

Secondary forest structure and biomass following short and extended land-use in central and southern Amazonia

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ABSTRACT. A study was conducted on the effect of extended land-use on secondary forest biomass accumulation in the Amazon. Structural measurements were made in a series of secondary forest stands, from 4–30 y old, in Brazil and Bolivia. Half of the stands were forest regrowth following clearance and only 1 y of cultivation; the other half were regrowth following 4 y or more of continuous pasture in Brazil and three or more rotations of medium-fallow agriculture in Bolivia. Above-ground live biomass was estimated using published allometric equations. Total biomass ranged from 17 to 207 Mg ha⁻¹. Biomass of pioneer trees was poorly related to stand age, while that of later-successional trees increased linearly with age. Total biomass accumulation in Bolivia averaged 5.4 Mg ha⁻¹ y⁻¹ over the entire age sequence. Biomass accumulation for regrowth following short-term use was not greater than that for regrowth following medium-fallow agriculture. In Brazil, biomass accumulation averaged 9.1 Mg ha⁻¹ y⁻¹ over the first 12 y of regrowth and 5.9 Mg ha⁻¹ y⁻¹ over the entire age sequence. Biomass accumulation was significantly slower, around 5.0 Mg ha⁻¹ y⁻¹, for regrowth following continuous pasture than for regrowth following 1 y of cultivation.

KEY WORDS: Amazon land use, biomass accumulation, fallow agriculture, forest regrowth

INTRODUCTION

Amazonian agricultural fallows are typically a regrowth of common pioneer shrub and tree species in an abandoned farm or pasture. They usually are unmanaged (but see Padoch *et al.* 1988) and dominated by trees within only 3–4 y. Several biophysical characteristics of tropical forest fallows demonstrate their potential significance to local ecosystems and global climate. Tropical secondary forests rapidly achieve high leaf area (Ewel & Benedict 1982, Jordan 1989, Saldarriaga & Luxmore 1991, Unruh 1991). This enables more efficient

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light gathering capabilities, higher rates of transpiration and more rapid biomass production than in non-forested communities. Rates of above-ground live biomass production for tropical regrowth are typically from 4 to 12 Mg ha⁻¹ y⁻¹ over the first 5 y (Alves *et al.* 1997, Brown & Lugo 1990, Faber-Langendoen 1992, Foody *et al.* 1994, Salimon *et al.* 2000, Uhl 1987).

The majority of tropical regrowing forests sampled for biomass have been cases of regrowth following very light, if any, agricultural usage. While this is common in the newest frontiers, most of the land-use in the Amazon is either rotational agriculture in sites that had previously been sown or longer-term agriculture and pasture. Uhl (1987) compared biomass accumulation for regrowth following increasing levels of disturbance in San Carlos del Río Negro, Venezuela. Disturbance was determined by the method used to clear forest: cutting with no burning or cultivation, cutting with burning and 3 y of cultivation and cutting with burning and 6 y of cultivation. Biomass accumulated after 5 y of regrowth was 35.2 Mg ha⁻¹ for the light disturbance case, 26.5 Mg ha⁻¹ for the moderate disturbance case and 7.1 Mg ha⁻¹ for the high disturbance case.

Further comparative studies have been conducted in the drier forests of the eastern Amazon. Uhl *et al.* (1988) compared biomass accumulation rates among a series of fallows near Paragominas, Pará. Biomass accumulation in sites that had not been burned or weeded averaged 10 Mg ha⁻¹ y⁻¹. Accumulation in sites that had been burned repeatedly during 6 to 12 y of pasture management averaged 5 Mg ha⁻¹ y⁻¹. The most heavily disturbed sites were those that had been subjected to mechanized clearing, in which the mostly non-woody biomass accumulation was as slow as 0.6 Mg ha⁻¹ y⁻¹. Guimarães (1993, in Fearnside & Guimarães 1996) examined the biomass–age relationship of secondary forests in Altamira, Pará. They varied in regeneration age and length of time under pasture prior to abandonment. She found that biomass accumulation rates of regrowth were reduced by 2.6 Mg ha⁻¹ y⁻¹ under pasture prior to abandonment. The implication of these findings is that extended land-use in the Amazon reduces the potential for forest regeneration.

This paper reports a comparison of structure and above-ground live biomass of secondary forests of varying ages and land-use histories. It was carried out in three areas of Amazonian colonization, two near Manaus, Brazil and one in Santa Cruz, Bolivia. Two questions are addressed in this study: (1) how does biomass production in regrowth following only 1 y of cultivation compare for the central and southern Amazon and (2) are rates of biomass production sustained in regrowth following more extended land uses?

STUDY AREAS

Amazonas, Brazil

The first Brazilian study area was in the zone of settlement along highways BR174 and AM10, north of Manaus, Amazonas, Brazil. The second was in a

caboclo community around Lago Janauaca, c. 40 km south of Manaus, across the Río Solimões. These two study areas are referred to as AM10 and Janauaca.

Manaus, located at 60°W 3°S, has a mean annual temperature of 25.6 °C and annual precipitation of 2100 mm y⁻¹, with a dry season from June to September (Junk 1997). The soils at AM10 are mostly clayey oxisols with patches of sandy soils in valley bottoms. All but one of the stands sampled were on clayey soils. Dias & Nortcliffe (1985) described samples collected nearby as having a thin A horizon over a heavy clayey B horizon that is deep, permeable and well-drained with low cation exchange capacities and pH values. Estimates of the total above-ground biomass estimated for three nearby mature forest stands on these soils are 275, 309 and 406 Mg ha⁻¹ (Klinge *et al.* 1975, McWilliam *et al.* 1993). The soils around Lago Janauaca have been classified as plinthic dystric podsols (EMBRAPA 1985), are characteristic of much of alluvial Amazonia and are locally recognized as more fertile than oxisols for cultivation.

During the past decades, small-scale agriculture and cattle ranching has proliferated at AM10. Many pastures were abandoned during the 1980s and since then much of the recovering vegetation has been re-cleared by recent settlers. Rice and citrus production is also common in the area.

The banks of the Lago Janauaca, along with those of neighbouring lakes and varzeas, have long been settled by caboclos, agriculturists of mixed Amerindian and European descent (Grenand & Grenand 1993, Parker 1985). They are largely dependent on fishing and rotational manioc cultivation, although some pastures are maintained. The settlement around Lago Janauaca forms a relatively large caboclo community that sells much of its productive and extractive resources in Manaus.

Santa Cruz, Bolivia

Peoples of the Altiplano have densely settled the Yapacaní and Surutú basins, in eastern Santa Cruz, Bolivia, for over 40 y (Fifer 1982, Stearman 1985). Most of the agriculture practiced here is short-term rice and manioc followed by 4–7 y of fallow. Small pastures are also common and continuous rice and soy bean production is more common in the adjacent colonies of San Juan, Antofogasta and Portachuelo, to the north and east of the study area. Land clearance over the past decade has encroached northward into the Chore forest reserve and southward into Amboró National Park, the southernmost extent of Amazonian rain forest.

