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Net nitrogen mineralization and net nitrification rates in soils following deforestation for pasture across the southwestern Brazilian Amazon Basin landscape

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Abstract Previous studies of the effect of tropical forest conversion to cattle pasture on soil N dynamics showed that rates of net N mineralization and net nitrification were lower in pastures compared with the original forest. In this study, we sought to determine the generality of these patterns by examining soil inorganic N concentrations, net mineralization and nitrification rates in 6 forests and 11 pastures 3 years old or older on ultisols and oxisols that encompassed a wide variety of soil textures and spanned a 700-km geographical range in the southwestern Brazilian Amazon Basin state of Rondônia. We sampled each site during October-November and April-May. Forest soils had higher extractable NO_3^--N and total inorganic N concentrations than pasture soils, but substantial NO_3^--N occurred in both forest and pasture soils. Rates of net N mineralization and net nitrification were higher in forest soils. Greater concentrations of soil organic matter in finer textured soils were associated with greater rates of net N mineralization and net nitrification, but this relationship was true only under native forest vegetation; rates were uniformly low in pastures, regardless of soil type or texture. Net N mineralization and net nitrification rates per unit of total soil organic matter showed no pattern across the different forest sites, suggesting that controls of net N mineralization may be broadly similar across a wide range of soil types. Similar reductions in rates of net N transformations in pastures 3 years old or older across a range of textures on these soils suggest that changes to soil N cycling caused by deforestation for pasture may be Basin-wide in extent. Lower net N mineralization and net nitrification rates in established pastures suggest that annual N losses from largely deforested landscapes may be lower than losses from the original forest. Total ecosystem N losses since deforestation are likely to depend on the balance between lower N loss rates from established pastures and the magnitude and duration of N losses that occur in the years immediately following forest clearing.

Key words Brazilian Amazon · Tropical forest · Tropical pasture · Nitrification · Nitrogen mineralization

Introduction

Large areas of tropical forest in the Brazilian Amazon have been cleared for agriculture, especially in states such as Rondônia and Pará, where fiscal incentives and government settlement programs encouraged extensive cattle ranching (Hecht 1985). Pasture is now the dominant use of deforested lands (Fearnside and Salati 1985; Skole et al. 1994). Important changes in soil physical and chemical characteristics and biogeochemical cycles follow pasture establishment and can affect soil fertility and the interaction of soils with the atmosphere and downstream aquatic ecosystems. Some of these changes, such as the increases in pH and exchangeable bases that follow the forest cutting and burning for pasture creation, are nearly universal and occur in a wide variety of sites and on different soils (Brinkman and Nascimento 1973, Serrão et al. 1979; Martins et al. 1990; Luizão et al. 1992). Changes to other biogeochemical attributes, such as soil organic matter stocks, are more variable, increasing under pasture in some locations (Choné et al. 1991; Moraes et al. 1996) and decrease in others (Detwiler 1986; Trumbore et al. 1995). A better understanding of the biogeochemical changes that follow

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forest conversion to pasture, their variability, and their controls is important for managing pastures in a sustainable manner and for interpreting the consequences of deforestation for the Amazon Basin as whole.

In a variety of ecosystems, rates of net N mineralization and the total quantity of soil N are indicators of soil fertility (Nadelhoffer et al. 1983; Pastor et al. 1984; Vitousek and Matson 1985). Net nitrification rates can reflect the potential for N losses, either through leaching or by gaseous emission (Likens et al. 1969; Vitousek and Melillo 1979; Krause 1982; Vitousek and Matson 1985). In previous studies of N cycling following tropical forest conversion to pasture at Nova Vida in the rapidly-developing Brazilian Amazon Basin state of Rondônia, we found higher soil N stocks and lower inorganic N concentrations in pasture soils compared with the original forest soils (Piccolo et al. 1994; Neill et al. 1995). Pasture soils also showed lower rates of net N mineralization and net nitrification than forest soils (Neill et al. 1995).

Tropical regions, including the Amazon Basin, contain a diversity of landforms and soil types comparable to that in temperate regions (Vitousek and Sanford 1986; Richter and Babbar 1991; Sanchez and Logan 1992). We expect that this diversity plays a large role in the response of N biogeochemistry to forest clearing and pasture creation. But because nutrient cycling studies in Amazonia have been limited to a small number of sites, we still know little about the consequences of landscape-level heterogeneity for the control of soil nitrogen biogeochemistry. In this study, we attempted to determine the extent to which patterns of nitrogen cycling in forests and established pastures vary across the landscape in Rondônia. We examined changes to inorganic N concentrations, net N mineralization and net nitrification rates following forest clearing and pasture planting in six chronosequences of forest and different-aged pastures along a 700-km transect. Our goals were: (1) to evaluate soil N concentrations and dynamics in forest and pastures on a range of soil types, and (2) to determine if seasonal patterns, represented by samples taken in October-November and in April-May, were similar to the annual patterns previously observed at intensively studied locations.

Materials and methods

Study areas

We conducted field measurements in chronosequences of forest and pastures distributed along a transect from Porto Velho to Vilhena (Fig. 1; Table 1). These locations covered a wide geographic distribution of soil types and moist upland *terra firme* evergreen tropical forest vegetation (Table 1). Soils ranged from very clayey yellow latosols (Hapludox) to sandy red-yellow podzolics (Paleudult). Ultisols and oxisols are the dominant soil types in the Brazilian Amazon Basin and cover approximately two-thirds of its total area (Cochrane and Sanchez 1982; Moraes et al., 1995). Vegetation was characteristic of the open tropical forest in Rondônia with high numbers of palms (Projeto Radambrasil 1978; Pires and Prance 1986). At Vilhena, the forest represented the transition between closed forest and open campo cerrado vegetation (Pires and Prance 1986). Because of their proximity to roads, all forests were influenced by human activities. Information provided by land owners indicated that 1–3 trees ha^{-1} were removed from all of the forests by selective logging during the previous 10 years. This level of disturbance is typical for all but the remotest forest reserves in central Rondônia. One location, Nova Vida, was the site of our previous investigations (Neill et al. 1995; Moraes et al. 1996).

