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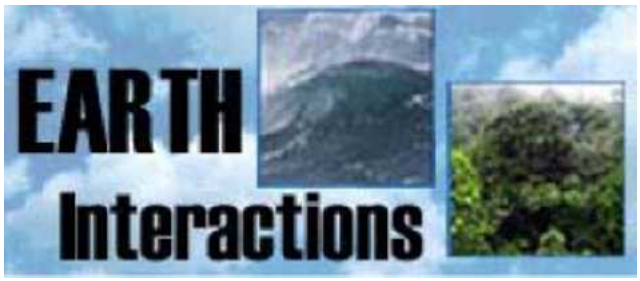

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Development of Forest Structure and Leaf Area in Secondary Forests Regenerating on Abandoned Pastures in Central Amazônia

Ted R. Feldpausch*

Department of Crop and Soil Sciences, Cornell University, Ithaca, New York

Susan J. Riha

Department of Earth and Atmospheric Sciences, Cornell University, Ithaca, New York

Erick C. M. Fernandes

Department of Crop and Soil Sciences, Cornell University, Ithaca, New York

Elisa V. Wandelli

Embrapa Amazônia Ocidental, Manaus, Brazil

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ABSTRACT: The area of secondary forest (SF) regenerating from pastures is increasing in the Amazon basin; however, the return of forest and canopy structure following abandonment is not well understood. This study examined the development of leaf area index (LAI), canopy cover, aboveground biomass,

* Corresponding author address: Ted R. Feldpausch, Department of Earth and Atmospheric Sciences, College of Agriculture and Life Sciences, Cornell University, 1126 Bradfield Hall, Ithaca, NY 14853.

E-mail address: trf2@cornell.edu

stem density, diameter at breast height (DBH), and basal area (BA) by growth form and diameter class for 10 SFs regenerating from abandoned pastures. Biomass accrual was tree dominated, constituting ≥94% of the total measured biomass in all forests abandoned ≥4 to 6 yr. Vine biomass increased with forest age, but its relative contribution to total biomass decreased with time. The forests were dominated by the tree *Vismia* spp. (>50%). Tree stem density peaked after 6 to 8 yr (10 320 stems per hectare) before declining by 42% in the 12- to 14-yr-old SFs. Small-diameter tree stems in the 1–5-cm size class composed >58% of the total stems for all forests. After 12 to 14 yr, there was no significant leaf area below 150-cm height. Leaf area return (LAI = 3.2 after 12 to 14 yr) relative to biomass was slower than literature-reported recovery following slash-and-burn, where LAI can reach primary forest levels (LAI = 4–6) in 5 yr. After 12 to 14 yr, the colonizing vegetation returned some components of forest structure to values reported for primary forest. Basal area and LAI were 50%–60%, canopy cover and stem density were nearly 100%, and the rapid tree-dominated biomass accrual was 25%–50% of values reported for primary forest. Biomass accumulation may reach an asymptote earlier than expected because of even-aged, monospecific, untiered stand structure. The very slow leaf area accumulation relative to biomass and to reported values for recovery following slash-and-burn indicates a different canopy development pathway that warrants further investigation of causes (e.g., nutrient limitations, competition) and effects on processes such as evapotranspiration and soil water uptake, which would influence long-term recovery rates and have regional implications.

KEYWORDS: Deforestation; Succession; Land-cover change

1. Introduction

As the largest remaining expanse of contiguous tropical rainforest, the forests of the Amazon basin have an important global function. The removal of primary forest cover, 6.7×10^6 hectares between 2001 and 2003 for Brazilian Amazônia [(Instituto Nacional de Pesouisas Espaciais) INPE 2004], has been predominately for pasture development (Moran et al. 1994; Fearnside 1996) as well as cropping and timber harvest. Deforestation has left large areas of the Amazon basin in various states of management, degradation, abandonment, or spontaneous forest recovery. Primary forest conversion to pasture differs from traditional slash-and-burn agriculture in that the patch of land cleared, the intensity of disturbance, and the time interval of use are greater for pasture (Uhl et al. 1988). Forest recovery following slash-and-burn agriculture, the predominant historical anthropogenic disturbance in the Amazon basin, has been well studied (Ewel 1971; Uhl et al. 1981; Uhl 1987; Saldarriaga et al. 1988; Brown and Lugo 1990; Kennard 2002). Pasture formation and abandonment, however, are relatively recent phenomena in tropical wet forests of the Amazon basin. The redevelopment of forest structure on abandoned pastures (Uhl et al. 1988; Honzák et al. 1996; Steininger 2000; Lucas et al. 2002; Davidson et al. 2004), in particular canopy structure and leaf area index (LAI) in central Amazônia, has received less attention than recovery following slash-and-burn agriculture.

Well-managed pastures in the Amazon have been reported to remain productive for 20 yr or more. In these pastures, burning is avoided and forage productivity is maintained via adequate stocking rates and cattle rotation. In many cases, however,

crude establishment techniques (Fernandes et al. 1997; Kauffman et al. 1998) and subsequent mismanagement (Serrão et al. 1993) result in nutrient loss and rapid pasture degradation and abandonment. The invasion of unpalatable plants into pastures reduces the forage to weed ratio, contributing to grass decline and eventual abandonment. Typical pasture management in the region includes hand weeding and burning to maintain grass productivity and to discourage the regrowth of aggressive forb and tree species. Pastures planted to *Panicum maximum* Jacq. or *Brachiaria* spp. may lose vigor within 3 to 8 yr (Uhl et al. 1988; Serrão et al. 1993) because of nutrient limitations, and the "degraded" pastures may be abandoned. The pastures may then be left indefinitely to the development of secondary vegetation or cleared after <6 yr of fallow regrowth for a cropping cycle or pasture reestablishment (Guimarães 1993).

Woody plant invasion may be delayed for many years on some abandoned pastures (Aide et al. 1995), although in general, despite losses of grass productivity, the invading woody secondary vegetation appears highly productive rather than inhibited (Uhl et al. 1988; Steininger 2000; Feldpausch et al. 2004). Seed bank impoverishment in the pasture soils affects species composition of the regenerating secondary forest (SF); (Vieira et al. 1994), and seedling establishment can be impeded because of herbivory and soil moisture stress (Nepstad et al. 1996). The development of roots suckers and sprouts from stumps may be an important source of stem development in young fallows (Kammesheidt 1998).

The effect of land use on regrowth remains controversial. Some intensively used pastures develop biomass more slowly compared to those subjected to slash-and-burn agriculture (Aide et al. 1995; Fearnside and Guimaraes 1996). Biomass recovery rates for other SFs, however, do not differ by land use (Steininger 2000; Zarin et al. 2001). Despite the debate over type of land use, biomass accumulation remains higher in lightly used pasture (Uhl et al. 1988; Steininger 2000; Feldpausch et al. 2004) than following extended land use as pasture (Uhl et al. 1988).

Understanding recovery processes becomes more complicated as the focus shifts from biomass alone to forest and canopy structure, species composition, the expression of dominance, and self-thinning. In a review of secondary forest growth, Guariguata and Ostertag (Guariguata and Ostertag 2001) reported a lack of detailed information about the light environment, senescence, and gap formation of secondary stands. In a second review, Finegan (Finegan 1996) concluded that we still have a poor understanding of the population dynamics of early succession, in particular, the replacement of short-lived by long-lived pioneers. Recent research in central Amazônia indicated that land use may have a significant effect on successional pathways. For example, Mesquita et al. (Mesquita et al. 2001) reported *Vismia* dominated succession following pasture abandonment and *Cecropia* dominated following slash-and-burn alone. This pattern may affect stand structure for at least 30 yr (Lucas et al. 2002). The length of land use, rather than the type of land use, may be more important to predict stand structure (Gehring et al. 2005). The early development of forest structure and the expression of dominance may have a long-term effect on the time needed for these forests to develop characteristics typical of primary forests.

