CARBON AND NUTRIENT ACCUMULATION IN SECONDARY FORESTS REGENERATING ON PASTURES IN CENTRAL AMAZONIA

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Abstract. Over the past three decades, large expanses of forest in the Amazon Basin were converted to pasture, many of which later degraded to woody fallows and were abandoned. While the majority of tropical secondary forest (SF) studies have examined post-deforestation or post-agricultural succession, we examined post-pasture forest recovery in 10 forests ranging in age from 0 to 14 years since abandonment. We measured above-ground biomass and soil nutrients to 45 cm depth and computed total site carbon (C) and nutrient stocks to gain an understanding of the dynamics of nutrient and C buildup in regenerating SF in central Amazonia.

Aboveground biomass accrual was rapid, 11.0 Mg·ha^{-1}·yr^{-1}, in the young SFs. Within 12–14 yr, they accumulated up to 128.1 Mg/ha of dry aboveground biomass, equivalent to 25–50% of primary forest biomass in the region. Wood nitrogen (N) and phosphorus (P) concentrations decreased with forest age. Aboveground P and calcium (Ca) stocks accumulated at a rate of 1.2 and 29.4 kg·ha^{-1}·yr^{-1}; extractable soil P stocks declined as forest age increased. Although soil stocks of exchangeable Ca (207.0 ± 23.7 kg/ha) and extractable P (8.3 ± 1.5 kg/ha) were low in the first 45 cm, both were rapidly translocated from soil to plant pools. Soil N stocks increased with forest age, probably due to N fixation, atmospheric deposition, and/or subsoil mining.

Total soil C storage to 45 cm depth ranged between 42 and 84 Mg/ha, with the first 15 cm storing 40–45% of the total. Total C accrual (7.04 Mg C·ha^{-1}·yr^{-1}) in both aboveground and soil pools was similar or higher than values reported in other studies. Tropical SFs regrowing on lightly to moderately used pasture rapidly sequester C and rebuild total nutrient capital following pasture abandonment. Translocation of some nutrients from deep soil ($>$45 cm depth) may be important to sustaining productivity and continuing biomass accumulation in these forests. The soil pool represents the greatest potential for long-term C gains; however, soil nutrient deficits may limit future productivity.

Key words: abandoned pasture; Amazon Basin; carbon sequestration; deforestation; fallow; nutrient cycling; Oxisol; plant nutrient stocks; secondary forest; soil nutrient stocks; succession.

INTRODUCTION

Primary forest conversion for subsistence agriculture, industrial logging, and pasture establishment continues to be the predominant causes of tropical deforestation (Laurance 1999). These activities have left a large portion of the tropical biome disturbed and in various states of natural regeneration (Brown and Lugo 1990), stagnation (Fearnside and Guimaraes 1996, Sarmiento 1997, Silver et al. 2000), or managed recovery (Fernandes and Matos 1995, Parrotta et al. 1997). Of the estimated 58.8 million ha of forest cleared in Brazilian Amazonia over the past three decades (Instituto Nacional de Pesquisas Espaciais [INPE] 2002), ~24 million ha were converted to pastures (Serrão et al.

1995). Depending on management (e.g., replacement of exported or lost nutrients, stocking rates, burning frequency, etc.), region, and soil type, pasture productivity may decline after 7–10 yr and pastures may be recleared or abandoned to recolonizing secondary vegetation; ~50% of the first-cycle pastures have reached this advanced stage of degradation (Serrao et al. 1993). Based on an analysis of 1990 land use data in the Amazon, Fearnside (1996) calculated an equilibrium will be reached where ~47% of all deforested land would be regenerating forest on degraded or abandoned pastures.

Although highly altered, these lands are valuable for human use (Brown and Lugo 1990), and provide important ecosystem services such as watershed protection, sources and havens of biodiversity, erosion prevention, soil fertility recovery by improved fallows (Szott et al. 1991), and atmospheric C sinks (Fearnside and Guimaraes 1996, Silver et al. 2000). However, the

potential of the abandoned land to recover and maintain these roles is dependant on the intensity of previous land use (Uhl et al. 1988, Nepstad et al. 1990, Aide et al. 1995, Alves et al. 1997), soil nutrient limitations (Cochrane and Sanchez 1982, Smyth and Cravo 1992, Laurance et al. 1999), and seed inputs and seedling establishment (Nepstad et al. 1996). These impediments to vegetation regrowth may be more extreme in abandoned pastures compared to agricultural land, resulting in lower aboveground productivity (Fearnside and Guimaraes 1996, Silver et al. 2000) and longer regeneration times.

Pasture productivity declines rapidly with decreasing soil P availability, facilitating invasion by secondary forest (SF) species better adapted to infertile soil (Toledo and Navas 1986); yet, soil fertility and biomass recovery is variable and dependant upon several factors. Degraded pastures are characterized by depleted soil nutrient stocks, low vegetation biomass, low primary forest seed inputs, high seed predation, depleted seed bank of forest species, and low stump sprouting (Nepstad et al. 1990), as well as soil surface sealing and compaction (Eden et al. 1991). Consequently, predicting the long-term growth rate of secondary vegetation on degraded pastures and the return of primary forest characteristics becomes a complex task.

New attention has focused on fast-growing SF due to their potential to sequester large quantities of C in short time-periods. For example, worldwide, tropical forests store ~2.06×10^{17} g C in the soil (Eswaran et al. 1993), and tropical SF of less than 20 years age have the potential to accrue soil C at a rate of 1.3 Mg·ha^{-1}·yr^{-1} (Silver et al. 2000). The growth rate of young SF is expected to increase with rising atmospheric CO_2 levels (DeLucia et al. 1999); however, high C allocation to short-lived tissues such as leaves and faster turnover of litter C may limit the potential C sink (Schlesinger and Lichter 2001). Furthermore, soil nutrient limitations may constrain primary productivity under CO_2 enrichment (Oren et al. 2001).

Soil nutrient impediments to productivity under native vegetation are substantial in Brazilian Amazônia. Cochrane and Sanchez (1982) estimated that only 7% of the land area is free from major plant growth limitations; soil P deficiencies (<7 mg/kg) constrain productivity in 90% (436 million ha), and Al toxicity (Al saturation of ≥60%) occurs over 73% of Brazilian Amazonia. Low soil Ca (Smyth and Cravo 1992) restrains productivity, P (Gehring et al. 1999) and N deficiencies (Davidson et al. 2004) limit SF growth; however, the vegetation is unable to effectively capture leaching soil N (Schroth et al. 1999). Mismanagement may compound these deficiencies since pasture-use intensity appears to negatively influence regenerating vegetation biomass (Uhl et al. 1988) and nutrient stocks (Buschbacher et al. 1988). Because SF recovery is variable and dependent on previous land-use and soil fer-

tility, the magnitude and rate of the above- and below-ground C and nutrient accumulation in these regenerating SF is still relatively unknown.

