Loss of Nutrients From Terrestrial Ecosystems to Streams and the Atmosphere Following Land Use Change in Amazonia

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Rates of deforestation in the Amazon region have been accelerating, but the quantity and timing of nutrient losses from forested and deforested ecosystems are poorly understood. This paper investigates the broad variation in soil properties of the Amazon Basin as they influence transfers of plant nutrients from the terrestrial biosphere to the atmosphere and the aquatic biosphere. The dominant lowland soils are highly weathered Oxisols and Ultisols, but significant areas of Alfisols also exist, resulting in a wide range of weatherable primary minerals. Despite this considerable variation among Amazonian soils, a common feature in most mature lowland Amazonian forests is a conservative P cycle and excess N availability. In cattle pastures and secondary forests, however, low rates of internal terrestrial N cycling, low N export to streams, and low gaseous N emissions from soils are common, due to significant previous losses of N through repeated fire. Export of P to streams may increase or remain nearly undetectable after forest-to-pasture conversion, depending on soil type. Oxisols exhibit very low P export, whereas increased P export to pasture streams has been observed in Ultisols of western Amazonia. Calcium is mostly retained in terrestrial ecosystems following deforestation, although increased inputs to streams can be detected when background fluxes are naturally low. Because soil mineralogy and soil texture are both variable and important, the effects of land-use change on nutrient export to aquatic ecosystems and to the atmosphere must be understood within the context of varying soil properties across the Amazon Basin.

INTRODUCTION

Some essential plant nutrients are lost and others are redistributed within terrestrial ecosystems when forests are cut and burned for timber harvests or for conversion to agricultural uses. Losses from the terrestrial ecosystem include harvest products, transport of gases, aerosols, and ash following fire, trace gas emissions from soils, soil erosion, and leaching to surface and ground waters. Redistribution includes incorporation of slash and ash material into soils and sedimentation of eroded soil in toeslope positions and streams. Several of these processes, such as ion retention in soils, flow

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paths for leaching, surface erosion, and microbial production of trace gases, are affected both by soil mineralogy and by changes in soil and landscape properties resulting from the intensity of land use. Hence, the effects of land use change on stream chemistry and on emissions of atmospheric greenhouse gases may vary locally and regionally, depending upon variation in soil properties. Similarly, the soil nutrient stocks and soil physical properties that influence rates of regrowth of secondary forests after agricultural abandonment also depend upon the inherited soil properties as well as management history.

The variability in soil properties in tropical regions such as the Amazon Basin may be underappreciated by many. Soils of the Amazon region range in texture from nearly 100% sand to over 80% clay. While the dominant soils in the lowlands are highly weathered Oxisols and Ultisols, significant areas of Alfisols can also be found [*Richter and Babbar*, 1991]. Hence, the abundance of weatherable primary minerals ranges from practically none to very significant quantities [*Sombroek*, 2000]. Mineralogy, topography, drainage, and many other factors also vary at local and regional scales. Although this huge variability appears daunting, and the number of published studies on this topic and region are relatively few, some identifiable patterns have emerged. The objective of this paper is to investigate some of the broad variation in soil properties of the Amazon Basin as they influence transfers of plant nutrients from terrestrial ecosystems to aquatic ecosystems and to the atmosphere.

Annual rates of deforestation in the Brazilian Amazon region have ranged from 11,000 to 29,000 km^2 since 1988 [*INPE*, 2002], with the 2001–2002 year being the second highest on record. About 15% of the forested area (nearly 600,000 km^2) has been deforested. Most of the deforested land has been used either for extensive cattle pastures or for small-holder slash and burn agriculture [*Fearnside*, 1993], although a trend of increasing intensification of large scale production of corn, rice, and soybeans appears to be accelerating [*Fearnside*, 2001].

Secondary forests are an important part of the slash-and-burn agriculture rotation, when aboveground biomass accumulates nutrients that are subsequently released to crops during the next slash and burn cycle. Secondary forests also develop when degraded cattle pastures are abandoned once the control of weeds becomes difficult [*Serrão and Toledo*, 1990]. Some secondary forests are often cleared again for creating new pastures and more intensive agriculture [*Rignot et al.*, 1997; *Salimon and Brown*, 2000]. The dynamic and complex interactions of social and economic factors make it difficult to predict the future importance of secondary forests, although it is clear that a large fraction of deforested land at least passes through a phase of secondary regrowth. Therefore, the effects of land use change on ecosystem stocks and flows of nutrients should be viewed as a dynamic mosaic of land uses and land covers superimposed over a landscape of widely varying geomorphology and soil type. We first examine patterns of nutrient cycling in mature Amazonian forests, and then consider the effects of land use change.

NITROGEN AND PHOSPHORUS CYCLING IN MATURE LOWLAND AMAZONIAN FORESTS

A common simplification about forest nutrient cycling is that temperate forests are nitrogen (N) limited, while tropical forests are phosphorus (P) limited. This simplification clearly ignores much of the variability among soils in both temperate and tropical regions. It also assumes that net primary productivity (NPP) is limited by a single resource, *sensu* Liebig's law of the minimum, but this may not be valid for many ecosystems of complex assemblages of species competing for multiple resources [*Ollinger et al.*, 2003].

Nitrogen is a resource that is often in short supply relative to plant demand in many terrestrial and aquatic ecosystems [*Vitousek and Howarth*, 1991]. The explanation for why more N fixation does not occur in N-limited ecosystems is still a topic of intense curiosity [*Vitousek and Field*, 1999]. Moreover, a large fraction of N that accumulates in terrestrial ecosystems is held in soil organic matter pools that cycle very slowly and is not available for plant uptake. Even when total soil N is abundant, much of the accumulated N is often effectively inactive.

In contrast to N, P is often present in primary minerals, and it adsorbs strongly to secondary minerals. Hence, plant-available P is often abundant in young and intermediate aged soils but becomes largely "occluded" into fractions bound to secondary minerals and in organic matter in highly weathered old soils [*Walker and Syers*, 1976]. The highly weathered Oxisols and Ultisols of lowland tropical regions often exhibit large stocks of total soil P, but relatively small stocks of P in forms that are readily available to plants.

Johnson et al. [2003] recently challenged this paradigm of P limitation of NPP on highly weathered soils. Their literature review of soil P chemical fractionation analyses showed that the operationally defined "plant available" pools from so-called "Hedley fractionation" exceeded annual plant demand for P in most sites. In one respect, this analysis helps resolve the paradox of how large-statured tropical forests can develop on highly weathered soils, where the secondary soil minerals are known to have great affinity for adsorbing P. Apparently, enough P cycles efficiently through organic forms (which can be measured semiquantitively by Hedley fractionation) to maintain plant needs despite strong competition with P adsorption on mineral surfaces. On the other hand, this result does not necessarily contradict the notion that P is conservatively cycled in these forests. Although plant-available P supply may be sufficient to meet plant demands, it is not so abundant as to avoid evolutionary pressure for P conservation strategies, such as resorption of P from leaves before litterfall [*Vitousek*, 1984] and mycorrhizal associations that facilitate P acquisition [*Herrera et al.*, 1978].

