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NUTRIENT LOSS AND REDISTRIBUTION AFTER FOREST CLEARING ON A HIGHLY WEATHERED SOIL IN AMAZONIA

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Abstract. Over the past three decades, tropical forest clearing and burning have greatly altered the Amazonian landscape by increasing the cover of pastures and secondary forests. The alteration of biogeochemical processes on these lands is of particular interest on highly weathered Oxisols that cover large areas in the region because of concerns regarding possible nutrient limitation in agricultural land uses and during forest regrowth. The objectives of this study were to quantify (1) the reaccumulation of nutrients in biomass of secondary land uses, (2) changes in soil nutrient contents, (3) internal nutrient cycles, and (4) input–output budgets for the landscape mosaic.

Nutrient stocks and fluxes were quantified from 1996 to 1998 in mature forest, 19-yr-old secondary forest, degraded pastureland, and managed pastureland in the Brazilian state of Pará. Mature forests contain 130 Mg C/ha in aboveground biomass while secondary forest, degraded pasture, and managed pasture contain 34, 4, and 3 Mg C/ha, respectively. Reaccumulation of N, P, K, Ca, and Mg in aboveground biomass of secondary forest was 20%, 21%, 42%, 50%, and 27% of that present in mature forest, while degraded pasture contained 2%, 4%, 15%, 11%, and 6%. Managed pasture had similar accumulations as degraded pasture except for Ca (3%).

Changes in soil stocks of C, N, and P were not detected among land uses, except in fertilized managed pastures, where total soil P (0–10 cm) was elevated. Conversely, Mehlich-III-extractable P of all secondary lands were very low (<1 μg/g) and were 1 kg/ha less than contents (0–10 cm) in mature forest. NaOH-extractable P was present in 100-fold higher concentrations and may gradually contribute to meeting plant demands over decadal time scales. Soil cation contents (0–20 cm) were elevated in secondary lands with increases of ~85, 500, and 75 kg/ha for K, Ca, and Mg, respectively. These increases could account for a substantial portion of cation contents originally in the aboveground biomass of mature forest.

The recycling of nutrients through ~9.0 $Mg \cdot ha^{-1} \cdot yr^{-1}$ of litterfall in secondary forest of 132, 2.8, 32, 106, and 23 $kg \cdot ha^{-1} \cdot yr^{-1}$ for N, P, K, Ca, and Mg, respectively, is similar to mature forest. Nutrient returns in both pasturelands were smaller for all elements except K, which was similar to the forested sites. In these pasture ecosystems, grass turnover has replaced litterfall return as the predominate mechanism of nutrient recycling.

Soil solution fluxes of total N were higher in mature forest (12 $kg \cdot ha^{-1} \cdot yr^{-1}$ at 25 cm depth) compared to secondary lands (<4 $kg \cdot ha^{-1} \cdot yr^{-1}$), indicating that cycling of available forms of N has diminished. Conversely, fluxes of cationic elements appear elevated in secondary lands and are charge balanced in solution by HCO_3^- derived from biological activity in the soil surface. Despite detectable increases in soil cation fluxes, rainwater inputs and stream water outputs of these elements across the watershed were not significantly different.

The aggregate picture for this landscape is one in which the secondary forest, although still of smaller stature and lower in species diversity compared to mature forest, is recuperating important nutrient cycling functions. Conversely, pasturelands, which dominate the landscape, are not only of smaller stature, but are also accumulating and cycling a smaller total mass of nutrients. This ecosystem conversion has released C and N from biomass mostly to the atmosphere and has redistributed K, Ca, and Mg from biomass mostly to the soil. Presently, base cation enriched soils are slowly re-equilibrating to an acidic condition through decadal-scale processes of plant uptake and biogenically driven soil leaching. Our mass balance approach has revealed low soil available N and P, diminished rates of cycling of these elements in secondary lands, and low precipitation inputs of P, which may constrain long-term recuperation of ecosystem carbon.

Key words: *Amazon; land use change; nutrient cycles, soil change; stream water; tropical forests.*

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Introduction

The effects of tropical forest clearing and burning on future forest productivity, forest habitat, soil fertility, and water quality are important issues concerning landscape conversion in the Amazon basin. Rates of tropical forest clearing have increased in recent years (Houghton et al. 2000; Instituto Nacional de Pesquisas Espaciais [INPE] data),[4] and pastures and secondary forests now cover over 15% of the Brazilian Amazon. It was once hypothesized that tropical forest clearing would lead to irreparable nutrient loss and an arrested state of forest succession (Goodland and Irwin 1975). This hypothesis was based on the observation that large-statured tropical forests grow atop highly weathered and generally infertile soils (Whittaker 1975). It was surmised that nutrient elements were stored disproportionately in forest biomass compared to forest soils (Hardy 1936, Milne 1937). Thus, it was believed, if forest nutrients were lost from the ecosystem, the soils would not provide adequate substrate for regeneration. With an increasing amount of information becoming available throughout the Amazon Basin, and the regrowth of young secondary forests apparent on a variety of cut-over lands, some of these fears have been belayed. At the same time, however, nutrient losses after tropical forest clearing have been reported from both fire (Kaufmann et al. 1995) and soil leaching (Uhl and Jordan 1984, Williams and Melack 1997).

Some of the early hypotheses about tropical forest recovery were guided by the misconception that tropical soils were universally acid and infertile. Infertile, clay rich Oxisols are a predominant component of the Amazon basin, but reviews of Vitousek and Sanford (1986), Proctor (1987), and Richter and Babbar (1991) stress the importance of not categorizing tropical forests and tropical soils as a single entity. Prior to adequate soil surveys, it was estimated that >65% of the Amazon basin was covered with Oxisols and that most of these soils would turn to laterite, a brick hard substance, shortly after forest clearing. Currently, it is recognized that only about 40% of the basin is covered with Oxisols (Richter and Babbar 1991) and <7% of these soils can potentially turn to hardened laterite (Sanchez and Logan 1992).

Although widespread laterization is unlikely, research results on the effects of forest clearing on hydrology and nutrient input-output budgets as reviewed by Bruijnzeel (1990, 1991) indicate a sensitivity of certain soil types, namely infertile Oxisols and Spodosols, to significant nutrient losses following forest clearing. Vitousek and Sanford (1986) demonstrated higher nutrient use efficiencies for P and Ca on Oxisols, and Proctor (1987) points out that these same common soil types possess a preponderance of nutrients in aboveground biomass compared to the top 50 cm of soil. Jordan and Herrera (1981) proposed the notion of oligotrophic forest types to distinguish forest and soil ecosystems that possess important nutrient conserving mechanisms that could be lost upon forest disturbance. Thus, although broad stereotypical generalizations concerning tropical forests or tropical soils are inappropriate, concerns regarding infertile Spodosols and highly weathered Oxisols merit continued investigation.

In this research, we investigated changes in ecosystem biogeochemistry including aboveground nutrient stocks, soil chemistry, and nutrient leaching, 28 yr after initial clearing of forests on a Haplustox. Soils in the great group Haplustox are simple or typical Oxisols (i.e., possess no other defining feature) that have an ustic (seasonally dry) soil moisture regime. Based on climatological data for the Amazon region (Marengo et al. 2001) soils in the suborder Ustox probably account for >50% of all Oxisols in the region. The objectives of this study were to (1) assess the reaccumulation of nutrients in biomass of secondary land uses, (2) evaluate changes in soil nutrient concentrations and contents, (3) quantify internal nutrient cycles, and (4) quantify input-output budgets for the landscape mosaic of this study site.

Methods

Research site

The study was carried out at Fazenda Vitoria, an active cattle ranch 6 km north of the town of Paragominas (2°59′ S, 47°31′ W) in the Brazilian state of Pará, in northern Amazonia (Fig. 1). Fazenda Vitoria has been the site of studies on C and N cycling, trace gas emissions, secondary forest succession, water use, and soil faunal activity during the last 16 yr (Bushbacher et al. 1988, Uhl et al. 1988, Nepstad et al. 1994, Davidson and Trumbore 1995, Trumbore et al. 1995, Jipp et al. 1998, Moutinho 1998, de Camargo et al. 1999, Verchot et al. 1999, 2000, Davidson et al. 2000, Markewitz et al. 2001, Nepstad et al. 2001). This area was settled in the early 1960s following the construction of the Belém–Brasilia highway and has become a regional center for logging and ranching (Nepstad et al. 1991). The 3500-ha ranch is a mosaic of primary forest (tropical moist forest according to Tosi et al. 1983), logged forest, secondary forest, and pasture with moderately dissected topography (Fig. 1). The areas that are now in pasture and secondary forest were originally cleared and burned in 1969. After 6–8 yr of pasturing, some of the area was abandoned to fallow. Where fire did not subsequently enter, a secondary forest is now growing. In contrast, accidental fires have frequently entered another area due to proximity to charcoal producing facilities, and this area has therefore remained a degraded pasture site. Some limited grazing has continued in the degraded pasture. A third area, which we call managed pastures, and which tend to be lands bordering streams (Fig. 1), received management inputs such as

[4] ⟨http://www.inpe.br/Informacoes_Eventos⟩

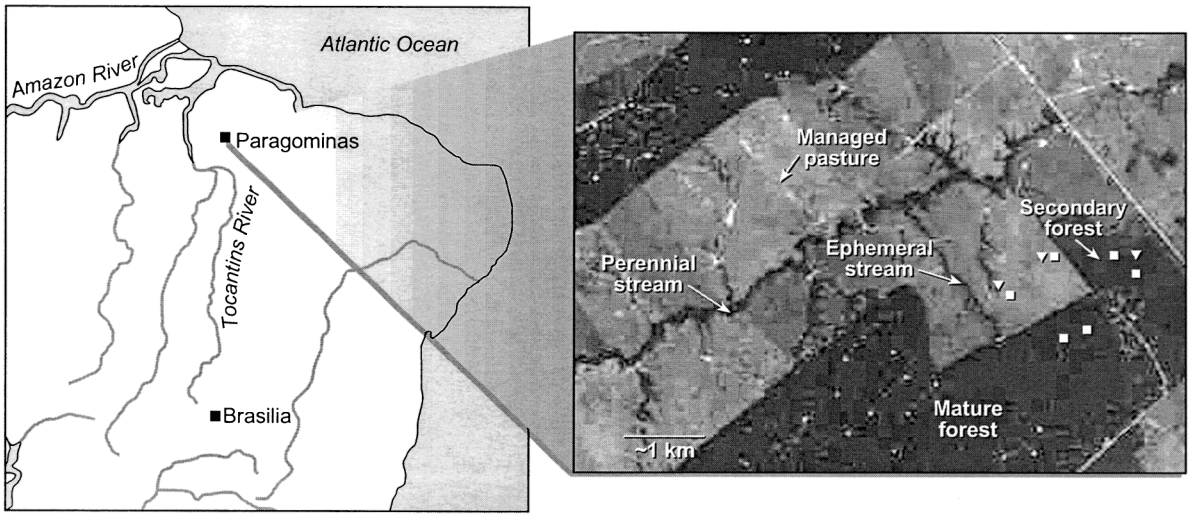

FIG. 1. A 2001 IKONOS image of research sites in Paragominas, Brazil. Squares indicate the location of deep soil shafts used for solution collections, and triangles indicate the location of rainwater collection. The perennial stream (Igarape 54) was sampled for stream water solutions. The sampled degraded pastures are just off the lower right-hand corner of the image.

disking, P fertilization (~50 kg/ha), and planting with an African grass (*Brachiaria brizantha*) in 1987 and has been actively grazed since. At times, we refer to this secondary forest, degraded pasture, and managed pasture collectively as ''secondary lands.''

Rainfall distribution in this region has a strong seasonality with <15% of the total annual precipitation falling between June and November. Average annual precipitation is 1803 ± 555 mm (1972–1994 mean ± 1 SD; Jipp et al. 1998). Soils of this region are deeply weathered Oxisols (Haplustox) derived from the Belterra clay formation that developed on the top and upper slopes of a Pleistocene terrace. Belterra clays consist mainly of kaolinite, with minor fractions of quartz and hematite, and are widespread at elevations below 200 m in the Amazon Basin (Clapperton 1993). These soils are classified as Latasolos Amarelos in the Brazilian classification (Carmargo et al. 1986). In the undisturbed condition, soils of the mature forest have a small O horizon (2–5 cm) that contacts a shallow A horizon (0–20 cm). Carbon contents are elevated in the A horizon (1.9%; Table 1) and clay content is high, 78% by weight (D. C. Nepstad, *unpublished data*). Clay content increases gradually to a peak of 95% at ~50 cm and then gradually decreases to 73% at 8 m. These soils have a slight color discontinuity with the upper 3-m having a reddish yellow color (7.5YR 7/8, Munsell notation; Munsell Color Inc., Baltimore, Maryland, USA) and the lower portions having a red color (10R 5/6). Plinthite has been encountered on portions of the landscape at depths from 2 to 10 m in a general relationship with landscape position (i.e., closer to the surface in lower slope positions). Bulk densities of the profile are quite uniform (1.2–1.3 g/cm^3) with only the upper A horizon (0.9–1.1 g/cm^3) being slightly less dense (Markewitz et al. 2001). Soils are acidic with $pH_w < 5.0$ at all depths. The delta pH (i.e., $pH_w - pH_s$) is positive in all cases, indicating a net negative charge throughout the upper 8.5 m. (The pH_w is the pH measured in deionized water in a 1:2 soil mass to water volume ratio. The pHs is measured in 0.01 mol/L $CaCl_2$ in a 1:2 soil mass to solution volume ratio.) All other components (except total P) decrease in concentration with depth. Total P decreases through the upper 3 m of the profile but then increases to 8 m depth (Table 1).

