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The globalization of N deposition: ecosystem consequences in tropical environments

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Abstract. Human activities have more than doubled the inputs of nitrogen (N) into terrestrial systems globally. The sources and distribution of anthropogenic N, including N fertilization and N fixed during fossil fuel combustion, are rapidly shifting from the temperate zone to a more global distribution. The consequences of anthropogenic N deposition for ecosystem processes and N losses have been studied primarily in N-limited ecosystems in the temperate zone; there is reason to expect that tropical ecosystems, where plant growth is most often limited by some other resource, will respond differently to increasing deposition. In this paper, we assess the likely direct and indirect effects of increasing anthropogenic N inputs on tropical ecosytem processes. We conclude that anthropogenic inputs of N into tropical forests are unlikely to increase productivity and may even decrease it due to indirect effects on acidity and the availability of phosphorus and cations. We also suggest that the direct effects of anthropogenic N deposition on N cycling processes will lead to increased fluxes at the soil-water and soil-air interfaces, with little or no lag in response time. Finally, we discuss the uncertainties inherent in this analysis, and outline future research that is needed to address those uncertainties.

Introduction

Human activity has more than doubled the quantity of nitrogen (N) fixed in terrestrial ecosystems, due to industrial N fixation, the mobilization and inadvertent fixation of nitrogen during fossil fuel combustion, and cultivation of nitrogen fixing crops (Smil 1990; Galloway et al. 1995; Vitousek et al. 1997). The mobility of fixed N within and between terrestrial ecosystems has also been enhanced as a consequence of land clearing, biomass burning, wetland drainage, and other processes (Vitousek & Matson 1993; Vitousek et al. 1997). Enhanced inputs of N are spread unevenly over Earth, being concentrated in and near areas where intensive agriculture is widespread, and in industrial regions (Matthews 1994; Townsend et al. 1996). In regions where N inputs have been altered substantially, ecosystem properties as fundamental and as disparate as C storage, trace gas exchange, cation leaching, biodiversity, and estuarine eutrophication have been affected (Schindler & Bayley 1993; Howarth et al. 1996; Vitousek et al. 1997).

Until recently, enhanced inputs of N were concentrated in economically developed regions of the temperate zone – and research on the consequences of enhanced N inputs was even more strongly focused on temperate ecosystems. Temperate and boreal forest and grassland ecosystems are often limited by the supply of fixed N, in the sense that additions of fixed N increase plant growth and C storage therein (Vitousek & Howarth 1991; Aber et al. 1995; Schimel 1995). The term 'nitrogen saturation' (Agren & Bosatta 1988; Aber et al. 1989; Aber 1992) has been applied to changes in ecosystem functioning that occur as N additions relieve N limitation to biological activity. In general, the paradigm of N saturation predicts that N-limited forests initially retain anthropogenic N by using it for vegetation and microbial growth and accumulation in biomass; N can also be accumulated in soil organic matter. At some point, however, inputs of N exceed the biological demands for N within the ecosystem, and the system begins to lose its ability to retain N. As this capacity to retain N is exceeded, excess N can move from the system via solution losses and gas fluxes.

The N saturation model has been evaluated extensively through observations on N deposition gradients and through experimental studies in temperate forests (cf. Grennfelt and Hultberg 1986; Schulze et al. 1989; Bowden et al. 1991, 1992; Aber et al. 1993, 1995; McNulty & Aber 1993; Nadelhoffer et al. 1995; Wright & van Bremen 1995). In general, such studies report a delay between the commencement of N additions and the observation of increased losses. Added N is more or less quantitatively retained within systems for a number of years, but with continued additions, N dynamics within systems are altered progressively and the ability of forests to retain added N is reduced (Wright & van Bremen 1995; Peterjohn et al. 1996).