Determining nutrient constraints to regrowth and the status of secondary vegetation is an important step in managing and/or enhancing abandoned site rehabilitation. We examined the dual roles of SF to rehabilitate site productivity and to increase C sinks and investigated potential soil nutrient limitations to these two processes. We examined aboveground and soil C accrual and nutrient stocks in degraded pastures that had been abandoned for a varying number of years. Our objective was to study the influence of regenerating vegetation on C and nutrient budgets following pasture abandonment. We hypothesized that C and N pools would recover with time following post-burn volatilization, while other nutrients would be redistributed from below- to aboveground pools resulting in reduced soil pools.

METHODS

Study area

The study areas are located in Amazonas, Brazil, in the Central Amazon Basin, north of the city of Manaus along the road BR-174. The study area spans ~26 km (2°34′ S, 60°02′ W and 2°20′ S, 60°04′ W). The terrain is undulating with an elevation of 50–150 m. The plateau soil is classified as dystrophic, isohyperthermic, clayey kaolinitic, Hapludox with ~80–85% clay (*latossolo amarelo* according to the Brazilian classification system). Slope soils are composed of Ultisols and valley bottoms by Spodosols. The plateau soils have a low cation exchange capacity and are infertile but are strongly aggregated and well drained (Van Wambeke 1992).

The regional climate is tropical humid and the mean temperature is 26.7°C. Mean annual rainfall in Manaus is 2.2 m, with March and April as the wettest months with over 300 mm of precipitation. A mild dry season occurs from August through October, with mean monthly precipitation falling below 100 mm (Lovejoy and Bierregaard 1990).

The native vegetation of this region is closed-canopy, dense, evergreen terra firme forest (Veloso et al. 1991). Species recovery with SF development is significantly different in areas used as pasture compared to areas cut but not managed (Mesquita et al. 2001). Old growth, native vegetation remains the dominant cover in this area. The establishment of new pastures is now rare, and active pastures are a diminishing, short-lived feature of the landscape north of Manaus. However, SF are increasingly found along the primary roads where efforts to raise cattle on large ranches failed some 10 to 20 years ago.

A majority of the pastures were mechanically cleared in the early 1980s, commercial timber may or may not have been removed, the slash burned in place or me-

TABLE 1. Mean C and nutrient concentrations in foliage and wood from 10 secondary forests (SF) regenerating from degraded pastures in Central Amazonia, Brazil.

SF age (yr)	Fazenda and forest no.	C (%)	N (g/kg)	P (g/kg)	K (g/kg)	Ca (g/kg)	Mg (g/kg)
Foliage							
0–2	DAS-1 and Rodão-1	46.65 (1.80)	17.11 (0.78)	0.87 (0.04)	3.71 (0.35)	7.25 (0.74)	2.31 (0.06)
2–4	Rodão-4	45.51 (0.33)	16.42 (0.06)	0.65 (0.03)	2.75 (0.00)	6.42 (0.17)	1.88 (0.02)
4–6	DAS-2 and Rodão-3	48.25 (1.26)	16.08 (0.82)	0.89 (0.04)	5.59 (1.16)	5.28 (0.14)	2.04 (0.28)
6–8	Dimona-1, -3 and Rodão-2	45.69 (0.59)	14.60 (0.50)	0.56 (0.03)	5.38 (0.71)	6.59 (0.41)	2.13 (0.19)
12–14	DAS-3 and Dimona-2	49.38 (0.64)	15.02 (0.16)	0.58 (0.02)	5.14 (0.29)	7.86 (0.12)	2.77 (0.12)
Overall mean		47.12 (0.54)	15.66 (0.31)	0.70 (0.03)	4.78 (0.36)	6.70 (0.24)	2.25 (0.10)
Wood							
0–2	DAS-1 and Rodão-1	51.40 (0.49)	3.71 (0.31)	0.31 (0.01)	2.23 (0.33)	4.05 (0.58)	0.98 (0.11)
2–4	Rodão-4	47.64 (0.41)	2.99 (0.39)	0.19 (0.01)	1.19 (0.10)	2.76 (0.29)	0.69 (0.05)
4–6	DAS-2 and Rodão-3	47.45 (1.16)	2.80 (0.15)	0.21 (0.03)	1.69 (0.31)	2.01 (0.21)	0.47 (0.04)
6–8	Dimona-1, -3 and Rodão-2	47.68 (1.05)	2.52 (0.14)	0.16 (0.01)	1.76 (0.17)	2.33 (0.19)	0.55 (0.06)
12–14	DAS-3 and Dimona-2	51.05 (1.99)	1.87 (0.12)	0.09 (0.02)	1.28 (0.11)	2.51 (0.30)	0.58 (0.07)
Overall mean		49.05 (0.63)	2.73 (0.14)	0.19 (0.01)	1.68 (0.12)	2.69 (0.19)	0.64 (0.04)

Note: Each mean nutrient concentration value represents $n = 3$ samples of a five-tree composite in each forest. Standard errors are reported in parentheses.

chanically piled in windrows, and the area planted with exotic African grasses such as *Brachiaria brizantha* or *B. humidicola* (Rendle). Standard pasture management for the region includes at least one application of 50 kg P/ha. The animal stocking rate and number of years that the pastures were grazed were variable. Overgrazing and annual burning to increase economic returns in the short-term accelerated pasture degradation through increased nutrient loss and soil compaction. However, even in the absence of overgrazing (1–2 animal/ha), increases in bulk density occur (0.4 g/cm^3 increase from forest values after 12 yr as pasture), leading to reduced infiltration, sheetwash, and pasture decline (Eden et al. 1991). Declining pasture productivity is characterized by a reduction in the forage to weed ratio as bare ground develops and herbaceous and woody plants begin to invade. When unpalatable plants begin to dominate, the pasture becomes ''degraded,'' livestock productivity drops, animal mortality increases and the pasture is eventually abandoned. Fire and/or labor intensive hand weeding of seedlings and roots may lengthen pasture life by reducing woody biomass while encouraging grass growth; however, species of *Vismia*, a fast-growing early successional tree, resprout rapidly after burning and dominate abandoned pastures.