The Bolivian field surveys were concentrated around Buena Vista, Huaytú and Yapacaní, in the Ichilo province of Santa Cruz. This study area is referred to as Surutú, for the main river basin in its centre. The area, centred at 63°30'W 17°30'S, receives on average 1600 mm of rain and has a mean annual temperature of 23 °C (Roche & Rocha 1985). A dry period from May to November averages less than 100 mm of rain per month with occasional strong cool winds that originate in the South Atlantic and last 3–5 d (Ronchail 1992).

The areas at Surutú can be grouped into dissected terraces and the alluvial

plains. Stands surveyed in the alluvial zone were on dystic and vertic eutrochrepts. The soils of the uplands are mostly quartzipsammentic haplothorps on dissected terraces to the north and typic paleudults on the piedmont to the southwest (CUMAT 1992). Soil analyses in rice farms on the piedmont west of the Yapacaní revealed that the most limiting nutrients there were nitrogen and zinc and that during cultivation the soils were subject to rapid acidification and losses in phosphorus, potassium, calcium and magnesium (Montenegro Hurtado 1987).

METHODS

Vegetation sampling

For the purpose of this study, I define a site subjected to 'short-term usage' (ST) as one that was covered by mature forest, cleared by slash-and-burn, cultivated for 1 y only and subsequently abandoned. I define 'long-term pasture' (LP) as continuous pasture for over 5 y, the most common long-term use in the area and in the Brazilian Amazon as a whole (Fearnside 1985). I define 'medium-fallow agriculture' (MF) as four or more cycles of medium-fallow agriculture, each cycle consisting of 1 y of cultivation followed by 5–8 y of fallow. All but two of the secondary forest stands surveyed were examples of recovery from one of these three types of land-use (Table 1). One stand in Brazil was an example of recovery from 4 y of continuous cultivation and another stand was an example of recovery from three cycles of 1 y of cultivation followed by 3 y of fallow. All the cases of land-use history in this study relate to Uhl's (1987) 'moderate' to 'high' intensity uses; no examples of 'abusive' use or mechanized agriculture classes are included.

Within the two study areas in Brazil 20 stands were surveyed during September to November 1995. Eleven of these stands were regrowth following long-term pasture and stand ages ranged from 4–30 y old, 19 of which were older than 10. In Bolivia, 13 secondary forest stands were surveyed in July 1995 and June 1996. Six of these stands were regrowth following short-term usage and seven were regrowth following medium-fallow agriculture.

The stands were mostly small, ranging from 2 to 8 ha. In Brazil, all stands had at least a portion of their edge bordering mature forest or old secondary forest; however in Bolivia most of the medium-fallow cases were surrounded by cleared and fallowed land. Within each stand transect plots 10 m in width by 70 to 100 m in length were marked, beginning 30 m from the stand edge and running toward the stand centre. Trees were identified to genus or family or recorded as unidentified, referring to Gentry (1993) and Freitas da Silva *et al.* (1977) in Brazil and Killeen *et al.* (1993) in Bolivia. Samples of the most common trees were collected and compared to collections at the Instituto Nacional de Pesquisas da Amazonia in Manaus and the Herbario Nacional at the Museo de Historia Natural Noel Kempff Mercado in Santa Cruz.

Table 1. Stands surveyed in all study areas. ST = short-term agriculture, LP = long-term pasture, MF = medium-fallow agriculture, SF = short-fallow agriculture (one case in Brazil) and LT = long-term agriculture (one case in Brazil). S/B indicates clearing by the slash-and-burn method.

Stand number	Age (y)	Stand area (ha)	Sampled area (ha)	Land-use	Land-use history
Bolivia, Piedmont:					
S3	10	4	0.09	MF	Forest, 4+ cycles of S/B, 1 y rice, 7 y fallow
S4	15	4	0.08	ST	Forest, S/B, 1 y rice
S12	20	2	0.10	ST	Forest, S/B, 1 y rice
S13	4	2	0.10	ST	Forest, S/B, 1 y rice
S14	10	4	0.10	ST	Forest, S/B, 1 y rice
S15	12	5	0.10	ST	Forest, S/B, 1 y rice
Bolivia, Alluvial:					
S5	25	3	0.10	MF	Forest, 4+ cycles of S/B, 1 y rice, 5 y fallow
S6	15	3	0.80	MF	Forest, 4+ cycles of S/B, 1 y rice, 5 y fallow
S7	5	4	0.10	LP	Forest, 3 cycles of S/B, 1 y rice, 5 y fallow, 7 y pasture
S8	6	4	0.10	MF	Forest, 4+ cycles of S/B, 1 y rice, 5 y fallow
S10	8	3	0.10	MF	Forest, 3 cycles of S/B, 1 y rice, 8 y fallow
S16	8	5	0.10	ST	Forest, S/B, 1 y manioc
S17	15	4	0.28	ST	Forest, S/B, 1 y manioc
S18	5	4	0.30	ST	Forest, S/B, 1 y rice
Brazil, AM10:					
A2	10	8	0.07	ST	Forest, S/B, 1 y rice
A3	4	4	0.07	LT	Forest, S/B, 6 y rice
A5	12	2	0.08	ST	Forest, S/B, seeded w/rice only + abandoned, sandy hilltop
A6	20	6	0.07	ST	Forest, S/B, 1 y rice
A7	23	5	0.09	ST	Forest, S/B, 1 y rice
A8	20	4	0.10	ST	Forest, S/B, 1 y pasture
A9	15	4	0.07	LP	Forest, S/B, 7 y pasture
A10	12	2.5	0.10	ST	Forest, S/no-burn, no cultivation
A11	12	3	0.08	ST	Forest, S/B, 1 y pasture
A12	7	1.5	0.08	LP	Forest, S/B, 6 y pasture
Brazil, Janauaca:					
J1	30	6	0.10	LP	Forest, S/B, 10 y pasture
J2	26	4	0.10	ST	Forest, S/B, 1 y manioc
J3	15	3	0.10	ST	Forest, S/B, 1 y manioc
J4	8	2	0.07	SF	Forest, 4 cycles of S/B, 1 y manioc, 3 y fallow
J5	12	4	0.08	ST	Forest, S/B, 1 y manioc
J6	15	3	0.09	LP	Forest, S/B, 1 y manioc, 5 y fallow, S/B, 5 y pasture
J7	20	8	0.07	LP	Forest, S/B, 1 y manioc, 3 y fallow, S/B, 10 y pasture
J9	10	2	0.10	LP	Forest, S/B, 1 y manioc, 3 y fallow, S/B, 5 y pasture
J10	5	1.5	0.08	LP	Forest, S/B, 1 y manioc, 3 y fallow, S/B, 6 y pasture
J11	5	2	0.08	ST	Forest, S/B, 1 y manioc

All trees greater than 5 cm diameter at breast height (DBH; 1.3 m above ground) whose stem centres were within the plots were recorded. The DBH of the few trees with developed buttresses were measured just above the buttress. Heights were estimated using a measuring tape and clinometer. Heights only were recorded for stemmed palms; non-stemmed palms were not recorded.

