of slowing or even reversing the downward pH shift, effectively equilibrating soil pH close to soil PZC, since as pH begins to rise above the PZC denitrification will again fall off as the availability of NO_3^- ions declines from the loss of anion exchange capacity.

At present such a model is hypothetical, although it suggests feedback loops in the system that might be manipulated to sustain site fertility following clearing and conversion to agriculture. Clearly such indirect relationships in the system must be clarified if we are to manage humid tropical systems effectively.

TABLE 3. Response of denitrifiers in intact soil cores from primary forest and mid-successional (*c.* 20 years since clearing from primary forest) sites at La Selva, Costa Rica, to added water and water + nitrate. Cores were assayed for nitrate response after an initial no-amendment denitrification assay. Values are means (\pm S.E.) of ten cores; asterisks indicate significant differences between treatments ($p < 0.05$) (from Robertson & Tiedje (1988))

Site and soil type	Water $\text{N}_2\text{O-N}$ ($\text{mg cm}^{-2} \text{h}^{-1}$)	Water + nitrate
Primary forest		
WP (Andic Humitropept)	87.7 (5.4)	77.2 (4.4)
SOC (Andic Humitropept)	111.0 (5.1)	91.6 (5.2)
BP (Andic Dystropept)	12.3 (3.9)	12.7 (0.9)
SWT (Typic Humitropept)	49.0 (4.0)	38.1 (9.0)
Mid-successional sites		
PAS (Andic Dystropept)	2.7 (1.5)	9.0 (2.2)*
GC (Oxic Dystropept)	0.2 (1.4)	148.0 (5.4)*

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