A comparison of the N and P cycles of the well known Hubbard Brook temperate deciduous forest in New Hampshire, USA, with the mature evergreen moist tropical forest in Paragominas, Brazil, illustrates the classical simplified dichotomy of N and P conservation strategies in temperate and tropical forests (Figures 1 and 2). These examples are not presented as being representative of their respective biomes, as we have already emphasized that considerable variation occurs within each biome. Rather, we simply wish to illustrate a pattern that occurs frequently enough to be noteworthy. It should also be noted that the Hubbard Brook forest is an aggrading secondary forest (55 years old at the time of Bormann and Likens' 1979 classic works); whereas, the Paragominas forest is mature, which, again, is a common occurrence for North and South America, respectively. Finally, some nutrient fluxes for the Hubbard Brook watershed have been changing during recent decades [*Driscoll et al.*, 2001], and we present here the classic original budgets for the watershed.

The stocks of C, N, and P (kg ha^{-1}) in aboveground biomass are 130,000, 1400, and 41 in the Paragominas forest and are 66,000, 350, and 34 for the Hubbard Brook forest. The Paragominas forest has twice as much aboveground biomass as the Hubbard Brook forest, but contains 4 times as much N and only 20% more P (Figures 1 and 2). Hence the Paragominas forest produces much more biomass per unit of P, whereas the Hubbard Brook forest produces much more biomass per unit of N. Litterfall C:N:P ratios show a similar pattern: 1500:45:1 at Paragominas and 620:14:1 at Hubbard Brook (Figures 1 and 2). Hence, P is very conservatively cycled relative to N at Paragominas, and N more conservatively cycled at Hubbard Brook. In the absence of significant atmospheric inputs of P (Figure 2) and in the absence of P in primary

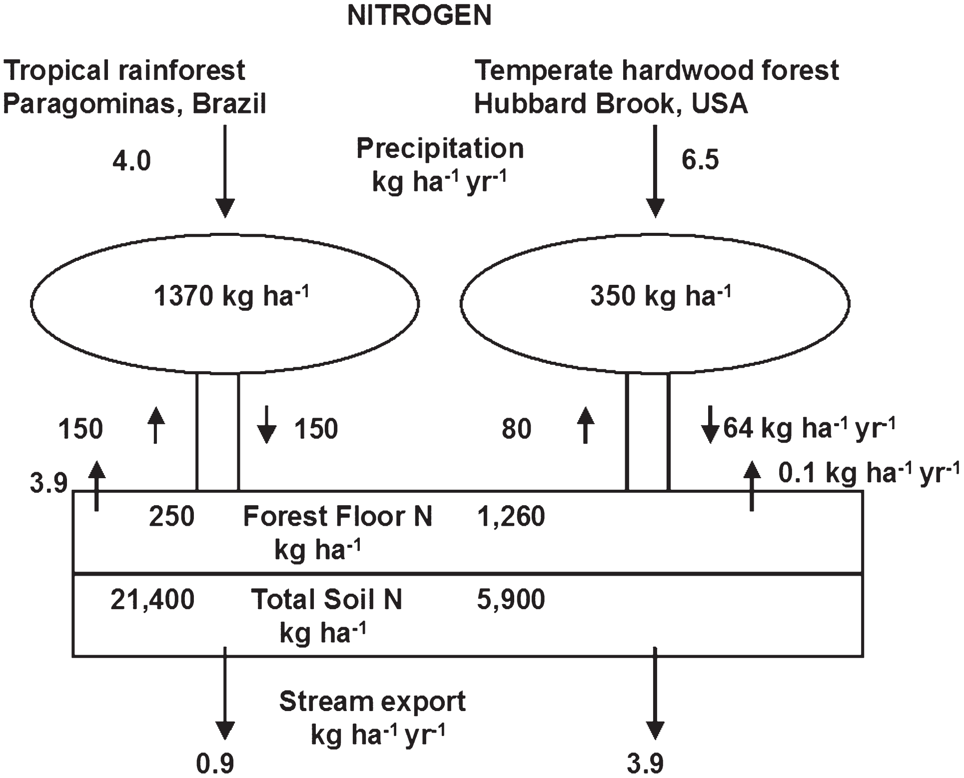

Figure 1. Comparison of nitrogen cycles at the mature moist tropical evergreen forest at Fazenda Vitória, Paragominas, Pará, Brazil [*Markewitz et al.*, 2004] and at the 55-year-old temperate mixed deciduous forest at Hubbard Brook, New Hampshire [*Boremann and Likens*, 1979]. Arrows indicate bulk precipitation inputs, plant uptake, litter and throughfall return to the soil, soil surface emissions of NO+N_2O, and stream export of total dissolved N. Soils stocks were sampled to 8m depth at Paragominas, whereas the soil depth averages about 0.5m to the underlying glacial till at Hubbard Brook.

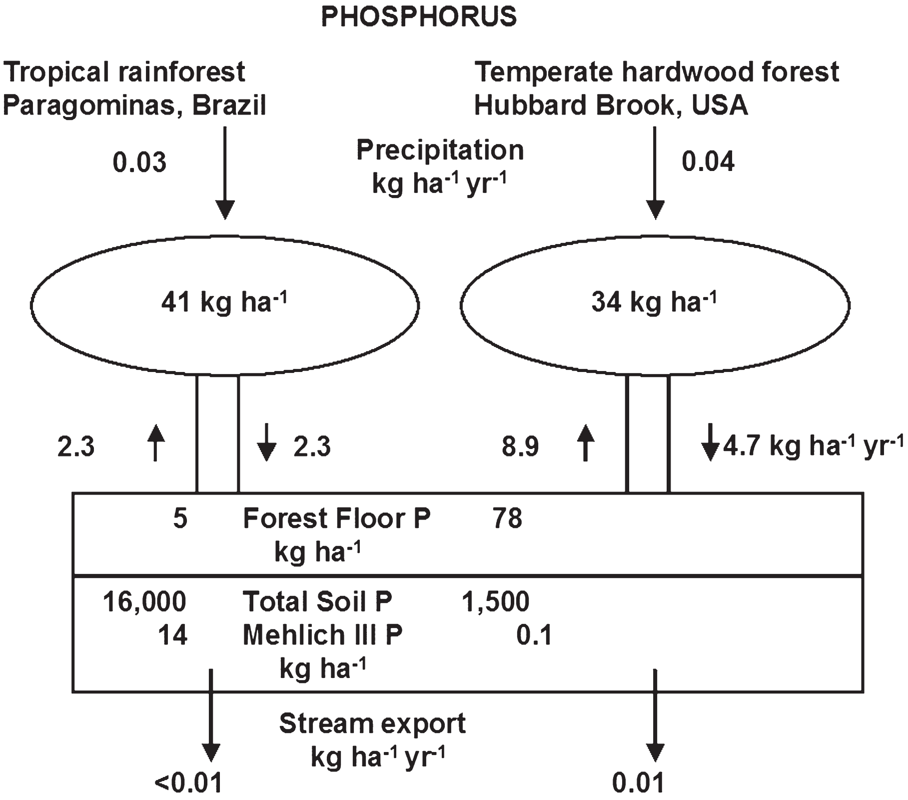

Figure 2. Comparison of phosphorus cycles at the mature moist tropical evergreen forest at Fazenda Vitória, Paragominas, Pará, Brazil [*Markewitz et al.*, 2004] and at the 55-year-old temperate mixed deciduous forest at Hubbard Brook, New Hampshire [*Boremann and Likens*, 1979]. Arrows indicate bulk precipitation inputs, plant uptake, litter and throughfall return to the soil, and stream export of total dissolved P. Soils stocks were sampled to 8m depth at Paragominas, whereas the soil depth averages about 0.5m to the underlying glacial till at Hubbard Brook.

minerals at the Paragominas site, the demand for P must be met almost entirely through efficient internal cycling of P within the terrestrial ecosystem.