Site and plot selection

Ten SF were selected within three fazendas (cattle ranches) now in various stages of grazing, pasture abandonment, or pasture reclamation: Fazenda Rodão (kilometer 46), the Brazilian Agency for Agricultural Research (Embrapa Amazônia Ocidental) Agricultural District of SUFRAMA (DAS) pasture research site (kilometer 53), and Fazenda Dimona (kilometer 72), all along the road BR-174. Within each forest located on plateau Oxisols, we established four plots of 100 m^2 to 400 m^2, each with three subplots ranging in size

from 35 to 225 m^2 depending on forest age. Forests ranged from 0–2 yr to 12–14 yr since pasture abandonment. Secondary forest selection was based on forest age and independence from adjacent plots within the same ranch. We selected a range of forests spanning the age of available SF in the area; however, all SF age classes do not occur at all farms. We conducted farmer interviews to determine site histories and when grazing was abandoned. The date at which the pastures were abandoned is not definitive, as cattle may infrequently graze the area until all palatable forage is replaced by woody successional vegetation. The regenerating forests within the ranches are biologically and physically distinct, each with a unique management history and vegetation cover.

Biomass and tissue analysis

Within each subplot, we measured the diameter at breast height (dbh at 1.3 m above ground level; *Cecropia* were measured above prop roots) for all live tree stems ≥1 cm, labeled the stems, and recorded all species. Using two sets of allometric equations; from Nelson et al. (1999) for stem >5 cm dbh and R. C. G. Mesquita (*unpublished manuscript*) for those 1–5 cm dbh, we calculated dry biomass for each tree and converted the estimates to megagrams per hectare. The two sets of equations were developed either on the Embrapa research site (Nelson et al. 1999) or within the same region (R. C. G. Mesquita, *personal communication*). They provide a better estimate of SF biomass than previous equations (see Saldarriaga et al. 1988, Uhl et al. 1988, Brown et al. 1989, Overman et al. 1994) developed in the Amazon Basin (Nelson et al. 1999). The Nelson equations provide valid biomass estimates from 1 to 30 cm dbh. However, since these SF have more stems in the smaller diameter range of the Mesquita
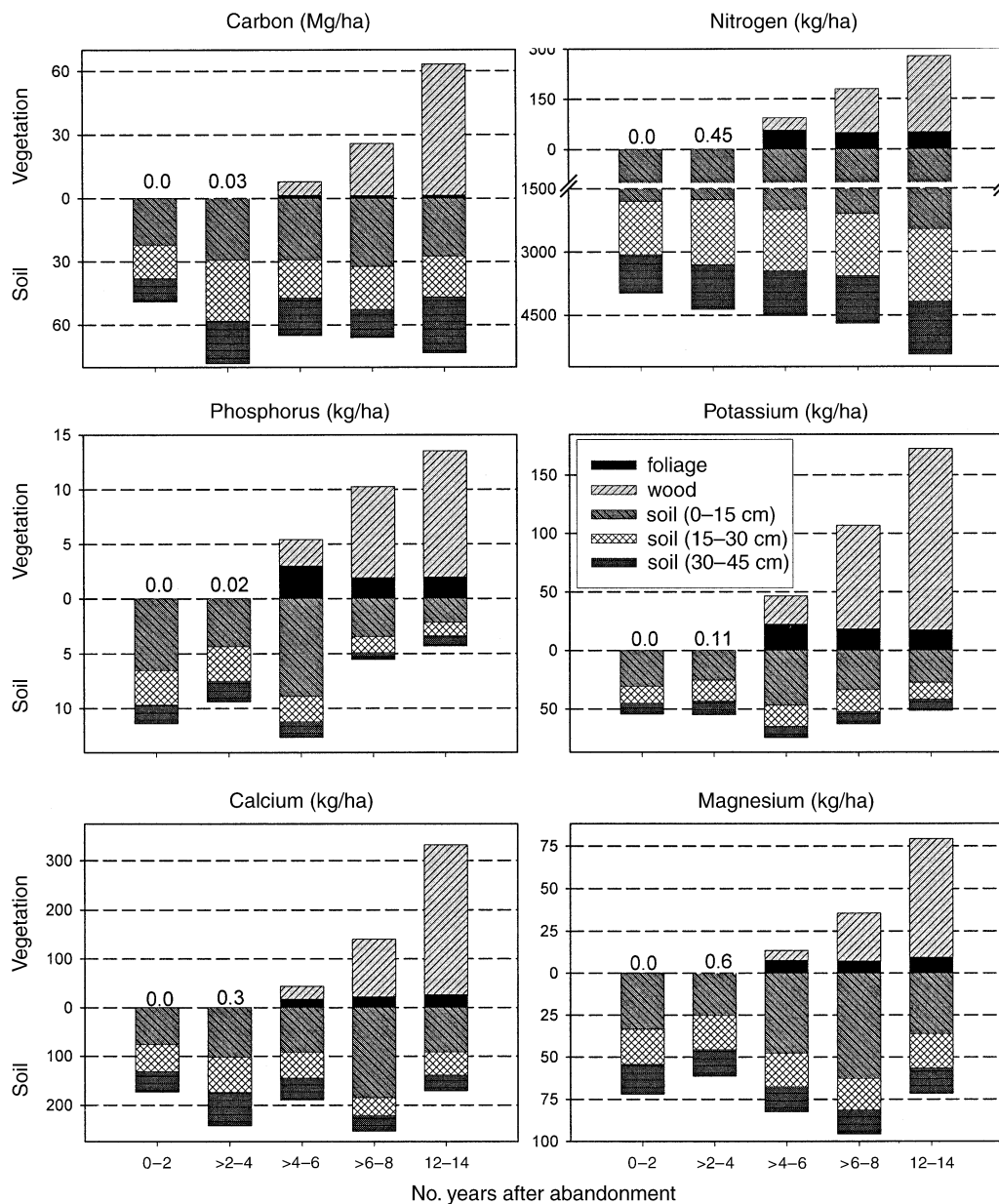
FIG. 1. Total C and N, Mehlich-I extractable P and exchangeable K, and exchangeable Ca and Mg in soils to 45 cm depth and live aboveground vegetation ≥1 cm dbh in 10 secondary forests regenerating from degraded pastures in central Amazonia, Brazil. Mean nutrient stocks for each forest (see Table 1 for forest grouping by age class) are calculated from soil and vegetation nutrient concentrations times soil bulk density or aboveground biomass. Note the scale difference between N soil and aboveground stocks. Values above time 0–2 and 2–4 indicate aboveground quantities only.

equations (1–5 cm dbh), by using the two sets of equations rather than one, we improve biomass estimates.