During the surveys, means of plot density, basal area and volume were calculated at each 10-m interval. Plot size was assumed sufficient when the means had changed by less than 10% after three consecutive 10-m intervals, thus varying plot sizes. Sampled areas for all but two stands are from 0.07 ha to 0.10 ha in size. One 0.30-ha plot in a 5-y-old stand and one 0.28-ha plot in a 15-y-old stand were surveyed to further assess subplot variability over varying sizes.

Field estimation of structure and biomass

Stand density, basal area and wood volume were estimated for each stand and converted to comparable units. Volumes were estimated using a general form factor of 0.62 calculated from Brown *et al.* (1995). As an index of canopy height I used the mean plus 25/SD of all tree heights in each plot. All structural and biomass data were calculated for the stand as a whole as well as for pioneer trees and later-successional trees. Pioneer refers to trees, many with low wood density, which rapidly colonize disturbed areas and senesce when shaded by over-storey trees. Based in part on Faber-Langendoen & Gentry (1991), Saldarriaga *et al.* (1988) and Uhl (1987), genera recorded as pioneer in the Brazilian stands for this study are *Bellucia* and *Miconia* (Melastomataceae), *Vismia* (Guttiferae), *Cecropia* (Moraceae) and *Iserfia* (Rubiaceae). Genera recorded as pioneer in the Bolivian stands are *Miconia*, *Vernonia*, *Senecio* (Compositae), *Piper* (Piperaceae), *Psidium* (Myrtaceae), *Guadua* (Gramineae), *Psychotria* (Rubiaceae), *Cecropia* and *Pourouma* (Moraceae), *Pseudobombax* and *Ochroma* (Bombacaceae) and *Heliocarpus* (Tiliaceae). All other trees recorded are considered later-successional.

Tree biomass was estimated using a set of allometric relations derived from destructive samples in previous studies (Table 2). Only the above-ground live biomass was estimated, believed to comprise roughly 80% of total live biomass for secondary forests of these ages. Equations from Uhl (1987) and Scatena *et al.* (1993) were applied for small softwoods, large softwoods and small hardwoods. The biomass of the remaining trees was estimated using the equation from Saldarriaga *et al.* (1988). This approach was used because of the floristic similarities between these studies and this one and because of the variation in form factors among small and large trees. It also allows for specification of wood density (S = dry weight per unit green volume, g cm^{-3}) in the latter group. Table 2 reports how the allometric equations were applied to taxonomic groups according to similarities in form and density.

Linear regressions of stand total above-ground live biomass vs. age were developed for both the Bolivian and Brazilian stands. Two regressions were developed: biomass accumulation for all stands in a study area and for stands up to 12 y old. Within Bolivia and Brazil, the effect of land-use history on the relationship between biomass and age was assessed using the F-ratio test (Neter *et al.* 1990). Biomass accumulation among regrowth stands in Bolivia and Brazil was compared using only the short-term usage sites.

Table 2. Allometric equations and densities used to estimate above-ground live biomass. M = above-ground standing dry biomass in Mg ha⁻¹, DBH = diameter at breast height in cm, H = tree height in m, S = density (= dry weight per unit fresh volume, g mm⁻³). Densities are averages among the most common taxa in each group and are used only in the calculation of biomass for dense tall trees.

Allometric class	Height range	Equation	r ²	Mean density (g mm ⁻³)	Taxonomic group applied to	Reference ¹
Light-short	< 11m	$M = 0.134(DBH^2 \cdot H \cdot 100) + 15.54 + 0.464(H \cdot 100 - 32.078)$	0.97		<i>Dichymopanax</i> , <i>Cecropia Helicarpus</i> , <i>Jacaranda</i> , <i>Naucleopsis</i> , <i>Ochroma</i> , <i>Pourouma</i> , <i>Scleronoma</i>	1
Light-tall Dense-short	≥ 11m	$M = \exp(2.475 \cdot \ln(DBH) - 2.40)$	0.97			2
	< 16m	$M = 10^{(0.360 \cdot \log(DBH \cdot DBH \cdot H \cdot 100) + 0.26)}$ $+ 10^{(0.612 \cdot \log(DBH \cdot DBH \cdot H) + 0.40)}$	0.97		<i>Pourouma</i> , <i>Scleronoma</i> All others < 16 m	1
Dense-tall	≥ 16m	$M = \exp(-1.09 + 0.876 \cdot \ln(DBH^2) + 0.604 \cdot \ln(H) + 0.871 \cdot \ln(S))$	0.93	0.42	Anacardiaceae, Amnonaceae, Pithecellobium, Simaruba, Apocynaceae, Bursaceae	3
	”	”		0.55	Cordiaceae, Lauraceae, Mimosoidaceae, Moraceae, Sapindaceae, Sapotaceae, <i>Anadenanthera</i> , <i>Astronium</i> , <i>Tabebuia</i>	
Palms	”	”		0.65	All other ≥ 16 m (Brazil)	
	All	$M = 0.0101(DBH^2)^{1.136} + 0.0379(DBH^2)^{0.712}$		0.70	All other ≥ 16 m (Bolivia)	
	stems	$DBH = 1.17 + H/1.311$		0.72	Araliaceae	4

¹Allometric equations are from 1. Uhl (1987), 2. Scatena *et al.* (1993), 3. Saldarriaga *et al.* (1988), 4. Fölster *et al.* (1976); wood densities are from Hidayat & Simpson (1994), Brown *et al.* (1995) and Finegan (1992). r² values are as reported in the original studies.

Estimation of error in stand biomass

Both the errors caused by measurement and plot size were examined in this study. Errors of measurement were estimated from the coefficient of variation (CV) of repeated measurements of diameter and height for a set of trees (Steininger 1998). The CV of diameter measurements for trees of 5.3 to 6.7 cm DBH was 1.5 to 3.8% and that for trees of 38.8 to 39.9 cm DBH was 1.7 to 3.7%. The CV of dbh measurements for the same trees was only 0.2 to 0.7 and 0.3 to 0.4%, respectively. The CV of volume was from 1.2 to 3.8 for the smaller trees and 1.8 to 4.2 for the larger trees.

Errors from the allometric equations may be estimated from the regression correlations reported in Table 2. However, this does not explain possible errors from applying the equations to different taxa or areas. Brown *et al.* (1995) conducted a cross-validation of a general allometric equation provided by Brown *et al.* (1989). They found that when using both DBH and height, 95% of the biomass estimates using the equation in Brown *et al.* (1989) were within 15% of the estimate calculated using locally derived allometry and most of the errors over 5% from the mean were for trees of less than 20 cm dbh. This demonstrates a high degree of generality of allometric relationships for neotropical trees.