We can conclude that P may be among the resources that limit NPP in the Paragominas forest, and, compared to P, N is a relatively abundant nutrient there. Additional indications of N abundance are the relatively large fluxes of N_2O and NO emitted from the soils [Figure 1; *Verchot et al.*, 1999], which indicates that nitrifying and denitrifying bacteria are able to obtain inorganic-N substrates that exceed plant demand [*Davidson et al.*, 2000]. Interestingly, hydrologic losses of N are not larger in Paragominas than in Hubbard Brook, although this comparison may not be valid because the Paragominas watershed is not entirely forested [*Markewitz et al.*, 2001; 2004]. Moreover, periodic hydrologic losses of N often occur in temperate ecosystems despite strong plant demand for N because of asynchrony of the plant growing season with the hydrologic pulses of N loss during winter and snowmelt seasons. In contrast, the tropical Paragominas forest experiences wet and dry seasons, but the potential hydrologic flushing of nutrients during the wet season occurs synchronously with vigorous plant growth and uptake.

The large stocks of N and P in the Paragominas soil are due to its clayey texture and its great depth. *Markewitz et al.* [2004] stopped sampling at 8m, although several more meters of clayey subsoil extend deeper. Very deep soil is another common, although not ubiquitous, feature of highly weathered soils [*Richter and Markewitz*, 1995]. The huge nutrient stocks shown in Figures 1 and 2 are somewhat misleading because the stocks are dependent upon somewhat arbitrary decisions about sampling depth, and because much of the soil N and P is stabilized in forms that do not actively cycle within the ecosystem. Using radiocarbon, *Trumbore et al.* [1995] estimated that 80–90% of the soil organic carbon below 1m depth in the Paragominas forest soil can be characterized as "passive," with a mean residence time of many thousands of years. Much of the deep soil N and P is likely to be similarly isolated from contemporary cycling processes.

Of the total soil N pool in the top 800cm of the Paragominas forest soil, about 10% occurs within the top 10cm of soil, and much of that cycles very actively. Several indicators of high N availability have been consistently demonstrated in Amazonian forests. First, emissions of NO and N_2O have been measured in the Brazilian states of Amazonas, Rondônia, and Pará, and all show remarkably similar and relatively high fluxes [see review by *Davidson et al.*, 2001]. Second, all of these sites, which include clayey Oxisols and sandy Ultisols, show a preponderance of nitrate over ammonium in the KCl-extractable mature forest soil [*Luizao et al.*, 2004; *Neill et al.*, 1995; *Verchot et al.*, 1999], which is another indicator of N availability in excess of plant demand [*Vitousek et al.*, 1979; *Davidson et al.*, 2000]. Third, most N in soil solution is in inorganic forms [*Markewitz et al.*, 2004; *Neill et al.*, 2001], compared with many temperate forests where dissolved organic N dominates total soil solution N [*Currie et al.,* 1996; *Perakis and Hedin,* 2002]. The predominance of inorganic-N indicates availability of N for mineralization and nitrification compared with more conservative internal cycling of organic-N in many temperate forest ecosystems. A fourth indicator of significant loss of inorganic-N from these tropical forests is the natural abundance of ^{15}N. *Martinelli et al.* [1999b] demonstrated that most Amazonian forests have foliage and soil organic matter that are relatively enriched in ^{15}N, indicating fractionation that occurs when lighter N is preferentially lost in a nonconservative N cycle.

Relatively abundant N in the soils of tropical forests appears to be related to N concentrations in streamwater. In a survey across forested watersheds of varying soil types in Rondônia, *Biggs et al.* [2004] found that streamwater nitrate concentrations were positively correlated with soil sand content, indicating that even fairly sandy Ultisols had abundant N. The authors interpreted the observed variability in nitrate export as a function of leaching characteristics of the soil (higher leaching rates in sandy soils) rather than soil fertility or nitrate production. Hence, despite considerable variability among soil types, abundantly cycling N in mature forests of Amazonia appears to be common. An important exception may be Spodosols and Psamments that are common in northwestern lowland Amazonia, where stocks of soil organic matter and N cycling rates may be lower [*Luizao et al.*, 2004].

In comparison to N, soil solution concentrations of both inorganic and dissolved organic P are low in most Amazonian soils, indicating efficient retention of both inorganic and organic P relative to N. This is consistent with high N:P ratios in tree biomass and litterfall and a conservative P cycle. The extremely low P availability in the Paragominas forest soil may be near the low end of the range for Amazonian soils [*McGrath et al.*, 2001; *Garcia-Montiel et al.*, 2000]. Consistent with this observation, ranchers in the Paragominas region (eastern Amazonia) find it necessary to use P fertilizers to maintain pasture productivity [*Dias-Filho et al.*, 2001], whereas P fertilization of pastures is uncommon in western Amazonia. In a study of numerous watersheds within the Brazilian western Amazonian state of Rondônia, *Biggs et al.* [2004] found that total dissolved P and particulate P in streamwater covaried with an extractable soil P pool (Mehlich I acid extraction), which is often used as an index of plant-available-P. Similarly, streamwater concentrations of Ca, Mg, and K were also significantly correlated with mineralogical differences among watersheds within Rondônia [*Ballester et al.*, 2003; *Biggs et al.*, 2002]. Variation in mineralogy on degrees of P availability within the basin is important and will be discussed further with respect to effects of land use change.

BIOGEOCHEMICAL CONSEQUENCES OF AMAZONIAN DEFORESTATION

Nitrogen

Just as a nonconservative N cycle is a common feature in mature Amazonian forests growing on Oxisols and Ultisols, a conservative N cycle is commonly established soon after deforestation. The disturbance phase of nutrient losses from deforested soils described by *Bormann and Likens* [1979] for Hubbard Brook is widely applicable [*Vitousek and Reiners*, 1975]. For example, increased hydrologic export of N and P was measured after clearing of forest cover in a small watershed near Manaus [*Williams and Melack*, 1997]. However, the period of hydrologic and gaseous nutrient loss is often quite short in Amazonia. Soil solution concentrations of nitrate and cations tend to decline within one or two years after cutting and burning [*Uhl and Jordan*, 1984; *Williams et al.*, 1997]. *Melillo et al.* [2001] measured increased soil ammonium and nitrate concentrations for 6 months after forest clearing and higher fluxes of N_2O from young pastures for 2 years after clearing on an Ultisol in Rondônia. After 3 years, N_2O emissions from pastures declined to below rates measured in the forest. *Verchot et al.* [1999] detected no elevated N_2O emissions from Oxisols in eastern Pará, even from pastures as young as 6 months. Concentrations of nitrate in soil solution were lower in pastures compared to forests in both eastern Pará [*Markewitz et al.*, 2004], and Rondônia [*Neill et al.*, 2001]. In all but the most severely degraded sites, growth of grasses and secondary vegetation is usually rapid and vigorous, thus limiting the period of low nutrient uptake by plants and significant nutrient loss after forest clearing. Furthermore, the stocks of actively cycling N in the terrestrial ecosystem appear to decline with pasture age, thus further lowering losses of N via gaseous emissions and hydrologic fluxes.