Aboveground biomass

Biomass estimates for mature forest have been made previously at our site (Buschbacher et al. 1988, Nepstad 1989). To convert biomass to C, we used a factor of 0.5. Nutrient contents of this forest were not measured directly but are estimated using nutrient ratios of other South American humid tropical forests on infertile soils (Table 2). Coefficients of variation (CV) for absolute amounts of C and the macronutrients N, P, K, Ca, and Mg in the nine forests of Table 2 are 21, 30, 32, 44, 55, and 41%, respectively. The CVs of C-to-nutrient ratios are similar: 27, 42, 33, 57, and 58% for C:N, C:P, C:K, C:Ca, and C:Mg, respectively. Using the mean of these reported C-to-nutrient ratios and the biomass estimate for the Paragominas forest from Nepstad (1989), we estimated the stocks of each element for the Paragominas mature forest.

In the secondary forest, biomass estimates were made from inventories of the diameter at breast height (~1.4 m) and height made by W. Stanley (*unpublished data*) and Moutinho (1998). The former work used 12 permanent plots established in 1986 by Chris Uhl, the latter work used a point-quarter method along two

TABLE 1. Soil chemical and physical parameters (mean ± 1 SD) for a Haplustox under mature forest in Paragominas, Brazil, 1996.

Soil depth (cm)	C (g/kg)	N (g/kg)	Total P (μg/g)	Mehlich III P (μg/g)	pH_w	Exchangeable acidity (1×10^{-2} mol_c/kg)
0–10	23.9 ± 0.6	2.19 ± 0.07	189 ± 2	1.6 ± 0.2	4.35 ± 0.13	0.81 ± 0.35
10–20	14.3 ± 0.7	1.33 ± 0.01	177 ± 3	0.6 ± 0.2	4.27 ± 0.03	1.14 ± 0.33
20–50	9.5 ± 0.1	0.83 ± 0.05	157 ± 1	0.2 ± 0.0	4.37 ± 0.28	0.89 ± 0.29
50–100	5.2 ± 0.2	0.46 ± 0.00	146 ± 9	0.1 ± 0.0	4.74 ± 0.05	0.64 ± 0.05
100–200	3.0 ± 0.4	0.26 ± 0.01	137 ± 5	0.1 ± 0.1	4.80 ± 0.16	0.30 ± 0.10
200–300	2.2 ± 0.4	0.19 ± 0.01	130 ± 15	0.2 ± 0.0	4.85 ± 0.06	0.17 ± 0.02
300–400	1.3 ± 0.3	0.11 ± 0.01	147 ± 6	0.1 ± 0.0	4.73 ± 0.02	0.11 ± 0.06
400–500	1.1 ± 0.1	0.09 ± 0.02	157 ± 20	0.2 ± 0.2	4.79 ± 0.11	0.11 ± 0.00
500–600	1.2 ± 0.1	0.10 ± 0.00	153 ± 38	0.2 ± 0.2	4.73 ± 0.03	0.14 ± 0.02
725–750	1.0 ± 0.3	0.07 ± 0.00	181 ± 28	0.1 ± 0.2	4.68 ± 0.15	0.09 ± 0.06
825–850	1.0 ± ND	0.08 ± 0.ND	174 ± ND	0.1 ± ND	4.64 ± ND	0.17 ± ND
Plinthite	0.4	0.01	112	0.23	5.40	ND

Notes: Soils are an integrated collection through the sampling layers up to 600 cm. The 725- and 825-cm samples were collected by augering >1.5 m into the sidewall of a soil shaft. Upper 0–20 cm samples are composite samples from transects ($N = 3$). Samples below 20 cm are average values of two auger holes. Plinthite is a single sample (pulverized for analysis) from 8 m depth in nearby secondary forest. Bulk density, pH, and exchangeable cation data were reported previously in Markewitz et al. (2001). ND, no data available.

† Total soil cation exchange capacity.

‡ Nonexchangeable = cations removed during soil digestion with H_2SO_4/H_2O_2 minus exchangeable cations.

200-m transects. Biomass was estimated using allometric equations derived for this same forest when it was 8-yr-old (Uhl et al. 1988), as well as two allometric equations developed during the current study for the species with the largest diameters (*Inga heterophylla Willd.* and *Ocotea glomerata* (*Nees*) *Mez.*). Based on these estimates, 11 tree species accounted for 83% of the forest biomass. We used these 11 species to estimate nutrient stocks based on foliage, branch, stem wood, and stem bark nutrient concentrations ($n = 4$–7 trees per species). The estimated nutrient contents of these species were multiplied by 1.20 (=1/0.83) to approximate the nutrient contents of all tree biomass. Understory components of the secondary forest were estimated by complete harvest of four 2 × 2 m plots.

Vegetation within the pastures was estimated by complete harvest. In the degraded pasture, where grasslands were relative evenly dispersed among regenerating tree islands, three randomly located plots of 3 × 3 m were manually cleared within each vegetation type. Biomass components were separated into foliage, live wood, dead wood, grasses, and forbes for measurements of wet-to-dry mass corrections and chemical analysis. For the managed pasture, four 2 × 2 m randomly located plots were cleared in 1996 in the late part of the rainy season (April) in areas that had not been recently grazed. Biomass was weighed in the field using a suspended spring-loaded scale, and a subsample composed of live and dead grasses was taken for moisture correction and nutrient analysis. An additional three plots were harvested in April/May of both 1997 and 1998 for further biomass estimates.

The internal cycling of litterfall biomass was determined in mature and secondary forest, and in degraded pasture within and next to tree islands. Fine litterfall (foliage, fruits, and twigs <1 cm in diameter) was collected in four litterfall traps of ~0.5 m^2 per land use. Collections were made once every month during the dry season (July 1997 to December 1997) and once every two weeks during the wet season (January 1998 to June 1998). Litterfall traps were randomly relocated quarterly. Collections were oven dried at 65°C for 48 h, separated into foliage, twigs, and miscellaneous fractions (i.e., fruits), weighed, and analyzed for macronutrients.

All biomass components were oven dried and ground in a Wiley mill with a 1 mm (40 mesh) screen. Samples were digested following Parkinson and Allen (1975). Total N and P were analyzed by ammonium salicylate and phosphomolybdate chemistries, respectively. Ca, Mg, and K were determined by atomic absorption spectrophotometry after the addition of $LaCl_3$.

Soils

Soil O horizon was sampled along three 200-m transects in each land use. Three to five collections were made using a 25 × 25 cm wood frame and the samples from each transect were composited for analysis ($n = 3$ per land use). Upper 0–10 and 10–20 cm mineral soils were collected along similar transects ($n = 3$). A stainless steel corer with a serrated edge was used to cut through the soil; this allowed extraction of discrete soil layers while minimizing compaction and interlayer contamination. To estimate soil nutrient stocks in this upper soil layer contents were normalized to an equal mass basis among land uses (Davidson and Ackerman 1993, Veldkamp 1994). This normalization assumes that any bulk density increases observed in pastures are due to compaction by cattle trampling, but erosional loss of a less dense surface layer could produce a sim-

TABLE 1. Extended.

Base saturation (%)	Total acidity (1×10^{-2} mol_c/kg)	CEC† (1×10^{-2} mol_c/kg)	Nonexchangeable‡ (1×10^{-2} mol_c/kg)		
			Ca	Mg	K
69.3	13.8 ± 1.0	15.8 ± 1.4	0.67 ± 0.14	0.48 ± 0.10	0.35 ± 0.02
39.0	11.3 ± 0.2	12.0 ± 0.2	0.35 ± 0.22	0.67 ± 0.34	0.37 ± 0.06
34.9	8.2 ± 0.1	8.7 ± 0.3	0.22 ± 0.12	0.65 ± 0.07	0.33 ± 0.02
25.5	6.8 ± 1.2	7.0 ± 1.1	0.21 ± 0.11	0.52 ± 0.14	0.34 ± 0.02
43.2	6.7 ± 0.4	6.9 ± 0.6	0.13 ± 0.01	0.36 ± 0.08	0.27 ± 0.05
43.2	6.4 ± 0.0	6.5 ± 0.2	0.15 ± 0.02	0.25 ± 0.07	0.24 ± 0.00
37.6	5.9 ± 0.7	5.9 ± 0.8	0.17 ± 0.06	0.26 ± 0.03	0.18 ± 0.05
27.7	5.4 ± 0.3	5.4 ± 0.3	0.21 ± 0.10	0.31 ± 0.08	0.16 ± 0.00
16.7	5.6 ± 0.1	5.6 ± 0.1	0.17 ± 0.01	0.32 ± 0.04	0.16 ± 0.01
23.5	6.2 ± 0.7	6.2 ± 0.6	0.15 ± 0.02	0.28 ± 0.14	0.16 ± 0.03
11.2	7.0 ± ND	7.0 ± ND	0.15 ± ND	0.29 ± ND	0.18 ± ND
	4.10	4.16	0.02	0.10	0.01

ilar bulk density difference. If erosional loss is in fact responsible for the measured change in bulk density, then we have underestimated nutrient losses. Soils were air dried and sieved through a 2-mm screen prior to analysis. Charcoal was present sporadically in the sieved material; we did not quantify the contribution of this material to soil C stocks. Analyses included soil pH in water and 0.01 mol/L $CaCl_2$ in a 1:2 soil mass to solution volume ratio (m/v); Mehlich-III exchangeable cations and P in a 1:10 m/v (Tran and Simard 1993); 1 mol/L KCl exchangeable acidity in a 1:10 m/v (Thomas 1982); BaCl in a triethanolamine buffer for total titratable acidity (Thomas 1982); total C and N with a Perkin-Elmer CHN analyzer (Perkin-Elmer, Shelton, Connecticut, USA) on pulverized samples; total P in mineral soil and total N, P, and cations in the O horizon by H_2SO_4-H_2O_2 digest (Parkinson and Allen 1975). In addition, a NaOH extract following the methods of Tiessen and Moir (1993) was preformed on all surface samples and on the deep profile samples of mature forest and managed pasture soils. Differences in soil concentrations were tested with a one-way ANOVA using land uses as a main effect.

Solution collection

Solutions were collected from May 1996 to May 1998. Bulk precipitation was collected 1.5 m from the soil surface using 16-cm funnels placed at three locations within the 280-ha study area (Fig. 1). Vegetation was periodically cut to maintain a sufficient opening. All bulk precipitation funnels fed through looped tubing to restrict evaporation (Likens and Bor-

TABLE 2. Estimates of nutrient contents in aboveground biomass in mature Amazonian forest ecosystems on soils of the Ultisol and Oxisol orders within the Amazon basin.

Location	C (Mg/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)	Reference
A) Measured nutrients from previous studies							
Brazil							
Jacunda, Para	146	1400	62	550	900		Kaufman et al. (1995)
Maraba, Para	217	2300	88	940	1280		Kaufman et al. (1995)
Santa Barbara, Rondonia	145	2020	55	400	330		Kaufman et al. (1995)
Jamari, Rondonia	181	2400	62	520	940		Kaufman et al. (1995)
Manaus	212	1375	30	324	359	194	Fernandes et al. (1997)
Amazonas	218	2724	62	442	445	219	Klinge (1976)
Columbia							
Magdalena	119	1413	45	309	526	161	Folster et al. (1976)
Magdalena	189	1650	54	419	899	250	Folster et al. (1976)
Venezuela							
San Carlos	145	1182	34	257	216	60	Uhl and Jordan (1984)
Mean (± 1 SD)	175 (37)	1829 (548)	55 (17)	462 (203)	655 (360)	177 (73)	
B) Paragominas							
Measured†	130						
Estimated‡		1368	41	343	487	131	

† Aboveground biomass content is from Nepstad (1989).
‡ Estimates are based on the Paragomas C contents and on mean nutrient ratios from previous studies in panel (A). Nutrient ratios are as follows: C:N = 95, C:P = 3181, C:K = 379, C:Ca = 267, C:Mg = 989.

TABLE 3. Carbon and nutrient contents (mean ± 1 SD) for aboveground components for contrasting land uses in Paragomians, Brazil, 1997.