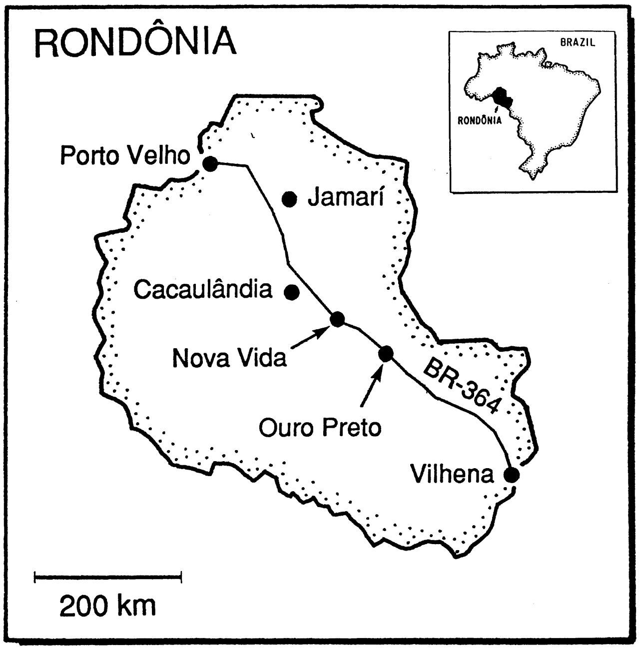

Fig. 1 Location of Rondônia and the chronosequences studied along a 700-km transect from Porto Velho to Vilhena

Mean annual rainfall along the transect ranges from 2.3 m in Porto Velho to 2.1 m at Vilhena (SUDAM 1984). The dry period typically lasts from May to September (Bastos and Diniz 1982). Mean annual temperature was 24.4–25.6°C in Porto Velho and 18.8–20.3°C in Vilhena (Bastos and Diniz 1982). Mean monthly temperature varied less than 4°C at all sites.

We selected pastures that were converted directly from forest by cutting, burning and seeding pasture grasses. The typical clearing sequence was as follows: brush was cut in March, large trees were cut in June or July, all the cut biomass was burned following the beginning of the rainy season in late August or September and pasture grasses were seeded in December or January. A second burn to kill tree stump sprouts and to reduce the volume of downed wood typically occurred 2–3 years after the initial clearing. Pastures were never mechanized nor was chemical fertilizer used. Pasture vegetation consisted of the grasses most commonly planted in Rondônia, *Panicum maximum*, *Brachiaria humidicola*, *B. decumbens* and *B. brizantha* (Table 1). Newer pastures were typically planted with *B. brizantha.* In some cases older pastures were converted to *B. brizantha* by burning and reseeding. All pastures were actively grazed. All sites were located in areas of flat or very gently rolling topography.

Field and laboratory methodology

We collected soils from all forest and pasture sites during October-November 1993 and April-May 1994. The October-November collection represented the transition between the dry season and the rainy season and the April-May collection represented the end of wet season. Five cores at 0–5 cm and 5–10 cm depths were col-

Table 1 Chronosequence location, land use and pasture age, pasture vegetation, soil type, soil texture and soil carbon and nitrogen concentrations along the Rondônia transect. Pasture age represents the age at the first sampling in 1993. Percent clay, soil texture class and carbon and nitrogen concentrations are for 0–10 cm depth

Chrono sequence	Location	Land use	Pasture vegetation	Soil type	Percent clay	Texture class	Carbon mg C g^{-1}	Nitrogen mg N g^{-1}
Porto Velho	EMBRAPA.5 km SE of Porto Velho on BR-364 (8°47′S / 63°52′W)	Forest		Red-yellow latosol (Hapludox)	58	clay	29.2	2.37
		7-year-old pasture	*Brachiaria brizantha*	Red-yellow latosol (Hapludox)	55	clay	28.1	2.14
Jamarí	Floresta Nacional do Jamarí. Santa Barbara mine, 8 km from BR-364 (9°11′S / 63°07′W)	Forest		Red-yellow podzolic latosol (Kandiudult)	33	sandy clay loam	20.5	1.44
		3-year-old pasture	*B. brizantha*	Red-yellow latosol (Hapludox)	61	clay	33.8	2.41
		7-year-old pasture	*B. brizantha*	Red-yellow lastosol (Hapludox)	65	clay	34.9	2.65
Cacaulândia	Fazenda Rancho Grande. Line road C-20, 9 km NE of Cacaulândia (10°09′S / 62°49′W)	Forest		Red-yellow podzolic (Paleudult)	16	sandy loam	17.1	1.86
		8-year-old pasture	*B. humdicola*	Red-yellow podzolic (Paleudult)	13	loamy sand	14.7	0.90
Nova Vida	Fazenda Nova Vdia, Retiro Aldeia. Km 472 of BR-364, 50 km SE of Ariquemes (10°09′S /62°49′W)	Forest		Red-yellow podzolic latosol (Kandiudult)	22	sandy loam	12.8	1.09
		4-year-old pasture	*B. brizantha*	Red-yellow podzolic latosol (Kandiudult)	24	sandy loam	12.5	0.90
		21-year-old pasture	*B. brizantha*	Red-yellow podzolic latosol (Kandiudult)	23	sandy clay loam	16.4	1.13
Ouro Preto	Fazenda Benjamin. Line Road 4, 4 km, N-NW of Ouro Preto do Oeste (10°42′S/62°12′W)	Forest		Red-yellow podzolic (Paleudult)	12	loamy sand	10.5	0.66

Table 1. (Continued)

Chrono sequence	Location	Land use	Pasture vegetation	Soil type	Percent clay	Texture class	Carbon	Nitrogen
							mg C g^{-1}	mg N g^{-1}
		6-year-old pasture	*Panicum maximum*	Red-yellow podzolic (Paleudult)	26	sandy clay loam	13.8	1.37
		11-year-old pasture	*P. maximum*	Red-yellow podzolic (Paleudult)	16	loamy sand	15.5	1.20
		23-year-old pasture	*B. brizantha* *B. decumbens*	Red-yellow podzolic (Paleudult)	16	sandy clay loam	15.3	1.28
Vilhena	3 km E of BR-364, 4 km on the Mato Grosso side of the RO/MT border (12°52′S /60°03′W)	Forest		Yellow latosol (Hapludox)	75	clay	37.0	2.63
		7-year-old pasture	*B. brizantha*	Yellow latosol (Hapludox)	76	clay	29.1	1.90
		12-year-old pasture	*B. brizantha*	Yellow latosol (Hapludox)	67	clay	34.2	2.23

lected with a 5-cm-diameter corer from locations 3 m apart in a line beginning at a random point. Total soil C and N concentrations were analyzed by combustion on a Perkin-Elmer 2400 Elemental Analyzer after drying at 60°C. Soil texture was analyzed on a composite 50-g sample from each site by the hydrometer method after dispersion with sodium hexametaphosphate and digestion of the organic matter with 30% H_2O_2 (Anderson and Ingram 1989).