Fire, commonly used for site preparation and for subsequent weed control, results in significant loss of N through transport of gases, aerosols, and ash [*Hölscher et al.*, 1997; *Kauffman et al.*, 1995, 1998]. Some of the ash usually remains on site, but some may also be transported away by wind and surface runoff. Mass balance studies have shown that losses of N from the terrestrial ecosystem caused by fire are 51–62% and 36–86% of the aboveground biomass N in Amazonian forests and pastures, respectively [*Kauffman et al.*, 1995, 1998].

In addition to lower gaseous emissions and lower nitrate concentrations in soil solutions, another common indicator of N impoverishment in pasture soils is the ratio of extractable soil nitrate to ammonium [*Davidson et al.*, 2000]. Whereas extractable nitrate:ammonium ratios >1 in forests indicate excess N availability that supports nitrification, ratios <1 have been commonly found in pastures [*Neill et al.*, 1995; *Verchot et al.*, 1999], indicating less nitrification and a more conservative N cycle in pastures. Assays of net N mineralization and net nitrification are also lower in pasture soils compared to mature forest soils in both regions [*Neill et al.*, 1997; *Verchot et al.*, 1999].

Perhaps the most unambiguous test of nutrient availability is experimental manipulation of nutrient resources. Although correlations of secondary forest regrowth with results of soil testing revealed no evidence of soil nutrient limitation [*Buschbacher et al.*, 1988], agronomic soil testing may not be suited for determining nutrient limitations for native vegetation. Fertilization experiments of fallow secondary forest vegetation have been conducted following slash and burn agriculture [*Gehring et al.*, 1999] and cattle pasture abandonment [*Davidson et al.*, 2004] in eastern Pará. Fires had been used intentionally or had entered accidentally numerous times at both sites. Responses to fertilizers were species specific, but total growth of secondary vegetation responded positively to fertilizer addition in both experiments. *Davidson et al.* [in press] found that remnant pasture grasses responded to P addition and N+P addition, whereas the majority of tree species responded only to N addition. *Gehring et al.* [1999] found increased growth of the nodulated legume, *Inga macrophylla*, only when P was included in the fertilizer complement. Although present, native N fixing species are not abundant and are usually slow growing in these young secondary forests. If many tree species grow better following N addition, it is puzzling why N fixing species would not have a greater advantage, but perhaps competition for other resources, such as P, light, and water preclude a positive return on investment in an N fixation strategy [*Vitousek and Field*, 1999]. In any case, the fertilizer amendment studies demonstrate that N is one of the resources that limits rates of biomass accumulation in abandoned agricultural lands that have experienced frequent fire.

Phosphorus

Phosphorus is already conservatively cycled in mature Amazonian forests, and so loss of P during disturbance is likely to exacerbate any P limitation that might exist. Although there is no gaseous form of P that can be lost in significant amounts either during fire or from soils, there may be significant P lost in particulates during fires or in ash that is lost through subsequent wind or water-driven erosion. Mass balance studies have shown that losses of P from the terrestrial ecosystem caused by fire are 7–32% and 1–36% of the aboveground biomass P in Amazonian forests and pastures, respectively [*Kauffman et al.*, 1995, 1998]. However, the situation is more complicated than this, because P availability changes with soil acidity, which also changes with land use. Some of the ash enters the soil, raising the pH of the soil and rendering soil P more available to plants [*Uehara and Gilman*, 1981]. In a pasture chronosequence study in Rondônia, *Garcia-Montiel et al.* [2000] found an initial increase in available-P pools during the first 3–5 years following pasture establishment and a gradual decline thereafter. *Townsend et al.* [2002] also observed declines in plant-available P forms with increasing pasture age in pasture chronosequences on Oxisols and Entisols near Sanaterem, Pará. The process of gradual reacidification of the soil, as cations from ash inputs are lost or as they accumulate in biomass, requires several decades [*Markewitz et al.*, 2001; *Moraes et al.*, 1996], which probably affects the dynamic of P availability as pastures age. Some of the P also appears to become bound into slowly cycling soil organic matter fractions with increasing pasture age [*Garcia-Montiel et al.*, 2000; *Townsend et al.*, 2002].

Calcium, Magnesium, and Potassium

Because wood stores relatively large quantities of Ca, Mg, and K and because these elements are largely conserved as ash following fire, Amazonian deforestation usually results in significant redistribution of these important plant nutrients from aboveground biomass to the soil. *Markewitz et al.* [2004] demonstrated a nearly stoichiometric recovery of aboveground forest stocks of Ca and Mg in the exchangeable cation pool of pasture and secondary forest soils. The more mobile K was partially lost from the terrestrial ecosystem. Although Oxisols have inherently low cation exchange capacity due to nearly nonexistent permanently charged minerals, the organic matter and some of the edges of kaolinite have modest pH-dependent cation exchange capacity [*Uehara and Gilman*, 1981]. The ash inputs following clearing and burning both increase this cation exchange capacity and provide the Ca, Mg, and K that become electrostatically bound to the exchange sites. Hence, the growth of pasture or secondary forest vegetation is probably not limited by availability of these cations for several decades following deforestation. An important exception may be the highly infertile and very ancient Oxisols (Acristox) of the *cerrado* region near Brasilia, where stream conductivity and cation concentrations are extremely low (Table 1). Ash inputs from burning the native *cerrado* (woodland/savanna) vegetation are usually insufficient for pasture establishment, and lime is usually applied. Although outside the Amazon Basin, this example is given to illustrate how even within the soil order of highly weathered Oxisols, considerable variation exists with respect to nutrient availability that has important management and ecological implications. At the other extreme, cation-rich, eutrophic soils can also be found within the Amazon region, such as where intrusions of utlramafic and mica-schist parent material occur on the craton of the Brazilian shield [*Biggs et al.*, 2002; *Sombroek*, 2000].

INFLUENCE OF AMAZONIAN DEFORESTATION ON STREAM SOLUTE CONCENTRATIONS

Streams act as integrators of processes of nutrient retention and release in watersheds. Stream solute concentrations are influenced by the diversity of soil types in the Amazon Basin, by changes in soils brought about by deforestation, and by the interactions among these changes and soil type. In a survey of watersheds across Rondônia, a region that included soils with both high and low cation (Ca, Mg, K) stocks, *Biggs et al.* [2002] found a strong correlation between soil cation stocks and their respective streamwater concentrations. All of the comparisons of *Biggs et al.* [2002] are limited by the fact that land use is not independent of soil type and cation content, because agricultural development has been most extensive on soil with higher base saturation. *Ballester et al.* [2003] found that 90% of pastures but only 48% of remaining forests in the 76,000 km^2 Ji Paraná river basin were located in areas mapped as having eutrophic soils. These authors found that both the percentage of pasture cover and the effective cation exchange capacity of the soil covaried with stream Ca and Mg. *Biggs et al.* [2002] were unable to find a deforestation signal for Ca and Mg that could be distinguished statistically from the natural variation among soil types and watersheds.