Land use type and component	C† (Mg/ha)	N (kg/ha)	P (kg/ha)	K (kg/ha)	Ca (kg/ha)	Mg (kg/ha)
Mature forest (see Table 1)						
total	130	1370	41	343	487	131
Secondary forest‡						
foliage	2.54 ± 0.64	74.9 ± 25.1	2.6 ± 1.0	26.6 ± 8.2	29.0 ± 10.3	6.7 ± 2.2
fine branches	1.61 ± 0.45	17.9 ± 9.9	0.9 ± 0.4	14.0 ± 6.6	22.7 ± 11.2	2.6 ± 1.1
coarse branches	7.07 ± 4.86	60.2 ± 101.5	2.1 ± 3.7	34.5 ± 48.9	59.0 ± 71.6	7.3 ± 5.9
wood/bark	21.3 ± 12.7	105.5 ± 101.7	2.7 ± 2.7	60.8 ± 47.8	116.6 ± 62.5	15.4 ± 4.0
understory foliage	0.23 ± 0.11	7.2 ± 3.8	0.2 ± 0.1	3.7 ± 1.6	5.8 ± 3.5	1.3 ± 0.7
understory twigs	0.75 ± 0.25	6.8 ± 1.7	0.3 ± 0.1	6.0 ± 1.5	10.6 ± 5.5	1.5 ± 0.9
total‡	33.5 ± 19.0	273 ± 244	8.8 ± 8.0	146 ± 115	244 ± 165	35 ± 15
Degraded pasture§						
foliage	0.21 ± 0.05	7.6 ± 3.4	0.3 ± 0.1	4.3 ± 2.2	6.3 ± 1.6	1.2 ± 0.4
wood/bark	0.77 ± 0.88	5.0 ± 5.6	0.3 ± 0.3	7.1 ± 10.3	7.9 ± 9.2	1.1 ± 1.3
standing dead wood	0.77 ± 0.87	4.7 ± 5.6	0.2 ± 0.2	2.1 ± 2.2	28.3 ± 42.6	0.7 ± 0.7
vines	0.39 ± 0.31	4.3 ± 3.0	0.2 ± 0.1	3.0 ± 1.8	3.3 ± 2.7	0.5 ± 0.2
grasses/forbes	1.78 ± 0.48	13.3 ± 4.2	0.9 ± 0.3	38.3 ± 10.5	5.8 ± 1.8	3.3 ± 0.9
total	3.91 ± 2.59	34.8 ± 21.8	1.9 ± 1.0	54.9 ± 26.8	51.5 ± 58.0	6.8 ± 3.5
Managed pasture‖						
grasses	2.70 ± 0.7	20.4 ± 5.4	1.4 ± 0.4	50.7 ± 13.4	12.7 ± 3.4	10.1 ± 2.7

† Carbon is estimated as 50% of biomass.

‡ Carbon contents are estimated from dbh of all tree species. Nutrient contents are based on 11 tree species that account for 83% of biomass; thus these values were augmented by 20.4% to estimate nutrient contents for 100% of the biomass.

§ Secondary forest and degraded pasture were first cleared in 1969, and abandoned from grazing in 1976.

‖ Managed pastures were first cleared in 1969, were grazed at varying intensities through 1987, and were then tilled, fertilized, and planted to *Brachiaria brizantha* prior to continued grazing.

mann 1995) and collection bottles were shielded from direct sunlight with small housings. Volume-weighted mean annual element concentrations and inputs were estimated for each collector. The average of the three precipitation collectors was then used to describe deposition inputs to all land uses. Within each land use, two deep (6–8 m) soil pits that had been randomly located and dug for previous studies of deep rooting and soil water use (Nepstad et al. 1994) were selected as the centers of solution collection plots (Fig. 1). In addition, for O horizon and 25-cm solution collections, two new small pits were randomly located and dug <10 m distant from the main pit to avoid areas previously disturbed by foot traffic. Each small pit consisted of a 25×9 cm PVC trough for throughfall collection, a 30×7 cm PVC trough placed below the O horizon for leachates, a 25×10 cm trough placed horizontally into the soil for 25-cm deep zero tension solutions, and one Prenart superquartz lysimeter (Prenart Equipment ApS, Frederiksberg, Denmark) also at 25 cm depth for tension solutions. The large pits all contained a set of collectors at 3 m and a second set at 6–8 m depending on pit depth. Each collection depth contained two 1 m $\times$ 10 cm PVC troughs placed horizontally for zero tension solutions and one Prenart lysimeter for tension solutions. Throughfall collectors contained evaporation loops and were spray painted silver while all samplers at the litter layer or below were placed within the relatively constant temperature environment of the pits. All tension lysimeters were placed under a vacuum of 0.06 MPa on a weekly basis. Water samples were also collected from Igarape 54, a stream draining Fazenda Vitoria (Markewitz et al. 2001).

Solutions within the above samplers were collected once every two weeks. All funnels, troughs, and bottles were rinsed with deionized water after collection. If any excessive algae or insect contamination was apparent, collectors were returned to the laboratory for acid washing. During collection, sample volume was measured and a subsample transferred to a previously acid-washed (1 mol/L HCl) polypropylene bottle. Samples were returned to a field laboratory in Paragominas, and within 48 h, were filtered through 0.4-μm polycarbonate filters (Nucleopore, Cambridge, Massachusetts, USA) and measured for conductivity, pH, and alkalinity. Alkalinity determinations were by endpoint titrations with 1 mmol/L HCl to pH 4.5 (Clesceri et al. 1998).

All samples were analyzed for dissolved organic carbon (Shimadzu TOC 5000, Columbia, Maryland, USA), total N, and total P following persulfate digestion (Koroleff 1983); PO_4 by the Murphy-Riley method (Clesceri et al. 1998); NH_4 by the Berthelot method (Clesceri et al. 1998); Cl, SO_4, and NO_3 by ion chromatography (Dionex DX 500, Sunnyvale, California, USA); and Ca, Mg, K, and Na by atomic absorption spectrophotometry after addition of $LaCl_3$. Standard solutions (Environmental Research Associates, Ar-

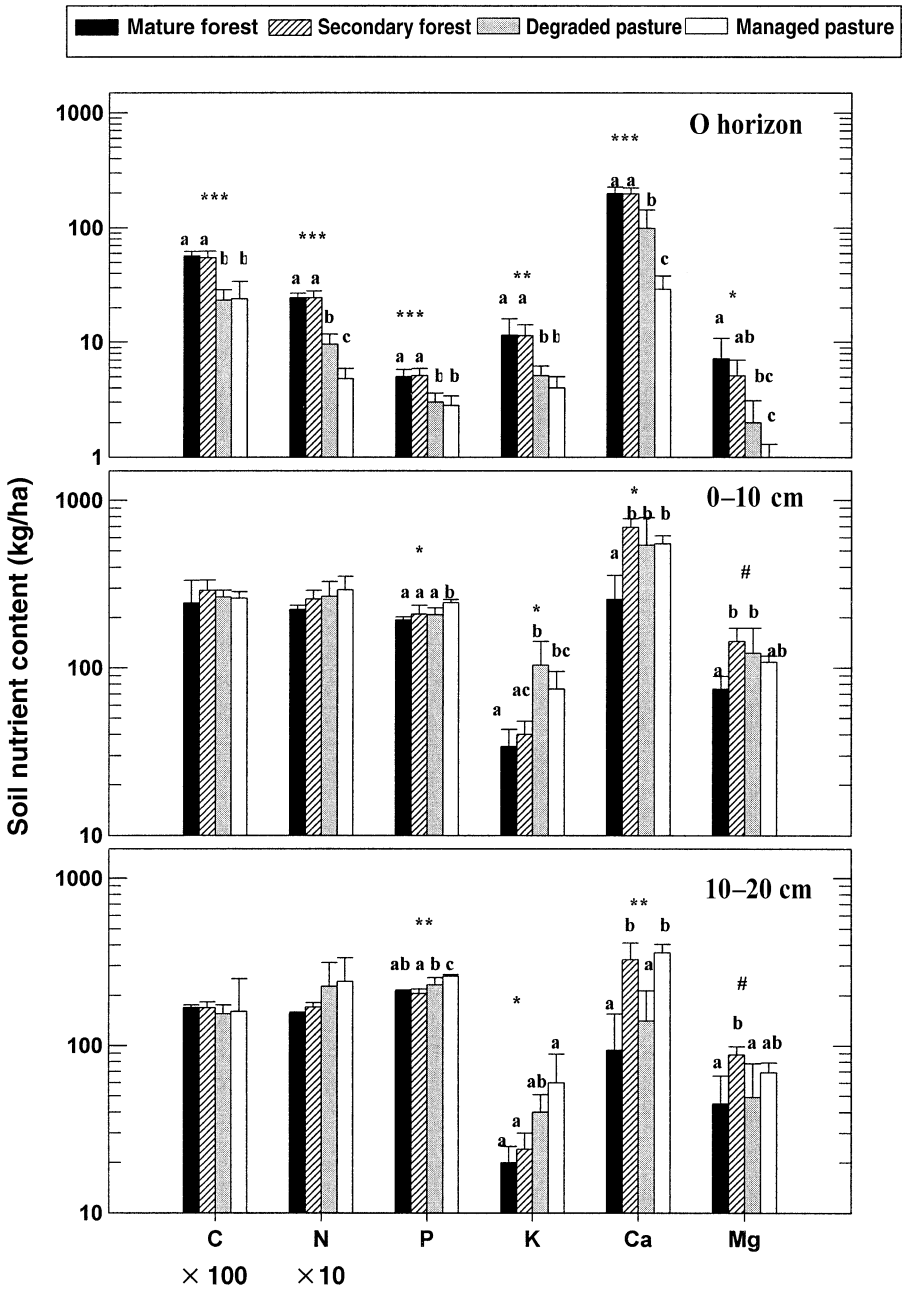

FIG. 2. Nutrient contents in O horizon and upper 20 cm of mineral soils (mean + 1 SD) for contrasting land uses in Paragominas, Brazil. Mineral soil contents in pasture are corrected for bulk density increases due to compaction. Soils were collected in 1996. Differences at the 0.1, 0.05, 0.01, and 0.001 level of significance are indicated by #, *, **, and ***, respectively; these results are from a one-way ANOVA with land use as the treatment and $N = 3$ per treatment). Different letters indicate significant differences from post hoc tests using Tukey's honestly significant difference ($P < 0.05$).

vada, Colorado, USA) were used with all analyses to maintain quality assurance and to minimize analytical bias through time. Differences in solution concentrations were tested with a one-way ANOVA using land use as a main effect. The 2 yr of volume-weighted mean concentrations were treated as the measurement unit of interest, with $n = 2$ for all land uses. In the case of total P, only one year of measurements was available.

To estimate nutrient fluxes in solution, element concentrations were multiplied by the hydrologic flux of water. Precipitation volume was estimated from our three solution collectors as well as three additional volume collectors that were measured on a daily basis. Throughfall and litter leachate fluxes were estimated from the volumes collected in our PVC troughs. The flux of water through the upper soil horizon was es-

TABLE 4. Soil chemical and physical parameters (mean ± 1 SD) for surface soils from contrasting land uses in Paragominas, Brazil.

Land use	C (g/kg)	N (g/kg)	P (μg/g)	pH_w†
A) Soil depth 0–10 cm				
Mature forest	24.0 ± 0.6	2.19 ± 0.07	189 ± 2[a]	4.35 ± 0.13[a]
Secondary forest	29.0 ± 6.8	2.57 ± 0.60	209 ± 12[ab]	5.47 ± 0.10[b]
Degraded pasture	26.3 ± 2.5	2.66 ± 0.57	207 ± 22[ab]	5.40 ± 0.43[b]
Managed pasture	25.5 ± 2.6	2.87 ± 0.58	240 ± 12[b]	5.71 ± 0.13[b]
B) Soil depth 10–20 cm				
Mature forest	14.3 ± 0.7	1.33 ± 0.01	180 ± 3[a]	4.27 ± 0.03[a]
Secondary forest	14.8 ± 1.8	1.50 ± 0.14	181 ± 6[a]	4.95 ± 0.15[b]
Degraded pasture	12.6 ± 1.3	1.84 ± 0.65	188 ± 12[a]	4.61 ± 0.30[c]
Managed pasture	12.9 ± 0.7	1.95 ± 0.75	209 ± 4[b]	5.39 ± 0.09[d]

Notes: Different superscript letters indicate significant differences by post hoc tests using Tukey's honestly significant difference for ANOVAs with $P < 0.05$. Bulk density, pH, and exchangeable cation data were reported previously in Markewitz et al. (2001).

† Soil pH is in deionized water (pH_w) in a 1:2 weight-to-volume ratio.

‡ ECEC is cation exchange capacity by the sum of cations methods.

§ CEC is cation exchange capacity by the sum of cations method using total acidity.

timated using the volumetric water content data measured by time domain reflectometry of Jipp et al. (1998). In their work, the removal of plant available water from a depth interval of 0–2 m was estimated from 1991 to 1994. In this horizon, we weighted water removal by root biomass to estimate uptake from 0.25 m (Nepstad et al. 1994). In the lower horizons, 300 and 700 cm, no estimate of nutrient flux was attempted. Estimation of stream water fluxes was described in Markewitz et al. (2001).

The uncertainties in estimating solution input–output budgets for large watersheds are considerable. This uncertainty is due in part to the propagation of errors to obtain an estimate and also in part to the absence of quantification for particular components (i.e., storm flow). To quantify these errors we used a reduced form of an error propagation equation (Lesack 1993):

$$S_y = (V^2 S^2_{cvm} + C^2_{vm} S^2_v)^{1/2}$$

where V is the volume of solution, C is the volume-weighted mean concentration, and S^2 is the associated variance of the estimates (i.e., S^2_v for volume and S^2_{cvm} for concentration). This reduced form of the equation assumes that the errors of the associated variances are independent and random, and thus no covariance term is required.

This error propagation for element inputs incorporated variation in rainfall volume (~4%), solute concentrations (~1–26%), and interannual variability (~10–300%). For element outputs the error propagation included stream water discharge (10%), stream water concentration (~1% as estimated by a bootstrap analysis with replacement [Schreuder et al. 1993]), watershed area (~10%), and interannual variability (~15%). This error analysis indicates that estimates for rainfall inputs (±10%) and stream water outputs (±16%) might only be considered significant if they differ >30%. We have used this as a guide in the following results and discussion of input-output budgets.