Soils for measurement of N pools, mineralization and nitrification rates were prepared the same day they were collected by removing roots and stones. One subsample ca.10 g fresh soil was extracted in 50 ml of 2M KCl to determine inorganic N concentrations. After 24 h, these extracts were filtered and preserved with phenyl mercuric acetate at a final concentration of 0.5 mg L^{-1}. A second subsample of approximately 5 g was dried to constant weight at 105°C for gravimetric moisture determination. Percent soil moisture was expressed as g H_2O 100 g^{-1} dry soil. At third subsample of approximately 50 g was incubated in the dark at room temperature between 25°C and 28°C for 7 days to determine net N mineralization and net nitrification rates. We have found that 7-day laboratory incubations provide a reliable index for comparing forest and pasture soils (Piccolo et al. 1994). After 7 days, a 10-g subsample of the incubated sample was extracted with 2M KCl for 24 h, then filtered and preserved.

We analyzed extracts for NH_4^+-N and $NO_3^- + NO_2^-$-N colorimetrically using an automated flow injection system (Ruzicka and Hansen 1981). NH_4^+-N was measured by the phenolate method and NO_3^--N was measured as NO_2^--N following reduction with a Cd catalyst. Net N mineralization was calculated as the change in NH_4^+-N plus NO_3^--N during the 7-day incubation. Net nitrification equaled final concentration of NO_3^--N minus initial concentration of NO_3^--N.

Tests for differences in soil moisture, inorganic N concentrations, net nitrogen mineralization rates and net nitrification rates between chronosequence, land use and season were made using analysis of variance. We specified an overall ANOVA model using the GLM Procedure of SAS (SAS 1987) that contained chronosequence (e.g., Porto Velho, Jamarí), land use (forest or different aged pasture) and season (October–November or April–May) as main effects. Chronosequence and season were fixed effects; land use was a random effect and nested within chronosequence. We conducted statistical tests using the 0–5 cm depth only to limit the total number of interaction terms and because differences among between factors were greater at the shallower depth.

Results

Soil conditions

Soil clay content along the transect varied from 12 to 16% in the red-yellow podzolics to 67–75% in yellow latosols (Table 1). Soil texture classes ranged from clays to loamy sands. Carbon concentrations in the top 10 cm of forest soil varied from 10.5 mg C g^{-1} to 37.0 mg C g^{-1} (Table 1). Pasture soil C concentrations spanned approximately the same range, from 12.5 mg C g^{-1} to 34.9 mg C g^{-1}. Nitrogen concentrations in the top 10 cm of forest and pasture soils ranged from 0.66 mg N g^{-1} to 2.63 mg N g^{-1} (Table 1).

Percent soil moisture varied from 12.71–34.74% in October-November and from 11.88 to 44.78% in April-May across all sites and depths (Table 2). The highest soil moistures occurred in Porto Velho and Vilhena where soil clay contents were highest. Overall, differences in soil moisture between forest and pastures were on the order of 5% or less; the exception was Jamarí,

Table 2 Percent soil moisture (g H_2O 100 g^{-1} dry soil) at 0–5 and 5–10 cm depths collected in October–November and April–May from forest and pasture soils along the Rondônia transect. Values are means ± SE

Chronosequence		October–November		April–May	
		0–5 cm	5–10 cm	0–5 cm	5–10 cm
Porto Velho	Forest	32.04 ± 1.09	32.50 ± 1.12	31.26 ± 0.91	29.26 ± 0.40
	7-year-old pasture	27.41 ± 0.50	27.80 ± 0.43	26.84 ± 0.43	25.72 ± 0.05
Jamari	Forest	15.41 ± 1.24	15.02 ± 0.51	16.49 ± 0.74	15.26 ± 0.62
	3-year-old pasture	28.70 ± 2.77	26.38 ± 1.45	31.61 ± 2.26	30.74 ± 3.07
	7-year-old pasture	26.77 ± 2.08	22.84 ± 1.11	35.69 ± 2.77	30.55 ± 1.71
Cacaulândia	Forest	20.20 ± 0.87	18.73 ± 0.76	18.78 ± 0.97	16.83 ± 0.54
	8-year-old pasture	21.38 ± 2.36	17.90 ± 2.29	13.04 ± 1.34	11.88 ± 0.66
Nova Vida	Forest	14.85 ± 1.61	14.38 ± 1.45	15.47 ± 1.07	15.08 ± 0.26
	4-year-old pasture	16.51 ± 1.27	13.95 ± 0.81	15.00 ± 0.63	13.58 ± 0.32
	21-year-old pasture	12.71 ± 0.78	12.73 ± 0.48	20.85 ± 2.03	15.72 ± 0.90
Ouro Preto	Forest	17.08 ± 1.80	16.11 ± 0.46	21.58 ± 1.02	17.03 ± 0.30
	6-year-old pasture	19.69 ± 2.30	17.15 ± 0.56	16.17 ± 0.86	14.88 ± 0.49
	11-year-old pasture	21.12 ± 1.10	17.74 ± 0.88	16.20 ± 0.18	15.80 ± 0.23
	23-year-old pasture	21.41 ± 1.07	18.24 ± 1.06	15.92 ± 0.53	13.85 ± 0.55
Vilhena	Forest	34.74 ± 0.85	32.55 ± 0.95	44.78 ± 2.54	35.81 ± 1.18
	7-year-old pasture	24.93 ± 1.29	28.10 ± 0.48	25.33 ± 0.97	24.28 ± 0.29
	12-year-old pasture	27.07 ± 1.67	26.89 ± 0.71	22.80 ± 0.33	24.26 ± 1.21

where soil moisture in pastures was nearly double that in forest. A significant land use by season interaction (Table 3) indicated that whether soil moisture was higher in forest or in pastures depended on the season sampled.

Inorganic nitrogen concentrations

The highest NH_4^+-N concentrations occurred in Porto Velho, Jamarí, Ouro Preto and Vilhena (Table 4). Both NH_4^+ and NO_3^- were important components of soil inorganic N concentrations at all chronosequences along the transect (Table 4). Chronosequence, land use, season and interactions of chronosequence and season all influenced NH_4^+ concentrations (Table 3). The interaction of chronosequence and season on NH_4^+-N concentrations was evident where concentrations increased between October-November and April-May sampling dates in some chronosequences (e.g., Porto Velho and Nova Vida) but changed relatively little in other chronosequences (e.g., Cacaulândia and Vilhena) (Table 4).