In contrast, where weatherable minerals and soil cation stocks are much lower, as in the Oxisols of Paragominas, a deforestation signal was clear, with higher exchangeable and soluble Ca, Mg, and K in the pasture soils compared to forest soils [*Markewitz et al.*, 2004]. Like a needle in a haystack, the deforestation signal of these cations in streamwater may be difficult to find when the haystack (cation leaching from forested soils) is moderate to large, but much easier to find when it is small.

The seasonal trend of Ca in the Paragominas stream was also contrary to the pattern typically reported in the literature [*Markewitz et al.*, 2001]. Where rock weathering contributes significantly to streamwater calcium, the highest concentrations occur at baseflow and become diluted at higher flows.

Table 1. Comparison of watershed and stream water characteristics in Rondônia (Fazenda Nova Vida; *Neill et al.*, 2001), Pará (Fazenda Vitória; *Markewitz et al.*, 2001), and *Brasília (Resende, Markewitz, Bustamante, and Davidson*, unpublished data).

	Rondônia		Pará	Brasília
Stream characteristic	Forest	Pasture	Forest & Pasture	Cerrado
Watershed area (ha)	1740	720	10,000	1000s
Soil type	Udult	Udult	Ustox	Ustox
Soil clay (%)	22	24	60-80	65-85
Annual precipitation (mm)	2200	2200	1800	1500
Dry season duration (mos)	4	4	6	6
Conductivity (μS/cm)	50	75	30	6
pH	6.6	6.2	4.9	5.6
Alkalinity (μequiv HCO_3^-/L)	175	200	56	44
K^+ (μequiv/L)	60	132	22	2
Mg^{2+} (μequiv/L)	121	155	42	10
Ca^{2+} (μequiv/L)	136	177	40	32
Na^+ (μequiv/L)	57	66	151	6
$Na^+/(Na^+ + Ca^{2+})$	0.33	0.30	0.79	0.15
NH_4^+ (μequiv/L)	2.9	6.6	2.4	0.5
NO_3^- (μequiv/L)	5.4	2.5	7.9	0.8
PO_4^{3-} (μequiv/L)	1.8	12.0	0.1	<0.1
Dissolved oxygen (mg/L)	6-7	0-1	3-7	No data

In contrast, the Paragominas stream had very low Ca concentrations during the dry season, and increased throughout the wet season. This effect was not simply higher concentrations during peak storm flow, as has been observed in other Amazonian watersheds [*Elsenbeer and Lack*, 1995; *Lesack*, 1993], but rather sustained high concentrations throughout the wet season, including periods between rainfall events. *Markewitz et al.* [2001] ascribed this increased wet season cation leaching to loss of small amounts of the cations held on surface soil cation exchange sites, when water and carbonic acid (derived from dissolved CO_2 produced by root and soil microbial respiration) leach the surface soil cations. This increased wet season input of cations to the stream is apparent when the background baseflow concentrations are extremely low due to lack of weatherable minerals. It is unclear if this pattern also applies to native forests on Oxisols or if it is only apparent with land-use change to ash-enriched pastures on highly weathered Oxisols. This pattern has not been observed in the western Amazon region, where weatherable minerals are more common

Changes to the availability of inorganic N in soil following deforestation are reflected, at least in some cases, in the concentration of nitrate draining small streams. *Neill et al.* [2001] found higher nitrate concentrations in headwater forest streams compared with pasture streams during the dry season when deeper groundwater flowpaths dominate stream discharge. Although nitrogen availability and nitrate leaching decline with pasture age to values below those found in the native forest, *Biggs et al.* [2004] observed higher concentrations of total dissolved N in streams draining watersheds that had been at least 75% deforested in Rondônia. This pattern was also found by *Neill et al.* [2001]. It is possible that dissolved organic N (DON) losses to streams may be important even when low nitrate and low emissions of NO and N_2O indicate conservative N cycling in pastures. Export of DON from ecosystems thought to be N limited is becoming increasingly recognized [*Campbell et al.*, 2000; *Goodale et al.*, 2000; *Hedin et al.*, 1995; *Perakis and Hedin*, 2002], but it has not been discussed with regard to tropical cattle pastures.

Unlike N, the availability of P does not appear to change consistently with deforestation in the limited number of studies available. *Neill et al.* [2001] found higher concentrations of P in first and second order streams draining pasture compared to streams draining forest, both on sandy Ultisols in Rondônia (Table 1). In contrast, *Markewitz et al.* [2004] found no increase in soil solution P or stream P in pastures on clayey Oxisols in Paragominas. The P concentrations in the pasture stream in Rondônia are not high compared to many other regions of the world, but they are significantly elevated compared to adjacent forest streams. This Ultisol contains small amounts of primary minerals that may be supplying P through weathering, whereas the Oxisol is virtually void of primary minerals. Higher concentrations of cations and higher conductivity and alkalinity in the Rondônia streams compared to the Pará stream supports the inference that weathering inputs are higher from the Ultisol (Table 1). The very deep clays at the Paragominas site may also be more effective in retaining phosphate than are the less deep and sandy Ultisols.

The paired watershed study by *Neill et al.* [2001] was corroborated at a larger scale by a statewide study of watersheds in Rondônia [*Biggs et al.*, 2004], where total dissolved P and particulate P were correlated with both extractable P (Mehlich I) of forest soils and the extent of watershed deforestation. Similarly, *Ballester et al.* [2003] found that the percentage of pasture cover in watersheds from 100 to 10,000 km^2 was the best predictor of streamwater phosphate concentration. Hence, both soil type and land use affect P export from soils to streams within that region, while the comparison with Pará studies demonstrates that the effects of land use may depend upon soil type. In other words, an interaction of land use change and soil type can be expected for P cycling across the basin.

Such local and regional variation is important for at least two reasons. First, the differences in streamwater chemistry are consistent with differences in pasture management—i.e., ranchers must use P fertilizer in regions where the soils are so effective in adsorbing P that no hydrologic P loss can be detected following deforestation. Hence, streamwater chemistry may be a good indicator of regional differences in agricultural requirements for productive agriculture. In this sense, the water transported to the stream may be an equally reliable "extractor" and broad integrator of P availability than is traditional agronomic soils testing. However, riparian and channel processes may also influence P retention and release, thus potentially masking some direct soil-stream links (see next section).

The second reason that local and regional variation of soil properties is important is related to the consequences of altered stream inputs on aquatic ecosystems. *Neill et al.* [2001] demonstrated that algal growth in the pasture streams of Rondônia becomes N limited because of the reduced N inputs and increased P inputs to pasture streams compared to forest streams. Therefore, the interaction of land use change and soil properties helps explain the consequences of deforestation on in-stream processes and water quality, which may be regionally specific.

IN-STREAM PROCESSES MAY COMPLICATE DEFORESTATION SIGNALS

It is also possible that processes other than those controlling solution N concentrations in upland *terra firme* soils dominate the control over the concentrations of N found in streams.