To estimate the error due to plot size, within-stand variability in biomass was calculated for larger plots in two stands in Bolivia. A 300 m-long transect was surveyed in a 5-y-old stand and a 280 m-long transect in a 15-y-old stand. The 0.30-ha and 0.28-ha plots were divided into 0.01-ha subplots. This enabled a comparison of biomass estimates from a sample of subplots of varying sizes. Error due to plot size was estimated as the maximum coefficient of variation of subplots of 0.07-ha area or greater, since this was the smallest sampled area for any of the surveyed stands (Table 3).

RESULTS

Stand structure and general composition

A shrub layer of *Vernonia*, *Senecio*, *Psychotria* and *Miconia* dominated the youngest stands in Bolivia (Figure 1). Stands up to 10 y old were dominated by *Ochroma pyramidale* (Cav. ex Lam.) Pers., *Cecropia*, *Heliocarpus americanus* L. and *Inga* with *Cecropia* as the most common genus among all the stands in Bolivia. All of these genera were common in the canopies of older stands, with *Nectandra* (Lauraceae) and *Swartzia* (Papilionoideae), becoming equally important. Other taxa that were recorded in more than one of the stands in Bolivia are *Cupania* (Sapindaceae), *Trema* and *Urera* (Urticaceae), *Cordia* (Boraginaceae), *Anadenanthera colubrina* (Vell. Conc.) Benth. (Mimosoideae), *Piper*, *Rinorea* (Violaceae), *Ormosia* and *Centrolobium* (Papilionoideae), *Psychotria* and *Capirona* (Rubiaceae), *Astronium* (Anacardiaceae), *Bixa* (Bixaceae), *Himatanthus* (Apocynaceae), *Brosimum* (Moraceae), *Pseudobombax* and *Chorisia*

Table 3. Coefficients of variation of the standard errors of above-ground biomass for plots of varying sizes in Surutú Stand 18, 5 y old and Surutú Stand 17, 15 y old. Units are Mg ha⁻¹ in each subplot, n = number of subplots, mean = mean biomass among subplots, SD = standard deviation of the mean, SE = standard error of the mean and CV = coefficient of variation, expressed as percent of the mean.

	Subplot size (ha)					
	0.05	0.06	0.07	0.10	0.12	0.14
Surutú 18 (5 y)						
Subplot 1	47.9	44.0	47.1	46.1	46.3	45.8
Subplot 2	44.3	48.6	44.4	52.6	49.0	45.9
Subplot 3	47.9	53.8	55.9	41.7		
Subplot 4	57.3	44.1	36.0			
Subplot 5	36.9	43.5				
Subplot 6	46.5					
n	6	5	4	3	2	2
Mean (Mg ha ⁻¹)	46.8	46.8	45.9	46.8	47.6	45.8
SD (Mg ha ⁻¹)	6.6	4.4	8.2	5.5	1.9	0.1
SE (Mg ha ⁻¹)	2.7	2.0	4.1	3.2	1.3	0.1
CV (%)	5.7	4.2	8.9	6.8	2.8	0.2
Surutú 17 (15 y)						
Subplot 1	106	132	134	111	118	116
Subplot 2	117	103	98	126	140	135
Subplot 3	115	121	151			
Subplot 4	137	159	120			
Subplot 5	187					
n	5	4	4	2	2	2
Mean (Mg ha ⁻¹)	132	129	126	118	129	126
SD (Mg ha ⁻¹)	32.5	23.3	22.4	10.1	15.6	13.5
SE (Mg ha ⁻¹)	14.6	11.7	11.2	7.2	11.0	9.5
CV (%)	11.0	9.1	8.9	6.0	8.6	7.6

(Bombacaceae). Stemmed palms were rare in the stands surveyed, except for *Scheelea princeps* (C. Martius) G. Karsten.

Stand canopy heights ranged from 8 m in an 8-y-old to almost 30 m in a 15-y-old stand (Figure 2). Stem density ranged from 100 to 1300 ha⁻¹ for pioneers, 300 to 1400 ha⁻¹ for later-successional trees and was poorly related to age. There is slight indication that both basal area and volume of pioneers increased in stands from 4 to 12 y old and then decreased among older stands. Basal area and volume of later-successional trees were similar or less than those of pioneers for stands of up to 12 y, but were much higher in stands older than 12 y.

A mix of *Vismia*, *Miconia* and *Bellucia* dominated most of the early regrowth stands in Brazil (Figure 1). None of the stands surveyed in this study were dominated by *Cecropia* alone but by *Cecropia* plus a few other genera. Many dead *Cecropia* were noted in the younger stands surveyed, especially stand J11, although dead stems were not counted. *Vismia*, *Miconia* and *Bellucia* were more abundant in the short-term sites than in the long-term pasture sites. In the 5–10-y-old stands where these genera were less common, *Pithecellobium* (Mimosoideae), *Psidium* (Myrtaceae), *Scleronema* (Bombacaceae), *Sipurana* (Monimiaceae) and *Warszewitzia* (Rubiaceae) were most common.