Land use significantly affected soil NH_4^+-N concentrations, but the overall difference in NH_4^+-N concentrations between forests and pastures was small (Table 4). Overall, mean NH_4^+-N concentration over 0–10 cm was higher in forest soils (6.47 µg NH_4^+-N g^{-1} ds) than in pasture soils (5.52 µg NH_4^+-N g^{-1} dry soil, ds), although the ranges of forest soil NH_4^+-N concentrations (1.24–17.59 µg N g^{-1} ds) and pasture soil NH_4^+-N concentrations (0 to 15.64 µg N g^{-1} ds) were generally similar (Table 4). NH_4^+-N concentrations were generally higher in April–May than in October–November (Table 4).

Unlike its effect on NH_4^+-N concentrations, chronosequence did not exert a significant influence on NO_3^--N concentrations (Table 3). Instead, extractable NO_3^--N concentrations were strongly influenced by land use,

Table 3 Results of an analysis of variance to test for the effects of chronosequence (e.g., Porto Velho, Jamarí, land use (forest and different-aged pastures) and the season of sampling (October–November and April–May) on soil moisture, inorganic nitrogen concentrations and net N mineralization and net nitrification rates at 0–5 cm depth in soils across the Rondônia transect. Chronosequence and season were treated as fixed effects; land use was a random effect and nested within chronosequence

		Soil moisture		NH_4^+-N		NO_3^--N		Net N minerlization rate		Net nitrifrification rate	
Source	*df*	*F*	*P* <	*F*	*P* <	*F*	*P* <	*F*	*P* <	*F*	*P* <
Chrono sequence (C)	5	3.73	0.0320	3.69	0.0331	1.86	NS	0.44	NS	0.42	NS
Land use (L)	11	25.29	0.0001	6.13	0.0001	3.18	0.0007	27.38	0.0001	35.88	0.0001
Season (S)	1	0.03	NS	24.97	0.0004	27.58	0.0003	0.00	NS	0.13	NS
C × S	5	1.21	NS	8.38	0.0004	6.24	0.0056	0.38	NS	0.48	NS
L × S (C)	11	5.80	0.0001	0.91	NS	0.59	NS	1.87	0.0481	3.37	0.004
Error	136										

NS = not significant

Table 4 Mean soil inorganic N concentrations (μg N g^{-1} dry soil) at 0–5 cm and 5–10 cm depths from forest and pastures of different ages collected in October–November and April–May along the Rondônia transect. Values are mean ± SE

Site	Location	October–November				April–May			
		NH_4^+-N		NO_3^--N		NH_4^+-N		NO_3^--N	
		0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm
Porto Velho	Forest	8.58 ± 0.90	4.77 ± 1.91	9.20 ± 0.83	9.17 ± 0.97	17.59 ± 0.73	14.09 ± 0.37	2.49 ± 0.37	2.53 ± 0.27
	7-year-old pasture	4.57 ± 1.38	2.84 ± 0.51	1.25 ± 0.16	1.28 ± 0.18	15.64 ± 1.45	13.05 ± 0.62	1.38 ± 0.23	1.45 ± 0.18
Jamarí	Forest	4.56 ± 1.91	1.83 ± 0.22	3.21 ± 1.11	2.51 ± 0.53	3.53 ± 0.34	3.07 ± 0.34	1.07 ± 0.08	1.27 ± 0.18
	3-year-old pasture	5.85 ± 1.95	4.26 ± 1.42	1.72 ± 0.13	2.54 ± 0.29	9.06 ± 1.70	7.43 ± 1.10	0.90 ± 0.10	0.94 ± 0.14
	7-year-old pasture	5.77 ± 1.00	3.94 ± 0.61	1.47 ± 0.09	1.43 ± 0.20	6.98 ± 1.59	3.72 ± 0.42	2.24 ± 0.74	1.79 ± 0.50
Caculândia	Forest	5.09 ± 0.76	4.91 ± 2.00	4.80 ± 0.59	3.30 ± 0.15	4.01 ± 0.53	2.67 ± 0.20	3.18 ± 0.45	2.31 ± 0.22
	8-year-old pasture	3.13 ± 0.61	2.05 ± 0.38	2.19 ± 0.62	2.54 ± 0.66	4.05 ± 0.35	3.51 ± 0.35	1.14 ± 0.12	1.33 ± 0.05
Novla Vida	Forest	1.83 ± 1.83	1.24 ± 1.24	6.43 ± 0.37	5.36 ± 0.42	3.60 ± 0.14	2.04 ± 0.14	4.63 ± 0.22	3.33 ± 0.24
	4-year-old pasture	2.60 ± 0.95	0.00 ± 0.00	2.09 ± 0.90	1.89 ± 0.97	5.73 ± 0.60	3.83 ± 0.55	1.59 ± 0.16	1.70 ± 0.12
	21-year-old pasture	3.87 ± 2.02	5.18 ± 3.21	4.50 ± 4.42	5.08 ± 4.97	4.23 ± 0.39	3.57 ± 0.53	1.44 ± 0.21	1.50 ± 0.17
Ouro Preto	Forest	6.51 ± 3.14	1.80 ± 0.20	11.87 ± 4.42	5.03 ± 0.77	9.90 ± 1.85	6.89 ± 1.03	9.11 ± 0.88	6.50 ± 0.60
	6-year-old pasture	8.67 ± 2.04	4.07 ± 0.58	1.69 ± 0.22	1.83 ± 0.29	5.80 ± 0.04	5.66 ± 0.23	1.49 ± 0.08	1.56 ± 0.18
	11-year-old pasture	6.45 ± 0.69	2.18 ± 0.29	3.64 ± 0.20	3.33 ± 0.16	6.04 ± 0.40	2.78 ± 1.17	0.95 ± 0.03	0.83 ± 0.35
	23-year-old pasture	7.17 ± 0.53	3.23 ± 0.52	1.57 ± 0.14	1.59 ± 0.22	9.00 ± 1.30	5.75 ± 0.27	1.21 ± 0.06	1.22 ± 0.14
Vilhena	Forest	14.44 ± 2.49	7.41 ± 2.30	10.58 ± 3.24	10.64 ± 2.84	15.63 ± 2.59	9.34 ± 1.00	3.52 ± 0.47	3.76 ± 0.36
	7-year-old pasture	5.22 ± 1.23	1.78 ± 0.48	11.58 ± 7.16	10.32 ± 6.83	7.13 ± 0.45	6.42 ± 0.36	2.73 ± 0.35	3.21 ± 0.21
	12-year-old pasture	5.76 ± 1.53	1.95 ± 0.40	17.52 ± 7.71	12.02 ± 3.14	6.86 ± 0.49	7.56 ± 1.00	3.40 ± 0.33	2.91 ± 0.17

Table 5 Net N mineralization and net nitrification rates (μg N g^{-1} dry soil day^{-1}) at 0–5 cm and 5–10 cm soil depths determined from 7-day laboratory incubations of forest and different-aged pasture soils collected in October–November and April–May along the Rondônia transect. Values are mean ± SE