Even in the undisturbed forested condition, the source of many elements to stream waters is not well understood. For example, *McClain et al.* [1994] demonstrated that upland and riparian groundwater concentrations of N differed from stream water characteristics in a forested watershed near Manaus, indicating that links between stream nitrogen chemistry with upland nutrient status were unclear. Using ^{15}N as an isotopic tracer, *Brandes et al.* [1996] showed that in-stream processes, not *terra firme* land cover, were controlling dissolved inorganic N concentrations. Subsequent studies in the same streams showed that dissolved organic C concentrations were also believed to be derived from riparian forests and not upland groundwater [*McClain et al.*, 1997]. In a tropical pasture stream, *Merriam et al.* [2001] showed that nitrification in the stream channel is a major source of streamwater nitrate. In Rondônia, *Thomas et al.* [2004] showed that a small pasture stream had lower nitrate concentrations consistent with lower rates of nitrate production in pasture soils and lower nitrate concentrations in pasture soil solution, but that a larger pasture stream had higher nitrate concentrations likely derived from in-channel nitrification, not inputs from soils of the watershed. Finally, nitrate removal in riparian forests may make it hard to detect reductions in nitrate delivery to streams caused by lower rates of nitrate production in pasture soils established after deforestation.

The structure and processes in stream channels may also account for changes to dissolved organic N concentrations in streams following deforestation. It is possible that the higher dissolved organic N concentrations in some pasture streams [*Neill et al.,* 2001] may be associated with the presence of abundant streamside vegetation in small pasture streams [*Thomas et al.,* 2004] and not necessarily with higher inputs of dissolved organic N from pasture watersheds.

Streamside vegetation may also affect P cycling in complicated ways. In the paired watershed study of *Neill et al.* [2001], for example, large mats of the grass, *Paspallum*, in the pasture stream channel consume oxygen, which, in turn affects iron solubility, which may reduce complexing of Fe and P, thus increasing P availability in the stream. Not only do such multi-element interactions deserve more attention [*Ollinger et al.*, 2003], but the distinction between altered inputs and altered in-stream processes also awaits clarification as explanations for the effects of deforestation on water quality.

UNDERSTUDIED TOPICS PERTAINING TO NUTRIENT LOSSES FOLLOWING LAND USE CHANGE

We have already mentioned the role of DON in losses from pastures and the role of in-stream processes as topics that merit further attention. Here we present additional topics that have not yet been covered in this paper, but that also deserve more research.

Very little research has been conducted on the effects of the accelerating trend towards intensification of Amazonian agriculture [*Fearnside*, 2001] on nutrient export from the terrestrial biosphere. This trend has potentially important consequences for exchanges between terrestrial ecosystems and the aquatic ecosystems and the atmosphere. Tilling and fertilization could increase gaseous emissions of N oxides [*Passianoto et al.*, 2003]. However, the strong potential for immobilization of N in soils of degraded lands and for fixation of P in Ultisols and Oxisols may buffer these systems from large exports of N and P, depending on the intensity of fertilization, soil type, and hydrology.

Both deforestation and intensification of agriculture are often followed by increased urbanization within the Amazon Basin [*Browder and Godfrey*, 1997]. *Biggs et al.* [2002; 2004] found a clear urbanization signal on stream water concentrations of sodium, chloride, sulfate, and total dissolved nitrogen across the state of Rondônia. Perhaps the most pronounced effect of land use change on water quality within the Amazon Basin will result from urbanization rather than from management of agricultural lands. A similar result has been demonstrated regarding the importance of human sewage for N inputs to rivers in agricultural regions of southern Brazil [*Figueiredo et al.*, 1998; *Martinelli et al.*, 1999a]. However, the effect of Amazonian urbanization on water quality has received little attention. In an urban neighborhood of the city of Ji-Paraná, Rondônia, where septic systems are used rather than dumping sewage directly into the river, nitrate concentrations were frequently >100 ppm in over 20 wells sampled throughout the neighborhood [*Silva*, 2001]. Transport of this nitrate to the Ji-Paraná river and possible dilution, adsorption, or denitrification along the way are poorly understood processes.

Another topic of surprisingly little research in the Amazon region is soil erosion. Perhaps the term "lowland" has been confused with "flat," but very little of the lowland Amazon region is actually flat. With the exception of floodplain areas, hill and valley topography is very common throughout most of the areas with well-drained soils, where deforestation for agriculture mostly occurs. Redistribution of soil nutrients through erosion has important impacts for water quality, agricultural productivity, and regrowth of secondary forests.

The flowpaths by which water, and the materials it carries, move from land to streams in tropical regions deserves more attention, both in native vegetation and in areas undergoing deforestation. Movement of surface waters and groundwater is often complicated by the presence of soil layers composed of secondary clays that restrict water infiltration and create a variety of overland or horizontal near-surface flowpaths. Many watersheds are not closed in the classical sense, and weirs may not measure all of the water exported from the watershed. Soils with aggregates dominated by secondary clays have very different infiltration properties than the more abundantly studied soils with predominantly primary minerals [*Tomasella et al.*, 2000]. The effects of these various factors on hillslope hydrology and flow paths are poorly understood.

The relative importance of overland flows, near-surface flows, throughflow, and groundwater flow and the nutrients that are transported by these flowpaths probably vary with topography, soil type, lithology, and management history [*Elsenbeer et al.*, 1999; *McClain and Elsenbeer*, 2001]. This variation may be key to understanding the variable effects of deforestation on stream water quality. The residence time in riparian zones of water feeding streams may be particularly important. *Williams et al.* [1997] provided evidence that riparian forests remove nutrients from runoff in a catchment of recent slash and burn agriculture, but few studies have addressed this topic, and clearing to the stream's edge is still very common in Amazonia. If intensification of agriculture continues, a better understanding of these processes may be important for developing management strategies to mitigate the effects of agricultural development on water quality.

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REFERENCES

Ballester, M. V. R., D. de C. Victoria, A. V. Krusche, R. Coburn, R. L. Victoria, J. E. Richey, M. G. Logsdon, E. Mayorga, and E. Matricardi, A remote sensing/GIS-based physical template to understand the biogeochemistry of the Ji-Paraná river basin (Western Amazon), *Remote Sensing of the Environment*, 87, 429–445, 2003.

Biggs, T. W., T. Dunne, T. F. Domingues, and L. A. Martinelli, The relative influence of natural watershed properties and human disturbance on stream solute concentrations in the southwestern Brazilian Amazon basin, *Water Resources Research*, 38, doi:10.1029/2001WR000271, 2002.

Biggs, T. W., T. Dunne, and L. A. Martinelli, Natural controls and human impacts on stream nutrient concentrations in a developing region of the Brazilian Amazon basin, *Biogeochemistry*, 68, 227–257, 2004.

Bormann, F. H. and G. E. Likens, *Pattern and process in a forested ecosystem*, Springer-Verlag, New York, 1979.

Brandes, J. A., M. E. McClain, and T. P. Pimental, 15N evidence for the origin and cycling of inorganic nitrogen in a small Amazonian catchment, *Biogeochemistry*, 34, 45–56, 1996.

Browder, J. O, and B. J. Godfrey, *Rainforest cities: Urbanization, development, and globalization of the Brazilian Amazon,* Columbia University Press, New York, 1997.

Buschbacher, R., C. Uhl, and E. A. S. Serrão, Abandoned pastures in eastern Amazonia II. Nutrient stocks in the soil and vegetation, *Journal of Ecology*, 76, 682–699, 1988.

Campbell, J. L., J. W. Hornbeck, W. H. McDowell, D. C. Buso, J. B. Shanley, and G. E. Likens, Dissolved organic nitrogen budgets for upland, forested ecosystems in New England, *Biogeochemistry*, 49, 123–142, 2000.