The most common taxa in the Brazilian stands older than 10 y were *Inga*

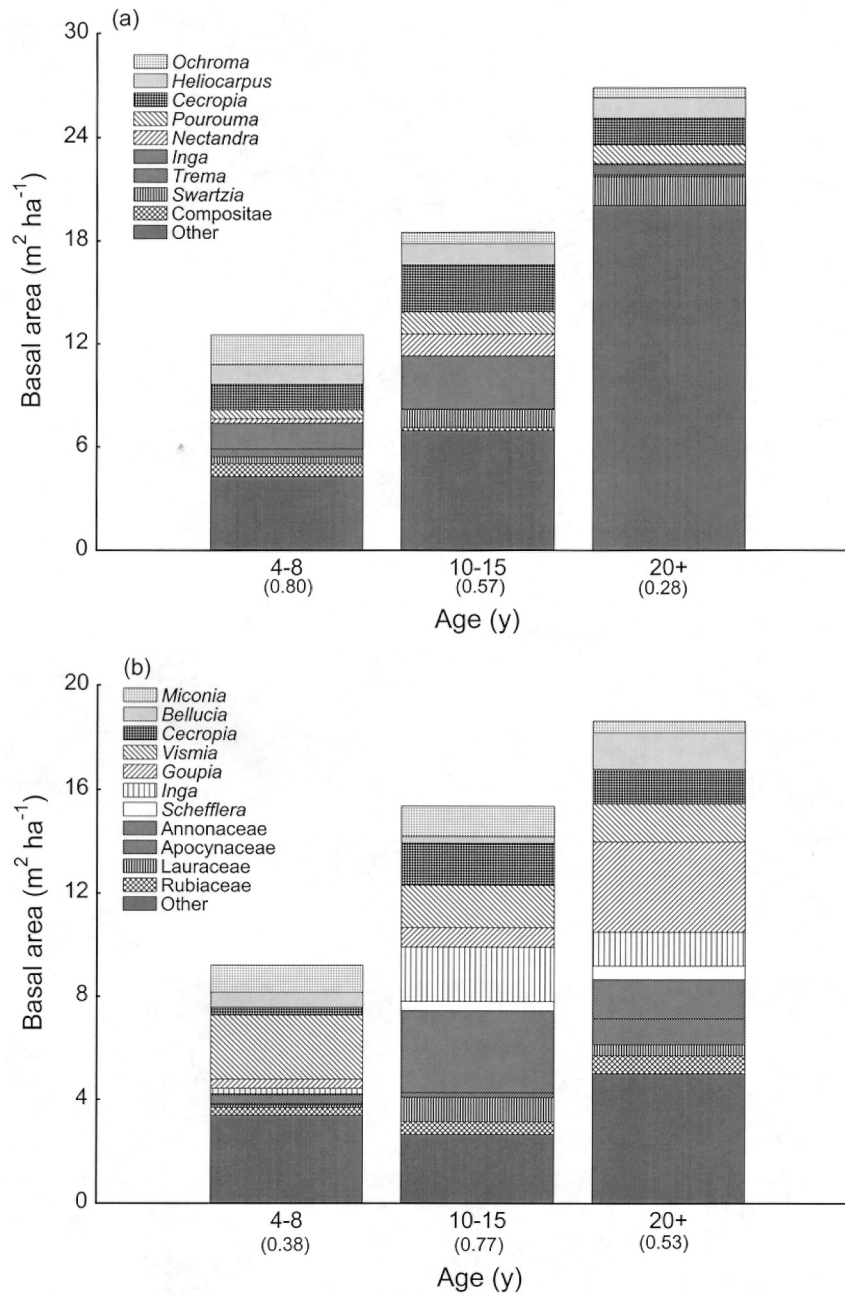


Figure 1. Basal area of most common genera and families by stand age for all stands surveyed in (a) Bolivia and (b) Brazil. Age is the range of regrowth stand ages for each age group. The total sampled area for each age group is shown in parentheses.

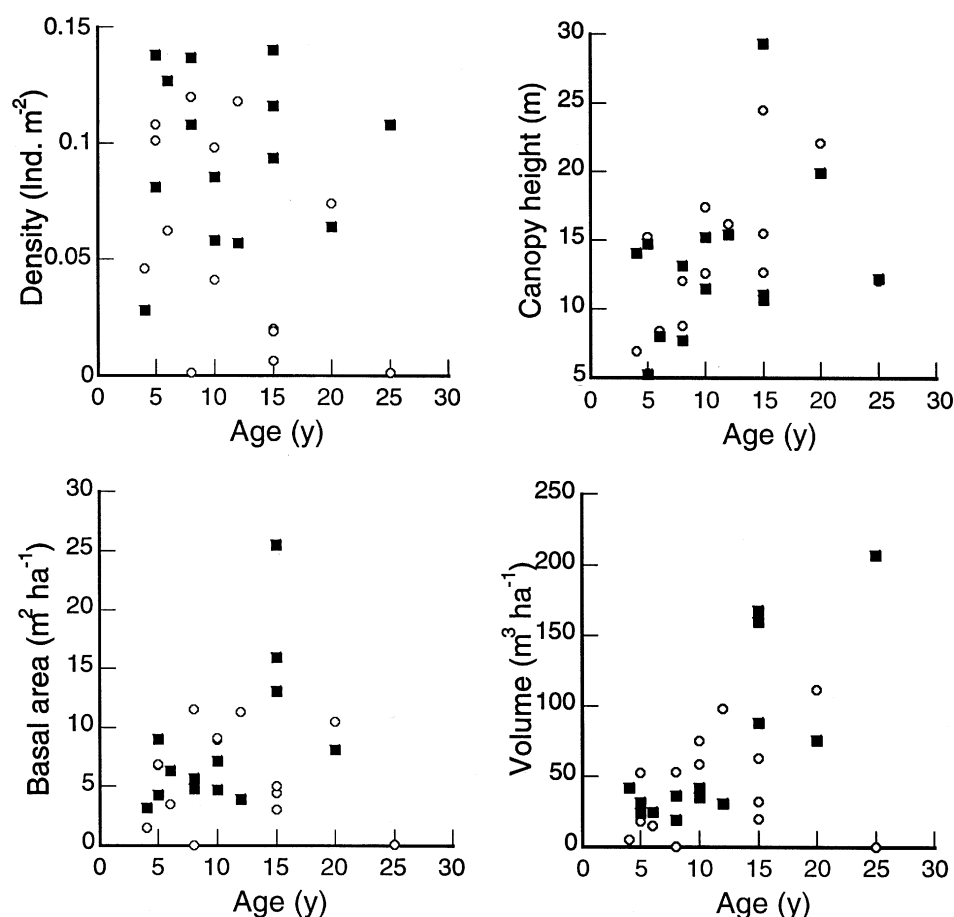


Figure 2. Regrowth structural characteristics for all stands surveyed in Bolivia. Open circles: pioneer species, closed squares: other species.

(Mimosoideae), *Goupia* (Celastraceae), *Schefflera morototoni* (Aublet) Maguire, Steyerl. & Frodin (Araliaceae) and genera of the Annonaceae, Lauraceae and Burseraceae. The importance of these genera can be interpreted as a second successional phase in forest regeneration in central Amazonia. Many of the common genera of mature forests in the area occurred in the stands 10 y and older. Other families with individuals recorded in more than one of these stands were Anacardiaceae, Apocynaceae, Bignoniaceae, Caryocaraceae, Caesalpinoideae, Cochlospermaceae, Chrysobalanaceae, Flacourtiaceae, Lecythidaceae, Malphiaceae, Meliaceae, Myrtaceae, Papilionoideae, Rubiaceae, Sapindaceae, Sapotaceae, Simaroubaceae and Sterculiaceae. Monocotyledonous genera recorded in more than one of the stands were *Astrocaryum*, *Bactris*, *Euterpe*, *Mauritia* and *Maximilia* (Araliaceae) and *Phenakospermum guianensis* (Rich.) Endl. (Strelitziaceae).

Among Brazilian stands, canopy height ranged from 6 to 30 m (Figure 3).