Determining the rates and pathways of forest structure recovery following pasture abandonment is important to understanding how these regenerating forests capture nutrients and light, evapotranspire, shift from early pioneer to late sec-

ondary to primary forest species, and redevelop primary forest function. Our objective was to determine the patterns of secondary forest regeneration on abandoned pastures. Specifically, we examined 1) the nature and rate of forest structure, LAI, and canopy structure development following pasture abandonment, and 2) the role of plant growth form (i.e., tree, shrub, and vine) on the redevelopment of structure. We determined LAI, canopy cover, aboveground biomass, plant stem density, and basal area by diameter classes and growth form for 10 forests regenerating from abandoned pastures on oxisols in an udic soil moisture regime to complement published studies on oxisols and ultisols in the seasonally drier ustic soil moisture regime in eastern Amazônia.

2. Methods

2.1. Study areas

The study was conducted at three fazendas (cattle ranches) spanning approximately 26 km along the federal road BR-174 from Manaus to Boa Vista: Fazenda Rodão (km 46), the Brazilian Agricultural Research Corporation (Embrapa Amazônia Ocidental) Superintendência da Zona Franca de Manaus (SUFRAMA) Distrito Agropecuário de SUFRAMA (DAS) research site (km 53), and Fazenda Dimona (km 72), Brazil, in central Amazônia (spanning 2°34′S, 60°02′W to 2°20′S, 60°04′W). Average annual rainfall in Manaus is 2200 mm, with over 300 mm month^{-1} of precipitation during the wettest months of March and April, and a mild dry season from August to October, when mean monthly precipitation falls to <100 mm (Ribeiro and Adis 1984). Undulating terrain characterizes the landscape with an elevation of 50–150 m above sea level. The plateau soil on which the study sites are located is classified as dystrophic, isohyperthermic, clayey kaolinitic, Hapludox (*latossolo amarelo* according to the Brazilian soil classification system). Detailed soil carbon and nutrient data for each forest in this study were presented by Feldpausch et al. (Feldpausch et al. 2004) (appendix). They reported calcium and phosphorus were low in both surface- and subsoil for all forests, and Mehlich-I extracted soil phosphorus concentrations declined over time, possibly because of uptake by fast-growing vegetation.

The old-growth, closed-canopy, dense, evergreen terra firme forest of the region remains the dominant land cover but is punctuated by open grassy hillsides and plateaus where the primary forest was cleared and cattle still, or once, grazed. Most of the cattle ranches are in some state of decline, conversion to plantations or other land use, or abandoned to secondary vegetation. Secondary forests are increasingly found along the primary roads where efforts to raise cattle on large ranches ended 10 to 20 yr ago. The primary forest was cleared in the early 1980s, and the clay, nutrient-deficient soil was sown with hardy African grasses such as *Brachiaria humidicola* (Rendle) Schweick. Many of the trunks and stumps—intact or undergoing termite degradation—are still visible in the pastures and the SFs in areas that were not mechanically cleared. Earthen mounds indicate where windrows were created when primary forest vegetation was pushed to field margins.

2.2. Site and plot selection

We selected 10 abandoned pastures reverting to SFs within the three fazendas. These fazendas represented typical management intensities and methodologies for

the area, with light to moderate grazing of less than 10 yr. Within each forest located on plateau oxisols with similar soil texture (~65%–90% clay in the top 50 cm), we established 12 parcels of 5 m × 7 m to 10 m × 10 m for a total of 0.56 ha measured for the 10 fazendas (Table 1). Younger sites had more heterogeneous vegetation (i.e., patchy with "islands" of emerging colonizing woody vegetation). We conducted farmer interviews to determine management histories and when grazing was abandoned. Defining "abandoned" is problematic since there may be an infrequent rotation of temporary contract grazing of a few cattle. The abandonment date is then indefinite since cattle may periodically graze the area until all palatable forage is replaced by woody successional vegetation. To address this issue, we present the data as age classes, rather than purport to define a fixed abandonment date. The regenerating forests within each fazenda represented individual pastures that were abandoned from 0–2 to 12–14 yr. Despite the major limitations of unknown management histories, carefully selected chronosequences can be cost-effective substitutes for expensive, long-term studies to measure the return of forest form and function.

2.3. Leaf area index and canopy openness

LAI, a measure of the one-sided leaf surface area per unit ground area, is a useful indicator of the potential of vegetation to exchange gas and capture photosynthetically active radiation. We measured LAI in December, two months after the onset of the wet season at random locations within each parcel per forest. Using a portable electronic digital handheld hemispheric (fisheye) lens (CI-110; CID, Inc., Vancouver, Washington) with the plane of the lens set parallel to the ground, we photographed at 5- and 150-cm height. This resulted in 12 LAI images per forest per height (240 total images). The differing measurement heights, 5 and 150 cm, allow the distinction of understory (leaf area below 150-cm height) and overstory leaf area. Strong direct sunlight is an impediment to obtaining accurate, high-resolution photos. To record the highest quality photos, we photographed using incident light during morning and evening twilight hours.

Leaf area index was calculated from the digital photos using the CI-110 software (version 3.0.1.1) on a high-resolution liquid crystal display (LCD) monitor. We reduced the image field of view from 180° to 150° to reduce the misclassification of stems as leaves. After setting an image-specific threshold to define leaf borders and differentiate between sky and leaf margins, the software uses inverse

Table 1. Experimental layout: Fazenda, years abandoned, number of parcels per fazenda, and total area sampled per age class.

Year (fazenda)	No. of parcels per fazenda	Parcel size (m)	Area sampled per fazenda (m^2)	Total area sampled per age class (ha)
0 to 2 (DAS-1 and Rodão-1)	12	10 × 10	1200	0.24
2 to 4 (Rodão-4)	12	10 × 10	1200	0.12
4 to 6 (DAS-2 and Rodão-3)	12	4 × 5	240	0.50
6 to 8 (Dimona-1, -3, and Rodão-2)	12	4 × 5	240	0.70
12 to 14 (DAS-3 and Dimona-2)	12	5 × 7	420	0.08
Total	120			0.56

gap-fraction analysis to calculate LAI for each image (Norman and Campbell 1989). Canopy cover, a measure of the percentage of leaf cover obscuring open sky as viewed from the ground, was calculated from the same digital photos with the software Gap Light Analyzer 2.0 (Frazer et al. 1999). Canopy cover was calculated using the canopy gap diffuse data, the fraction of pixels in each sky region that are open (white) on the fisheye photograph, weighted by hemispherical area.

2.4. Forest structure and biomass

We partitioned stem density, basal area (BA), biomass by vegetation growth form (tree, shrub, and vine), and diameter class [1 to 5, >5 to 10, >10 to 20, >20 cm diameter at breast height (DBH)]. Stand-level biomass and nutrient stock estimates for these forests were reported by Feldpausch et al. (Feldpausch et al. 2004). To generate a stand-level biomass estimate, they measured DBH (at 1.3 m above ground level or immediately above the buttress or prop roots) for all live tree stems $\geq$1 cm within each subplot. In addition, we measured all vine and shrub stem DBH at 1.3-m height within each subplot, enumerated, and painted the DBH measurement height for future measurements. Vines included herbaceous leafy climbers and the mostly woody bare-stemmed larger lianas (Hegarty and Caballé 1991). Using the individual tree and shrub DBH measurements, we calculated dry biomass by life-form and diameter class using two sets of allometric equations, Nelson et al. (Nelson et al. 1999) for stems >5 cm DBH and R. Mesquita (2005, personal communication) for those 1–5-cm DBH. Basal area provides a stand-level index of growth and dominance (Uhl and Jordan 1984). We calculated mean BA for all stems by converting individual stem DBH to the cross-sectional area and summing the values (m^2 ha^{-1}). Using an allometric equation for vines constructed from Amazônian terra firme sites (Putz 1983), we converted individual vine BA to dry biomass.