Currie, W. S., J. D. Aber, W. H. McDowell, R. D. Boone, and A. H. Magill, Vertical transport of dissolved organic C and N under long-term N amendments in pine and hardwood forests, *Biogeochemistry*, 35, 471–505, 1996.

Davidson, E. A., M. M. C. Bustamante, and A. S. Pinto, Emissions of nitrous oxide and nitric oxide from soils of native and exotic ecosystems of the Amazon and Cerrado regions of Brazil, *in Optimizing Nitrogen Management in Food and Energy Production and Environmental Protection: Proceedings of the 2nd International Nitrogen Conference on Science and Policy*, edited by J. Galloway, E. Cowling, J. Erisman, J. Wisniewski, and C. Jordan, pp. 312–319, A.A. Balkema Publishers, Lisse, 2001.

Davidson, E. A., M. Keller, H. E. Erickson, L. V. Verchot, and E. Veldkamp, Testing a conceptual model of soil emissions of nitrous and nitric oxides, *BioScience*, 50, 667–680, 2000.

Davidson, E. A., C. J. R. Carvalho, I. C. G. Vieira, R. O. Figueiredo, P. Moutinho, F. Y. d. S. M. T. P. Ishida, J. B. Guerrero, K. Kalif, and R. T. Sabá, Nutrient limitation of biomass growth in a tropical secondary forest: early results of a nitrogen and phosphorus amendment experiment, *Ecological Applications*, 14, S150–S516, 2004.

Dias-Filho, M., E. A. Davidson, and C. J. R. de Carvalho, Linking biogeochemical cycles to cattle pasture management and sustainability in the Amazon Basin, *in The Biogeochemistry of the Amazon,* edited by M. E. McClain, R. L. Victoria, and J. E. Richey, pp. 84–105, Oxford University Press, New York, 2001.

Driscoll, C. T., G. B. Lawrence, A. J. Bulger, T. J. Butler, C. S. Cronan, C. Eagar, K. F. Lambert, G. E. Likens, J. L. Stoddard, and K. C. Weathers, Acidic deposition in the northeastern United States: Sources and inputs, ecosystem effects, and management strategies, *BioScience*, 51, 180–198, 2001.

Elsenbeer, H., B. E. Newton, T. Dunne, and J. Dm de Moraes, Soil hydraulic conductivities of latosols under pasture, forest and teak in Rondonia, Brazil, *Hydrological Processes*, 13, 1417–1422, 1999.

Elsenbeer, H., A. Lack, and K. Cassel, Chemical fingerprints of hydrological compartments and flow paths at La Cuenca, western Amazonia, *Water Resources Research*, 31, 3051–3058, 1995.

Fearnside, P. M., Soybean cultivation as a threat to the environment in Brazil, *Environmental Conservation*, 28, 23–38, 2001.

Fearnside, P. M., Deforestation in Brazilian Amazonia: The effect of population and land tenure, *Ambio*, 22, 537–545, 1993.

Figueiredo, R. O., and A. R. C. Ovalle, Fluvial hydrogeochemistry in a sub-tropical coastal watershed in Brazil, *Water, Air, and Soil Pollution*, 105, 399–407, 1998.

Garcia-Montiel, D. C., C. Neill, J. M. Melillo, S. Thomas, P. A. Steudler, and C. C. Cerri, Soil phosphorus transformations following forest clearing for pasture in the Brazilian Amazon, *Soil Science Society of America Journal*, 64, 1792–1804, 2000.

Gehring, C., M. Denich, M. Kanashiro, and P. L. G. Vlek, Response of secondary vegetation in Eastern Amazonia to relaxed nutrient availability constraints, *Biogeochemistry*, 45, 223–241, 1999.

Goodale, C. L., J. D. Aber, and W. H. McDowell, The long-term effects of disturbance on organic and inorganic nitrogen export in the White Mountains, New Hampshire, *Ecosystems*, 3, 433–450, 2000.

Hedin, L. O., J. J. Armesto, and A. H. Johnson, Patterns of nutrient loss from unpolluted, old-growth temperate forests: Evaluation of biogeochemical theory, *Ecology*, 76, 493–509, 1995.

Herrera, R., T. Merida, N. Stark, and C. Jordan, Direct phosphorus transfer from leaf litter to roots, *Naturwissenschaften*, 65, 208–209, 1978.

Hölscher, D., R. F. Möller, M. Denich, and H. Fölster, Nutrient input-output budget of shifting agriculture in Eastern Amazonia, *Nutrient Cycling in Agroecosystems*, 47, 49–57, 1997.

INPE (Instituto Nacional de Pesquisas Espaciais), Monitoramento da floresta Amazônica Brasiieira por Satélite 2000–2001, Brazilian National Institute for Space Research, 2002. Available online at: http://sputnik.dpi.inpe.br:1910/col/dpi.inpe.br/lise/2002/06.12.13.16/doc/Capa.htm.

Johnson, A. H., J. Frizano, and D. R. Vann, Biogeochemical implications of labile phosphorus in forest soils determined by the Hedley fractionation procedure, *Oecologia*, 135, 487–499 doi:10.1007/s00442–002–1164–5, 2003.

Kauffman, J. B., D. L. Cummings, and D. E. Ward, Fire in the Brazilian Amazon 2. Biomass, nutrient pools, and losses in cattle pastures, *Oecologia*, 113, 415–427, 1998.

Kauffman, J. B., D. L. Cummings, D. E. Ward, and R. Babbitt, Fire in the Brazilian Amazon: biomass, nutrient pools, and losses in slashed primary forests, *Oecologia*, 104, 397–409, 1995.

Lesack, L. F. W., Export of Nutrients and Major Ionic Solutes from a Rain-Forest Catchment in the Central Amazon Basin, *Water Resources*, 29, 743–758, 1993.

Luizão, R. C. C., F. J. Luizão, R. Q. Paiva, T. F. Monteiro, L. S. Sousa, and B. Kruijt, Variation of carbon and nitrogen cycling processes along a topographic gradient in a central Amazonian forest, *Global Change Biology*, 10, 592–600, 2004.

Markewitz, D., E. A. Davidson, R. Figueiredo, R. L. Victoria, and A. V. Krusche, Control of cation concentrations in stream waters by surface soil processes in an Amazonian watershed, *Nature*, 410, 802–805, 2001.

Markewitz, D., E. A. Davidson, P. Moutinho, and D. C. Nepstad, Nutrient loss and redistribution after forest clearing on a highly weathered soil in Amazonia, *Ecological Applications*, 14, S177–S199, 2004.

Martinelli, L. A., A. V. Krusche, R. L. Victoria, P. B. de Camargo, M. Bernardes, E. S. Ferraz, J. M. D. de Moraes, and M. V. Ballester, Effects of sewage on the chemical composition of Piracicaba River, Brazil, *Water, Air, and Soil Pollution*, 110, 67–79, 1999a.

Martinelli, L. A., M. C. Piccolo, A. R. Townsend, P. M. Vitousek, E. Cuevas, W. McDowell, G. P. Robertson, O. C. Santos, and K. Treseder, Nitrogen stable isotopic composition of leaves and soil: Tropical versus temperate forests, *Biogeochemistry*, 46, 45–65, 1999b.

McClain, M. E. and H. Elsenbeer, Terrestrial inputs to Amazon streams and internal biogeochemical processing, in *The Biogeochemistry of the Amazon Basin*, edited by M. E. McClain, R. L. Victoria, and J. E. Richey, pp. 185–208, Oxford University Press, New York, 2001.