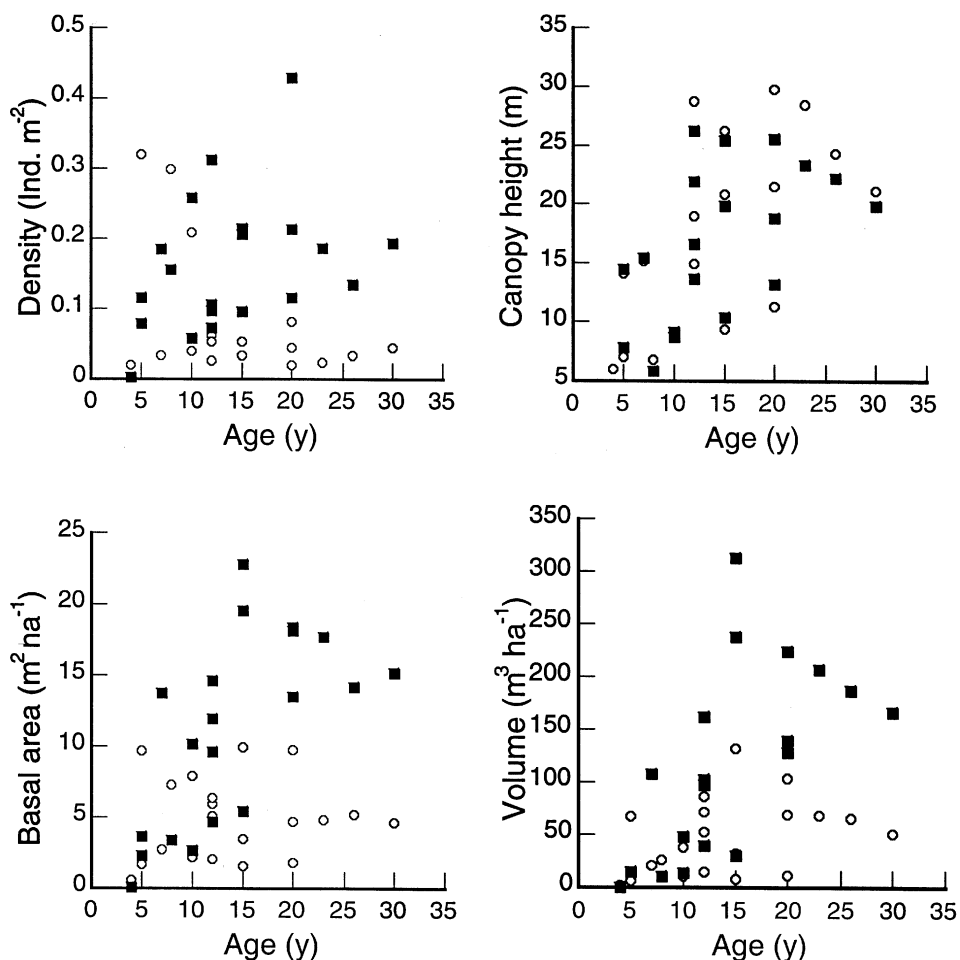


Figure 3. Regrowth structural characteristics for all stands surveyed in Brazil. Open circles: pioneer species, closed squares: other species.

The density of pioneers peaked at 3000 ha⁻¹ for stands 4–5 y old and decreased to around 500 ha⁻¹ for the remainder of the chronosequence. The frequency, basal area and volume of later-successional trees were low for stands from 4–5 y old and highly variable among stands from 12–15 y old.

Patterns of biomass accumulation

In Bolivia, total above-ground live biomass estimates of trees > 5 cm dbh for all stands ranged from 3 to 170 Mg ha⁻¹. The average rate of biomass accumulation throughout the age sequence was 5.4 Mg ha⁻¹ y⁻¹. Pioneer trees represented a relatively small component of total biomass, even in the stands in which they dominated the canopies (Figure 4). This is because all of the dominant pioneer trees had very low wood density. Among the Bolivian stands 10 y

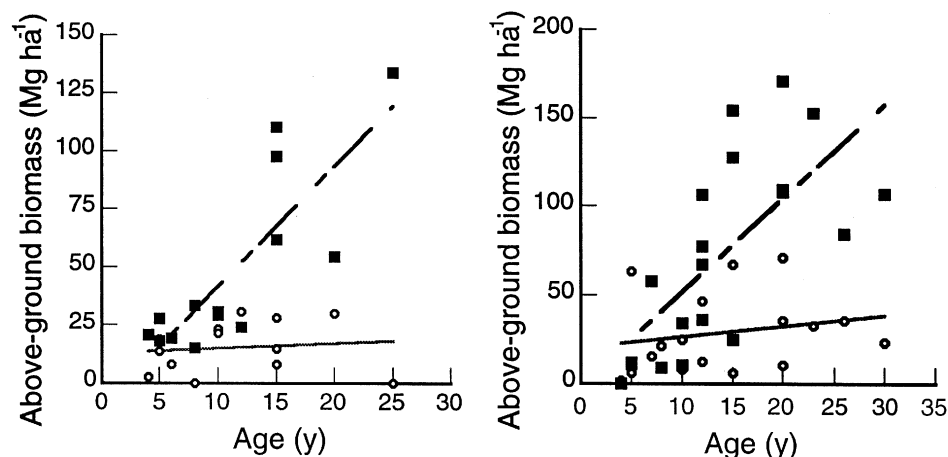


Figure 4. Above-ground biomass for all stands surveyed in (a) Bolivia and (b) Brazil. Open circles: pioneer species, closed squares: other species.

and older *Inga*, *Nectandra*, *Cordia*, *Swartzia* and *Anadenanthera colubrina* contributed the greatest amount of biomass.

Stands on both soil types were included in a comparison of short-term versus medium-fallow cases, as there was no significant effect of soil type on the biomass accumulation of the stands in Bolivia ($F = 2.64$, $df = 13$, $P > 0.133$). An F-ratio test indicated no significant difference in regrowth biomass accumulation rates between these land uses ($F < 0.001$, $df = 13$, $P > 0.99$).

Among the stands in Brazil, total stand biomass ranged from 10 to 200 Mg ha⁻¹. Biomass of pioneer trees varied around 2.5 Mg ha⁻¹ over the entire chronosequence, while biomass of later-successional species increased linearly at over 5.0 Mg ha⁻¹ y⁻¹.

Like volume, total biomass was most variable among stands 12 to 15 y old. The sample of fallows from AM10 includes three stands of 12 y recovering from short-term use. The first, A10, was cleared, not burned and then immediately abandoned without any cultivation (Table 1). This stand had an above-ground biomass of over 140 Mg ha⁻¹. The second case, A5, recovered from 1 y of manioc cultivation and grew to just over 110 Mg ha⁻¹. The third case was also in use for only 1 y, although it was the sole example in this study of regrowth on a sandy oxisol hilltop. The biomass of this stand was 80 Mg ha⁻¹. The two 15-y-old stands at Janauaca had particularly high biomass densities. Most of the biomass in these stands was in the largest 11 *Miconia*, *Inga* and Lauraceae trees with DBH up to 40 cm, however, no individual tree accounted for more than 5% of the total estimated biomass in any stand. The 12–15-y-old stands with the lowest biomass densities were dominated by *Miconia* and *Goupia*, although at smaller DBH and lower heights.

Selecting only stands up to 12 y in age, the average rate of above-ground live

Table 4. Regression statistics for relationships of above-ground live biomass versus age for all stands at AM10 and Janauaca. M = above-ground standing biomass in Mg ha⁻¹, A = age (y), L = land-use: short-term = 0, long-term pasture = 1. ST = short-term agriculture, LP = long-term pasture, MF = medium-fallow agriculture.