The concentration of research on the consequences of N deposition into north-temperate forests made sense until recently – most N deposition occurred there. Now, however, 40% of global applications of industrial N fertilizer take place in the tropics and subtropics, and over 2/3 are expected to occur in now-developing regions by 2020 (Matthews 1994; EPA 1990). Similarly, fossil fuel combustion is increasing dramatically in less economically developed parts of Earth, including much of the tropical and subtropical region. Galloway et al. (1994) estimate that by 2020, nearly 2/3 of Earth's energy-related N inputs will take place in the tropics and subtropics. Finally, N emissions associated with biomass burning are already heavily concentrated in the tropics, and likely will remain so for decades (Andreae 1993).

We suggest that most tropical forests function quite differently from most temperate forests with regard to N cycling, and that the effects of anthropogenic N inputs on tropical ecosystem processes may also differ. As discussed by Martinelli et al. (this volume), there is substantial although mostly indirect evidence that N supply does not limit plant production in the majority of tropical forests, while most temperate systems are N-limited. Thus, additions of N may have little direct effect on plant production and carbon storage, but may substantially affect the rate and timing of N losses. Also, many tropical forests soils are highly acidic; additions of anthropogenic N may increase that acidity, leading to increased losses of cations and decreased availability of phosphorus and other limiting nutrients, ultimately reducing plant production and other ecosystem functions.

In this paper, we assess the likely consequences of enhanced N inputs in tropical forests. Before enhanced deposition becomes more widespread, it is important to identify the direct and indirect effects of N additions to tropical forests, and to determine their probable consequences to aquatic systems and the atmosphere locally, regionally, and globally. In this analysis, we identify unknowns and uncertainties that constrain our ability to predict the consequences of this already significant – and rapidly growing – component of environmental change.

Direct effects of altered N on tropical forest processes

Whereas NPP and NEP in temperate ecosystems are largely N-limited, a range of evidence suggests that biological activity in many tropical forests, especially those on highly weathered soils, is not limited by N but rather by some other nutrient (e.g., P, Ca) or by other resources (Vitousek 1984; Jordan 1985). The one forest fertilization experiment we are aware of that was carried out on a highly weathered tropical soil demonstrated limitation by P and not N (Herbert & Fownes 1995; Vitousek & Farringon 1997). Studies that have used the growth response of roots to split additions of nutrients have yielded responses to nutrients other than N, except on white sand soils and montane forest soils (Cuevas & Medina 1988; Luizao 1995). Unlike the situation in temperate ecosystems, where anthropogenic N stimulates plant growth, probably creating a significant sink for excess atmospheric CO_2 (Peterson & Melillo 1985; Schindler & Bayley 1993; Townsend et al. 1996), additions of anthropogenic N are likely to have little direct effect on carbon uptake in most tropical forests.

Nitrogen biogeochemical processes in soils strongly reflect the greater availability of N in many tropical soils. Studies of N cycling and N trace gas emissions across a range of tropical ecosystems suggest that N gas fluxes (as a proportion of N mineralization) are greater in tropical than in temperate systems, and that quantitatively, N trace gas fluxes are on average much greater in tropical than in temperate systems (Keller et al. 1986; Matson & Vitousek 1987; Matson et al. 1990; Hall et al. 1996). While Vitousek and Matson (1988) reported a range in microbial uptake of applied ^{15}N depending on tropical soil type, microbial immobilization of ^{15}N generally was much less than in temperate systems where similar measurements have been made (e.g., Matson et al. 1992). Thus, it seems likely that retention of anthropogenic N will be much less in most tropical systems than in most temperate systems, due to reduced microbial uptake and retention in soil organic matter as well as reduced uptake and retention in plant biomass.

The rather limited data from upland tropical forests also suggests that most mineralized N is quickly nitrified (Vitousek & Matson 1988; McDowell et al. 1992, 1996). In contrast, in many temperate forests, not all N that is mineralized to ammonium is oxidized to nitrate (Vitousek et al. 1982). Indeed, one of the hypothesized responses of temperate soils to long-term anthropogenic N inputs is a gradual shift in the nitrogen economy of soils, from ammonium-dominated to nitrate-dominated systems (Melillo et al. 1989; Aber 1992). Upland tropical soils are likely to display little delay in nitrification in response to increasing N additions.