Site	Location	October–November				April–May			
		Net N mineralization		Net nitrification		Net N mineralization		Net nitrification	
		0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm	0–5 cm	5–10 cm
Porto Velho	Forest	2.69 ± 0.43	1.23 ± 0.10	3.46 ± 0.48	1.63 ± 0.26	2.87 ± 0.56	1.42 ± 0.28	3.79 ± 0.73	2.46 ± 0.39
	7-year-old pasture	−0.05 ± 0.12	0.05 ± 0.05	0.23 ± 0.03	0.18 ± 0.05	−0.90 ± 0.11	−0.98 ± 0.15	0.14 ± 0.04	0.01 ± 0.05
Jamari	Forest	1.95 ± 1.08	0.88 ± 0.14	1.74 ± 0.48	0.99 ± 0.14	2.55 ± 0.39	1.13 ± 0.13	2.04 ± 0.19	1.34 ± 0.14
	3-year-old pasture	0.40 ± 0.31	1.33 ± 0.83	0.93 ± 0.21	1.58 ± 0.91	0.36 ± 0.23	−1.16 ± 0.22	0.07 ± 0.14	0.49 ± 0.15
	7-year-old pasture	−0.04 ± 0.12	0.14 ± 0.11	0.23 ± 0.14	0.36 ± 0.12	1.14 ± 0.56	0.41 ± 0.26	0.98 ± 0.73	0.53 ± 0.26
Cacaulândia	Forest	3.08 ± 0.63	1.20 ± 0.70	3.62 ± 0.68	1.86 ± 0.61	2.17 ± 0.58	1.40 ± 0.15	1.60 ± 0.19	1.25 ± 0.14
	8-year-old pasture	−0.16 ± 0.07	−0.26 ± 0.08	0.06 ± 0.10	−0.05 ± 0.10	0.30 ± 0.07	0.22 ± 0.04	0.28 ± 0.02	0.27 ± 0.02
Nova Vida	Forest	0.93 ± 0.35	0.52 ± 0.30	0.96 ± 0.38	0.70 ± 0.47	2.08 ± 0.46	1.16 ± 0.29	2.34 ± 0.43	1.28 ± 0.31
	4-year-old pasture	0.38 ± 0.14	0.06 ± 0.11	0.31 ± 0.15	−0.08 ± 0.07	−0.27 ± 0.10	−0.16 ± 0.13	0.10 ± 0.10	0.05 ± 0.07
	21-year-old pasture	0.35 ± 0.29	0.58 ± 0.55	0.60 ± 0.54	1.04 ± 0.92	−0.23 ± 0.02	−0.27 ± 0.03	−0.02 ± 0.04	−0.03 ± 0.02
Ouro Preto	Forest	1.29 ± 0.77	0.67 ± 0.09	1.81 ± 0.44	0.85 ± 0.09	1.65 ± 0.23	0.49 ± 0.10	2.24 ± 0.41	1.09 ± 0.23
	6-year-old pasture	−0.83 ± 0.12	−0.34 ± 0.08	0.05 ± 0.04	0.14 ± 0.03	−0.36 ± 0.07	−0.53 ± 0.02	−0.06 ± 0.01	−0.06 ± 0.02
	11-year-old pasture	0.56 ± 0.14	−0.15 ± 0.07	0.95 ± 0.11	0.04 ± 0.07	−0.33 ± 0.55	0.02 ± 0.20	0.03 ± 0.02	0.08 ± 0.04
	23-year-old pasture	−0.56 ± 0.16	−0.25 ± 0.07	0.22 ± 0.20	0.21 ± 0.07	−0.22 ± 0.12	−0.29 ± 0.02	0.22 ± 0.18	0.04 ± 0.04
Vilhena	Forest	4.32 ± 0.73	1.77 ± 0.15	3.73 ± 0.36	2.37 ± 0.35	5.47 ± 1.28	2.39 ± 0.36	4.79 ± 0.56	3.16 ± 0.42
	7-year-old pasture	0.72 ± 0.24	0.70 ± 0.22	0.76 ± 0.24	0.57 ± 0.21	−0.04 ± 0.09	−0.07 ± 0.09	0.67 ± 0.12	0.56 ± 0.12
	12-year-old pasture	0.58 ± 0.20	0.65 ± 0.16	0.91 ± 0.26	0.57 ± 0.12	−0.12 ± 0.12	−0.27 ± 0.07	0.41 ± 0.13	0.45 ± 0.11

season and an interaction of land use and season (Table 3). Overall mean NO_3^--N concentration at 0–10 cm was higher in forest soils (5.24 μg NO_3^--N g^{-1} ds) than in pasture soils (2.97 μg NO_3^--N g^{-1} ds), but the range of values in forest soils (1.07–11.87 μg NO_3^--N g^{-1} ds) and pasture soils (0.90–17.52 μg NO_3^--N g^{-1} ds) was similar (Table 4).

Season affected soil NO_3^--N concentrations but the magnitude of this effect differed between chronosequences as indicated by a significant chronosequence by season interaction (Table 3). NO_3^--N concentrations were generally higher in October–November than in April–May (Table 4). Two pastures, in Porto Velho and one in Jamarí, were exceptions to this pattern and had higher NO_3^--N concentrations in April–May (Table 4).

Net N mineralization and net nitrification rates

Forest soils exhibited only positive rates of net N mineralization; pasture soils showed either positive rates of smaller magnitude or negative rates (net NH_4^+ or NO_3^- immobilization) (Table 5). Net N mineralization rates in forest soils ranged from 1.17–3.48 μg N g^{-1} ds, compared with a range of −0.51 to 0.48 μg N g^{-1} ds day^{-1} in pasture soils (Table 5). Net nitrification rates in forest soils ranged from 1.32 to 3.51 μg N g^{-1} ds day^{-1} compared with lower rates of 0.02–0.77 μg N g^{-1} ds day^{-1} in pasture soils (Table 5). Land use and an interaction of land use with season had significant effects on net N mineralization and net nitrification rates, but chronosequence and season had no effects (Table 3). The magnitude of the land use effect varied with season but the basic pattern was the same.