We used species-specific equations for the dominant tree species *Vismia cayennensis* (Jacq.) Pers., *V. japurensis* Reich. (Clusiaceae); *Cecropia* (Moraceae; mainly *C. sciadophylla* Mart. and *C. purpurascens* C.C. Berg); *Bellucia* (Melastomataceae); *Goupia glabra* Aubl. (Celastraceae); *Laetia procera* (Poepp.) Eichler (Flacourtiaceae), and a mixed-species equation for all others. To produce an aboveground forest estimate of nutrient concentrations (and nutrient stocks on a per hectare basis) within each forest, we randomly selected 15 trees ≥1 cm dbh and collected mature, upper-canopy, sun leaves using a telescoping tree pruner or by climbing the boles. From the same trees, we drew two wood core samples (wood and bark) at 1.3 m height

TABLE 2. Rate of total nutrient accumulation, vegetation immobilization, and soil nutrient flux to 45 cm depth.

	N			P		
Source	Accumulation (kg·ha^{-1}·yr^{-1})	r^2	P	Accumulation (kg·ha^{-1}·yr^{-1})	r^2	P
Total vegetation and soil	142.4	0.52	<0.01	0.55	0.2	0.18
Total foliage and wood	24.7	0.90	<0.001	1.2	0.76	<0.001
Total soil†	117.8	0.44	0.04	−0.66	0.34	0.08

Notes: Results are shown from 10 secondary forests regenerating from degraded pastures in Central Amazonia, Brazil. Nonsignificant change is indicated by NS.

† Total nitrogen, extractable P, and exchangeable K, Ca, and Mg.

on opposite sides of the bole. Foliage and wood samples were pooled into three sample composites of five trees, oven dried at 70°C, ground and homogenized, and analyzed for C, N, P, K, Ca, and Mg using standard Embrapa laboratory operating procedures (Silva 1999).

Vegetation stocks calculations

Using a species-specific foliage:wood ratio (R. C. G. Mesquita, *unpublished manuscript*), we partitioned the biomass estimate into wood and foliar components. We then estimated aboveground carbon and nutrient stocks in each forest by multiplying site specific mean nutrient concentrations for foliage and wood samples by the allometric estimates of each biomass component as partitioned by the foliage to wood ratio for individual trees. Our estimates of nutrient pools do not include aboveground biomass <1 cm dbh, forest litter, root biomass, or standing dead trees.

Soil analysis

We sampled soil to 45 cm in three depth classes (0–15, 15–30, 30–45 cm) within each of four plots per forest. The four soil samples per depth in each forest (120 soil samples) represent a composite of four to six subsamples per sample. Soil composites were combined in the field, air dried in solar dryers, charcoal and roots removed, hand milled with a roller, sieved to 2 mm, and analyzed for C, N, P, K, Ca, and Mg. Charcoal is common in local surface soils and is present at times to 45 cm depths in both pasture and forest soils. As charcoal is heterogeneously distributed in the soil, charcoal contamination poses an important impediment to resolution in reporting soil C concentrations. We estimate that carbon concentrations in this study, as with other studies within the Amazon basin, may generally overestimate total soil carbon stocks as a result of charcoal contamination (M. A. Rondon, *unpublished data*). To reduce the large bias of charcoal contribution to soil C estimates, large pieces were removed while the samples were wet and again with a forceps after drying before grinding; however, the small fragment size made total removal difficult.

Extractable soil P and exchangeable K were analyzed using a Mehlich-I double acid extraction (0.05 mol/L hydrochloric acid and 0.0125 mol/L sulfuric acid) and

exchangeable Ca and Mg with 1 mol/L potassium chloride. Total soil N was determined by the Kjeldahl technique and percent soil C by wet digestion (Silva 1999). Soil nutrient pools (kg/ha) of C, N, P, K, Mg, and Ca were calculated using mean soil bulk density data measured to 45 cm depth from abandoned pastures and SF in the same area (T. R. Feldpausch and S. A. Welch, *unpublished data*). Nutrient concentrations were multiplied by bulk densities for each depth class to provide soil nutrient stocks on a per hectare basis.

Statistical analysis

Statistical analyses were performed using Minitab 12.1 (Minitab, Inc., State College, Pennsylvania, USA). Statistical comparisons for C and nutrient concentrations and stocks were conducted separately for the different vegetation tissue types and soil depths using linear and loglinear regression and a $P < 0.05$ significance level. Soil and vegetation concentrations and soil stocks values were log transformed. Pooling the data for SF age classes and using regression analysis, we tested for trends in C and nutrients within aboveground and soil pools, as partitioned by depth, foliage or wood, versus time (years after pasture abandonment).

RESULTS

A total of 1901 stems were measured in 2320 m^2, of which 138 standing dead and 177 lianas were excluded from biomass calculations due to allometric equation limitations in computing such components. Of those stems considered in biomass estimations, 68% were less than 5 cm dbh, while no stems were greater than 30 cm dbh. The two recently abandoned pastures of 0–2 yr had no stems ≥1 cm dbh, the minimum diameter used for the allometric equations.

Vegetation nutrient concentrations

Wood N and P concentrations declined with SF age ($r^2 = 0.85$, 0.75; $P < 0.001$), with an average reduction of 50 and 60% in wood N and P from the youngest to the oldest forests. Foliage N and P concentrations tended to decline with forest age, although nonsignificantly. Compared to wood, foliage contained an average of 5.7 times more N and 3.7 times more P (Table 1).

TABLE 2. Extended.

K			Ca			Mg		
Accumulation (kg·ha^{-1}·yr^{-1})	r^2	P	Accumulation (kg·ha^{-1}·yr^{-1})	r^2	P	Accumulation (kg·ha^{-1}·yr^{-1})	r^2	P
15.0	0.76	<0.001	28.7	0.73	<0.01	7.4	0.56	<0.01
15.4	0.88	<0.001	29.4	0.91	<0.001	7.0	0.94	<0.001
~0	NS	NS	~0	NS	NS	~0	NS	NS

Foliar and wood Ca concentrations did not show a trend with age, but the concentrations were high relative to other nutrients. Calcium concentrations in wood were comparable and at times higher than wood N values. In the foliage, Ca concentrations represented an average of 43% of N values. Foliage contained an average of 2.5 times more Ca than wood. Potassium and Mg foliar and wood concentrations showed no trends with forest age (Table 1).