Since we focus on stem density and biomass for trees, vines, and shrubs $\geq$1 cm DBH, our estimates underrepresented total aboveground biomass and stem density (e.g., grasses and sedges, herbaceous, standing dead, stems < 1 cm DBH, etc.). Statistical analyses were performed using the software Minitab 13.1 (Minitab 2000). Not all SF age classes occurred at all fazendas, so that we had an incomplete sampling design. The data were tested for normality and homogeneity of variance. Log transformations were necessary to normalize some data. The data were partitioned by vegetation growth form (tree, shrub, vine). Trends were analyzed using analysis of variance (ANOVA) and regression analysis, with LAI, canopy openness, basal area, biomass, DBH, and stem density as the response variables by time after pasture abandonment (midpoint of each age class).

3. Results

3.1. Plant community transition

Across the successional sequence spanning more than a decade, the pioneering vegetation converted the abandoned pastures from a low biomass, grass–forb–shrub-dominated community with species from the genera *Borreria* (Rubiaceae),

Brachiaria (Poaceae), *Clidemia* (Melastomataceae), *Lantana* (Verbenaceae), *Piper* (Piperaceae), and *Rolandra* (Asteraceae) to a high biomass, closed canopy tree-dominated community (Figure 1a). The low-stature ground cover invading the pastures (0 to 4 yr) was replaced by high tree density (6 to 8 yr), which later thinned with the closing tree canopy (12 to 14 yr); (Figure 1b). The forests were dominated by tree species from the genus *Vismia* [Clusiaceae; mainly *V. cayennensis* (Jacq.) Pers., *V. japurensis* Reich.]. Other common genera included *Cecropia* (Moraceae; mainly *C. sciadophylla* Mart. and *C. purpurascens* C.C. Berg); *Bellucia* (Melastomataceae); *Laetia procera* (Poepp.) Eichler (Flacourtiaceae); and *Goupia glabra* Aubl. (Celastraceae). No palms occurred in the plots and were rare to absent in the SFs.

3.2. Forest structure

3.2.1. Stem density

A total of 1763 living stems ≥1 cm DBH were measured in the 10 SFs, of which 1499 were trees, 87 were shrubs, and 177 were vines (Table 2). Of all trees ≥1 cm DBH, 50%–85% were from the genus *Vismia* in all but one forest. There was a prevalence of tree stems in the 1–5-cm DBH class for all forests, with >58% of the stems always in this class, even in the most mature forest (Figure 2a). All tree stems in the 2- to 4-yr-old forests fell into this size class, and stem occurrence in this class peaked at 6 to 8 yr with 8070 ± 2081 stems per hectare before declining by 57% in the oldest forests. The number of tree stems per hectare in the oldest forests (12 to 14 yr) declined by one-half with each 5-cm increase in size class.

Considering growth-form stem density, trees dominated all forests ≥4 to 6 yr. Tree stem density followed a modal distribution over time, increasing to 10 320 ± 2389 stems per hectare after 6 to 8 yr before declining by 42% over the next 6 yr (Figure 1b). Shrubs accounted for 80% of the total stems in the 2- to 4-yr-old forest, increased to a maximum density 4 to 6 yr following pasture abandonment (1500 ± 375 stems per hectare; 22% of the total), before rapidly declining to less than 24 stems per hectare in the oldest forests. Vine stem density, unlike trees and shrubs, continued to increase over time, from 8% of the total stems in the 6- to 8-yr-old forests to 17% of the total in the 12- to 14-yr-old forests (Figure 1b).

3.2.2. Basal area

Total BA per hectare, including trees, shrubs, and vines, increased rapidly with time ($R^2 = 0.94$, $p < 0.08$), almost identical to tree BA alone (Figure 1c). The 12- to 14-yr-old forests had 42% more BA than the 6- to 8-yr-old forests. Shrubs accounted for 77% of the total BA in the 2- to 4-yr-old forests and less than 1% in the ≥6- to 8-yr-old forests. Vines contributed little to BA, even in the oldest forests (1.5% of total BA); (Figure 1c). Tree stem girth growth in the forests of this study was delayed until 4 to 6 yr following pasture abandonment, when a large uniform cohort of individuals simultaneously matured into the 1- to 5-cm DBH class (Figure 2a). After 12 to 14 yr, mean tree DBH was 5.8 ± 0.4 cm and mean vine diameter was about 2 cm. No trees were >30 cm and no vines were >4.7 cm DBH in any of the forests.