RESULTS AND DISCUSSION

Biogeochemical patterns and processes

To assess changes in the biogeochemical cycles of the contrasting landscapes, we used a mass balance approach in which we evaluated both nutrient stocks and nutrient fluxes. We first compare the content of elements in mature forest biomass (Table 2) to those in smaller stature secondary land biomass (Table 3) to estimate loss of aboveground nutrient storage during conversion of mature forest. Using this change in aboveground biomass storage as an upper bound on potential nutrient inputs to the soil caused by forest clearing and burning, we evaluate changes in surficial (0–20 cm) soil nutrient contents (Table 4 and Fig. 2). Observed differences in soil content and concentration data are then compared to litterfall flux (Table 5) and solution nutrient concentrations and fluxes for the differing land uses (Tables 6 and 7, and Fig. 3) to assess internal cycling processes. Finally, we endeavor to present an integrated biogeochemical picture across these four land uses by combining the above data with chemical concentration data in stream water drainage (Figs. 4–6).

Carbon

Much recent tropical landscape biogeochemistry has focused on the effect of forest clearing on C budgets (Houghton et al. 2000). The aboveground biomass in the mature forest at this site was estimated to contain 130 Mg/ha of C (Table 2). The secondary forest at this site that is less than half the height of the 35 m tall primary forest canopy and possesses a smaller number of tree species, 82 species (W. Stanley and C. Uhl, *unpublished data*) compared to the 171 species found

TABLE 4. Extended.

Exchangeable acidity ($cmol_c$/kg)	ECEC ($cmol_c$/kg)‡	Total acidity ($cmol_c$/kg)	CEC ($cmol_c$/kg)§
0.81 ± 0.35a	2.80 ± 0.22	13.8 ± 1.0	15.8 ± 1.4
0.11 ± 0.04b	4.88 ± 0.83	12.3 ± 2.8	17.1 ± 3.6
0.24 ± 0.27b	4.25 ± 1.40	13.0 ± 0.9	17.0 ± 0.8
0.08 ± 0.02b	3.86 ± 0.35	11.4 ± 1.7	15.2 ± 1.9
1.14 ± 0.32a	1.93 ± 0.10	11.3 ± 0.2a	12.0 ± 0.2a
0.35 ± 0.10bc	2.50 ± 0.38	9.2 ± 0.5bc	11.3 ± 1.0a
0.96 ± 0.47ab	1.98 ± 0.59	10.6 ± 0.5ab	11.6 ± 1.0a
0.13 ± 0.01c	2.20 ± 0.29	8.0 ± 0.8b	10.1 ± 0.7b

by Nepstad (1989) in the primary forest has reaccumulated ~26% of the mature forest C as aboveground biomass (i.e., 33.5 ± 19.0 Mg C/ha [mean ± 1 SD]) since pasture abandonment (Table 3). For a 19-yr-old forest, these rates of average annual accumulation are modest, 1.8 Mg $C \cdot ha^{-1} \cdot yr^{-1}$. The recovery of forest biomass on a variety of soils has been measured across Amazonia and range between 0.3 and 9.6 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ (Uhl and Jordan 1984, Buschbacher et al. 1988, Sanchez et al. 1989, Szott 1989, Vierra et al. 1996, Johnson et al. 2001). Rates of reaccumulation can be affected by previous land use history (Buschbacher et al. 1988, Nepstad et al. 1996) and possibly by nutrient limitation as investigated here.

The 19-yr-old degraded pasture has accumulated only 7.8 ± 5.2 Mg/ha of biomass (Table 3). Tree islands within the degraded pasture share some species with secondary forest but trees are of smaller stature, <8 m in height. The predominant grass species is *Brachiaria humidicola*. Carbon accumulated in the degraded pasture biomass accounts for <4% of the original forest C. The small biomass accumulation and large variability in degraded pasture is partly attributable to repeated fire observed within different portions of the degraded pasture in 1995, 1996, and 1997, and thus there is currently a large contribution of standing dead wood to aboveground C content of ~20%. Biomass estimates for this site in 1994 were 27.6 ± 16.8 Mg/ha (D. C. Nepstad, *unpublished data*), but repeated fire continues to set back this accumulation.

In comparison to the degraded pastures, the managed pastures of our research site are productive systems when properly fertilized (Dias-Filho and Serrão 1987, Dias-Filho et al. 2001). Managed pastures, which are relatively homogeneous fields with a small percentage of woody species, had aboveground biomass averaged over three consecutive years (1996–1998) of 5.4 ± 1.4 Mg/ha. Regardless of the managed pasture productivity, these grass dominated systems that lack a woody component will likely never reclaim a substantial portion of the original aboveground C stored in mature forests.

The above data indicate large losses of aboveground biomass C. Changes in soil C stocks that accompany

TABLE 5. Fine litterfall return (mean ± 1 SD) to contrasting land uses in Paragominas, Brazil, 1997–1998.

Land use and component	Biomass (Mg/ha)	Litter nutrients ($kg \cdot ha^{-1} \cdot yr^{-1}$)				
		N	P	K	Ca	Mg
Mature forest						
foliage	6.1 ± 1.3	95.2 ± 18.5	1.9 ± 0.5	23.0 ± 7.2	66.8 ± 11.8	16.8 ± 3.8
twig	2.5 ± 1.1	26.3 ± 8.4	0.5 ± 0.2	4.0 ± 1.9	30.7 ± 13.3	3.6 ± 0.5
misc.	1.7 ± 1.2	21.4 ± 8.0	0.8 ± 0.4	8.4 ± 6.3	12.3 ± 7.0	2.6 ± 1.2
total	10.3 ± 3.6	143 ± 35	3.3 ± 1.0	35.4 ± 15.4	109 ± 32	23.0 ± 5.5
Secondary forest						
foliage	6.3 ± 1.0	74.7 ± 13.0	1.7 ± 0.4	27.2 ± 6.9	70.2 ± 10.1	13.2 ± 2.8
twig	1.6 ± 1.0	13.5 ± 7.6	0.3 ± 0.2	3.4 ± 1.6	19.6 ± 11.7	2.6 ± 2.0
misc.	1.0 ± 0.4	16.0 ± 5.1	0.8 ± 0.3	7.7 ± 4.7	8.2 ± 3.2	2.0 ± 0.6
total	8.9 ± 2.4	104 ± 26	2.8 ± 0.9	38.3 ± 13.2	98.0 ± 25.0	17.8 ± 5.4
Degraded pasture						
foliage	1.9 ± 0.7	23.5 ± 9.0	0.6 ± 0.2	12.2 ± 6.3	23.9 ± 12.3	4.7 ± 2.0
twig	0.4 ± 0.2	4.2 ± 2.2	0.1 ± 0.1	1.4 ± 1.0	5.6 ± 3.9	0.7 ± 0.4
misc.	0.4 ± 0.1	6.9 ± 2.2	0.3 ± 0.1	3.1 ± 0.8	4.0 ± 2.7	0.9 ± 0.3
total	2.7 ± 1.0	34.6 ± 13.4	1.0 ± 0.4	16.7 ± 8.1	33.5 ± 18.9	6.3 ± 2.7

Notes: In the degraded pasture, traps were located within or in proximity to tree islands and were corrected based on percent tree cover. Collections extended from July 1997 to June 1998.

TABLE 6. Mean (± 1 SD) solution concentrations for two years of volume-weighted mean concentrations in contrasting land uses in Paragominas, Brazil.

Solution type by land use†	n‡	Conductivity (μs/cm)	pH	Alkalinity (μeq/L)	DOC§ (mg/L)	Total N (μg/L)	NO_3-N (μg/L)
All							
Bulk precipitation	88	10.2 ± 5.8	4.90 ± 0.24	22 ± 2	9.6 ± 5.0	314 ± 262	19 ± 16
Mature forest							
TF	133	25.3 ± 7.6	5.84 ± 0.06	108 ± 29	8.1 ± 1.2[a]	936 ± 332	171 ± 94
LL	109	38.2 ± 7.3	5.89 ± 0.17	132 ± 7[a]	16.0 ± 2.1	2548 ± 959	966 ± 477
T25	20	29.1 ± 2.2	5.15 ± 0.07	59 ± 0[a]	1.8 ± 0.2	1482 ± 112[a]	1163 ± 94[a]
T300	2	64.1 ± 50.8	3.97 ± 1.18	16 ± 23	1.2 ± 0.3[a]	902 ± 547	555 ± 277
T750	0						
Z20	33	65.1 ± 9.8	4.55 ± 0.03	12 ± 2	8.5 ± 0.5	6133 ± 750	3375 ± 354
Z300	2	21.1	4.98	50	0.8	1250	1197
Z700	0						
Secondary forest							
TF	135	24.1 ± 7.5	5.87 ± 0.16	110 ± 11	6.2 ± 0.1[ab]	654 ± 256	84 ± 42
LL	102	62.6 ± 14.7	6.00 ± 0.20	174 ± 30[b]	19.6 ± 1.4	2206 ± 443	709 ± 121
T25	21	34.0 ± 21.0	5.70 ± 0.12	179 ± 75[b]	1.8 ± 0.3	264 ± 99[b]	84 ± 111[b]
T300	1	24.8	5.55	88			
T750	0						
Z20	45	49.8 ± 12.2	5.67 ± 0.32	132 ± 9	13.5 ± 6.8	2212 ± 853	1070 ± 443
Z300	2	30.7	5.33	83	15.3	732	35
Z700	0						
Degraded pasture							
TF	133	13.9 ± 2.0	5.90 ± 0.23	81 ± 4	4.3 ± 0.3[b]	271 ± 61	28 ± 22
LL	99	37.6 ± 1.5	6.24 ± 0.27	182 ± 1[b]	16.7 ± 1.4	1280 ± 176	233 ± 97
T25	11	33.7 ± 3.8	5.51 ± 0.12	128 ± 22[b]	2.7 ± 2.4	536 ± 365[b]	69 ± 95[b]
T300	11	13.6 ± 0.1	4.99 ± 0.31	42 ± 7	1.7 ± 0.4[a]	283 ± 1	39 ± 37
T750	1	80.9	4.19	16	12.1	5404	115
Z20	17	47.5 ± 35.1	5.70 ± 0.20	90 ± 23	11.2 ± 4.9	4788 ± 5501	841 ± 3144
Z300	10	34.6 ± 17.0	5.55 ± 0.10	78 ± 14	5.6 ± 1.3	2416 ± 2052	1603 ± 1357
Z700	7	26.7 ± 7.9	5.59 ± 0.03	132 ± 52	4.8 ± 0.1	1564 ± 1315	121 ± 104
Managed pasture							
TF	61	24.9 ± 11.9	5.91 ± 0.15	100 ± 17	7.1 ± 0.6[a]	579 ± 233	47 ± 23
LL							
T25	34	40.1 ± 7.1	5.47 ± 0.14	108 ± 24[b]	2.2 ± 0.6	250 ± 89[b]	54 ± 70[b]
T300	2	19.0	5.25	41	4.6[b]	1022	233
T750	11	13.4 ± 3.2	5.07 ± 0.20	38 ± 3	2.2 ± 1.1	692 ± 359	255 ± 100
Z20	6	92.0	6.69	239	12.5	12 975	185
Z300	0						
Z700	0						
All							
stream	406	29.6 ± 0.4	4.92 ± 0.20	55.7 ± 8.0	1.3 ± 0.1	277 ± 33	110 ± 7

Notes: Different superscript letters indicate significant differences between land uses ($P < 0.1$) for a one-way ANOVA with land use as treatment and $n = 2$ years per treatment.

† Solution types: TF = throughfall, LL = litter leachate, T = tension lysimeter, Z = zero tension lysimeter.

‡ Total no. samples collected over two years; samples were collected biweekly from May 1996 to 1998.

§ Dissolved organic carbon.

mature forest clearing are less clear, with results of previous studies reporting some losses, gains, or no change (Veldkamp 1994, Trumbore et al. 1995, de Moraes 1996, Neill et al. 1997, de Camargo et al. 1999, Neill and Davidson 2000). At this research site, modest increases in mineral soil C (~2 Mg C/ha) were found previously in the managed pasture and a small decrease (~1 Mg C/ha) was found in degraded pasture using C isotope techniques (Trumbore et al. 1995). In the present study, in the soil O horizon significant differences were apparent in C stocks among the four land uses (Fig. 2). In the degraded pasture, where fire has become an important ecological variable, and in the managed pasture, with its different plant physiology, the soil O horizon has not completely reestablished after disturbance. In contrast, the secondary forest O horizon has reaccumulated as much organic matter as that present in the O horizon of the mature forest (Fig. 2). These patterns in the O horizon are consistent for the other elements (Fig. 2). The upper mineral soil layers, 0–10 cm and 10–20 cm, were also measurably affected by land-use conversion (Table 4). The bulk density of the present surface soil is higher in both the degraded and managed pasture compared to the mature forest (Markewitz et al. 2001)—a result that has been documented previously in forest to pasture conversion (de Moraes

TABLE 6. Extended.