Vegetation nutrient stocks

The SF regrowth rapidly restored aboveground nutrients lost via deforestation and burning, with the greatest nutrient gains in wood as the forests matured (Fig. 1). Total Ca aboveground stocks increased most quickly as a result of the high wood Ca concentrations followed by N (Table 2). Phosphorus accumulation, slow relative to other nutrients, did not exceed 15 kg/ha after 12–14 yr.

Soil nutrient concentrations

Within each forest, soil carbon and nutrient concentrations generally decreased with depth (Table 3). Total soil N concentrations decreased with depth; however, deeper soil profile (30–45 cm depth) N concentrations increased with time after pasture abandonment (r^2 = 0.75; P < 0.001), with the shallower depths showing a weaker soil N increase trend with time. Soil extractable P concentrations tended to decrease at all soil depths over time, with significant reductions in surface layers (0–15 cm depth) with increasing time after abandonment (r^2 = 0.46, P < 0.05). Near-surface Ca levels (0–15 cm depth) ranged from 0.13 to 0.33 cmol$_{(+)}$/kg. Calcium concentrations were low below 15 cm depth, with overall means of 0.07 cmol$_{(+)}$/kg at 15–30 cm and 0.07 cmol$_{(+)}$/kg at 30–45 cm depths, where cmol$_{(+)}$ indicates centimoles of positive charge (Table 3, Fig. 1).

Soil nutrient stocks

Soil extractable nutrient stocks were generally lower in deeper soil pools. Within the oldest forests, soil C and N stocks were greater than aboveground stocks while the other nutrients resided predominantly within forest vegetation (Fig. 1).

Soil N stocks, relative to aboveground stocks, were high, and increased with forest age (r^2 = 0.44, P < 0.05). Pastures abandoned for twelve or more years stored 1.5 Mg/ha more total N to 45 cm depth than

areas abandoned for two or fewer years (5.4 and 3.9 Mg N/ha). In all forests, surface nitrogen stocks (0–15 cm) represented ~40–45% of the total soil nitrogen to 45 cm depth (total 45 cm range: 3.3–5.5 Mg N/ha; Fig. 1).

Extractable soil P stocks to 45 cm tended to decline with increasing forest age (−0.66 kg·ha^{-1}·yr^{-1}), a trend most pronounced within the upper 0–15 cm. This surface layer represented 46–70% of total soil P stocks to 45 cm depth, with the younger areas, on average, storing 4.2 kg/ha more P in the first 15 cm than the oldest areas. Considering the entire measured soil profile (0–45 cm depth) higher extractable soil P stocks were observed in stands of 0–6 yr (11.5 ± 4.6 kg/ha) compared to stands of 6–14 yr (5.1 ± 2.1 kg/ha). Soil P in the 0–15 cm class was more variable than in deeper layers. K, Ca, and Mg stocks remained constant with time after abandonment (Table 2).

Total nutrient stocks

There was a significant net gain of total system nutrient stocks (in vegetation and soil) for all nutrients except P (Table 2); however, in soils alone, only N increased significantly. Total system N stocks increased most rapidly over time followed by Ca. The total system P accumulation rate was slow and reflective of the counteracting decrease in soil P stocks with increasing forest age.

Carbon sequestration

Standing biomass.—Average biomass accrual for all SF through the first 12–14 yr after pasture abandonment was 11.0 Mg·ha^{-1}·yr^{-1} (r^2 = 0.95, P < 0.001), or 5.6 Mg C·ha^{-1}·yr^{-1} (r^2 = 0.94, P < 0.001) (Fig. 1). The greatest total biomass (128.1 Mg/ha) was measured in a SF with 12–14 yr since abandonment; the areas abandoned 6–8 yr had an average biomass of 54.4 Mg/ha, while the areas abandoned 4–6 yr an average of 16.4 Mg/ha (Fig. 1). Woody biomass in the 10 SF by years after pasture abandonment was 0.0, 0.05, 12.92, 50.89, 120.92 Mg/ha in the forests of ages 0–2, 2–4, 4–6, 6–8, and 12–14 yr.

Soil carbon.—Soil C storage (excluding roots) tended to increase with forest age, with the oldest forests storing an average of 25 Mg/ha (65%) more total soil C to 45 cm depth than the youngest forests. Surface layers (0–15 cm) stored significantly more C (28.4 ± 2.4 Mg/ha) than deeper layers (18.3 ± 1.5 Mg/ha), from

TABLE 3.   Mean soil carbon and nutrient concentrations and pH from 10 secondary forests (SF) regenerating from degraded
pastures in Central Amazonia, Brazil.

SF age (yr)	Fazenda and forest no.	C (g/kg)	N (g/kg)
0–15 cm depth			
0–2	DAS-1 and Rodão-1	15.39 (2.27)	1.23 (0.13)
2–4	Rodão-4	20.77 (2.64)	1.25 (0.09)
4–6	DAS-2 and Rodão-3	20.71 (2.01)	1.42 (0.16)
6–8	Dimona-1, -3 and Rodão-2	22.91 (0.85)	1.49 (0.05)
12–14	DAS-3 and Dimona-2	19.51 (2.77)	1.75 (0.04)
Overall mean		20.19 (0.94)	1.46 (0.05)
15–30 cm depth			
0–2	DAS-1 and Rodão-1	9.17 (1.43)	0.74 (0.06)
2–4	Rodão-4	17.14 (0.70)	0.91 (0.06)
4–6	DAS-2 and Rodão-3	10.63 (1.08)	0.86 (0.08)
6–8	Dimona-1, -3 and Rodão-2	12.09 (0.55)	0.88 (0.02)
12–14	DAS-3 and Dimona-2	11.46 (0.76)	1.01 (0.01)
Overall mean		11.65 (0.52)	0.88 (0.03)
30–45 cm depth			
0–2	DAS-1 and Rodão-1	6.57 (0.57)	0.55 (0.02)
2–4	Rodão-4	12.25 (0.86)	0.65 (0.07)
4–6	DAS-2 and Rodão-3	10.84 (2.36)	0.65 (0.02)
6–8	Dimona-1, -3 and Rodão-2	8.12 (0.66)	0.69 (0.01)
12–14	DAS-3 and Dimona-2	16.08 (2.49)	0.77 (0.02)
Overall mean		10.46 (0.89)	0.67 (0.01)

Note: Mean values are $n = 4$ per depth in each forest from a composite of four to six subsamples per sample and summarized
by age class, for total C and N, Mehlich-I extractable P and exchangeable K, and exchangeable Ca and Mg. Standard errors
are reported in parentheses.