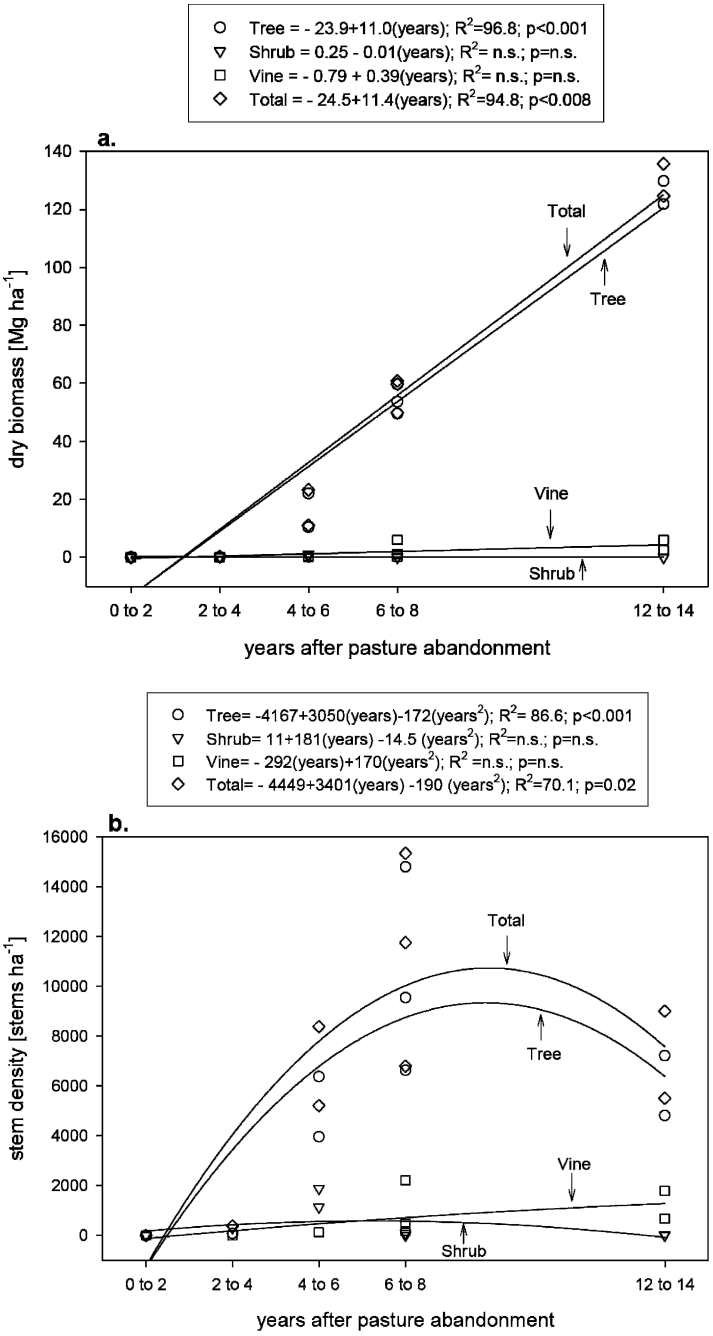

Figure 1. Relationship between years after pasture abandonment (X) and forest and canopy structure (Y) for (a) aboveground biomass (Mg ha^{-1}), (b) stem density (stems per hectare), (c) basal area (m^2 ha^{-1}), and (d) LAI for 10 secondary forests regenerating from abandoned pastures in central Amazônia, Brazil. The midpoint of each age class was used as the predictor in the regression analysis. The lines represent best-fit lines. The data is partitioned by (a)–(c) growth form and (d) the shrub layer (5–150-cm height), canopy (≥150 cm height), and total (≥5 cm height).

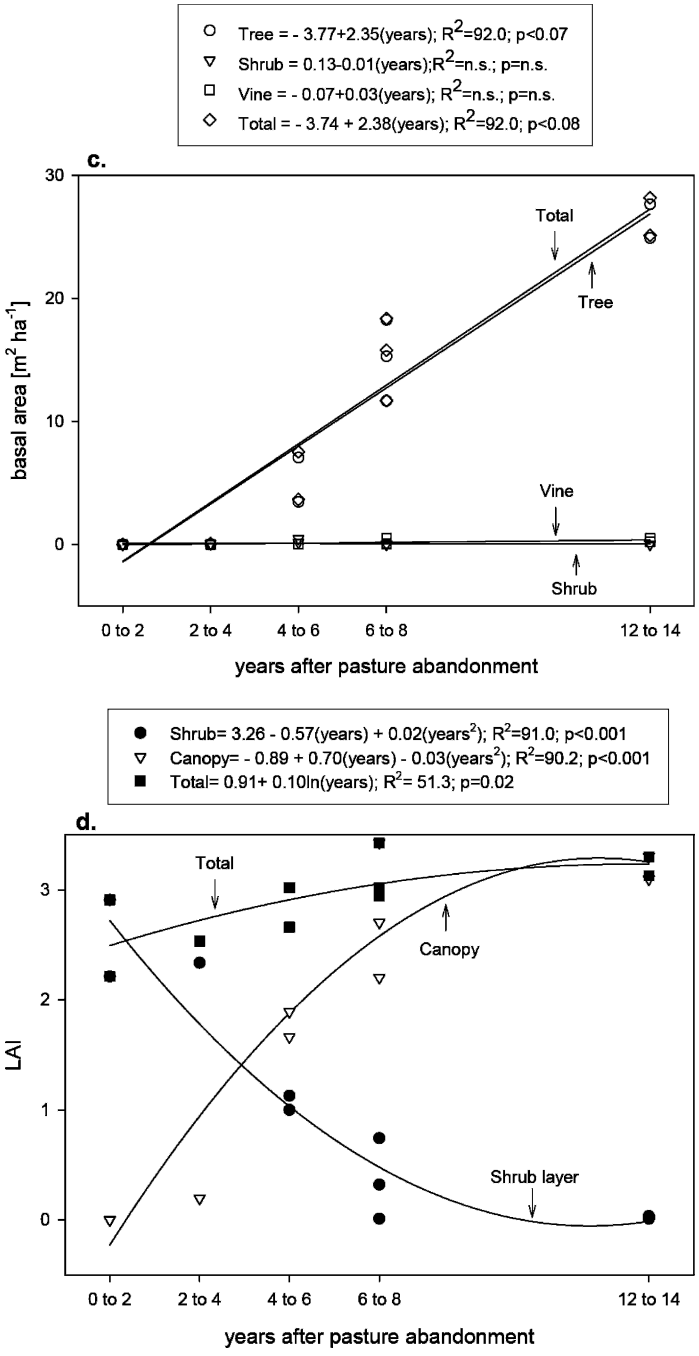

Figure 1. *(Continued)*

3.2.3. Biomass

Nonwoody genera dominated the recently abandoned areas, and shrubs only contributed significant biomass in the 2- to 4-yr-old forests (74% of the total). In the more mature forests (>4 yr), trees contributed more than 94% of the total biomass

Table 2. Mean dry biomass (Mg ha^{-1}), DBH (cm), stem density (stem ha^{-1}), and basal area (m^2 ha^{-1}) by growth form for all live stems ≥1 cm DBH for 10 secondary forests regenerating from abandoned pastures in central Amazônia, Brazil. Mean (±SE).

	Biomass				DBH		
Year and (fazenda)	Tree	Shrub	Vine	Total	Tree	Shrub	Vine
0 to 2 (DAS-1, Rodão-1)*	0	0	0	0	0	0	0
2 to 4 (Rodão-4)	0.08 (0.05)	0.18 (0.10)	0	0.25 (0.13)	0.86 (0.52)	0.73 (0.43)	0
4 to 6 (DAS-2)	22.27 (3.06)	1.10 (0.54)	0.20 (0.08)	23.62 (3.11)	3.05 (0.30)	1.81 (0.10)	0.95 (0.34)
4 to 6 (Rodão-3)	10.45 (2.59)	0.35 (0.15)	0.38 (0.23)	11.18 (2.58)	2.88 (0.29)	1.00 (0.34)	0.89 (0.51)
6 to 8 (Dimona-1)	54.00 (14.50)	0	6.05 (0.50)	60.00 (14.00)	3.88 (0.36)	0	1.65 (0.12)
6 to 8 (Dimona-3)	49.80 (12.90)	0	0.23 (0.17)	50.00 (12.80)	3.80 (0.37)	0	0.59 (0.34)
6 to 8 (Rodão-2)	59.25 (8.72)	0.03 (0.03)	1.10 (0.49)	60.38 (8.92)	3.57 (0.12)	0.38 (0.38)	1.42 (0.089)
12 to 14 (DAS-3)	120.6 (10.40)	0	2.55 (1.18)	123.40 (10.30)	6.23 (0.21)	0.37 (0.37)	2.03 (0.16)
12 to 14 (Dimona-2)	128.1 (30.70)	0	6.00 (2.14)	134.10 (31.80)	5.39 (0.26)	0	1.65 (0.18)

	Stem density				Basal area			
Year and (fazenda)	Tree	Shrub	Vine	Total	Tree	Shrub	Vine	Total
0 to 2 (DAS-1, Rodão-1)*	0	0	0	0	0	0	0	0
2 to 4 (Rodão-4)	75 (50)	300 (173)	0	375 (165)	0	0.1 (0.03)	0	0.1 (0.1)
4 to 6 (DAS-2)	6375 (463)	1875 (949)	125 (42)	8375 (1239)	7.0 (0.9)	0.5 (0.2)	0	7.6 (1.0)
4 to 6 (Rodão-3)	3958 (571)	1125 (416)	125 (80)	5208 (632)	3.5 (0.8)	0.2 (0.1)	0.03 (0.03)	3.7 (0.8)
6 to 8 (Dimona-1)	9542 (1096)	0	2208 (602)	11750 (1013)	15.3 (3.5)	0	0.5 (0.05)	15.8 (3.5)
6 to 8 (Dimona-3)	6625 (1244)	0	167 (118)	6791 (1322)	11.7 (1.5)	0	0.03 (0.03)	11.7 (1.5)
6 to 8 (Rodão-2)	14792 (2367)	83.3 (83)	458 (172)	15333 (2493)	18.3 (2.2)	0.03 (0.03)	0.08 (0.05)	18.4 (2.2)
12 to 14 (DAS-3)	4810 (499)	23.8 (24)	666 (358)	5500 (738)	24.9 (2.2)	0	0.2 (0.1)	25.1 (2.2)
12 to 14 (Dimona-2)	7214 (798)	0	1786 (437)	9000 (1130)	27.7 (5.9)	0	0.6 (0.2)	28.2 (6.0)

* Sites in the 0- to 2-yr age class lacked stems ≥1 cm DBH.