NH_4-N (μg/L)	Total P (μg/L)	K (mg/L)	Ca (mg/L)	Mg (mg/L)	Na (mg/L)	Cl (mg/L)	SO_4 (mg/L)
121 ± 163	2	0.39 ± 0.10	0.25 ± 0.10	0.09 ± 0.04	0.36 ± 0.088	0.82 ± 0.14	0.18 ± 0.04
285 ± 141	10	3.51 ± 1.75	0.86 ± 0.16	0.49 ± 0.09	1.23 ± 0.03[a]	2.82 ± 1.01	1.35 ± 0.05[ab]
498 ± 348	20	4.65 ± 0.08[a]	2.22 ± 0.70[a]	0.94 ± 0.16	1.37 ± 0.04	2.89 ± 0.35	1.80 ± 0.12[ab]
127 ± 23[a]	1	0.16 ± 0.07[a]	1.22 ± 0.07	0.62 ± 0.16[ac]	2.58 ± 0.50	3.82 ± 0.64	0.77 ± 0.12[ab]
202 ± 285	0	0.49 ± 0.45	0.58 ± 0.29	0.22 ± 0.12	1.45 ± 1.50	17.04 ± 17.08	1.23 ± 0.59
2233 ± 790	14	3.75 ± 1.45	2.11 ± 0.34	0.84 ± 0.02	2.53 ± 0.56	4.76 ± 0.83	3.45 ± 0.00
19	1	0.11	1.20	0.31	1.69	1.72	0.32
217 ± 161	5	4.01 ± 1.02	0.87 ± 0.18	0.46 ± 0.14	0.62 ± 0.07[b]	2.89 ± 1.09	1.53 ± 0.80[a]
538 ± 303	17	9.72 ± 2.57[b]	3.63 ± 0.04[b]	1.36 ± 0.31	1.43 ± 0.19	8.00 ± 3.34	3.72 ± 1.16[a]
17 ± 8[b]	2	0.98 ± 1.36[a]	1.92 ± 0.79	0.34 ± 0.04[b]	1.69 ± 1.09	4.94 ± 3.82	0.25 ± 0.29
324 ± 1	18	5.36 ± 4.02	3.47 ± 0.59	0.97 ± 0.28	1.48 ± 0.11	5.14 ± 1.58	3.60 ± 0.72
33	8	3.22	1.86	0.81	1.25	4.61	0.80
49 ± 24	2	1.66 ± 0.11	0.85 ± 0.01	0.29 ± 0.07	0.47 ± 0.04[b]	1.86 ± 0.47	0.57 ± 0.00[bc]
146 ± 153	7	6.96 ± 1.05[ab]	2.22 ± 0.04[a]	0.86 ± 0.03	1.14 ± 0.07	3.91 ± 0.75	1.59 ± 0.04[b]
13 ± 13[b]	1	0.21 ± 0.00[a]	1.86 ± 0.72	0.50 ± 0.05[ab]	1.35 ± 0.37	4.40 ± 1.20	1.93 ± 0.76[a]
58 ± 71	0	0.21 ± 0.24	0.67 ± 0.27	0.26 ± 0.18	0.62 ± 0.22	1.52 ± 0.05	1.19 ± 0.53
1142	0	1.12	0.86	0.29	1.13	22.60	2.06
1659 ± 2290	7	4.35 ± 1.82	2.58 ± 1.82	0.68 ± 0.31	0.92 ± 0.35	2.81 ± 2.04	1.89 ± 0.05
31 ± 31	4	2.28 ± 0.16	3.24 ± 2.52	0.87 ± 0.21	0.63 ± 0.02	1.77 ± 0.08	3.08 ± 2.39
1123 ± 1073	4	2.10 ± 0.64	2.27 ± 2.26	0.56 ± 0.37	0.79 ± 0.68	1.42 ± 0.22	0.96 ± 0.50
168 ± 165	4	3.14 ± 0.10	1.94 ± 1.93	0.53 ± 0.12	0.45 ± 0.09[b]	4.37 ± 3.28	0.38 ± 0.03[c]
40 ± 12[b]	4	4.58 ± 0.29[b]	2.00 ± 0.88	0.82 ± 0.00[c]	1.08 ± 0.04	7.90 ± 1.73	1.95 ± 0.73[a]
298	5	0.57	0.61	0.23	2.64	4.22	1.55
128 ± 83	1	0.27 ± 0.11	0.40 ± 0.32	0.33 ± 0.01	0.83 ± 0.10	1.39 ± 0.31	0.85 ± 0.07
16 252	183	7.83	12.38	6.32	1.36 ± 0.07	3.44 ± 0.53	2.78 ± 0.03
34 ± 5	2	0.85 ± 0.13	0.79 ± 0.07	0.51 ± 0.01	3.47 ± 0.07	7.07 ± 0.53	0.72 ± 0.03

et al. 1996, Neill et al. 1997). After normalization for bulk density differences, however, the content of soil C did not differ between the different land uses (Fig. 2).

The majority of C present in the original aboveground forest biomass was not transferred to the soil, was apparently lost from the ecosystem, and has not been replaced by soil C derived from grass inputs. The overall loss of ecosystem C during mature forest conversion either through decomposition or burning is consistent with all previous studies. In one study of pre- and postfire forest contents, up to 56% of the C was lost due to fire (Kaufmann et al. 1995). Indisputably, any reported increase in soil C from conversion to pasture is likely to be dwarfed by the loss of C from burning of aboveground mature forest biomass. Similarly, reaccumulation of C in secondary forest biomass is likely to dwarf accumulations of soil C during secondary forest succession over decades (Schlesinger 1990, de Camargo et al. 1999, Richter et al. 1999).

Despite the large changes in aboveground C standing stocks, the rate of C cycling through the biomass of these ecosystems are of comparable magnitude. The rate of C and nutrient cycling among the different ecosystems can be compared based on the return of elements to the soil surface and the total annual uptake by plants:

$$\text{Return } (R_T) = R_{FL} + R_{TF} \qquad \text{Uptake} = R_T + \Delta WS$$

where R_T is total return, R_{FL} is return in fine litterfall, R_{TF} is return in net throughfall (throughfall minus precipitation), and ΔWS is change is wood storage (Cole and Rapp 1982). This definition ignores certain cycling components such as gaseous uptake and release of C

TABLE 7. Two-year mean solution nutrient fluxes for contrasting land uses in Paragominas, Brazil.

Land use and solution type	H_2O (cm)	Solution components (kg/ha)										
		DOC	Total P	Total N	NH_4-N	NO_3-N	Cl	SO_4	Ca	Mg	K	Na
All												
Precipitation input	132	123.4	0.03	4.0	1.5	0.2	10.7	2.4	3.2	1.2	5.0	4.7
Mature forest												
TF	103	83.1	0.2	9.5	2.9	1.7	28.5	13.9	8.7	5.0	35.1	12.6
LL	92	146.6	0.4	23.1	4.4	8.7	26.6	16.6	20.2	8.6	43.0	12.7
T25	81	14.2	0.1	12.0	1.0	9.4	30.8	6.2	9.9	5.2	1.4	20.8
Secondary forest												
TF	103	64.2	0.1	6.6	2.1	0.8	29.1	15.3	8.9	4.6	40.7	6.4
LL	92	180.7	0.4	20.2	4.8	6.6	72.3	33.8	33.5	12.4	88.6	13.1
T25	81	14.6	0.1	2.1	0.1	0.6	38.3	2.1	15.3	2.8	8.7	13.2
Degraded pasture												
TF	103	43.7	0.1	2.8	0.5	0.3	18.9	5.8	8.8	2.9	17.0	4.8
LL	92	154.8	0.2	11.7	1.3	2.1	36.5	14.7	20.5	8.0	64.9	10.5
T25	81	20.6	0.0	4.2	0.1	0.6	35.3	15.3	14.8	4.1	1.7	10.8
Managed pasture												
TF	103	73.7	0.1	5.8	1.6	0.5	43.2	3.9	18.9	5.4	32.3	4.6
LL												
T25	92	19.8	0.1	2.3	0.4	0.5	71.7	18.3	17.9	7.5	42.3	9.9
All												
Streamwater output	30	4.1	0.0	0.9	0.1	0.3	21.8	2.2	2.4	1.6	2.6	10.7

Notes: Solutions were collected and concentration analyzed biweekly during May 1996–May 1998. Hydrologic fluxes were measured during this same period for precipitation inputs and streamwater outputs, while fluxes through the land uses are estimated from collected volumes and four years (1991–1994) of soil moisture measurements (Jipp et al. 1998).

as CO_2 and is less appropriate for pastures than forests, because it does not account for annual production of grasses. Nor does it account for accumulation of nutrients in the foliar canopy of young forests. Regardless, it provides an estimate of internal biomass cycling and ecosystem nutrient demand. In pastures, we assume an annual turnover of grass biomass, which may be conservative, because grass productivity can be higher (Resende et al. 1999). On the other hand, these pastures suffer a long dry season, during which time the grass goes dormant. Vigorous grass growth occurs only during the five-month rainy season.

The return of C to the soil surface is similar in both forest ecosystems (Fig. 4A). This result is driven by the similar rate of litterfall biomass in the two ecosystems (Table 5). Earlier collections of litterfall from

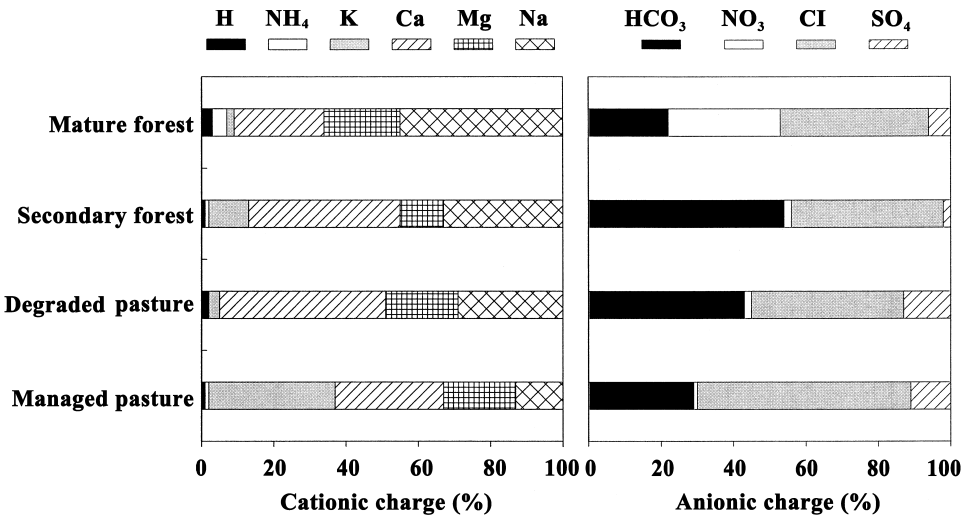

FIG. 3. Contribution (as a percentage) to cationic or anionic charge for surface 25-cm soil leachate solution components collected with tension lysimeters. Estimates are based on volume-weighted mean concentrations for two years (1996–1998) of biweekly solution collections at the Fazenda Vitoria in Paragominas, Brazil.

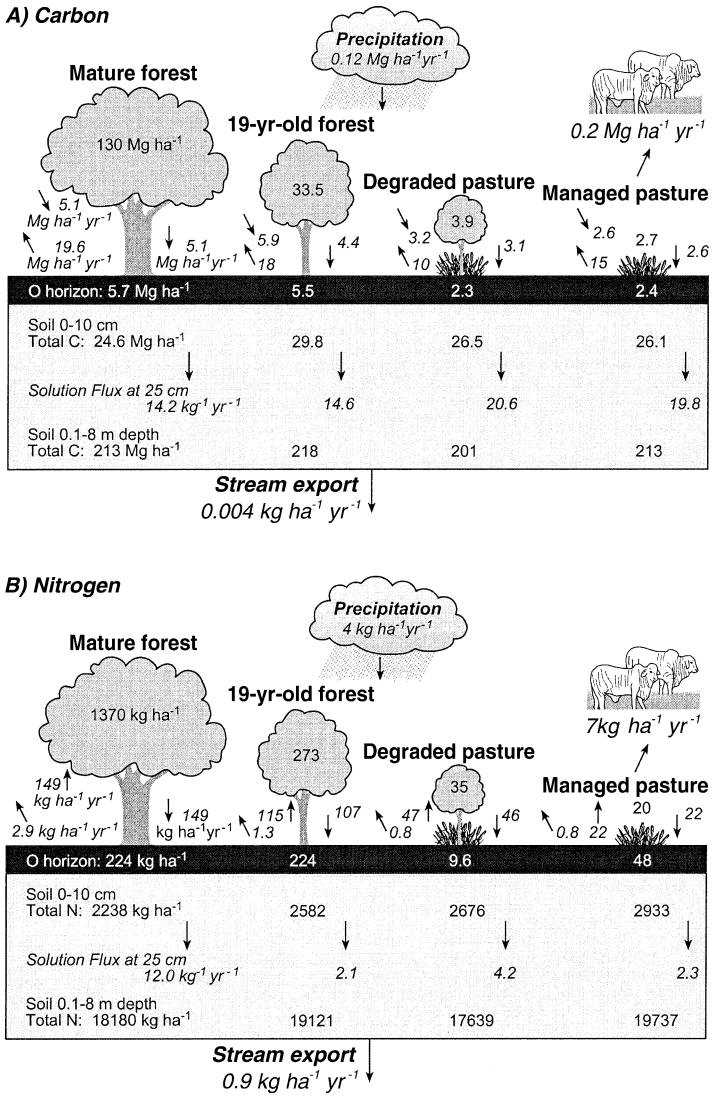

FIG. 4. Biogeochemical balances for (A) carbon and (B) nitrogen in mature and secondary forest, and degraded and managed pastures in the Fazenda Vitoria, Paragominas, Brazil. Element contents are in nonitalicized bold with fluxes in italicized bold numbers. Data were collected between 1996 and 1998.