24 to 50% of the total soil carbon to 45 cm depth in
all forests ($P < 0.001$). However, the oldest forests,
12–14 yr old, stored as much carbon in the 30–45-cm
layer as in the 0–15-cm surface layer. Additionally, the
deeper soil profile (30–45 cm) was the only depth
showing significantly increasing C stocks with time
after abandonment ($r^2 = 0.21$, $P < 0.001$). Considering
all forests, total soil C to 45 cm depth increased non-
significantly at a rate of 1.49 Mg·ha^{-1}·yr^{-1} during the
first 12–14 yr of succession (Table 4).

Total carbon accrual.—In vegetation and soil (ex-
cluding roots), the 10 SFs accrued a total of 7.04 Mg
C·ha^{-1}·yr^{-1} during the first 12–14 yr after abandonment
($r^2 = 0.85$, $P < 0.001$) (Table 4).

DISCUSSION

Nutrient accrual

The vegetation withdrew large quantities of ex-
changeable Ca from low exchangeable soil Ca reserves,
as vegetation Ca stocks were accumulating most quick-
ly with forest age. Wood and foliage N:Ca ratios were
low, ranging from 0.7 to 1.4 for wood and 1.9 to 3.0
for foliage. In contrast, primary forest vegetation re-
ported N:Ca ratios were 3.1 for trunks, branches, and
coarse roots, and 4.4 for leaves (Fernandes et al. 1997).

The high rate of Ca immobilization in vegetation but
lack of reduced soil exchangeable Ca over time in our
study indicates that (1) soils adequately replenish im-
mobilized Ca from unavailable forms (Table 2); and/
or (2) the vegetation is withdrawing Ca from deeper
than 45 cm depth. A similar trend of a high percentage

of total system Ca content in vegetation and high Ca
uptake from low soil reserves of exchangeable Ca has
been reported for temperate forests (Johnson and Hen-
derson 1989). The highly weathered Oxisols of our
study provide negligible Ca from parent materials;
however, atmospheric deposition may replenish de-
pleted soil reserves by adding 0.8–12 kg·ha^{-1}·yr^{-1} (Vi-
tousek and Sanford 1986, Schroth et al. 2001). For
young tropical fallow vegetation, low root length den-
sity and low nutrient demand make Ca and nitrate ions
susceptible to downward movement (Szott et al. 1999);
these nutrients may be retrieved with increased rooting
depth in later successional stages. Trees have been re-
ported to increase soil nutrient availability over time
(Sanchez et al. 1985); and, net increases in total system
stocks of N and Ca have been observed in older fallows,
probably as a result of atmospheric deposition, N_2 fix-
ation, and uptake from subsoil (Szott et al. 1991). How-
ever, pasture soils were found to have higher exchange-
able soil Ca concentrations than plantations and SFs
(McGrath et al. 2001), indicating that after the initial
increase of soil Ca from cutting and burning, colonizing
trees act as sinks, reducing soil Ca. Although soil Ca
stocks are currently maintained in these SFs, the high
rate of Ca relocation from soil to vegetation, large veg-
etation Ca stocks, and high concentrations relative to
N indicate extreme Ca demands for biomass produc-
tion, which may create a soil Ca deficit and limit future
vegetation growth.

The rapid total soil N stock and N concentration
increase below 30 cm depth with forest age can be only

Table 3. Extended.

P (mg/kg)	K (mg/kg)	Ca (cmol$_{(+)}$/kg)	Mg (cmol$_{(+)}$/kg)	pH (KCl)
4.83 (0.57)	20.98 (2.40)	0.13 (0.02)	0.09 (0.01)	4.1 (0.03)
3.09 (0.17)	18.11 (0.82)	0.18 (0.01)	0.07 (<0.01)	4.0 (0.02)
6.30 (0.86)	33.20 (4.76)	0.16 (0.04)	0.14 (0.02)	4.0 (0.03)
2.46 (0.30)	23.92 (2.49)	0.33 (0.11)	0.18 (0.04)	4.0 (0.03)
1.55 (0.17)	19.45 (0.55)	0.16 (0.05)	0.11 (<0.01)	4.0 (0.01)
3.55 (0.36)	23.78 (1.52)	0.21 (0.04)	0.13 (0.02)	4.0 (0.01)
2.03 (0.53)	8.46 (0.71)	0.08 (0.01)	0.05 (<0.01)	4.2 (0.02)
1.87 (0.17)	10.53 (0.47)	0.11 (0.01)	0.05 (0.01)	4.2 (0.02)
1.40 (0.13)	10.86 (1.63)	0.08 (0.01)	0.05 (0.01)	4.1 (0.02)
0.86 (0.13)	11.19 (0.88)	0.05 (0.01)	0.04 (0.01)	4.1 (0.02)
0.70 (0.00)	8.56 (0.31)	0.07 (0.02)	0.05 (<0.01)	4.1 (0.02)
1.25 (0.13)	10.02 (0.48)	0.07 (0.01)	0.05 (<0.01)	4.1 (0.01)
1.15 (0.41)	5.56 (0.28)	0.06 (0.01)	0.04 (0.01)	4.2 (0.02)
1.15 (0.16)	7.14 (0.46)	0.10 (0.02)	0.04 (<0.01)	4.2 (0.02)
0.86 (0.09)	5.84 (0.97)	0.07 (0.01)	0.04 (<0.01)	4.2 (0.02)
0.39 (0.10)	6.28 (0.58)	0.05 (0.01)	0.04 (0.01)	4.1 (0.02)
0.58 (0.09)	5.84 (0.39)	0.05 (0.01)	0.04 (<0.01)	4.1 (0.01)
0.74 (0.09)	6.06 (0.28)	0.06 (0.01)	0.04 (<0.01)	4.2 (0.01)

partially explained by external inputs (Fig. 1, Table 3). Nitrogen-fixing plants may contribute 10–150 kg·ha^{-1}·yr^{-1} to soils (Fernandes et al. 1997, Szott et al. 1999) and atmospheric deposition may add 5.5–11.5 kg·ha^{-1}·yr^{-1} (Jordan et al. 1982, Vitousek and Sanford 1986, Schroth et al. 2001), explaining a fraction of the increasing total soil N. The remaining contribution to the high soil N accumulation rates could be subsoil mining of leached nitrate. Increasing extractable soil N with depth below topsoil has been measured in young SFs (J. Lehmann, *personal communication*); high deep-soil N concentrations may be attributable to leaching from surface layers after slash and burning and cropping, followed by a reduced nutrient capture potential of shallow rooted colonizing secondary vegetation. Primary forest also loses nitrate to the subsoil (Schroth et al. 1999). These large N pools were deep (1–2 m) and considered at the lower limit of uptake by young SFs. Leaching of surface N can be rapid in Oxisols because of the high macroporosity and hydraulic conductivity, but leaching below 0.6 m is delayed, apparently because of NO_3^- adsorption to the net positively charged subsoil (Melgar et al. 1992). Deep nutrient pools may provide a source of N as forests mature and root systems develop. Leaching of surface N (0–15 cm) to deeper layers could also explain the increase in N concentrations we observed below 30 cm depth with forest maturation. Unless deep N mining occurs with root development, N losses to subsoil due to leaching may negatively affect surface soil fertility.