Dependent variable	Equation	df	F	P	r ²
<i>Bolivia:</i>					
1 M pioneer	M = 13.02 + 0.21 A	13	0.2	0.680	0.015
2 M non-pioneer	M = -10.21 + 5.19 A	13	26.1	0.001	0.685
3 M all 4–12 y	M = 14.04 + 3.33 A	8	8.6	0.022	0.550
4 M all stands	M = 2.81 + 5.40 A	13	36.5	0.001	0.753
5 M ST	M = -2.68 + 5.85 A	6	32.4	0.003	0.867
6 M MF	M = 10.12 + 4.71 A	6	7.1	0.045	0.585
<i>Brazil:</i>					
7 M pioneer	M = 20.32 + 0.61 A	19	0.9	0.368	0.045
8 M non-pioneer	M = -1.65 + 5.32 A	19	17.3	0.001	0.490
9 M all 4–12 y	M = -17.08 + 9.08 A	10	7.6	0.023	0.458
10 M all stands	M = 18.67 + 5.93 A	19	13.8	0.002	0.403
11 M all stands	M = -102.7 + 81.7 log(A)	19	18.4	0.001	0.506
12 M all stands	M = 47.52 + 5.35 A -45.99 L	19	10.9	0.001	0.561
13 M all stands	M = -62.7 + 72.7 log(A) -38.9 L	19	12.4	0.001	0.594
14 M ST	M = 40.31 + 5.82 A	10	6.1	0.036	0.404
15 M LP	M = 5.77 + 5.01 A	8	6.5	0.038	0.481
16 M ST	M = -85.4 + 81.4 log(A)	10	6.8	0.029	0.430
17 M LP	M = -89.1 + 67.4 log(A)	8	8.3	0.024	0.544

biomass accumulation for early regrowth in Brazil was 9.0 Mg ha⁻¹ y⁻¹, almost three times the rate in Bolivia (Table 4, eqns 3 and 9). Regression equations for all stands were not significantly different between AM10 and Janauaca (F = 0.33, df = 19, P > 0.57). Data from AM10 and Janauaca were combined to compare all cases of recovery from short-term versus long-term pasture in Brazil. The regression slopes of biomass versus age did not differ significantly, yet the intercepts did differ by over 45 Mg ha⁻¹ (F = 4.92, df = 19, P < 0.05; Figure 5b). The average rate of biomass accumulation for regrowth following long-term pasture was 5 Mg ha⁻¹ y⁻¹. An F-test between the short-term cases from Bolivia and Brazil also revealed a significant difference in intercept but not in slope (F = 4.6, df = 17, P < 0.05; Figure 6).

DISCUSSION

Successional changes and vegetation structure

In Brazil, most of the stands were dominated by *Vismia* and to a lesser extent *Miconia*, *Bellucia* and *Cecropia*. This was also the case in stands surveyed along the upper Río Negro and in eastern Pará (Saldarriaga *et al.* 1988, Uhl 1987, Uhl *et al.* 1988). Foody *et al.* (1994) have suggested that in the area around Manaus, *Cecropia* dominate young stands regenerating in sites cleared for the first time and *Vismia* dominate in sites burned multiple times. In the present study, *Cecropia* was more abundant in the short-term cases than in the long; however, *Vismia*, *Miconia* and *Bellucia* were not more common in *Cecropia*'s

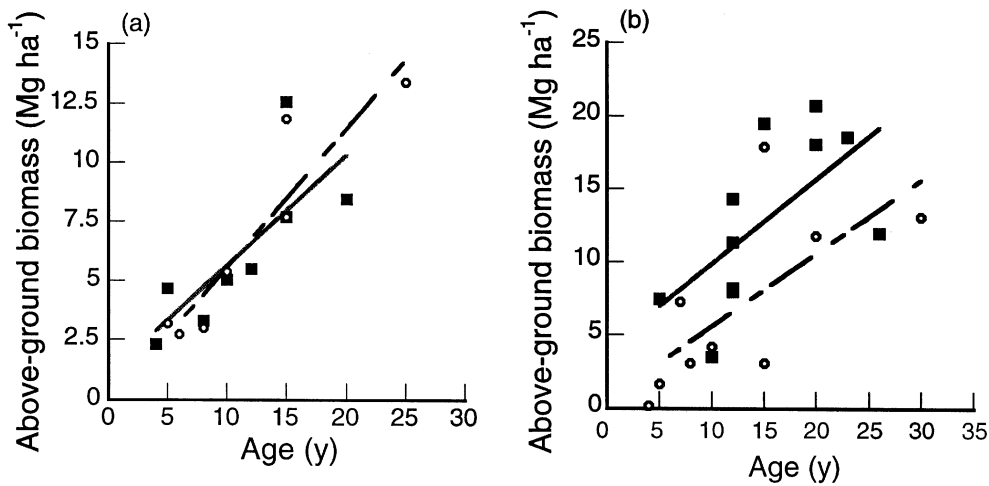


Figure 5. Above-ground biomass for all stands surveyed in (a) Bolivia and (b) Brazil. For Bolivian regrowth, open circles: regrowth following medium-fallow agriculture, closed squares: regrowth following short-term agriculture. For Brazilian regrowth, open circles: regrowth following long-term pasture, closed squares: regrowth following short-term agriculture.

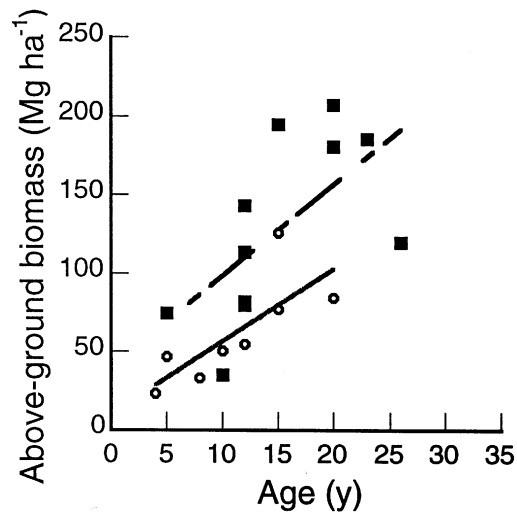


Figure 6. Above-ground biomass for regrowth following short-term agriculture only. Open circles: Bolivian regrowth, closed squares: Brazilian regrowth.

absence. Furthermore, while *Cecropia* trees were more common in recovery from short-term disturbance, their dominance was short-lived. This may depend on stand size, as the stands surveyed in Brazil were from 2 to 8 ha and all had at least a partial border with mature forest.

In Bolivia, dominant pioneer trees were *Ochroma*, *Cecropia*, *Pourouma* and *Heliconia americana* and dominant later-successional trees were *Inga*, *Nectandra*, *Cordia*, *Swartzia* and *Anadenanthera colubrina*. Despite the persistence of pioneer

tree genera in the older regrowth in both study areas, they accounted for a small portion of the total biomass as they all had low density wood. Among the stands from 4–8 y old in both Bolivia and Brazil, those with the highest biomass had a high density of pioneer trees that accounted for most of the biomass. The variability in biomass was greatest among 12–15-y-old stands and appeared to be dependent on the timing of canopy recruitment of later-successional trees versus the senescence of larger pioneers.