Indirect effects of anthropogenic N on ecosystem processes

The biogeochemical consequences of enhanced N inputs to terrestrial ecosystems can range well beyond direct alterations of nitrogen cycling and plant response. Numerous studies in natural and agricultural systems of the temperate zone have shown that both atmospheric and fertilizer inputs of N can lead to soil acidification, depletion of base cations, and mobilization of potentially toxic aluminum (Al) ions (Johnson et al. 1982; Hallbacken & Tamm 1986; Aber et al. 1989; Schulze 1989; Lawrence et al. 1995; Likens et al. 1996). Moreover, many tropical soils have developed in place over a very long time, without rejuvenation by glaciation or loess deposition. Accordingly, these soils can be highly weathered, depleted in primary minerals, poorly buffered, and dominated by variable charge clays (Uehara & Gillman 1981; Sanchez & Logan 1992). These systems are therefore (1) poorly buffered against additional sources of acidity, and (2) potentially quite sensitive to base cation depletion. As N inputs increase in humid tropical regions, changes in soil acidity, base cation supply, P availability, Al mobility, and carbon storage are all possible, but the rates, consequences, and sometimes even the direction of such changes are likely to be markedly different in many tropical sites than what has been observed in the temperate zone.

Soil acidification

Elevated N inputs can lead to soil acidification via several pathways, with the overall change depending on the properties of the ecosystem, the form in which N is added, and the anion or cation associated with the added N (Ruess & Johnson 1986). Both fertilizer and atmospheric N inputs can lead to soil acidification; our focus here will be upon atmospheric inputs only. Added N can be acidifying regardless of the inorganic form by which it is added, but the net change in soil acidity due to inputs depends on plant uptake (Figure 1). For example, nitric acid inputs do not necessarily lead to soil acidification: if the nitrate ion is taken up and retained by plants, the proton is neutralized by release of a hydroxyl ion. However, if NO_3^- remains mobile and leaches out of the system, the proton's greater affinity for cation exchange sites in the soil will displace a base cation (potassium, calcium, magnesium, sodium) which will balance the charge of the leaching NO_3^- ion. The addition of one molecule of nitric acid would then cause a net increase of one proton in the soil and the net loss of one base cation. Addition of N as ammonium (NH_4^+) can produce the greatest per molecule effects. If the NH_4^+ ion is taken up, one proton is released. (When soil NH_4^+ is derived from decomposition of organic matter, this released proton is not an increase in acidity as it balances the consumption of a proton during conversion of NH_3 to NH_4^+.) If the added NH_4^+ ion is nitrified, two protons are released. If the resulting NO_3^- ion is then taken up by a plant, the net change is still an increase of one proton; if the NO_3^- is leached, two protons are added and one base cation is lost.

In temperate ecosystems, addition of excess N from the atmosphere has led to soil acidification and base cation depletion, but strong plant demand for N slows the rate of change. As discussed above, however, moist tropical systems frequently are rich in N relative to other essential elements. Thus, the majority of excess N inputs are likely to end up as NO_3^-, and much of this NO_3^- may not be taken up by plants. Leaching of NO_3^- from surface soils mobilizes a cation (Figure 1); as the base cation supply is progressively depleted, the leached cation will either be a proton or mobilized aluminum ion, both of which have potentially serious consequences for downstream aquatic systems (see below).