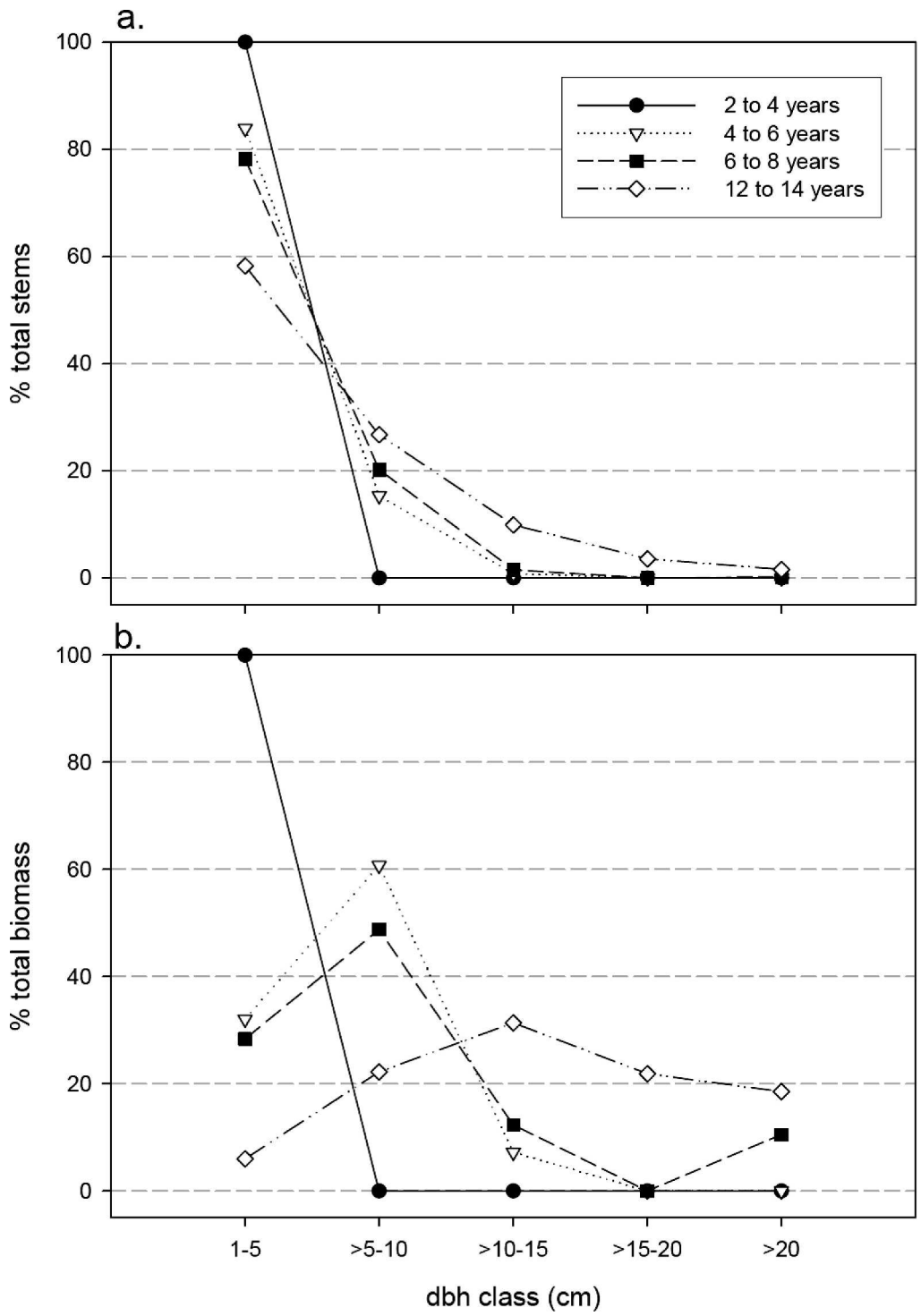

Figure 2. Distributions in 5-cm DBH classes of the mean (a) percent of total tree stems and (b) percent of total dry tree biomass in 10 secondary forests regenerating from abandoned pastures in central Amazônia, Brazil (live trees ≥1 cm DBH). Sites in the 0- to 2-yr age class lacked stems ≥1 cm DBH.

(Figure 1a). Total vine biomass increased with forest age, although its relative contribution to total biomass decreased from the 6- to 8-yr-old (4.4%) to the 12- to 14-yr-old forests (3.3%). During that same period tree biomass more than doubled (Figure 1a). Biomass was concentrated in the 1–5-cm DBH class in the younger forests (Figure 2b). With time, biomass was concentrated in subsequently larger DBH classes, with the highest concentration in the >10 to 15 cm DBH class. For example, in the 2- to 4-yr-old forests, 100% (0.1 Mg ha^{-1}) of the biomass was in the 1- to 5-cm DBH diameter class. In the 6- to 8-yr-old forest 60% of the total biomass was in the >5 to 10 cm DBH class. By 12 to 14 yr after pasture abandonment, biomass was distributed among all diameter classes, with a slightly greater dominance (31%) in the >10 to 15 cm DBH class (Figure 2b).

3.3. Canopy structure

3.3.1. Leaf area index

The three recently abandoned areas (0 to 4 yr) had a dense grass and shrub layer <150 cm tall that persisted until the woody vegetation invaded and the canopy closed. This shrub layer resulted in a high leaf area index at 5- to 150-cm height, comparable to the LAI >150 cm height in the tree-dominated stands ≥ 6 to 8 yr old (Figure 1d). The first contribution to canopy LAI ≥150 cm height began 2 to 4 yr after pasture abandonment, and by 4 to 6 yr more than half of the total leaf area was located ≥150 cm height. After 12 to 14 yr of pasture abandonment, there was a complete loss of a significant shrub layer in the forests, with all leaf area (LAI = 3.2) represented above 150-cm height (Figure 1d). Over 12 to 14 yr of succession, total LAI values (>5 cm height) increased from LAI = 2.7 in the most recently abandoned areas to LAI = 3.2 in the oldest.

The LAI above 150-cm height was strongly positively related with total BA [LAI = 1.60 + 0.40ln(BA); $R^2 = 91.0$, $p < 0.001$] and with total biomass [LAI = 1.27 + 0.34ln(biomass); $R^2 = 88.8$; $p < 0.001$]. The LAI development ≥150 cm height was asymptotic, with LAI only increasing by 0.4 between 6 to 8 and 12 to 14 yr. The LAI below 150-cm height was inversely related to BA and biomass accumulation.