1991 to 1993 for mature and secondary forests, 8.6 ± 1.4 and 7.5 ± 0.5 Mg·ha^{-1}·yr^{-1}, respectively, where similar (D. C. Nepstad, *unpublished data*). Furthermore, if we assume that the O horizon is near a steady-state condition for the two forest ecosystems, the equal mass of C in litterfall return and of forest floor C indicates comparable rates of turnover (~1.2 yr). Rates of soil respiration were also similar in the two ecosystems, Fig. 4A (Davidson et al. 2000). The total annual uptake of C from the atmosphere (note that C differs from the other nutrients in that uptake is from the atmosphere and not the soil) between the two forest ecosystems does differ, however, with rates tending to be higher in the secondary forest (Fig. 4A). The difference in uptake is driven by our assumption that the woody biomass in the mature forest is at steady state, while the secondary forest is currently in a state of woody biomass accretion. Recent eddy covariance studies have indicated that mature Amazonian forests may be accumulating C (Grace et al. 1995, Mahli et al. 1999). Although these eddy covariance estimates remain controversial, it is possible that we are underestimating uptake by the mature forest.

The pasture systems have lower amounts of foliar litterfall return, but higher rates of turnover for grass biomass. The inclusion of grass turnover results in return rates that are about two-thirds those of the forest ecosystems (Fig. 4A). Based on the same steady-state assumption as above, C turnover in the pasture O horizons is <1 yr. These smaller internal rates of cycling may, in part, be due to our conservative assumption of an annual turnover for pasture grasses but are also a function of the loss of the forest canopy, which cycles a large quantity of biomass C. The pasture ecosystems accumulate only small amounts of C in woody biomass but cycle a relatively large amount of C through annual

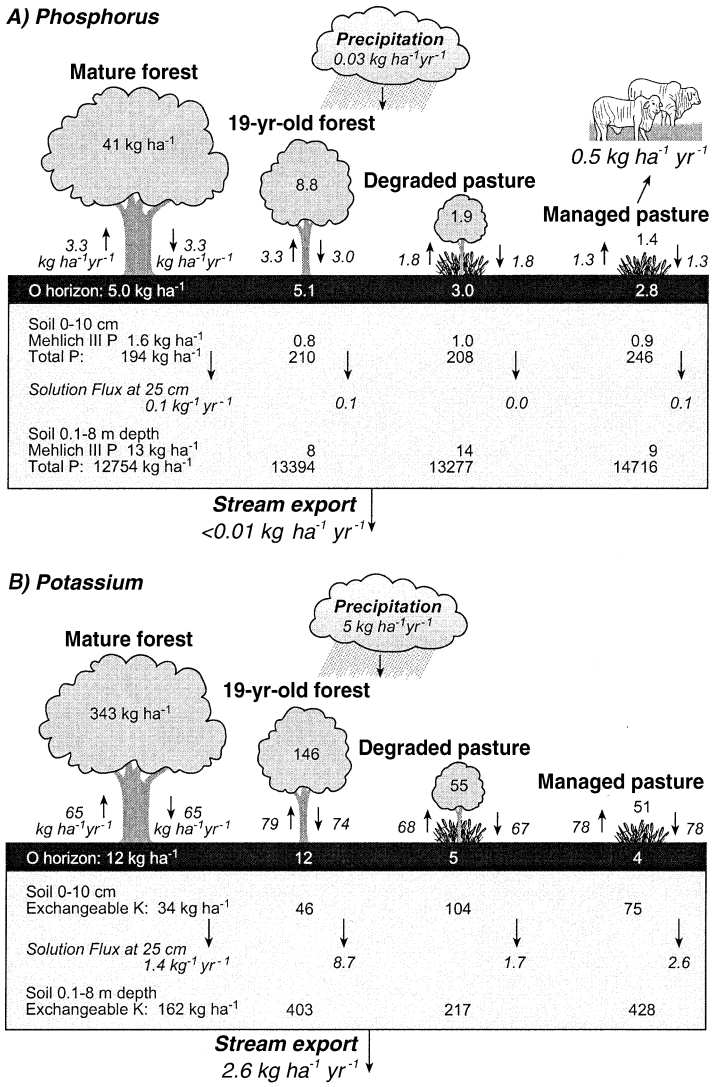

FIG. 5. Biogeochemical balances for (A) phosphorus and (B) potassium in mature and secondary forest, and degraded and managed pastures in the Fazenda Vitoria, Paragominas, Brazil. Element contents are in nonitalicized bold with fluxes in italicized bold numbers. Data were collected between 1996 and 1998.

foliar tissues. In addition, within pastures, export of C as cattle for meat production is estimated at 0.1 to 0.2 Mg C·ha^{-1}·yr^{-1} (Dias-Filho et al. 2001). These patterns in C cycling for the differing ecosystems will largely dictate the cycling of the other nutrient elements, i.e., N or Ca, although total quantities will be modified by differences in foliar concentrations and contributions from net throughfall.

Nitrogen

Lowland moist tropical forests such as the Paragominas study site, generally contain large stocks of aboveground N (Table 2) and soil N (Table 1). Reaccumulation of N in the woody biomass of the secondary forest ecosystem currently accounts for 20% of the original biomass N (Table 3) and is accumulating at ~9 kg·ha^{-1}·yr^{-1}. This accumulation rate is more than two times the estimated input of total N in bulk deposition of 4 kg·ha^{-1}·yr^{-1} (Table 7). Losses of N from this secondary forest include 1 kg N·ha^{-1}·yr^{-1} as NO + N_2O (Verchot et al. 1999), possibly some N_2 emissions from soils that have not been measured, and as much as 2 kg N·ha^{-1}·yr^{-1} leached to deep soils and perhaps to the groundwater (Tables 6 and 7). To balance this N budget, then, the processes of dry deposition, N fixation, and net N mineralization from soil organic matter must sum to ~8 kg N·ha^{-1}·yr^{-1}. Legumes are present but not abundant in the secondary forest, and so mineralization of soil organic N is the most likely source of the N needed to meet plant demand. Degraded and managed pasture sites only possess ~2% of the N originally present in the aboveground mature forest biomass (Table 3) and are accumulating N at rates below rainfall inputs, although in managed pastures an additional 7 kg/ha of N is exported as meat (Dias-Filho et al. 2001: Fig. 4B).

After clearing of forests at this site the N that had been present in the aboveground biomass of the cut

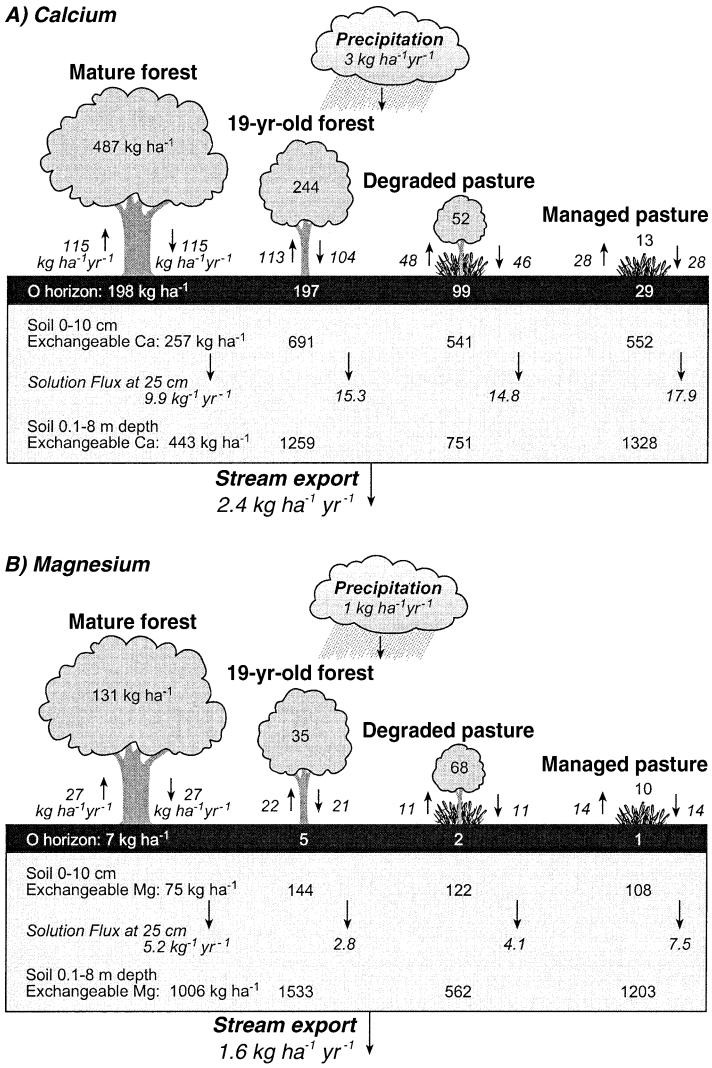

FIG. 6. Biogeochemical balances for (A) calcium, and (B) magnesium in mature and secondary forest, and degraded and managed pastures in the Fazenda Vitoria, Paragominas, Brazil. Element contents are in nonitalicized bold with fluxes in italicized bold numbers. Data were collected between 1996 and 1998.

forest was not detected as statistically significantly increased stocks of soil N in the upper 0–20 cm (Fig. 2). It is possible that some additional N was present in the surface or leached to lower portions of the soil profile but against a large background of soil N we could not detect any significant changes. Previous work of Neill et al. (1997) in forest to pasture conversions in the western Amazon, working with surface soils, found increases, decreases, and no change in total soil N for 18 paired sites. As for C, the absence of an increase in soil N indicates that the 1.4 Mg N/ha present in the forest biomass was not transferred to the soil and was apparently lost from the ecosystem. In a pre- and post-fire study, >70% of tropical forest N was lost during forest burning (Kaufmann et al. 1995). Additionally, short-term losses of N in soil solutions and stream water have been observed at other Amazonian locations (Uhl and Jordan 1984, Williams and Melack 1997). As with soil C, changes in soil N, when they occur, are relatively small compared to the loss of the original aboveground biomass N.

The cycling of N in total return remains somewhat higher in the mature forest (149 kg $N \cdot ha^{-1} \cdot yr^{-1}$) than in the secondary forest (107 kg $N \cdot ha^{-1} \cdot yr^{-1}$), but is diminished (46 kg $N \cdot ha^{-1} \cdot yr^{-1}$) in the degraded pasture (Table 5 and Fig. 4B). Gaseous N losses (Verchot et al. 1999) and leaching N losses (Tables 6 and 7) are higher in the mature forest and similar in the pastures, compared to the secondary forest.

The most evident difference in N cycling between the ecosystems is the large decrease in throughfall, litter leachate, and soil solution flux of N observed in secondary lands (Tables 6 and 7). In the mature forest, total N flux increased more than twofold while passing through the forest canopy, 4.0 to 9.5 kg/ha for precipitation and throughfall, respectively (Table 7). Furthermore, this increase in N flux persists in solutions passing from the upper 25 cm of the mineral soil (12.0

kg/ha). The abundance of N in these mature forest solutions is consistent with findings of N cycling processes in other mature tropical forests (Vitousek 1984) and the N mineralization assays of Verchot et al. (1999) for these same sites. The persistence of N in solutions through 3 m of soil (Table 6) may indicate potential losses of N from the rooting zone of the mature forest ecosystem. In contrast, although there is a similar increase in throughfall (6.6 kg/ha) and litter leachate N (20.2 kg/ha) in secondary forest solutions, soluble N fluxes decrease rapidly in upper soil solutions. At 25 cm depth, solution flux (2.1 kg/ha) is below levels of precipitation inputs. Degraded pastures share a similar pattern as those of secondary forests with decreased fluxes of N in mineral soils at 25 cm (4.2 kg/ha). In managed pastures, fluxes at 25 cm (2.3 kg/ha) also decrease in comparison to throughfall flux (5.8 kg/ha).

These results from secondary lands that were converted from primary forest 27 yr earlier contrast with the N flux results reported by Uhl and Jordan (1984) shortly following forest disturbance. In the previous work, N fluxes were found to increase during the first 3 yr after forest cutting but were concluded to return to baseline levels after ~5 yr. For the 19-yr-old forest and the old pastures of the current study, the N fluxes have decreased below fluxes observed in the mature forest. In addition, rates of net N mineralization, net nitrification, and emissions of NO and N_2O were also lower in the secondary forest and the pastures compared to the mature forest for this research site (Verchot et al. 1999). Apparently, the large total soil N stocks in these clayey soils belie a much smaller actively cycling N pool that is susceptible to depletion with land use change. Studies on a Tropohumult in Costa Rica also found diminished rates of net N mineralization after conversion to pasture (Reiners et al. 1994). These secondary ecosystems are reaccumulating N in foliar and wood tissues but apparently have not yet accumulated an abundance of actively cycling ecosystem N as is present in the mature tropical forest. It is this abundance of available N that leads to the high N fluxes present in both the soil liquid and gas phases of the mature ecosystem that are reduced in the secondary ecosystems. Lower rates of actively cycling N in the secondary lands, including mineralization of soil organic-N, may be indicative of N limitation to forest growth. This inference is consistent with results of a fertilizer application experiment in a repeatedly burned 6-yr-old secondary forest at the same ranch, where growth of trees responded to N fertilization and not P fertilization (Davidson et al. 2004).