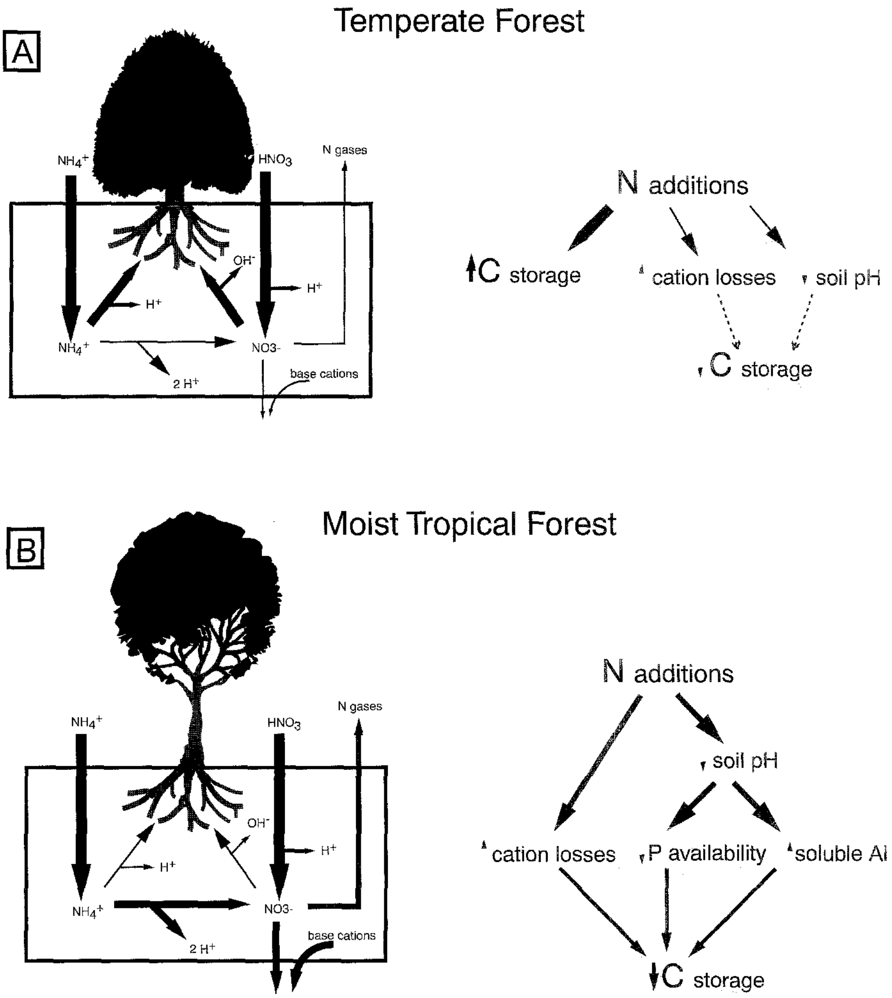

Figure 1. Diagram comparing initial responses of temperate (A) vs moist tropical (B) forests to elevated inputs of atmospheric nitrogen. The figure assumes that plant growth and carbon storage in the majority of temperate forests are initially limited by N supply, and that N functions in relative excess in the majority of lowland moist tropical forests. The thickness of the arrows represents the relative magnitude of fluxes of N in the diagrams on the left, and the relative magnitude of the effects of those fluxes in the summary flow charts on the right. Thus, in (A), we contend that most of the N additions will be retained in the system and initially lead to C storage, whereas in (B), we argue that most of the additional N inputs will be lost from the system, and that the consequences of increased nitrification rates and N losses will be losses of base cations and decreases in soil pH, which may in turn lead to decreases in C storage in moist tropical forests.

Anion adsorption capacity

The fate of excess N and the rate of soil acidification in tropical systems may also be affected by the surface charge properties of many tropical soils. Soil surface charge in the vast majority of temperate zone soils is both permanent and negative, so that anion adsorption capacity is usually quite low (Johnson & Cole 1980). However, iron (Fe) and Al oxide rich tropical soils are often of variable charge, meaning that overall net charge is a function of pH and soil solution chemistry. At the low pH's typical of these soils, net charge is frequently positive (Uehara & Gilman 1981). In addition, free Fe and Al oxides create significant sources of positive charge across a large range of pH values (Ji 1997). Thus, electrostatic adsorption of may be important in controlling losses of excess NO_3^- to aquatic systems.