Discussion

Effects of forest conversion to pasture

The pattern of lower net N mineralization and net nitrification rates in pastures soils compared with forest soils along the Rondônia transect was consistent across a range of soil types, soil textures and pasture ages. In forests, N transformation rates agreed well with rates measured both at Nova Vida and on oxisols and ultisols elsewhere in the Brazilian Amazon Basin (Matson and Vitousek 1987; Livingston et al. 1988; Vitousek and Matson 1988; Matson et al. 1990; Luizão et al. 1992; Neill et al. 1995). These rates are comparable to rates of N transformation in a variety of more fertile tropical soils (Vitousek and Denslow 1987; Matson et al. 1990; Reiners et al. 1994) and support the interpretation that phosphorus- and calcium-poor oxisols and ultisols are relatively rich in N (Vitousek and Sanford 1986; Vitousek and Matson 1988). These N transformation rates are higher than found on sandy soils or on nutrient poor soils of the Rio Negro region of the Amazon (Matson and Vitousek 1987; Montagnini and Buschbacher 1989).

In pastures, rates of net N mineralization and net nitrification along the transect were consistent with rates of < 1.0 μg N g^{-1} ds day^{-1} in established pastures 3 years old or older at Nova Vida (Neill et al. 1995). This pattern was different from that found at the few other locations in the Amazon Basin where these N transformations have been measured. Near Manaus, Luizão et al. (1992) found no difference over an annual cycle between net N mineralization and net nitrification rates in forest and a 1-year-old pasture. Also near Manaus, Matson et al. (1990) reported the same pattern from a one-time measurement in a forest and 3-year-old pasture. The young age of the pasture studied by Luizão et al. (1992) may have contributed to the similarity of rates of N transformation between pasture and forest. At Nova Vida, net N mineralization and net nitrification rates in 3-year-old pasture were lower than the original forest, and they continued to decline with increasing pasture age (Neill et al. 1995). It is likely that the pattern of lower rates of N transformations in pastures do not become clearly established until 2–3 years after pasture formation. In the pasture studied by Matson et al. (1990), fertilizer application of 36 kg N ha^{-1} may have resulted in unusually high net N mineralization and net nitrification rates. Along the Rondônia transect, lower rates of net N mineralization and net nitrification across soil types in pastures 3 years old or older suggests that this is likely the more general pattern. In contrast to Nova Vida, this study found no evidence of declining rates of N transformations in older pastures, but the range of pasture ages examined was smaller.

Variation in soil type and soil texture led to differences in soil moisture, inorganic N concentrations and net N mineralization and net nitrification rates in forests along the transect. Moisture, inorganic N concentrations and net mineralization and nitrification rates were highest in the forests at Porto Velho and Vilhena, where soil clay contents were greatest. Net N mineralization and net nitrification rates were higher on soils with higher clay contents (Fig. 2). This was consistent with higher total soil organic carbon concentrations in finer textured soils that occurs throughout Amazonia (Moraes et al. 1995), but these rates showed no trend across the range of soil textures when expressed per gram of available soil organic matter (SOM) (Fig. 2). This indicated that for a given unit of C in SOM under native forest, N transformation rates remained similar across a wide range of soil textures. In contrast, net mineralization and net nitrification rates across the range of clay contents were uniformly low in pastures (Fig. 2). Lower rates of net N mineralization and net nitrification in established pastures could not be explained by changes in soil total carbon or nitrogen concentrations, suggesting that some other factors control soil N turnover after pasture creation. This fundamental decoupling of rates of net N mineralization and net nitrification from total soil organic C stocks in pasture indicates that plant available N in pastures will not increase, even in those cases (e.g., Moraes et al. 1996; Neill et al. 1996) where

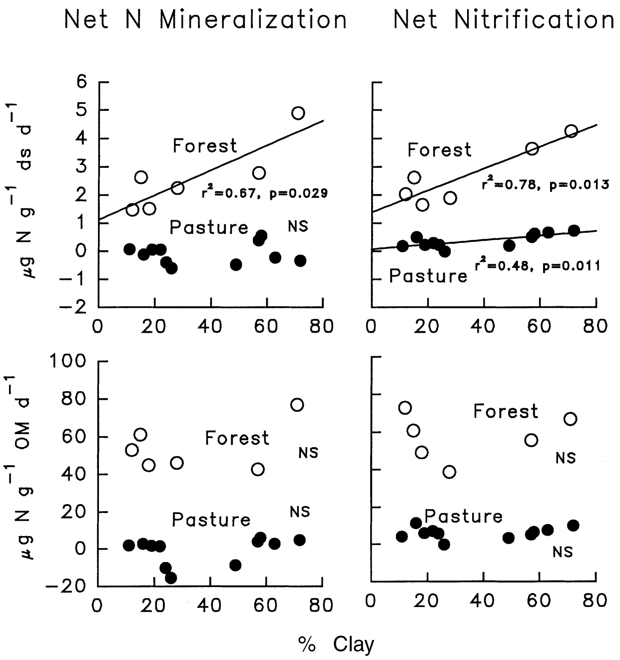

Fig. 2 *Top two panels* show rates of net N mineralization and net nitrification (μg N g^{-1} dry soil day^{-1}) plotted against soil percent clay. Regression lines and statistics are shown when there was a significant relationship. *Bottom two panels* show rates of net N mineralization and net nitrification normalized for soil organic matter (OM) concentration (μg N g^{-1} OM day^{-1}). Rates per g of available soil organic matter were similar across soil textures, but the large difference between rates in forests and pastures was retained. All values are means of the April–May and October–November sampling dates and are for 0–5 cm depth (*NS* not significant, $P < 0.05$)

pasture creation results in increased surface SOM stocks.

Seasonal patterns

The absence of a seasonal effect on net N mineralization or net nitrification rates along the Rondônia transect was consistent with results from some other tropical forests where net N mineralization and net nitrification rates are relatively aseasonal (Vitousek and Denslow 1986; Matson et al. 1987; Steudler et al. 1991; Neill et al. 1995). Rates measured in October–November and April–May generally reflected annual values at Nova Vida, but the relative similarity of soil moisture values to annual values at the other sites is difficult to determine because the two sampling periods did not capture the annual soil moisture extremes. Rates of net N mineralization and net nitrification in some seasonally dry tropical forests decrease during the dry season (García Méndez et al. 1991).

Seasonal differences in NH_4^+-N concentrations were statistically significant but relatively small, similar to soil NH_4^+-N concentrations at Nova Vida which showed a modest increase during the wet season (Neill et al. 1995). NO_3^--N concentrations everywhere along the transect were higher at the end of the dry season in October-November. This is likely associated with a prolonged period of lower soil moisture and is similar to the annual pattern at Nova Vida (Neill et al. 1995), although the substantial concentrations of NO_3^--N in some pasture soils along the transect indicated that elevated soil NO_3^--N concentrations may be more common than measurements at Nova Vida over one annual cycle suggested. Forest soils along the Rondônia transect had inorganic N concentrations about equally distributed between NH_4^+-N and NO_3^--N. This pattern was similar to the annual pattern at Nova Vida and a number of other tropical forests on a variety of soils (Vitousek and Denslow 1986; Matson et al. 1987; García Méndez et al. 1991), but substantial variation exists among tropical forests, with some soil N pools dominated by NH_4^+-N (Piccolo 1989; Livingston et al. 1988) and others dominated by NO_3^--N (Robertson 1984).