3.3.2. Canopy cover

Total cover (>5 cm height) varied little with forest development, beginning high (84%) in the grass–forb-dominated recently abandoned pastures and increasing to 94% in the oldest forests. The contribution to total cover by ground vegetation or canopy vegetation, however, changed dramatically (Table 3). In the recently abandoned pastures, 100% of the total cover was attributable to the grass–forb–shrub complex 5–150-cm height because of the absence of mature trees, but below canopy cover steadily declined to zero in the tree-dominated 12- to 14-yr-old forests. In the 2- to 4-yr-old forests canopy vegetation contributed 18% to the total cover. By 6 to 8 yr after abandonment, the canopy contributed 94% of the total cover. Canopy cover increased by more than 50% between the 2- to 4-yr old and 4- to 6-yr-old forests, but only increased by <25% over the next 8 to 10 yr, revealing the dominance of woody vegetation and full closure of the vegetation ≥150 cm height in the 12- to 14-yr-old forests.

Table 3. Vegetation cover (%) partitioned by total (>5 cm height), shrub layer (5–150-cm height), and canopy (≥150 cm height) in 10 secondary forests regenerating from abandoned pastures in central Amazônia, Brazil. Mean (±SE).

Year (fazenda)	Shrub layer	Canopy	Total
Intensive pasture*	84.0	0	84.0
0 to 2 (DAS-1 and Rodão-1)	84.4 (10.7)	0	84.4 (10.7)
2 to 4 (Rodão-4)	69.4	18.1	87.5
4 to 6 (DAS-2 and Rodão-3)	21.1 (8.7)	70.9 (10.9)	91.9 (2.2)
6 to 8 (Dimona-1, -3, and Rodão-2)	2.6 (2.4)	91.1 (3.7)	93.8 (1.3)
12 to 14 (DAS-3 and Dimona-2)	0 (0.2)	94.2 (1.0)	94.2 (0.8)

* Historic measurements for active pasture at Fazenda Dimona (from McWilliam et al. 1993).

4. Discussion

4.1. Forest structure development

When actively grazed, the areas we studied that are now abandoned had 84% grass, 11% bare soil, 5% trunk, and <1% shrub cover (Wright et al. 1992). The invading secondary vegetation rapidly altered previous pasture conditions, with the development of high tree stem densities and forest canopy cover (Table 3; Figure 1). A review of biomass accumulation in SF in Amazônia indicated that there is still no consensus as to the effect of land use on biomass accumulation rates. Zarin et al. (Zarin et al. 2001) suggested there is no difference between recovery following slash-and-burn and recovery following pastures, and Steininger (Steininger 2000) reported that biomass accrual on pastures can lag behind recovery from abandoned crop cultivation. The controlling factor may not be time, but rather burn frequency, since biomass accumulates more slowly in areas burned 5 times or more (Zarin et al. 2005, manuscript submitted to *Ecol. Lett.*). Compared to recovery following slash-and-burn, the postpasture forests of this study recovered biomass more slowly than *Piper*-dominated SFs in the humid lowlands of Papua New Guinea (Hartemink 2001), more rapidly than rates reported for Bolivian lowland SFs (Steininger 2000), at similar rates for a review of forest recovery following slash-and-burn in the Tropics (Brown and Lugo 1990), and much lower than after shifting cultivation 50–100 km from our study area (Gehring et al. 2005).

Annual biomass accumulation on recently abandoned (<15 yr) abandoned pastures ranges from 1 to 11 Mg ha^{-1} (Uhl et al. 1988; Aide et al. 1995; Steininger 2000; Feldpausch et al. 2004). The postpasture biomass accumulation rates for the forests of our study were similar to reported values for lightly used pastures in eastern Amazônia (Uhl et al. 1988) and young SFs regenerating from pastures in central Amazônia (Steininger 2000) and higher than rates reported for abandoned pastures in Puerto Rico (Aide et al. 1995).

Gehring et al. (Gehring et al. 2005) found that a moderate increase in the intensity of land use had only minor effects on biomass accumulation, but affected forest structure with the biomass being more evenly distributed among size classes. In the upper Rio Negro of the Amazon basin biomass increased linearly through the first 40 yr following clearcutting and abandonment, but did not change for the next 40 yr because of the death of long-lived successional species (Saldarriaga et

al. 1988). The successional species are similar between their study areas and ours, suggesting that the rapid tree-dominated biomass accumulation of the forests of our study is probably short-lived, especially considering the depletion of Mehlich-I extracted soil P (phosphorus) at our sites (Feldpausch et al. 2004). After 12 to 14 yr, the forests of our study have maintained high stem densities (Figure 2a) and biomass (Figure 2b) in the smaller DBH classes, indicating that dominance by individual large trees is slow to develop relative to slash-and-burn alone (e.g., Gehring et al. 2005).

Total stem density in our forests peaked at 6 to 8 yr, as also reported by Steininger (Steininger 2000). Our 12- to 14-yr-old forests, with 2250 stems per hectare ($\geq$ 5 cm DBH) had twice the stems than postpasture forests reported by Honzák et al. (Honzák et al. 1996) and Steininger (Steininger 2000) for similar-aged forests in the region. The large number of small individuals encountered in the 6- to 8-yr-old forests of this study were probably stump sprouts and root stuckers that had formed from the lateral roots of *Vismia*, the most frequent genus to colonize the pastures, which spouts profusely after fire and main stem damage (Williamson et al. 1998) and may account for up to 75% of the stems in young fallows (Kammesheidt 1998). This indicates more frequent disturbance on our sites, with the young trees being cut by machete or damaged by fire prior to abandonment. Stem density in Puerto Rican forests increased to 8000–10 000 stems per hectare between 25 and 35 yr after pasture abandonment (Aide et al. 1995), much delayed compared to the same densities found in our 6- to 8-yr-old forests. Stem density in primary forests is low (Hegarty and Caballé 1991), similar to that found in the 12- to 14-yr-old SFs of our study. After 12 to 14 yr, the forests of our study developed about 60% of the BA of primary forests of the region.

The general positive correlation between forest disturbance and vine density (Hegarty and Caballé 1991; Schnitzer and Bongers 2002; Gerwing 2004) conflicts with our results for central Amazônian pasture regrowth. As also reported for other SFs regenerating from pastures (McKerrow 1992), vines were infrequent on the <5 yr old abandoned pastures of our study (Figure 1b). The vines in the forests of our study were approaching primary forest values (Hegarty and Caballé 1991; Gerwing and Farias 2000) for ratios of the total:vine stem density, total:vine biomass, and total:vine basal area, which contrasts with the findings of Gehring et al. (Gehring et al. 2005) for other secondary forests near our sites where vine density was much higher. Canopy development is important to vine succession. Vines, which may have a density 3 times higher in the building phase than mature forest (Vidal et al. 1997), respond to irregularities in the forest canopy by forming aggregations and can be more abundant in rolling or abrupt landscapes where the forest canopy may be broken (Hegarty and Caballé 1991). Vine density in the forests of our study may be low relative to other types of disturbance because the regenerating forests are located on level plateaus and the unbroken canopy is dominated by a single genus, *Vismia*, of a relatively uniform height.

4.2. LAI and canopy cover

In early succession, the development of woody vegetation tends to progress in a stepwise manner at different stages of seedling growth, with energy first channeled into the development of leaf biomass, followed by stem and root biomass (Ewel

1971). The leaf area and canopy-cover measurements indicated that there was no significant shrub layer in our forests, in terms of LAI, by 12 to 14 yr after pasture abandonment (Figure 1d), even though all forests consistently contained a high number of small-diameter trees. The large number of tree stems in the 1–5-cm DBH class in the oldest forests, 3500 stems per hectare, indicates girth growth suppression of many small-diameter individuals and lack of dominance (Figure 2a).