Such adsorption may be especially important in deeper soil horizons. High concentrations of organic matter in surface horizons create negatively charged surfaces that make nitrate highly mobile. However, SOM decreases with depth while the density of positively charged sites increases. Matson et al. (1987) showed that significant amounts of N lost from surface horizons in a Costa Rican soil were retained as exchangeable NO_3^- in soil layers below 40cm. Soils in the lowland tropics frequently are very deep (>10 m, at times much greater – Nepstad et al. 1994; Richter & Markewitz 1995), thereby creating a long hydrologic path over which NO_3^- can be adsorbed. Thus, increases in NO_3^- leaching from surface soils due to greater N deposition in the tropics may not lead to similar increases in NO_3^- loading of aquatic ecosystems.

Prediction of the role of anion exchange in controlling NO_3^- losses is further complicated by the biogeochemistry of other elements. Where excess S inputs occur in addition to increasing N, ligand exchange of sulfate ions will decrease NO_3^- adsorption capacities (Zhang & Yu 1997). In addition, there is evidence that NO_3^- adsorption may vary considerably with the identity of its charge-balancing cation in soil solution. For example, Wang et al. (1987) found that NO_3^- adsorption in both a Brazilian and a Chinese oxisol was 15–20% greater when the accompanying cation was calcium as opposed to potassium. Given that soil acidification should result in base cation losses, NO_3^- retention may vary with time as the balance of cations in soil solution shifts.

Effects on carbon storage

Unlike the temperate zone, where increasing N deposition may cause at least a transient increase in carbon storage, we suggest that higher N inputs to moist tropical systems may lead to lower productivity and *reduced* carbon storage. This may occur via several mechanisms. First, because plant growth in many tropical systems appears limited by some combination of P and/or base cation availability, losses of base cations due to increased leaching of nitrate may cause reductions in plant growth and carbon storage. Furthermore, cation exchange capacity (CEC) in many tropical soils is largely a function of soil organic matter content (Tiessen et al. 1994a; Mogollon & Querales 1995). Thus, increasing N inputs could induce a positive feedback in which higher losses of cations decrease growth rates and organic matter pools, which in turn reduce the soil's capacity to retain base cations, further reducing productivity and C storage.[1]

Second, decreases in productivity and carbon storage may also occur due to the effects of increasing soil acidity on phosphorus availability. Phosphorus is the element most commonly associated with nutrient limitation in the lowland tropics (Sanchez et al. 1982). This deficiency occurs for two reasons. First, as with the base cations, the combination of extremely old soils and high weathering rates has led to severely depleted primary mineral pools of P (Tiessen et al. 1994b; Crews et al. 1995). Second, acidic soils rich in iron and aluminum oxides react with labile inorganic P, and fix some of that P into insoluble forms (Uehara & Gillman 1981). As a consequence, even tropical soils that have large total soil P pools may have scarce plant-available P. Additions of excess N to such soils may exacerbate P limitation, because rates of P fixation tend to increase with decreasing soil pH[2] (Edwards 1991; Pardo et al. 1992). In many tropical systems, lowered P availability is likely to result in less C uptake and storage.

Finally, the prevalence of aluminum oxides and low pH in many tropical soils means that even slight additional decreases in pH can lead to significant increases in the release of mobile Al ions into soil solution (Sanchez & Logan 1992). The solubility of Al in soils is a nonlinear function of pH, and many tropical soils have pH values well below 5, and at times below 4. Sharp increases in soluble Al occur at soil pH's below 4, thus Al mobilization is likely to occur following a much smaller increase in N deposition in the tropics than has been seen in temperate systems. Increases in soluble Al have a number of potentially deleterious effects, ranging from inhibition of plant and microbial activity to poisoning of fish and other aquatic organisms in downstream systems (NRC 1986; Ruess & Johnson 1986; Godbold et al. 1988; Shortle & Smith 1988). The inhibition of plant and microbial growth provides a third potential way in which elevated N deposition in the moist tropics may lead to net losses of carbon to the atmosphere (Figure 1).