Regional scale implications

Changes in rates of net N mineralization and net nitrification following pasture creation have important regional implications because of their potential links to ecosystem N losses, either through gaseous emissions or leaching. Tropical forests are the largest known global source of N_2O (McElroy and Wofsy 1986; Matson and Vitousek 1990), and several studies have linked tropical forest N_2O emissions to soil NO_3^--N concentrations (Keller and Reiners 1994) or net N mineralization rates (Matson et al. 1990). Relatively high rates of nitrification in soils of Amazon *terra firme* forests are also linked to high soil water NO_3^--N concentrations (McClain et al. 1994) and soil nitrification is an apparent source of NO_3^- to surface waters (Martinelli et al. 1992). Our findings of high rates of net N mineralization and net nitrification rates in Rondônia forests are consistent with high N_2O releases and soil NO_3^- leaching from these ecosystems.

Large areas of the Brazilian Amazon Basin, including Rondônia, are currently being cleared for cattle pasture (Fearnside 1993; Skole and Tucker 1993). The consequences of this change for regional N_2O losses will depend on the total deforested area and the magnitude of change in N_2O flux as land is converted from forest to pasture and as pastures age. Several studies suggest that N_2O emissions from young pastures (2–10 years) are up to an order of magnitude greater than fluxes from the original forest (Luizão et al. 1989; Matson et al. 1990; Keller et al. 1993). These fluxes are higher than indicated by soil inorganic N pools, net N mineralization or net nitrification rates, suggesting that the relationships between these measures of N cycling and N_2O fluxes that apply in forest ecosystems are less clear in younger pastures. Keller et al. (1993) also found that the period of elevated fluxes from pastures is relatively short; N_2O fluxes from 10-year-old and older pastures were lower than fluxes from the original forest. A relationship between low soil NO_3^--N concentrations and low N_2O

fluxes also appeared to hold for older pastures (Keller and Reiners 1994). We have data on N_2O fluxes from Nova Vida and the Rondônia transect (unpublished) that indicate: (1) N_2O fluxes from pastures are generally lower than from forests, and (2) any period of increased N_2O flux after pasture creation lasts less than 3 years, which is the age of the youngest pastures we examined. These data suggest that the lower NO_3^--N pools and rates of net N mineralization and net nitrification we measured in pastures across Rondônia are indicative of lower pasture N_2O fluxes. Because established pastures more than 3 years old now dominate cleared land in Rondônia (Fearnside 1993; Skole and Tucker 1993), the region as a whole may be currently losing less N as N_2O than it did prior to the onset of widespread forest clearance in the late 1970s. If upland-surface water N fluxes are also influenced by soil NO_3^--N concentrations and net nitrification rates, the same pattern may also hold for regional NO_3^- leaching losses. At the regional scale, the significance of forest to pasture conversion on cumulative ecosystem N losses will likely depend on the balance between lower N loss rates from established pastures and the magnitude and duration of higher losses in the years immediately following forest clearing.

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References

Anderson JM, Ingram JSI (1989) Tropical soil biology and fertility: a handbook of methods. CAB International, Wallingford

Bastos TX, Diniz TD AS de (1982) Avaliação do clima do Estado de Rondônia para desenvolvimento agrícola (Boletim de pesquisa 44). EMBRAPA-CPATU, Belém

Brinkman WLF, Nascimento JC de (1973) The effect of slash and burn agriculture on plant nutrients in the Tertiary region of Central Amazonia. Turrialba 23:284–290

Choné T, Andreux F, Correa JC, Volkoff B, Cerri CC (1991) Changes in organic matter in an oxisol from the central Amazonian forest during eight years as pastures, determined by ^{13}C composition. In: Berthelin J (ed) Diversity of environmental biogeochemistry. Elsevier, New York, pp 307–405

Cochrane TT, Sanchez PA (1982) Land resources, soils and their management in the Amazon region: A state of knowledge report. In: Hecht SB (ed) Amazonia: agriculture and land use research. Centro Internacional de Agricultura Tropical, Cali, Colombia, pp 137–209

Detwiler RP (1986) Land use change and the global carbon cycle: the role of tropical soils. Biogeochemistry 2:67–93

Fearnside PM (1993) Deforestation in Brazilian Amazonia: the effect of population and land tenure. Ambio 22:537–545

Fearnside PM, Salati E (1985) Explosive deforestation in Rondônia, Brazil. Environ Conserv 12:355–356

García-Méndez G, Maas JM, Matson PA, Vitousek PM (1991) Nitrogen transformations and nitrous oxide flux in a tropical deciduous forest in Mexico. Oecologia 88:362–366

Hecht SB (1985) Environment, development and politics: capital accumulation and the livestock sector in eastern Amazonia. World Devel 13:663–684

Keller M, Reiners WA (1994) Soil-atmosphere exchange of nitrous oxide, nitric oxide and methane under secondary succession of pasture to forest in the Atlantic lowlands of Costa Rica. Global Biogeochem Cycles 8:399–409

Keller M, Veldkamp E, Weitz AM, Reiners WA (1993) Effect of pasture age on soil trace-gas emissions from a deforested area of Costa Rica. Nature 365:244–246

Krause HH (1982) Nitrate formation before and after clearcutting of a monitored watershed in central New Brunswick, Canada. Can J For Res 12:922–930

Likens GE, Bormann FN, Johnson NM (1969) Nitrification: importance to nutrient losses from a cut-over forested ecosystem. Science 163:1205–1206

Livingston GP, Vitousek PM, Matson PA (1988) Nitrous oxide flux and nitrogen transformation across a landscape gradient in Amazonia. J Geophys Res 93:1593–1599

Luizão F, Matson PA, Livingston G, Luizão RC, Vitousek P (1989) Nitrous oxide flux following tropical land clearing. Global Biogeochem Cycles 3:281–285

Luizão RC, Bonde TA, Rosswall T (1992) Seasonal variation of soil microbial biomass – the effect of clearfelling a tropical rainforest and establishment of pasture in the central Amazon. Soil Biol Biochem 24:805–813

Martinelli LA, Victoria RL, Trivelin PCO, Devol AH, Richey JC (1992) ^{15}N natural abundance in plants of the Amazon River floodplain and potential atmospheric N_2 fixation. Oecologia 90:591–596