Considering some of the findings in earlier studies, this may in part be explained by biotic factors during early succession. Later-successional species were far less abundant than pioneer species in the seed banks of cleared fields and young fallows in Pará and San Carlos (Cardoso da Silva *et al.* 1996, Nepstad *et al.* 1989, Uhl 1987). Once established, however, the shade-tolerant later-successional trees grew rapidly under the pioneer canopies of young fallows (Uhl 1987). The return of the vectors of seed dispersal to an abandoned farm may be a major factor in how quickly those species eventually reach the canopy. Most of these species are dispersed by frugivorous birds and small mammals, few of which venture into fields and young fallows (Cardoso da Silva *et al.* 1996, Gorchoff *et al.* 1993, Nepstad *et al.* 1989, Schupp *et al.* 1989, Uhl 1987). Factors such as the distribution and habitat characteristics of neighbouring forests may be particularly important not only to composition but to changes in structure and biomass during the later stages of secondary regrowth.

Rates of biomass accumulation in Brazil and Bolivia

General patterns are evident when comparing biomass estimates of the younger stands in this study to those reported in previous studies. The average rate of above-ground biomass accumulation over the first 12 y of regrowth in Brazil was 9.1 Mg ha⁻¹ y⁻¹ and over the entire age sequence 5.9 Mg ha⁻¹ y⁻¹. Combining data from San Carlos, Venezuela with those from six other tropical lowland moist and wet sites, Uhl (1987) estimated an average rate of above-ground biomass accumulation of around 6.5 to 7 Mg ha⁻¹ y⁻¹ over the first 8 y of forest regrowth following short-term clearances. The rate from this study agrees with an estimated average of 10 Mg ha⁻¹ y⁻¹ for young forest regrowth in moist tropical environments by Brown & Lugo (1990) and is comparable with findings from other humid neotropical sites (Faber-Langendoen 1992, Fölster *et al.* 1976, Mesquita 1995, Szott & Palm 1994). It is probable that a rate of 9–10 Mg ha⁻¹ y⁻¹ is applicable to young regrowth following short-term usage in most of humid Amazonia. It is also likely that such rates of biomass accumulation are typical for most areas of low density caboclo settlements, where swidden fields are small and derived mostly from mature or old secondary forest.

The rate of biomass accumulation in Bolivia was *c.* 5.4 Mg ha⁻¹ y⁻¹ and linear throughout the age sequence. This rate is less than the average reported by Uhl (1987) and similar to rates reported for Rondônia (Alves *et al.* 1997) and Pará (Busbacher *et al.* 1988, Fearnside & Guimarães 1996). This rate is probably most applicable to young forest regrowth in the drier areas of the Amazon.

Few published data on the biomass of regrowth over 15 y old in Amazonia exist for comparison with this study. Saldarriaga *et al.* (1988) surveyed a series of stands up to 80 y old in the upper Río Negro and concluded that biomass increased linearly over the first 40 y of regeneration and changed little thereafter. In all of the stands surveyed by Saldarriaga *et al.* (1988), none of those younger than 30 y old had surpassed 100 Mg ha⁻¹ and none of those younger than 80 y old had surpassed 200 Mg ha⁻¹. Alves *et al.* (1997) reported a range of biomass estimates for 16-y and 18-y-old stands in Rondônia. Their high biomass estimates were over 200 Mg ha⁻¹, but the estimates using the allometry of Uhl (1987) are below 150 Mg ha⁻¹. Their estimate rate of biomass accumulation of 6.4 to 7.9 Mg ha⁻¹ y⁻¹ is slightly greater than the rate estimated for Bolivia in this study. In this study, regrowth younger than 30 y old had attained 130 Mg ha⁻¹ in Bolivia and 200 Mg ha⁻¹ in Brazil.

Impacts of extended land use on biomass accumulation

In Bolivia, all of the medium-fallow agriculture cases of regrowth had been re-cleared four or more times. These data do not support the idea that rates of biomass accumulation during regrowth are reduced with continued fallow agriculture. This contrasts reports of reduced crop productivity with continued fallow agriculture in this area and elsewhere (Barber 1995). Possible explanations for this are: (1) tropical secondary forest species are better adapted to low nutrient conditions than are crop species (Uhl 1987); (2) tropical secondary forests rapidly develop efficient mechanisms of nutrient cycling that permit rapid growth despite low soil nutrient levels (Jordan 1989); and (3) the lengths of the fallow periods relative to the cultivation periods in this study were long enough to maintain productivity.

The biomass recovery rates found in Bolivia suggest that carbon uptake is independent of stand age or time under shifting cultivation. Small-scale roadside shifting cultivation is probably the most common land use along the base of the Andean crescent. If the soils in this area are to be considered representative of much of the Andean crescent, then this result implies that the carbon sequestration in such areas depends primarily on the area of regrowth and local climate rather than factors such as regrowth age distribution and length of time since original forest clearance.

The comparison of regression equations of biomass in regrowth following short-term agriculture and long-term pasture in Brazil revealed a significant difference between intercepts but not between slopes. This agrees with Guimarães (1993), who reported a significant effect of years under pasture on the intercept of biomass-age regressions for regrowth in Para. The difference in intercepts suggests that differences in biomass already existed by the beginning of this age sequence, i.e. differences in biomass accumulation following these land uses mostly occurred during the first 5 y of regrowth. The similarity of slopes suggests that after this early phase, rates of above-ground biomass accumulation become more similar. In other words, the effects of extended

pasture use are less important to rates of biomass accumulation during later years of regrowth. This may be explained by contributions to soil organic matter by litter fall during fallow regrowth, rendering effects of soil nutrient changes less evident at later stages of regrowth.

It must be kept in mind that the 'long-term' pasture use in this study is most similar to the 'moderate' and 'high' intensity uses described by Fearnside and Guimarães (1993), Uhl (1987) and Uhl *et al.* (1988). These data do not indicate the biomass accumulation of regrowth following very intensive uses, such as mechanized agriculture and longer-term pasture. Both seedling establishment and growth of woody species in sites abandoned from such intensive uses are seriously inhibited (e.g. Purata 1986, Uhl 1987, Uhl *et al.* 1988, Zweetslot 1981), and forest regrowth in very large clearances may be inhibited due to slow seed arrival. Nevertheless, the reduced biomass accumulation in regrowth following over 5 y of pasture is consistent with findings elsewhere in the Amazon. This suggests that even in the highly productive regions of the Amazon, extended pastures consistently lead to reduced grazing potential (Fearnside 1985, Hecht 1990, Moran 1976) as well as reduced rates of forest recovery following abandonment.

In terms of biomass accumulation of forest regrowth, medium-fallow agriculture as practiced in Santa Cruz, Bolivia is sustainable, while extended grazing in the Brazilian Amazon is unsustainable. What is encouraging is that among all of the land-uses considered in this study, regrowth was always dominated by woody vegetation and the effect of extended pasture on regrowth biomass accumulation was less apparent among older fallows. This implies that the long-term protection of secondary forests in many areas of the Amazon may permit a rapid recovery of tropical forest structure, biomass and physical functioning.

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