Off site consequences

Land-water exchange

Increased N deposition in tropical landscapes is likely to have significant consequences for tropical aquatic and marine ecosystems. Although net primary productivity in most temperate lakes and rivers is P-limited, nutrient limitation appears to be less clear-cut in the tropics, where a significant number of lakes may be N-limited (Payne 1986; Vitousek & Howarth 1991) and some streams may be light-limited (Pringle et al. 1986). Near-shore marine embayments appear to be more commonly P-limited in the tropics than they are in the temperate zone, but off-shore waters are N-limited as they are in the temperate zone (Vitousek & Howarth 1991). Overall, it appears that the susceptibility of tropical waters to increased N run-off relative to their temperate zone counterparts is higher for fresh waters, less for near-shore coastal waters, and similar for off-shore ecosystems.

The extent to which increased N deposition in tropical ecosystems will affect water quality depends in part on N cycling at the land-water interface. Numerous studies in the temperate zone have shown that plant uptake and denitrification in the riparian zone typically remove 85% of dissolved N from shallow groundwater and thus protect water quality (reviewed by Triska et al. 1993). Maintenance of a riparian buffer strip in forestry and agricultural operations is considered to be ‘best management practice’ in many areas of the United States, as well as Europe (Lowrance et al. 1984; Vought et al. 1994).

Although fewer in number, studies of riparian N dynamics in tropical forests clearly show that N concentrations are reduced as water moves from upslope forests to streams (McDowell et al. 1992, 1996; McClain et al. 1994). In tropical forests, denitrification is thought to be the major mechanism driving this attenuation of N transfers (Bowden et al. 1992; Brandes et al. 1996). Although concentrations of NH_4^+ and DON also decline across tropical riparian zones (McDowell et al. 1996), denitrification is the process most likely to result in net loss of N from the terrestrial ecosystem to the atmosphere; thus, this pathway is most likely to provide effective long-term protection of water quality. The improvement in water quality is counterbalanced by the undesirable input of N_2O to the atmosphere, unless denitrification proceeds all the way to N_2.

The consequences of increased N loading for land-water interactions will depend in large part on the form of nitrogen lost from tropical forest soils, and on any changes in forest C dynamics that accompany increased N loading. For denitrification to proceed, anoxic conditions, a reduced carbon substrate, and nitrate must all be present. Declines in productivity and C availability are possible with increased N deposition in the tropics (as discussed above), potentially decreasing riparian denitrification. We expect, however, that at least in the short term, the complete conversion of NH_4^+ to NO_3^- in the upland soils will favor increased denitrification rates in the riparian and sediment systems. Although specific predictions about the magnitude of off-site effects are difficult to make, biogeochemical processes at the land-water interface will be crucial in determining the long-term impacts of increased N deposition on surface water quality.

Land-air exchange

After more than a decade of research, it is now apparent that tropical forests are important sources of several trace gases that play important roles at regional and global scales. Nitric oxide (NO) is a chemically reactive gas that regulates tropospheric ozone production and is a precursor to nitric acid deposition; dry tropical forests and savannas are the most important natural biogenic sources of this gas (Hall et al. 1996; Davidson & Kingerlee 1997). Nitrous oxide (N_2O), on the other hand, is not chemically active in the atmosphere but is an effective greenhouse gas, and once in the stratosphere, can regulate ozone concentrations there. Humid tropical forests are the most important background source for this gas (Matson & Vitousek 1990; Williams et al. 1992; Watson et al. 1992).

Both N_2O and NO are produced via nitrification and denitrification; nitrification produces relatively more NO while denitrification primarily produces N_2O (and N_2). Rates of both of these processes are likely to be very responsive to increases in N inputs to tropical forests – nitrification by increases in NH_4^+ inputs and by an increase of N cycling in soils; denitrification by an increase in NO_3^- production, availability, and accumulation in excess of plant and microbial demand.