The rapidly declining leaf area below 150-cm height and increasing leaf cover above 150-cm height was indicative of several important forest structure characteristics: 1) a uniform canopy has developed with few gaps dominated by understory vegetation, as evidenced by a low canopy-cover standard error (Table 3); 2) the canopy above 150-cm height has sufficiently closed to restrict the growth of shade-intolerant species, so that there is a decline of early pioneer plants intolerant of canopy LAI of 3.2; and 3) the development of shade-tolerant species may be slow.

A review of forest recovery reported that leaf area increases to a maximum within the first 15 yr of regeneration (Brown and Lugo 1990), which conflicts with our results. In the forests of our study, although the development of structural attributes characteristic of values reported for primary forest returned relatively quickly following pasture abandonment in terms of biomass, stem density, DBH, canopy cover, and basal area, we found the return of leaf area was very slow compared to values reported for other land uses. Leaf area index above 150-cm height in the forests of our study, increasing from 0 to 3.2 over the 12- to 14-yr period following abandonment, was still well below the indices (4.0–6.2) reported for primary forests in the region (McWilliam et al. 1993; Williams et al. 1998; Gerwing and Farias 2000; Wirth et al. 2001; Meir and Grace 2002). Leaf area accumulation stalled in our forests between the time 6 to 8 yr (LAI $= 3.1 \pm 0.3$) and 12 to 14 yr (LAI $= 3.2 \pm 0.2$), indicating our forests have different canopy developmental patterns.

Our results, when compared to other studies, indicate LAI recovers more slowly following extended use as pasture than recovery following slash-and-burn (Figure 3). For example, Uhl (Uhl 1987) reported LAI of 4.6 one year following agricultural site abandonment, higher than similar-aged and older SFs of our study. When the slash-and-burn areas were immediately abandoned rather than cultivated (Uhl and Jordan 1984), LAI approached estimated mature forest values within 5 yr (Jordan and Uhl 1978; McWilliam et al. 1993). When slash-and-burn areas are subjected to prolonged cycles (Vieira et al. 2003), LAI recovery corresponds more closely to that measured for our sites. Few studies report leaf area recovery in tropical SFs regrowing from pastures, and those reported are from the seasonally drier eastern Amazônia. A pasture abandoned 6 yr in eastern Amazônia (Davidson et al. 2004) had comparable LAI as our similar-aged forest that had 4 times the biomass, indicating the disproportionately low LAI relative to standing biomass at our sites.

The low LAI relative to biomass recovery measured in our forests may be explained by 1) the gap fraction analysis of hemispheric images is underestimating LAI. A comparison of LAI methods (Honzák et al. 1996) indicated that the gap fraction analysis of hemispheric images, as used in our study, rather than the sunfleck fraction, may be more appropriate to estimate LAI in tropical forests.

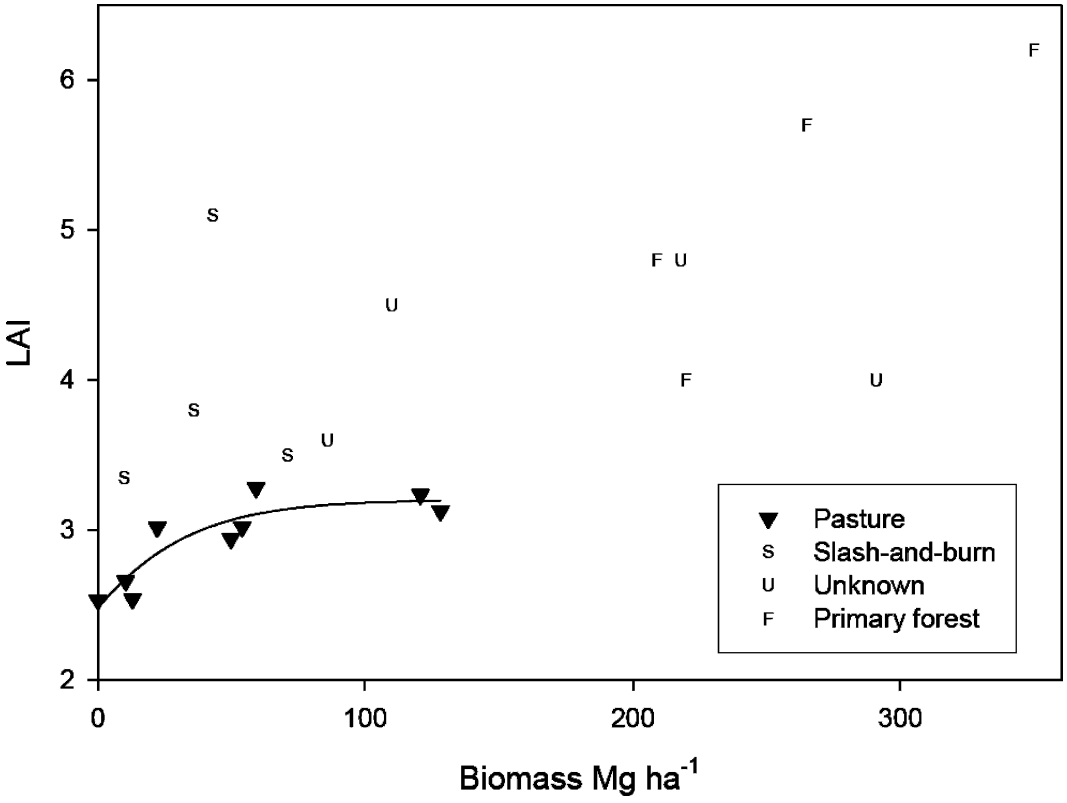

Figure 3. Prior land use and LAI: biomass (Mg ha^{-1}) vs LAI in primary forest and secondary forest regrowing after varying land-use pasture (this study and Davidson et al. 2004), slash-and-burn agriculture (Uhl and Jordan 1984; Uhl 1987; Lucas et al. 2002; Vieira et al. 2003), unknown land-use history (Lucas et al. 2002), and primary forest (McWilliam et al. 1993; Williams et al. 1998; Meir and Grace 2002).

2) The dense even-aged highly monospecific structure dominated by the tree genus *Vismia* results in an untiered canopy characterized by low LAI. 3) Recruitment of shade-tolerant species may be low. We found that nearly 60% of the stems were 1–5 cm DBH. 4) Low nutrient availability, especially phosphorus in the forests of our study (Feldpausch et al. 2004), limits LAI development. This is probable since Davidson et al. (Davidson et al. 2004) found SF LAI to increase with fertilizer additions in eastern Amazônia. The delayed LAI recovery relative to recovery at sites abandoned soon after slash-and-burn indicates land-use intensity—many cycles of slash-and-burn or prolonged periods as pasture—negatively affects LAI recovery (Figure 3).

4.3. Light capture and evaporative potential

The comparatively slow leaf area accumulation relative to biomass in our forests indicates an ineffective capacity of these forests to rebuild canopy structure, suggesting impediments to regeneration (e.g., shallow rooting, soil nutrient deficits,

low species diversity, etc.). This requires further research to understand leaf area development in these *Vismia*-dominated forests. Despite limited leaf area, radiation interception and evapotranspiration (ET) in our oldest forests (>94% cover) probably remains high, since Hölscher et al. (Hölscher et al. 1997) found that SFs <15 yr old returned ET to primary forest rates. Their reported recovery of ET within 15 yr to values for mature forest (Hölscher et al. 1997; Jipp et al. 1998) demonstrates that LAI, or stomatal conductance, which tends to be higher in early successional species, is not limiting water uptake in SFs. It should be noted that the forests of those studies are seasonally drier and the primary forests are lower in biomass than in our study region and would need to develop deeper root systems or suffer water deficits during the more pronounced seasonal precipitation depressions.