Phosphorus

As with C and N, the original biomass P present in mature forest (Table 2) has not yet reaccumulated in secondary forest biomass, where only 8.8 kg/ha of P is present in aboveground biomass. This accumulation represents a relatively meager annual accumulation of P in woody biomass (0.25 $kg \cdot ha^{-1} \cdot yr^{-1}$), but still far exceeds the annual input of dissolved P in bulk deposition (0.03 $kg \cdot ha^{-1} \cdot yr^{-1}$; Table 7). During the first 19 yr of forest regrowth, the soils of these ecosystems must have been contributing the bulk of bioavailable P.

In this study, 27 yr after forest clearing, none of the ~40 kg/ha of P originally present in the aboveground forest biomass was detected as an increase in total soil P. Again, the lack of a P increase in the secondary forest and degraded pasture soil compared to mature forest indicates that the P was not transferred to the soil and was lost from the ecosystem. This apparent P loss of ~30 kg/ha should have been detectable had it been retained in the surface soil (even if in an irreversibly adsorbed condition), because it is similar in magnitude to the P increase observed in the fertilized managed pasture soil (Fig. 2). Compared to the mature forest, secondary forest, and the degraded pasture sites, the managed pasture was elevated in total P in 0–10 cm and 10–20 cm soils as a result of fertilizer inputs. The net positive difference in total soil P between the mature forest and the managed pasture for the 0–10 cm and 10–20 cm layers, 190 ± 2 vs. 240 ± 12 and 180 ± 3 vs. 209 ± 4 kg/ha, respectively, is slightly more than the amount of fertilizer P that the rancher reported applying 8 yr previous (~50 kg/ha) but within uncertainties of soil analysis and fertilizer application rate. P is relatively immobile in mineral soils so likely was not leached to deeper soil depths. Oxidation of P may occur during hot fires caused by slash-and-burn practices, but the fraction of biomass P oxidized is typically lower (i.e., <30%) than for C and N (Kaufmann et al. 1995). Phosphorus that is converted to an inorganic state during organic matter destruction through burning can also be irreversibly adsorbed to soil oxides and in this way be lost from the biologically active P cycle of the secondary ecosystem, although this would not be measured as an ecosystem loss (Sanchez et al. 1989). In any case, most of the aboveground P of the mature forest was apparently lost from the ecosystem during or following clearing and burning. Other studies in tropical forests have also found losses of ecosystem P as great as 50% shortly after burning (Ewel 1981, Kaufmann et al. 1995) and some runoff losses of P have been observed in the western Amazon in small watershed studies (Williams and Melack 1997, Neill et al. 2001). About 0.5 kg $P \cdot ha^{-1} \cdot yr^{-1}$ is exported as meat from managed pastures stocked at about one head per hectare (Dias-Filho et al. 2001), partially explaining the need for periodic P fertilization of managed pasture. This export may have been higher when stocking rates were up to four head per hectare during early phases of pasture management.

In these highly weathered soils, bioavailable P can be difficult to measure and total soil P is not considered a good estimator of available P. Mehlich-III-extractable

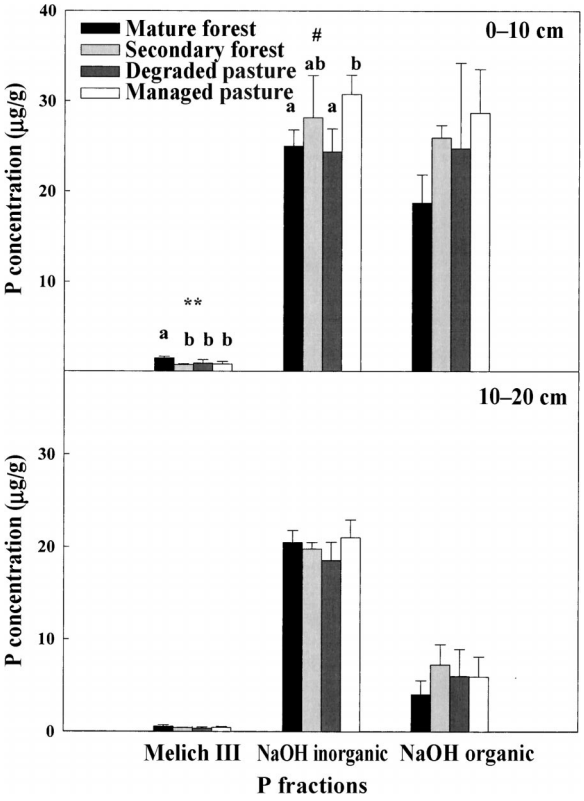

FIG. 7. NaOH-extractable inorganic and organic P, and Mehlich-III-extractable P concentrations (mean + 1 SD) in the upper surface soils of contrasting land uses in Paragominas, Brazil. Soils were collected in 1996. Differences at the 0.1 and 0.05 level of significance are indicated by # and *, respectively, for a one-way ANOVA with land use as the treatment and $N = 3$ per treatment. Different letters indicate significant differences by post hoc tests of significance using Tukey's honestly significant difference ($P < 0.05$).

P is used in agricultural systems to define available P (Tran and Simard 1993) and is designed for acid soils such as these Oxisols. Among these four land uses, mature forest has the highest level of Mehlich-III-extractable P, despite the inputs to secondary land soils from clearing and burning and fertilizer inputs (Fig. 7). In ecosystems investigated soon after disturbance, particularly burning, elevated concentrations of available P have been observed (Alegre et al. 1988). In our study, 27 yr after disturbance, vegetation regrowth or P loss has led to a depletion of ~1 kg/ha of Melich-III-extractable P in the upper 10 cm of soil compared to the mature forest. These low levels of P may also be limiting the rate of biomass accumulation.

Currently, the mass of Mehlich-III P in the upper 20 cm, <3 kg/ha, and even that throughout the entire 8 m soil profile, 14 kg/ha (Table 1), would not be sufficient to replenish the 40 kg P/ha needed in the aboveground biomass of a mature forest (Fig. 5A). Less easily extractable forms of soil P may also be bioavailable but at a slower kinetic rate (i.e., decadal timescale). The removal of 1 mol/L NaOH-extractable P, following a component of the Hedley fractionation (Tiessen and Moir 1993), recovered 10–30 times more P than Mehlich III in the upper 20 cm (Fig. 7), and could provide a sufficient pool of P to rebuild biomass, assuming a substantial portion of the pool were bioavailable over time. The inorganic NaOH fraction, however, may represent strongly bound Fe- or Al-P that is not bioavailable, while the organic fraction may be more indicative of available P. NaOH-extractable organic P was elevated (although not significantly) in 0–10 cm soil of secondary lands compared to mature forest (Fig. 7) but was a significant fraction of soil P only in the upper 100 cm of the profile (Fig. 8). The content of organic P in the top 1 m of soil (47 kg P/ha) is considerably more than the Mehlich-III pool, but still only slightly more than stocks in aboveground biomass of a mature forest.

The 8.5 kg P/ha already accumulated in the aboveground biomass of the secondary forest suggests that the less-available soil P pools may have already contributed to P uptake, and it is reasonable to speculate that mineralization of NaOH-extractable organic P might be one of the important processes limiting rates of forest growth (Schmidt et al. 1997, Richter and Markewitz 2001). Mycorrhizal infection of tree roots, demonstrated to 8 m depth in these soils (Nepstad et al. 2001), could facilitate the uptake of the less available P pools by native species. Davidson et al. (2004), however, found no response in tree growth to P addition in a nearby 6-yr-old successional forest regrowing on degraded pasture land, although remnant grasses grew

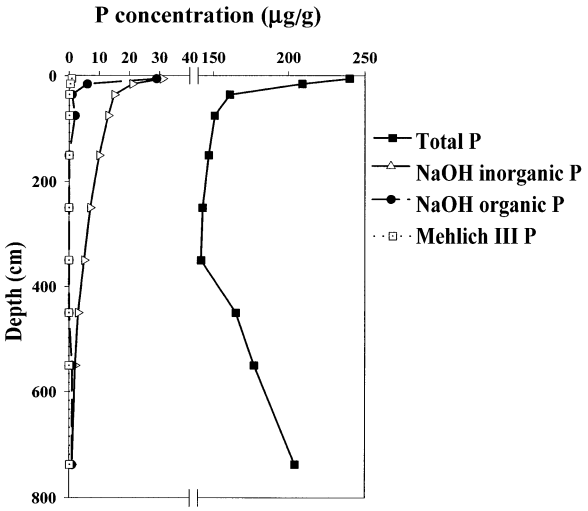

FIG. 8. Soil phosphorus fractions for the upper 825 cm of a Haplustox under managed pasture in northern Amazonia, Paragominas, Brazil. Soils were collected in 1996. Upper 0–20 cm samples are composite samples from transects ($n = 3$). Samples below 20 cm were collected by bucket auger as an integrated collection through the sampling layer. Data symbols represent the midpoint of the sampling layer.

better after P fertilization. The mechanisms and kinetics of P mineralization relative to demands of native and exotic plants may be critical for interpreting these results regarding factors limiting primary productivity during secondary succession.

The internal cycling of P is predominantly through litterfall and grass turnover with a small amount of P in throughfall solutions. Despite the relatively large differences in standing stock of P between mature forest and secondary ecosystems, the quantity of P return was relatively similar. Thus, in all secondary systems, a large portion of the standing stock of biomass P is being conservatively recycled annually (Fig. 5A).

The cycling of P in solutions was generally consistent with the low mobility of this element. The total flux of P increased from rainfall to throughfall and was greater in mature forest (0.2 kg/ha) compared to the other land uses (<0.1 kg/ha; Table 7). Litter leachate concentrations were elevated in both mature (0.4 kg/ha) and secondary forest (0.4 kg/ha) compared to the degraded pasture, which had 0.2 kg/ha of P as solution flux (Table 7). The fluxes of P in mineral soil solutions were all low (<0.1 kg/ha) although slight elevations in total P concentration were apparent for the 300-cm and 700-cm-tension lysimeters of the managed pasture (Table 6). Some amount of P was also present in soil solutions from zero-tension lysimeters for all depths and land uses (Table 6). The total number and volume of zero-tension solutions collected was limited, however, thus the flux of these waters as a pathway for P loss to groundwater cannot be accurately determined, although it is likely low.

Cations

The secondary forest currently contains 42, 50, and 27% of K, Ca, and Mg, respectively, originally present in aboveground biomass of mature forest (Table 3). The degraded pasture and managed pasture possess ~15, 11, and 6% of these same elements, respectively. The lower Ca contents in managed pasture, which possess little woody material, are the only exception in the latter case, representing only 3% of the Ca present in mature forest (Table 3). The mean annual accumulations in secondary forest woody biomass for K, Ca, and Mg were 4.9, 8.9, and 1.2 $kg \cdot ha^{-1} \cdot yr^{-1}$. Only for Ca does the annual accumulation substantially exceed the estimated precipitation input for the element of 3.2 $kg \cdot ha^{-1} \cdot yr^{-1}$ (Fig. 4E). The pasture ecosystems have retained relatively greater amounts of the original cationic contents compared to C, N, and P, but the total biomass accumulations are still relatively small.

The retention of cationic elements K, Ca, and Mg in mineral soils tells a strikingly different story than C, N, and P, with all the cationic components having significant increases in both concentration and content for secondary land uses relative to mature forest soils, Fig. 2 (see also Markewitz et al. 2001). One exception is the relatively small increases in K content of the secondary forest soil. The retention of cationic elements in the upper 20 cm of soil corresponds with an increase in soil pH and a decrease in exchangeable acidity (Table 4). In the upper 0–10 cm of soils, an increase in the effective cation exchange capacity (CEC measured at soil pH) was also evident, Table 4.

The cationic inputs to the soil resulting from clearing and burning of the mature forest biomass (estimated from mature minus secondary forest biomass contents) are ~200, 250, and 100 kg/ha of K, Ca, and Mg, respectively. These potential inputs from forest clearing approximate the measured increases of these nutrient stocks in the upper 20 cm of pasture and secondary forest soils compared to the mature forest soil (Fig. 2).

The retention of cationic elements after forest clearing through variable charge effects on ECEC has been found previously in tropical Oxisols (Sanchez et al. 1983, Reiners et al. 1994). An increase in ECEC is explained by an increase in soil pH due to the alkalinizing effect of base rich ash inputs. ECEC, estimated by the sum of cations method (Thomas 1982), is measured in unbuffered solutions, and thus reflects changes in soil pH. Further evidence that the increase in exchange capacity is due to the presence of pH-dependent variable-charged soils is provided by the lack of a change in the total cation exchange capacity (CEC), Table 4. CEC is also estimated by a sum of cations method but uses total acidity which is measured in a strongly buffered solution ($BaCl_2$ + Triethanolamine at pH 8.2, [Thomas 1982]). If organic matter had increased in surface soils, this would have increased ECEC, but it also would have increased CEC, which was not observed. Although soil response to ash inputs has been observed previously, the response is remarkable in this case because more than 27 yr have passed since initial forest clearing and burning. The response in ECEC is known to be rapid, but the longevity of this response is not well quantified. A few studies (McCraken et al. 1989, Reiners et al. 1994, Richter et al. 1994, de Moraes et al. 1996, Markewitz et al. 1998), including the present study, indicate that this effect might well persist over many decades. The abundance of these cationic elements in surface soils means that, in contrast to C, N, and P, a large fraction of the initial mature forest standing stocks were retained in the secondary forest and pasture soils (Fig. 2).