A large number of studies have reported increased N losses via dinitrogen, nitrous oxide, nitric oxide, and ammonia emissions from ecosystems receiving fertilizer inputs (see Eisner 1990; Williams et al. 1992; Schlesinger & Hartley 1992; Hall et al. 1996 for reviews). Much more limited evidence suggests that high levels of chronic N deposition cause increased N gas fluxes from temperate zone forest ecosystems (Papen et al. 1993). While most of these studies have been carried out in the temperate zone, the few studies carried out in the tropics suggest that tropical soils have proportionally higher rates of gaseous losses of fertilizer N than do temperate zone systems (Keller & Matson 1994; Matson et al. 1996; Veldkamp & Keller 1997). It seems probable that increasing deposition of anthropogenic N in tropical forest systems will result in increased fluxes of trace gases.

Future research directions

There are a number of important uncertainties in our analysis, and especially in its applicability to the approaching enhancement of N deposition to tropical forest ecosystems. First, we have discussed tropical soils as if they were all more or less one type – the highly weathered, cation-depleted, acid clay oxisols and ultisols that underlie approximately 55% of the moist tropics (Sanchez 1981). Other tropical soils and ecosystems can be quite different. Where geological activity (volcanoes, slides) is more recent, dry seasons relatively extended, or particular parent materials widespread, soils are more often alfisols with higher pH, more available cations and P, and generally very high levels of N in circulation (Vitousek & Sanford 1986). Other areas are underlain by white sand soils, or are subjected to cooler montane temperatures; N may be in as short supply in these ecosystems as in any temperate forest (Cuevas & Medina 1988; Tanner et al., in press; Martinelli et al., this volume), and the effects of enhanced N deposition are likely to be quite different from those in the more widespread oxisols and ultisols. How the distribution of future enhancements in N deposition maps out onto the distribution of tropical forest ecosystems is an important uncertainty.

Second, for those systems where N is abundant, it is important to know which other resources are in short supply. Where low cation availability represents the most important constraint on forest production (Medina & Cuevas 1989), enhanced N deposition is likely to have rapid and deleterious effects on forest production. Where P is in shortest supply, consequences will probably develop more slowly, in that a decrease in soil pH, which is relatively well-buffered and thus slower to respond, will drive any change in P availability. Also, no nutrients may be in short enough supply to constrain production in some forests.

Third, and related to the second, we lack experimental studies of the regulation of production and biogeochemistry in most tropical forest systems. Identification of the resource(s) in short supply requires manipulative experiments, but whole-system fertilization experiments in particular have been notable for their absence in lowland tropical forests. Experimental studies also represent an important opportunity in tropical forests; it is too late to know how many temperate forests functioned in the absence of anthropogenic N, but we can still do prospective experiments in most tropical (and southern temperate) forests.

Finally, whole-system simulation models represent a crucial tool for the integration and extrapolation of our understanding of the effects of N deposition on ecosystems. However, most of the processes that are crucial to evaluating the consequences of N deposition in tropical ecosystems are not even represented in widely used ecosystem models, and all of these models are built on the concept of N limitation, not over-abundance. Only Century (Parton et al. 1988, 1995) now simulates P cycling and availability – and there is evidence that it does not work very well for tropical soils (Glijsman et al. 1996). None of the widely used models (e.g. TEM and BIOME-BGC as well as Century) evaluate cation fluxes or potential limitation. These models are crucial tools for understanding the consequences of environmental change (Schimel et al. 1997), but they require extensive modification before they can be applied to analyzing N deposition in tropical forest ecosystems.

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Notes

1. This feedback could be counter-balanced by feedbacks to decomposition, in which reduced availability of limiting nutrients (base cations in this case) leads to lower decomposition rates and greater nutrient conservation (e.g. Vitousek 1982).
2. Although the overall effects of decreasing pH on P availability in variable charge soils are not clear – there is also some suggestion that lowering pH could cause greater anion retention, which could increase the amount of exchangeable P.

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