Compared to primary forest nutrient storage in soil (of the total aboveground and soil stocks), the SF stored comparable amounts of N, less P, but more Ca. Soil storage of exchangeable Ca and total N in the oldest SF accounted for an average of 34% and 95% of total nutrient storage, respectively, but just under 25% of extractable P (Fig. 1). This contrasts with compartmentalization within primary vegetation, where soil

Table 4. Relationship between the number of years after pasture abandonment (*X*) and the accumulation of aboveground biomass and carbon and soil carbon (Mg·ha^{-1}·yr^{-1}) in 10 secondary forests regenerating from degraded pastures in Central Amazonia, Brazil.

Dependent variable	Equation	r^2	P
Biomass†			
Total foliage and wood	$Y = 11.0 X - 23.92$	0.95	<0.001
Carbon			
Total foliage and wood†	$Y = 5.55 X - 12.54$	0.94	<0.001
Total soil‡	$Y = 1.49 X + 5.59$	0.20	0.20
Total foliage, wood, and soil	$Y = 7.04 X + 43.31$	0.85	<0.001

† All live trees ≥1 cm dbh with biomass converted to C, based on site-specific foliage and wood C concentrations.
‡ Total soil C, excluding roots, to 45 cm depth.

storage of exchangeable Ca and total N may account for <1% and 73% of total nutrient storage, and extractable P in soil accounts for 69% of the total storage (Sanchez 1987).

Increases in soil nutrient concentrations are followed by greater vegetation tissue concentrations in successional vegetation. Secondary forest vegetation growing on nutrient-poor soil produced wood with three times less P and leaves with 50% less P than vegetation where soil P limitations were removed through P fertilizer additions (Gehring et al. 1999). The reduction in foliar P concentrations with increasing forest age observed in our study (Table 1) may indicate that this nutrient is becoming limiting as soil P levels decline (Fig. 1).

Total aboveground and soil nutrient stocks increased as forests matured; yet, for P, uptake and soil-P supply indicates a potential growth limitation. Concomitant decrease in extractable soil P and increase in biomass over time may be attributable to relocation from below- to aboveground pools. Plants appear to be taking up more soil P than is available (Table 2). This suggests a rapid transfer of soil P from plant unavailable to available forms or deep soil mining as the available pool is depleted with plant growth. However, subsoil-P retrieval probably contributes <1 kg·ha^{-1}·yr^{-1} (Szott et al. 1999). The net reduction in soil P stocks from the soil (0.66 kg P·ha^{-1}·yr^{-1}) with increasing forest age, indicates inadequate replacement of available soil P with plant P uptake, a trend also observed elsewhere (Johnson et al. 2001). Should this trend continue, P may become limiting to growth unless other factors (1) reduce P uptake by plants, (2) increase P uptake from subsoil, or (3) increase the rate at which unavailable forms of soil P shift to plant available P forms to replenish immobilized plant available soil P.

Pools of plant available (extractable) nutrients are significantly lower than the total in soils (Brown and Lugo 1990), and the plant availability of the soil P depends on the extent of fixation or immobilization. Phosphorus fixation for Oxisols is lower in the central Amazon Basin than for Oxisols in other regions of the Amazon; however, levels of plant available P in the soils are similar (Lehmann et al. 2001). Pasture grasses such as *Brachiaria* spp. may increase P availability by exuding acid phosphatase into the rhizosphere and hydrolyzing plant unavailable forms of organic phosphates (Dias-Filho et al. 2001), a benefit lost as secondary vegetation replaces the pasture grasses. Root associations with both vesicular arbuscular mycorrhizae and ectomycorrhizae may help the colonizing vegetation access P even at low soil P concentrations; and, in the case of ectomycorrhizae, to access P from poorly accessible pools (Boot et al. 1994). Since these colonizing species have the ability to take up P in excess of immediate growth requirements (Boot et al. 1994), P uptake by maturing trees may decline before plant levels become limiting to biomass accumulation. Fal-

low vegetation increased mineralizable N and available P compared to continuous cropping, probably as a result of deeper rooting (Tian et al. 2001). Additional research is needed to develop and evaluate management strategies that promote soil-P acquisition, such as increasing rooting depth of regenerating vegetation.

Carbon accrual

Aboveground.—Rapid biomass accrual in the SF, 11.0 Mg·ha^{-1}·yr^{-1}, was similar to other Amazonian findings (Uhl et al. 1988, Brown and Lugo 1990, Alves et al. 1997), lower than (Hartemink 2001), and higher than a 20-yr mean annual rate (6.17 Mg·ha^{-1}·yr^{-1}) in a review of tropical SF succession (Silver et al. 2000). C storage in the 12–14-yr-old areas represents 25–50% of equivalent primary forest biomass (230–500 Mg/ha) in Amazonia (Alves et al. 1997, Fujisaka et al. 1998, Laurance et al. 1999).

Aboveground carbon accrual slows with age as colonizing trees mature, die, and are replaced by slower growing species. Secondary forests in the Bragantina region of the Amazon Basin were accruing biomass more rapidly in 10-yr-old (5.5 Mg·ha^{-1}·yr^{-1}) than in the 20–40-yr-old SF (3.3 Mg·ha^{-1}·yr^{-1}) (Johnson et al. 2001). And a review of 44 secondary tropical forests showed wet forests accumulating biomass significantly faster during the first 20 of 80 years of regrowth (Silver et al. 2000). Their rates through the first 10 and 20 yr were still less than the rate we report through the first 12–14 yr (Table 4).