The higher cation contents in the mineral surface soils of the secondary forest have not increased the cycling of these elements through biomass or net throughfall beyond the rates measured in the mature forest (Fig. 4D–F), but the fact that the 19-yr-old secondary forest already has cation returns as throughfall and litterfall similar to the mature forest is impressive. The return of elements to the soil surface in pasturelands is lower than in the forests, except for K, which has similar rates of return for all ecosystems. Cycling

of K differs from the other elements in that a substantial percentage of the return to soil is in net throughfall.

Within these secondary lands there also appears to be an increased solution flux of cations through the O horizon and enriched mineral surface layer relative to the mature forest (Tables 6 and 7). The mobility of the cationic elements (K, Ca, and Mg) is much greater than that of P, for example, and can potentially be leached from soils after forest disturbance (Richter et al. 1994, Likens and Bormann 1995). Potassium, the most mobile of the cationic elements, had an elevated flux in secondary forest litter leachate (89 kg/ha), and 25-cm-tension lysimeter (87 kg/ha) compared to mature forest (Table 7). Slight flux increases of K were also evident in managed pastures, but were less clear in degraded pastures (Table 7). Increased Ca fluxes in litter leachate solutions were also apparent in secondary forest (33.5 kg/ha) compared to mature forest (20.2 kg/ha). In fact, all secondary lands had elevated Ca flux at 25 cm depth for tension lysimeter solutions although all differences were not statistically significant (Tables 6 and 7). Fluxes of Mg in solution were positively correlated with those of Ca ($r = 0.84$ Pearson's correlation coefficient). Generally, there appears to have been an increase in cationic solution concentrations in secondary lands.

Whether plant roots or soil surface charge are capturing these increased solution fluxes below the 25 cm depth is uncertain. Previous studies that have investigated short-term effects of tropical forest disturbance on solution fluxes indicate that an initial and rapid increase in solution concentrations and mass flux, i.e., nutrient loss, is apparent, although a rapid return (<5 yr) to predisturbance solution concentrations was also observed (Uhl and Jordan 1984, Williams and Melack 1997). The current study indicates that concentration differences and thus gradual mass loss might continue to persist over many decades. Paired watershed work in the temperate region of the Hubbard Brook Experimental Forest, New Hampshire, in fact, found such a prolonged response with stream water fluxes of K elevated 25 yr after initial forest disturbance (Likens et al. 1994).

Additional evidence for a general change in the biogeochemical cycling of cationic as well as anionic elements in solution comes from the relative contributions of the individual elements to charge balance. For example, in the mature forests, NO_3^- is an important component in solution, particularly in mineral soils, where it accounts for up to 57% of the anionic charge (Fig. 3). Conversely, in all three secondary land uses, NO_3^- usually accounts for $<10\%$ of anionic charge in solution. In secondary lands, HCO_3^- accounts for a greater percent of anions, particularly in mineral soil solutions were pH has increased. A similar scenario is present for the cationic elements, where H^+ accounts for a smaller percentage of the sum of cations in secondary lands, while the nutrient cations Ca, Mg, and K account for a greater percentage (Fig. 3). In essence, these tropical lands have shifted from mature forests with low pH, acidic solutions that leach as nitrate salts, to secondary ecosystems with slightly elevated soil and solution pH that leach as bicarbonate salts.

Input–output budgets

Input–output budgets are of great interest in interpreting effects of land-use conversion because such budgets allow for estimates of nutrient loss or retention in watersheds. At the Fazenda Vitoria, solution inputs as precipitation for the May 1996 to 1998 periods were below the 22-yr annual average for the region due to the strong El Niño Southern Oscillation event of 1997 (Jipp et al. 1998). The hydrologic watershed flux estimated for this period was 142 and 122 cm of rainfall input and 32 and 31 cm of stream water output for year one and two, respectively. The stream water output estimated as percent runoff is 22% and 25% while the minimum evapotranspiration (assuming no change in soil moisture storage) is 111 cm and 91 cm, respectively. Jipp et al. (1998) measured a significant decrease in soil water storage ($\sim$130 cm in mature forest or $\sim$70 cm in pasture) during the dry years of 1992 and 1993, and so ET during our relatively dry study years probably also substantially exceeded our minimum estimate. Runoff estimates reported for Amazonian forests with similar rainfall regimes and soil types are in a similar range of 19–35%, but vary more broadly across the region at 19–65% (Franken and Leopoldo 1984, Bruijnzeel 1990, 1991, Lesack 1993). In the low rainfall years of 1992 (110 cm) and 1993 (149 cm) at the same ranch as the present study, Jipp et al. (1998) estimated evapotranspiration rates for mature forest (113 and 151 cm), secondary forest (110 and 141 cm), and pasture (93 and 135 cm). These estimates are only slightly higher than ours in the current study.

The hydrologic inputs of 123 $kg \cdot ha^{-1} \cdot yr^{-1}$ of C in precipitation and outputs of 4 kg $C \cdot ha^{-1} \cdot yr^{-1}$ in stream water (Fig. 4A) indicate retention or decomposition of solution C within the terrestrial ecosystem. The low activity clays of these weathered Oxisols are able to adsorb organic molecules (Torn et al. 1997), and organic matter decomposition is a rapid process in these warm tropical ecosystems. These solution fluxes of C are tiny in relation to ecosystem stocks and fluxes of C (Fig. 4A) and thus this small potential retention of C should not be construed to represent a significant C sink.

The input–output budget of N for the watershed integrates the observed differences among the ecosystems within our landscape mosaic. For example, the flux of N in solutions was substantial through both forest ecosystem litter layers ($\sim$20 $kg \cdot ha^{-1} \cdot yr^{-1}$), but was greatly diminished in pastures and through the lower portions of the soil profile. For the watershed, there was a net retention of total N based on precipitation

inputs and stream water outputs (4.0 and 0.9 $kg \cdot ha^{-1} \cdot yr^{-1}$, respectively), although there appears to be a net balance in the flux of NO_3 (Fig. 4B). Moreover, gaseous losses of N_2O and NO from the mature forest were ~3 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (Verchot et al. 1999), indicating close to a net balance of zero. However, biological N fixation and gaseous losses of N_2 have not been measured. The secondary lands had lower N_2O and NO losses (0.8–1.2 kg $N \cdot ha^{-1} \cdot yr^{-1}$), but N is either accumulating in aboveground biomass (secondary forest) or being exported in fires (degraded pasture) or as meat (active pasture) in these ecosystems. Losses of total N have been reported for mature tropical forests (Bruijnzeel 1991) but losses of N would be surprising in a watershed in which 80% of the area is covered by young, aggrading secondary vegetation. The concentration–discharge relationship for stream water NO_3 has a negative slope, indicating that concentrations decrease during periods of high flow (Markewitz et al. 2001). Flushing of N from organic enriched surface soils during periods of high flow such as snow melt or storm runoff, as observed in temperate forest ecosystems (Likens and Bormann 1995), is apparently not a predominant source of stream water N in this ecosystem. Nitrate moving through the forest soil profile and entering the groundwater may be a more important source of stream water NO_3 (but see McClain et al. 1994). The contribution of NO_3 to stream water may have diminished due to the loss of mature forest ecosystems rich in soil solution N near the stream. Such a pattern has been reported in Rondônia, Brazil, where streamwater in pastures has lower N and higher P than streamwater from forests (Neill et al. 2001).

The flux of P in the dissolved phase was generally small. There was a net retention of P in the watershed but the ecosystem inputs dissolved in solution were meager (0.03 $kg \cdot ha^{-1} \cdot yr^{-1}$), while the output in streamwater was near zero (<0.01 $kg \cdot ha^{-1} \cdot yr^{-1}$; Fig. 5A).

Calcium (3.2 $kg \cdot ha^{-1} \cdot yr^{-1}$) and K (5.0 $kg \cdot ha^{-1} \cdot yr^{-1}$) inputs from precipitation are slightly greater than streamwater outputs (2.4 and 2.6 $kg \cdot ha^{-1} \cdot yr^{-1}$, respectively), while input (1.2 $kg \cdot ha^{-1} \cdot yr^{-1}$) and output (1.6 $kg \cdot ha^{-1} \cdot yr^{-1}$) estimates for Mg indicate a small net loss to streamwater. Only for K do these apparent differences in inputs and outputs exceed our uncertainty estimate of $\pm 30\%$. Given the extent of mature forest clearing in this watershed and the observed retention of cation stocks in the surface soil of secondary lands, a relative balance in inputs and outputs or potential ecosystem retention for these elements is surprising.

The temporal patterns of streamwater K, Ca, and Mg in this tropical watershed indicated that these elements are reaching the stream during periods of high flow in the wet season (Markewitz et al. 2001). The positive discharge–concentration relationships observed for these elements usually implies an input of the elements from surface or interflow processes, such as a flushing of organic enriched surface soils that would contribute base cations and bicarbonate to streamwater. This conclusion for cationic elements differs dramatically from that interpreted previously in watersheds on younger soil substrates (Drever 1997). In these younger soil substrates, cationic element concentrations are generally highest during base flow periods and are predominantly derived from mineral weathering of rocks. The predominance of HCO_3 in these surface and interflow waters creates a bicarbonate salt solution akin to that observed to be leaching from secondary lands and implicates the surface soils of these secondary lands as the likely source of these inorganic ionic components.

Conclusions

Contrary to early concerns about loss of large fractions of total ecosystem nutrient stocks during and following deforestation, the deep, clayey Oxisol of our study site stores large stocks of C, N, P, K, Ca, and Mg relative to aboveground biomass stocks. Much of the N, P, or cations, however, does not actively cycle on annual time scales, thus reinforcing the concern that land-use change might still diminish nutrient stocks available to young successional forests.

The aggregate picture for this landscape is one in which ecosystem conversion has released C, N, and P from biomass to the atmosphere or solution losses and has redistributed K, Ca, and Mg from biomass to soil. Most clearly, the biomass contents of C, N, and P present in the original aboveground biomass have not been retained in the secondary ecosystems. Increases in soil stocks of these elements were not measurable in the upper 20 cm, except when P fertilizer was applied to managed cattle pastures. In contrast, an increase in exchangeable soil cation contents was measurable and is nearly equal to the cation stocks present in the original above ground biomass. Thus, K, Ca, and Mg were mostly retained within the ecosystems. Presently, however, base cation enriched soils appear to be re-equilibrating on decadal time scales to an acidic condition through processes of plant uptake and soil leaching, with the latter process potentially indicating continued nutrient loss.

Despite the observed nutrient redistributions and losses, forest succession is occurring on portions of this landscape, although the rate of biomass accumulation is comparatively low for secondary tropical forests. Nevertheless, the secondary forest, is recuperating important nutrient cycling functions. For example, secondary and mature forests both have similar amounts of fine litterfall and similar rates of turnover through the soil O horizon, an important nutrient recycling mechanism. In addition, secondary forests are accumulating nutrients in woody biomass making the elements unavailable for continued leaching loss. Conversely, pasturelands that dominate the landscape are not only cycling a smaller total mass of nutrients but

are also limited in woody biomass and thus provide little storage against continued leaching loss.

In the case of N, a large capital of plant available N has been lost from the ecosystem, and cycling of N has clearly diminished. Nitrogen fixation and N mineralization of the large total soil N pool may replenish actively cycling plant-available N pools, but this could be a rate-limiting process for secondary succession, especially where repeated fires has severely depleted the available N pool. For P, ecosystem losses are of concern because atmospheric inputs are small, and soil adsorption processes can effectively remove P from the biogeochemical cycle. Soil available P defined by Mehlich III, even when integrating over an 8 m soil profile, (i.e., ~14 kg/ha), is only about one-third of the P needed to regrow the aboveground biomass of a mature forest. Mineralization of NaOH-extractable organic P may contribute to bioavailable forms but even this pool remains limited (i.e., ~47 kg/ha), and the kinetics of mineralization of this organic-P pool is likely slow. Thus losses of P during mature forest cutting and burning may retard or even limit recovery of aboveground biomass. For both N and P, then, the soil is a reservoir of large but mostly recalcitrant stocks that must become available to plants to support future growth. The key to understanding limitation of these nutrients to growth of either native trees or exotic grasses is the kinetics of these mineralization processes, which remains poorly understood. Cationic elements seem less susceptible to limitations due to the abiotic retention of these elements through cation exchange. Thus, if forests are allowed to regrow shortly after mature forest clearing cation elements should be sufficient to meet demands. Conversely, if small stature pasture ecosystems persist for longer time periods (i.e., decades), either through altered environmental conditions or management options, continued cation loss could limit future soil stocks. Presently, exchangeable stocks over the 8 m soil profile for K (~420 kg/ha) appear more limited than Ca (1710 kg/ha) or Mg (1200 kg/ha) in relation to demands required to regrow a mature forest.

Although forests can and do regrow after agricultural abandonment on highly weathered Oxisols, this analysis of nutrient stocks and flows indicates that the rates of regrowth and the long-term magnitude of biomass accumulation may well be constrained by nutrient availability, particularly mineralization of N and P from recalcitrant soil stocks.

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