Martins PF S da, Cerri CC, Volkoff B, Andreux F (1990) Effeito do desmatamento e cultivo sobre características físicas e químicas do solo sob floresta natural na Amazônia oriental. Rev Inst. Geogr. Geol. São Paulo 8–10, 11:21–33

Matson PA, Vitousek PM (1987) Cross-system comparisons of soil nitrogen transformations and nitrous oxide flux in tropical forest ecosystems. Global Biogeochem Cycles 1:163–170

Matson PA, Vitousek PM (1990) Ecosystem approach to a global nitrous oxide budget. BioScience 40:667–672

Matson PA, Vitousek PM, Ewel JJ, Mazzarino MJ, Robertson GP (1987) Nitrogen transformations following tropical forest felling and burning on a volcanic soil. Ecology 68:491–502

Matson PA, Vitousek PM, Livingston GP, Swanberg NA (1990) Sources and variation of nitrous oxide flux from Amazonian ecosystems. J Geophys Res 95:16789–16798

McClain ME, Richey JE, Pimentel TP (1994) Groundwater nitrogen dynamics at the terrestrial-lotic interface of a small catchment in the central Amazon Basin. Biogeochem 27:113–127

McElroy MB, Wofsy SC (1986) Tropical forests: interactions with the atmosphere. In: Prance GT (ed) Tropical rain forests and the world atmosphere. Westview, Boulder, pp 33–60

Montagnini F, Buschbacher RJ (1989) Nitrification rates in two undisturbed tropical rain forests and three slash-and-burn sites of the Venezuelan Amazon. Biotropica 21:9–14

Moraes JFL, Cerri CC, Melillo JM, Kicklighter D, Neill C, Skole DL, Steudler PA (1995) Soil carbon stocks of the Brazilian Amazon basin. Soil Sci Soc Am J 59:244–247

Moraes JFL, Volkoff B, Cerri CC, Bernoux M (1996) Soil properties under Amazon forest and changes due to pasture installation in Rondônia/Brazil. Geoderma 70:63–81

Nadelhoffer KJ, Aber JD, Melillo JM (1983) Leaf-litter production and soil organic matter dynamics along a nitrogen-availability gradient in southern Wisconsin (USA). Can J For Res 13:12–21

Neill C, Piccolo MC, Steudler PA, Melillo JM, Feigl BJ, Cerri CC (1995) Nitrogen dynamics in soils of forests and active pastures in the western Brazilian Amazon Basin. Soil Biol Biochem 27:1167–1175

Neill C, Fry B, Melillo JM, Steudler PA, Moraes JFL, Cerri CC (1996) Forest- and pasture-derived carbon contributions to carbon stocks and microbial respiration of tropical pasture soils. Oecologia 107:113–119

Pastor J, Aber JD, McClaugherty CA, Melillo JM (1984) Aboveground production and N and P cycling along a nitrogen mineralization gradient on Blackhawk Island, Wisconsin. Ecology 65:256–268

Piccolo MC (1989) Dinámica do nitrogênio incorporado na forma orgánica em solos de várzea e terra firma na Amazônica central. MS Thesis, Centro de Energia Nuclear na Agricultura, University of São Paulo, Piracicaba

Piccolo MC, Neill C, Cerri CC (1994) Net nitrogen mineralization and net nitrification along a tropical forest-to-pasture chronosequence. Plant Soil 162:61–70

Pires JM, Prance GT (1986) The vegetation types of the Brazilian Amazon. In: Prance GT, Lovejoy TM (eds) Key environments: Amazonia. Pergamon, Oxford, pp 109–129

Projeto Radambrasil (1978) Folha SC-20, Porto Velho. Departamento Nacional de Produção Mineral (DNPM). Levantamento de Recursos Naturais, Rio de Janeiro

Reiners WA, Bouwman AF, Parsons WFJ, Keller M (1994) Tropical rainforest conversion to pasture: changes in vegetation and soil properties. Ecol Appl 4:363–377

Richter DD, Babbar LI (1991) Soil diversity in the tropics. Adv Ecol Res 21:315–389

Robertson GP (1984) Nitrification and nitrogen mineralization in a lowland rainforest succession in Costa Rica, Central America. Oecologia 61:99–104

Ruzicka J, Hansen EH (1981) Flow injection analyses. Wiley, New York

Sanchez PA, Logan TJ (1992) Myths and science about the chemistry and fertility of soils in the tropics. In: Lal R, Sanchez PA (eds) Myths and science of soils of the tropics (SSA special publication 29). American Society of Agronomy, Madison, Wisconsin, pp 35–46

SAS (1987) SAS/STAT guide for personal computers, version 6 ed. SAS Institute, Cary, North Carolina

Serrão EAS, Falesi IC, Veiga JB da, Teixeira Neto JB (1979) Productivity of cultivated pastures on low fertility soils of the Amazon of Brazil. In: Sanchez PA, Tergas LE (eds) Pasture production in acid soils of the tropics. Centro International de Agricultura Tropical, Cali, Colombia, pp 195–226

Skole DS, Tucker C (1993) Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. Science 260:1905–1910

Skole DS, Chomentowski W, Salas WA, Nobre AD (1994) Physical and human dimensions of deforestation in Amazonia. BioScience 44:314–322

Steudler PA, Melillo JM, Bowden RD, Castro MS, Lugo AE (1991) The effect of natural and human disturbances on soil nitrogen dynamics and trace gas fluxes in a Puerto Rican wet forest. Biotropica 23:356–363

SUDAM (Superintendência do Desenvolvimento da Amazônia) (1984) Projeto de Hidrologia e Climatologia da Amazônia. Ministério do Interior, Belém

Trumbore SE, Davidson EA, Camargo PB de, Nepstad DC, Martinelli LA (1995) Below-ground cycling of carbon in forests and pastures of eastern Amazonia. Global Biogeochem Cycles 9:515–528

Vitousek PM, Denslow JS (1987) Nitrogen and phosphorus availability in treefall gaps of a lowland tropical rainforest. J Ecol 74:1167–1178

Vitousek PM, Matson PA (1985) Disturbance, nitrogen availability and nitrogen losses in an intensively managed loblolly pine plantation. Ecology 66:1360–1376

Vitousek PM, Matson PA (1988) Nitrogen transformations in a range of tropical forest soils. Soil Biol Biochem 20:361–367

Vitousek PM, Melillo JM (1979) Nitrate losses from disturbed ecosystems: patterns and mechanisms. For Sci 25:605–619

Vitousek PM, Sanford RL Jr (1986) Nutrient cycling in moist tropical forest. Annu Rev Ecol Syst 17:137–167