Belowground.—Our study indicates a trend of increasing soil C storage through the first 12–14 yr (Fig. 1); however, the soils are storing comparable to less C than other SF of similar or greater age (Silver et al. 2000, Johnson et al. 2001). Although our forests only showed a weak C-storage gain, other studies indicated that soil C storage (excluding roots) increases significantly with SF age, and can approach mature forests levels after 80 years of regrowth (Silver et al. 2000).

Contrary to aboveground biomass accumulation rates, which proceed faster in SF following agriculture (Fearnside and Guimaraes 1996), soils accumulate C almost twice as fast when regeneration follows pasture rather than agriculture, although this effect is only distinguishable after 20 years of recovery (Silver et al. 2000). Delays in aboveground C accrual with forest growth in early years following pasture abandonment may be offset, to a certain degree, by enhanced soil C accumulation.

Compared with soil-C storage in pasture (49.5 Mg/ha, 0–30 cm depth; Moraes et al. 1996), tropical plantation (90 Mg C/ha) and SF (61 Mg C/ha, 0–25 cm depth; Silver et al. 2000), the SF soils in this study were storing 47.9 Mg C/ha to 30 cm and 66.1 Mg C/ha to 45 cm depth. Since aboveground C accrual appears higher than other sites, and soil C lower than other SF sites, high litter turnover and soil respiration

rates at our sites may be reducing soil C residence time in this high rainfall area.

These factors pose important management implications to carbon sequestration. By choosing to maintain areas as pasture, directing SF colonization and succession after abandonment, or establishing plantations or agroforestry systems, land managers can influence the distribution of aboveground- and soil-C storage and the rate at which carbon accumulates within those pools. Maintaining the land cover as forest for longer time periods rather than as degraded pasture is a more favorable practice to increase C storage.

Predictive limitations

The ≥1-cm-dbh limitation imposed by the allometric equations may significantly underestimate biomass and nutrient stocks in the absence of root and biomass measurements of young SF vegetation <1 cm dbh. Deep-rooted grasses tend to allocate a significant portion of total plant biomass within root structures (Nepstad et al. 1994); and, necromass, shrubs, and herbaceous vegetation dominating early pasture succession and SF understories contribute considerable quantities to C and nutrient stocks, especially P (McKerrow 1992). Wood core measurements may overestimate nutrient concentrations in young stands since a greater portion of the sample core is nutrient rich bark. Also, although we located our abandoned pasture study sites on plateaus, the pastures span the rolling topography. Nutrient limitations may be more severe on hillsides where erosion is more pronounced and forest recovery slower than the rates we predict. The variable time that each SF remained as pasture before abandonment could also influence initial C and soil nutrient stocks and accumulation rates since pasture-use could have a positive, negative, or no effect on these variables. Since younger forests passed more time as pasture, pasture activities would be more pronounced, and thus more prone to influence C and nutrient accumulation rates in the younger SF than in the older forests. These management activities may explain some of the high variability in estimated C and nutrient accumulation rates over the range of the chronosequence.

Implications for succession, carbon sequestration, and nutrient barriers

After several decades of neotropical studies of SF regeneration, we still lack the ability to make strong predictions about nutrient storage and successional shifts in forest development, and regeneration times for abandoned pastureland to attain primary forest equivalent biomass. This is largely due to a historic research focus on forest succession following agriculture rather than pasture. Since biomass recovery is significantly slower following pasture than following agriculture (Fearnside and Guimaraes 1996, Steininger 2000), it is important to increase our understanding of pasture succession and determine potential nutrient limitations.

The paucity of forest recovery studies on abandoned pastureland and lack of detailed soil C and nutrient data make predicting forest regeneration on highly altered lands difficult. In a review of SF biomass accumulation (Silver et al. 2000), only 13% of the SFs (18 of 134) were previously pastures. Additional data from SFs regenerating from pasture are needed to determine long-term C accumulation rates, potential nutrient limitations for regeneration, and the time needed to attain both structural and functional properties of mature forests. This is especially relevant since primary forest biomass is positively associated with soil nutrient levels, suggesting that soil nutrient loss through pasture installation may result in lower mature regenerated forest biomass than the original forest (Laurance et al. 1999). Although studies such as ours help to fill this void, there is a need for long-term rather than chronosequential studies of forest recovery following pasture abandonment.

SUMMARY

In this study, we show that during early successional years, biomass accumulation in light to moderately used pastures is rapid after abandonment, and that soil C storage is higher in older forests. However, a slower soil C accrual rate than in regenerating SFs in other regions may negatively offset total long-term C gains. The higher proportion of soil C storage compared to aboveground pools will be an important consideration of future ''carbon credit'' management, as this pool is more recalcitrant to perturbations. Aboveground C reaccumulation from post-burn values is high, yet represents a finite pool which is rapidly attained in a relatively short time period. Managing forest regeneration to maximize soil C storage, rather than aboveground pools, may prove to be more useful or meaningful when attempting to increase SF C sequestration.

Furthermore, the colonizing vegetation can extract large nutrient quantities from the soil, even when in low supply. In addition to a shift of nutrients from soil to aboveground pools, total system nutrient stocks were increasing over time. Within the oldest forests, most of the C and N were stored within the soil, while P, K, Mg, and Ca resided within the vegetation. This has important consequences to total forest nutrient stocks, in the event of removal of aboveground vegetation. In the absence of nutrient additions, removal of the vegetation a second time (e.g., pasture reclearing or logging) could compromise the SF potential to regenerate as a result of nutrient limitations. Even after P fertilization when the areas were pasture, soil P stocks remained low. The vegetation was withdrawing more soil P than could be replenished, creating a soil P deficit which may limit system productivity. Low exchangeable-soil-Ca stocks seemed to be adequately replaced,

apparently from atmospheric inputs and depths below 45 cm, as growing vegetation took up large nutrient quantities. Nevertheless, as vegetation Ca demands were high and soil stocks low, lack of Ca may limit future productivity.

These results demonstrate the regenerative capacity of tropical SFs to sequester C and to rebuild the nutrient capital following pasture abandonment. Aboveground carbon accrual is rapid but belowground gains represent the largest potential area for continued accumulation and management. Relocation of some nutrients from deeper soil layers may represent a substantial source of nutrients for plant growth and may be vital to sustaining long-term productivity and biomass accumulation. We recommend additional studies to explore P and Ca nutrient limitations to forest productivity and long-term measurements of soil nutrient fluxes and forest growth. Understanding nutrient limitations to resource capture will provide new options to manage forest regeneration and increase C accumulation on these globally important nutrient-limited soils.

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