McClain, M. E., J. E. Richey, and J. A. Brandes, Dissolved organic matter and terrestrial-lotic linkages in the central Amazon basin of Brazil, *Global Biogeochemical Cycles*, 11, 295–311, 1997.

McClain, M. E., J. E. Richey, and T. P. Pimental, Groundwater nitrogen dynamics at the terrestrial-lotic interface of a small catchment in the Central Amazon Basin, *Biogeochemistry*, 27, 113–127, 1994.

McGrath, D. A., C. K. Smith, H. L. Gholz, and F. deA. Oliveira, Effects of land-use change on soil nutrient dynamics in Amazônia, *Ecosystems*, 4, 625–645, 2001.

Melillo, J. M., P. A. Steudler, B. J. Feigl, C. Neill, D. Garcia, M. C. Piccolo, C. C. Cerri, and H. Tian, Nitrous oxide emissions from forests and pastures of various ages in the Brazilian Amazon, *Journal of Geophysical Research*, 106, 34,179–34,188, 2001.

Merriam, J. L., W. H. McDowell, J. L. Tank, W. M. Wollheim, C. L. Crenshaw, and S. L. Johnson, Characterizing nitrogen dynamics, retention and transport in a tropical rainforest stream using an *in situ* ^{15}N addition, *Freshwater Biology*, 47, 143–160, 2002.

Moraes, J. L., B. Volkoff, C. C. Cerri, and M. Bernoux, Soil properties under Amazon forest and changes due to pasture installation in Rondônia, Brazil, *Geoderma*, 70, 63–81, 1996.

Neill, C., L. A. Deegan, S. M. Thomas, and C. C. Cerri, Deforestation for pasture alters nitrogen and phosphorus in small Amazonian streams, *Ecological Applications*, 11, 1817–1828, 2001.

Neill, C., M. C. Piccolo, C. C. Cerri, P. A. Steudler, J. M. Melillo, and M. Brito, Net nitrogen mineralization and net nitrification rates in soils following deforestation for pasture across the southwestern Brazilian Amazon Basin landscape, *Oecologia*, 110, 243–252, 1997.

Neill, C., M. C. Piccolo, P. A. Steudler, J. M. Melillo, B. J. Feigl, and C. C. Cerri, Nitrogen dynamics in soils of forests and active pastures in the western Brazilian Amazon Basin, *Soil Biology and Biochemistry*, 27, 1167–1175, 1995.

Ollinger, S. V., O. Sala, G. Agren, B. Berg, E. Davidson, C. Field, M. Lerdau, J. Neff, Mary Scholes, Robert Sterner, New frontiers in the study of element interactions, in: *Interactions of the Major Biogeochemical Cycles*, edited by J. Melillo and C. Field, pp. 63–92, Scientific Committee on Problems of the Environment (SCOPE), Island Press Publishers, 2003.

Passianoto, C. C., T. Ahrens, B. J. Feigl, P. A. Steudler, J. B. do Carmo and J. M. Melillo, Emissions of CO_2, N_2O and NO in conventional and no-till management practices in Rondonia, Brazil, *Biology and Fertility of Soils*, 38, 200–208, 2003.

Perakis, S. S. and L. O. Hedin, Nitrogen loss from unpolluted South American forests mainly via dissolved organic compounds, *Nature*, 415, 416–419, 2002.

Richter, D. D. and L. I. Babbar, Soil diversity in the tropics, Advances in Ecological Research, 21, 315–389, Academic Press, 1991.

Richter, D. D. and D. Markewitz, How deep is soil?, *BioScience*, 45, 600–609, 1995.

Rignot, E., W. A. Salas, and D. L. Skole, Mapping deforestation and secondary growth in Rondonia, Brazil, using imaging radar and thematic mapper data, *Remote Sensing of the Environment*, 59, 167–179, 1997.

Salimon, C. I. and I. F. Brown, Secondary forests in western Amazonia: Significant sinks for carbon released from deforestation?, *Interciencia*, 25, 198–202, 2000.

Serrão, E. A. S. and J. M. Toledo, The search for sustainability in Amazonian pastures, in: *Alternatives to Deforestation: Steps toward sustainable use of the Amazon rain forest*, edited by A. B. Anderson, pp. 195–214, Columbia University Press, New York, 1990.

Silva, A. C. da, *Potabilidade das Águas Subterrâneas do Município de Ji-Paraná. Estudo de caso: Bairro Nova Brasília*, Masters thesis, Universidade Estadual Paulista, Instituto de Geociências e Ciências Exatas, 2001.

Sombroek, W., Amazon landforms, and soils in relation to biological diversity, *Acta Amazonica*, 30, 81–100, 2000.

Thomas, S. M., C. Neill, L. A. Deegan, A. V. Krusche, R. Victoria, and M. V. Ballester, Influences of land use and stream size on particulate and dissolved materials in a small Amazonian stream network, *Biogeochemistry*, 68, 135–151, 2004.

Tomasella, J., M. G. Hodnett, and L. Rossato, Pedotransfer functions for the estimation of soil water retention in Brazilian soils, *Soil Science Society of America Journal*, 64, 327–338, 2000.

Townsend, A. R., G. P. Asner, C. C. Cleveland, M. E. Lefer, and M. C. Bustamante, Unexpected changes in soil phosphorus dynamics along pasture chronosequences in the humid tropics, *Journal of Geophysical Research*, 107, doi:10.1029/2001JD000650, 2002.

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

Uehara, G. and G. Gillman, *The Mineralogy, Chemistry, and Physics of Tropical Soils with Variable Charge Clays*, Westview Press, Boulder, Colorado, 1981.

Uhl, C. and C. F. Jordan, Succession and nutrient dynamics following forest cutting and burning in Amazonia, *Ecology*, 65, 1476–1490, 1984.

Verchot, L. V., E. A. Davidson, J. H. Cattânio, I. L. Ackerman, H. E. Erickson, and M. Keller, Land use change and biogeochemical controls of nitrogen oxide emissions from soils in eastern Amazonia, *Global Biogeochemical Cycles*, 13, 31–46, 1999.

Vitousek, P. M., Litterfall, nutrient cycling, and nutrient limitation in tropical forests, *Ecology*, 65, 285–298, 1984.

Vitousek, P. M. and C. B. Field, Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications, *Biogeochemistry*, 46, 179–202, 1999.

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

Vitousek, P. M. and W. A. Reiners, Ecosystem succession and nutrient retention: A hypothesis, *BioScience*, 25, 376–381, 1975.

Vitousek, P. M., J. R. Gosz, C. G. Grier, J. M. Melillo, W. A. Reiners, and R. L. Todd, Nitrate losses from disturbed ecosystems, *Science*, 204, 469–474, 1979.

Walker, T. W. and J. K. Syers, The fate of phosphorus during pedogenesis, *Geoderma*, 15, 1–19, 1976.

Williams, M. R., T. R. Fisher, and J. M. Melack, Solute dynamics in soil water and groundwater in a central Amazon catchment undergoing deforestation, *Biogeochemistry*, 38, 303–335, 1997.

Williams, M. R. and J. M. Melack, Solute export from forested and partially deforested catchments in the central Amazon, *Biogeochemistry*, 38, 67–102, 1997.

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