The recovery of high ET rates has important implications for regional climate since as much as 25%–56% of the Amazon basin rainfall is derived from "recycling" water evaporated within the basin (Eltahir and Bras 1996). Because of the added productivity at forest edges as a result of vertical differentiation and high LAI, regional ET could be higher when the landscape is dominated by many patches of SFs like those of our study rather than large forest blocks (Veen et al. 1991). Furthermore, vines have been implicated in high soil water depletion rates relative to their occurrence. For example, vines accounting for 6% of the total BA in a young SF of eastern Amazônia contributed 8% of annual evapotranspiration (Restom and Nepstad 2001).

This study raises many questions that require further inquiry to understand the redevelopment of forest structure and function. For example, what is the role of dominant genera in the development of forest structure? Do fast-growing, short-lived vegetation negatively affect growth and survival of long-lived species? With the slow accrual of leaf area compared to other forests, is less soil water being withdrawn by the growing vegetation? And, how do those rates vary through the wet and dry seasons? How would forests of different ages respond to relaxed soil nutrient limitation? Would the forests exhibit structural and functional attributes characteristic of primary forest more rapidly? We have implemented nutrient limitation studies and continue to monitor forest development and function (e.g., soil water uptake) to answer these questions.

Our postpasture regeneration data on well-characterized clayey oxisols in an udic soil moisture regime (appendix) complement data from the seasonally drier ustic soil moisture regime in eastern Amazônia. Pasture establishment, grazing, and fire result in a cost to regeneration via impacts on nutrients, seed banks, and selection of sprouting species that give rise to uniform "clonal" stands of a few genera (e.g., *Vismia*) with distinct structural differences. The species depauperate and uniform stand structure affects both LAI and biomass accumulation relative to the species-rich forests regenerating after cropping, which may influence long-term recovery. High *Vismia* stem densities, indicating cutting and burning of early invading trees, has created simple-structured, monospecific, even-aged stands. The forests have begun to recover structural attributes characteristic of primary forests, but LAI return relative to biomass is delayed, indicating a different developmental pathway following pasture abandonment. Additional work is needed to determine if nutrient deficiencies limit leaf area development and if low LAI relative to biomass recovery results in lower soil water uptake and ET, which may influence

long-term primary productivity. Furthermore, the rapid tree-dominated biomass accumulation may stall because of lack of dominance and simple even-aged monospecific stand structure. Because of the widespread and increasing occurrence of SFs regenerating from pasture in the Amazon basin, recovering SFs will have a greater influence on the global carbon budget and local, regional, and global climate. Novel or altered successional pathways may modify long-term forest recovery of these globally important postpasture secondary forests.

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Appendix: Mean Soil Carbon and Nutrient Concentrations, and pH in 10 Secondary Forests Regenerating from Abandoned Pastures in Central Amazônia, Brazil*

Year	Fazenda and forest No.	C	N	P	K	Ca	Mg	pH
		— (g kg^{-1})—		— (mg kg^{-1})—		— ($cmol_{(+)}$ kg^{-1})—		(KCl)
0–15-cm depth								
0 to 2	DAS-1 and Rodão-1	15.39 (2.27)	1.23 (0.13)	4.83 (0.57)	20.98 (2.40)	0.13 (0.02)	0.09 (0.01)	4.1 (0.03)
2 to 4	Rodão-4	20.77 (2.64)	1.25 (0.09)	3.09 (0.17)	18.11 (0.82)	0.18 (0.01)	0.07 (<0.01)	4.0 (0.02)
4 to 6	DAS-2 and Rodão-3	20.71 (2.01)	1.42 (0.16)	6.30 (0.86)	33.20 (4.76)	0.16 (0.04)	0.14 (0.02)	4.0 (0.03)
6 to 8	Dimona-1, -3, and Rodão-2	22.91 (0.85)	1.49 (0.05)	2.46 (0.30)	23.92 (2.49)	0.33 (0.11)	0.18 (0.04)	4.0 (0.03)
12 to 14	DAS-3 and Dimona-2	19.51 (2.77)	1.75 (0.04)	1.55 (0.17)	19.45 (0.55)	0.16 (0.05)	0.11 (<0.01)	4.0 (0.01)
Overall mean		20.19 (0.94)	1.46 (0.05)	3.55 (0.36)	23.78 (1.52)	0.21 (0.04)	0.13 (0.02)	4.0 (0.01)
15–30-cm depth								
0 to 2	DAS-1 and Rodão-1	9.17 (1.43)	0.74 (0.06)	2.03 (0.53)	8.46 (0.71)	0.08 (0.01)	0.05 (<0.01)	4.2 (0.02)
2 to 4	Rodão-4	17.14 (0.70)	0.91 (0.06)	1.87 (0.17)	10.53 (0.47)	0.11 (0.01)	0.05 (0.01)	4.2 (0.02)
4 to 6	DAS-2 and Rodão-3	10.63 (1.08)	0.86 (0.08)	1.40 (0.13)	10.86 (1.63)	0.08 (0.01)	0.05 (0.01)	4.1 (0.02)
6 to 8	Dimona-1, -3, and Rodão-2	12.09 (0.55)	0.88 (0.02)	0.86 (0.13)	11.19 (0.88)	0.05 (0.01)	0.04 (0.01)	4.1 (0.02)
12 to 14	DAS-3 and Dimona-2	11.46 (0.76)	1.01 (0.01)	0.70 (0.00)	8.56 (0.31)	0.07 (0.02)	0.05 (<0.01)	4.1 (0.02)
Overall mean		11.65 (0.52)	0.88 (0.03)	1.25 (0.13)	10.02 (0.48)	0.07 (0.01)	0.05 (<0.01)	4.1 (0.01)
30–45-cm depth								
0 to 2	DAS-1 and Rodão-1	6.57 (0.57)	0.55 (0.02)	1.15 (0.41)	5.56 (0.28)	0.06 (0.01)	0.04 (0.01)	4.2 (0.02)

Year	Fazenda and forest No.	C	N	P	K	Ca	Mg	pH
		— (g kg^{-1})—		— (mg kg^{-1})—		— ($cmol_{(+)}$ kg^{-1})—		(KCl)
2 to 4	Rodão-4	12.25 (0.86)	0.65 (0.07)	1.15 (0.16)	7.14 (0.46)	0.10 (0.02)	0.04 (<0.01)	4.2 (0.02)
4 to 6	DAS-2 and Rodão-3	10.84 (2.36)	0.65 (0.02)	0.86 (0.09)	5.84 (0.97)	0.07 (0.01)	0.04 (<0.01)	4.2 (0.02)
6 to 8	Dimona-1, -3, and Rodão-2	8.12 (0.66)	0.69 (0.01)	0.39 (0.10)	6.28 (0.58)	0.05 (0.01)	0.04 (0.01)	4.1 (0.02)
12 to 14	DAS-3 and Dimona-2	16.08 (2.49)	0.77 (0.02)	0.58 (0.09)	5.84 (0.39)	0.05 (0.01)	0.04 (<0.01)	4.1 (0.01)
Overall mean		10.46 (0.89)	0.67 (0.01)	0.74 (0.09)	6.06 (0.28)	0.06 (0.01)	0.04 (<0.01)	4.2 (0.01)

* Mean (± SE) values are $n = 4$ per depth in each forest from a composite of four to six subsamples per sample and summarized by age class. Total C and N, Mehlich-I extractable P and exchangeable K, and exchangeable Ca and Mg from Feldpausch et al. (Feldpausch et al. 2004).

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