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Aboveground biomass and structure of rainforests in the southwestern Brazilian Amazon

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Abstract

The biomass of intact tropical forests must be known in order to quantify C pools and emissions arising from biomass burning associated with deforestation, land conversion, or fragmentation. To address this need, we quantified the total aboveground biomass (TAGB) and forest structure in 20 intact tropical forest sites in western Brazil. The sites were located in open, dense, and ecotone (to savanna) forest types. The TAGB of open forest ranged from 288 to 346 Mg ha^{-1}, with a mean of 313 Mg ha^{-1}; dense forest TAGB ranged from 298 to 533 Mg ha^{-1}, with a mean of 377 Mg ha^{-1}; and ecotone forests TAGB ranged from 298 to 422 Mg ha^{-1}, with a mean of 350 Mg ha^{-1}. Mean TAGB for all 20 sites was 341 Mg ha^{-1}. "live trees" (broad-leaved trees) comprised most of TAGB, averaging 280 Mg ha^{-1}. Mean aboveground biomass of trees $\geq$10 cm diameter at breast height (dbh) differed between open (239 Mg ha^{-1}) and dense forests (307 Mg ha^{-1}). Mean biomass of live "non-tree" components (predominantly palms) for all 20 sites was 22 Mg ha^{-1}. The combined biomass of coarse wood debris, forest floor (litter/rootmat), and standing dead plants (trees, palms and vines) averaged 38 Mg ha^{-1} or 12% of the TAGB. Forest structure and biomass distribution were not uniform among sites or forest types. For example, non-tree components ranged from 41% of the TAGB in one ecotone forest to as low as 7% in a dense forest site. Non-tree components comprised 22% of TAGB. This is noteworthy because the non-tree components are often omitted from forest biomass/carbon pool estimates.

Keywords: Amazon; Biomass; Rainforest

1. Introduction

Tropical rainforests are a significant global terrestrial C pool, thus, deforestation/land conversion contributes to rising levels of greenhouse gases in the atmosphere. Information on total aboveground biomass (TAGB) is scarce for Amazonian forests. Indirect estimates based on commercial volume from forest inventory data (Brown and Lugo, 1992; Fearnside, 1992a,b), as well as direct field measurements of individual trees have been used to predict TAGB (Jordan and Uhl, 1978; Klinge and Herrera, 1978; Russell, 1983; Higuchi et al., 1994). Estimates for TAGB in the Brazilian Amazon have ranged from 155 to 555 Mg ha^{-1} (Revilla Cardinas et al., 1982; Brown and Lugo, 1984).

Differences in estimates of TAGB arise in part from the methods used to measure it, as well as from the

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heterogeneity of the forests. Early studies involved destructive sampling to develop predictive models for tree biomass estimations based on combinations of tree diameter at breast height (dbh), specific gravity (sg), and height (*h*) (Jordan and Uhl, 1978; Klinge and Herrera, 1978; Russell, 1983; Higuchi et al., 1994). The models for individual tree biomass were then applied to measurements from trees. The application of destructive and field measurements is limited by the time and cost associated with collecting field data over a large area of tropical forests. To reduce the dependence on destructive or direct field measurements, commercial volumes derived from forest inventories have been used to estimate total tree biomass at large scales (Brown et al., 1989; Brown and Lugo, 1992; Brown, 1997). Based on a compilation of results from nine studies for which direct measurements of biomass were made, as well the indirect estimates of Brown and Lugo (1992), Fearnside (1992b) estimated the average TAGB for the Brazilian Legal Amazon at 335 Mg ha^{-1}. In another set of studies, Kauffman et al. (1995) and Guild et al. (1998) quantified TAGB for six slashed primary forests. Their biomass estimates ranged from 293 to 436 Mg ha^{-1}, with a mean of 362 Mg ha^{-1}. Although the tierra firme forest sampled by Jordan and Uhl (1978) was considered to be of low stature and biomass (335 Mg ha^{-1}) for the Amazon, their estimate was almost 100 Mg ha^{-1} more than the mean biomass for Amazonia (227 Mg ha^{-1}) that Brown and Lugo (1992) calculated through models based on forest inventories. However, the Brown and Lugo (1992) estimates ignored components of TAGB other than trees $\geq$10 cm dbh. Laurance et al. (1997) calculated TAGB and biomass losses from forest inventories by assuming that all non-tree biomass and trees <10 cm dbh made up 12% of the overstory (trees >10 cm dbh). Yet, in Amazonian forests studied by Kauffman et al. (1998), there was a significant negative relationship between overstory and understory biomass. Nevertheless, TAGB is often estimated by assuming a constant proportion between overstory trees and other biomass components (Fearnside, 1992a).

The RADAMBRASIL forest inventory project of the Departamento Nacional de Produção Mineral (DNPM) was a forest classification and mapping effort of much of the Amazon Basin. It classified forest into types and delineated the area covered by each (DNPM, 1978). RADAMBRASIL identified five regions or forest types and 15 geomorphic sub-regions in Rondônia, Brazil. This classification system was based on a hierarchy of ecological regions (forest types), sub-regions (ecological/geomorphology sub-groupings), and formations (topography). Information from the RADAMBRASIL inventory is currently being used in global models of carbon pools and flux (Houghton, 1991; Fearnside, 1992b, 1997; Fearnside et al., 1993; Dixon et al., 1994). However, because estimates of TAGB derived from models using the RADAMBRASIL data set are low compared with data collected in ecological studies, its use is controversial (Brown and Lugo, 1992; Fearnside, 1992a). The extrapolation of more detailed measurements to the larger forest inventory database would increase the accuracy of global carbon models essential to predicting climate change. The objectives of this study were to quantify forest structure and TAGB and its distribution in 20 intact Amazonian tropical forest stands on or near the RADAMBRASIL inventory plots in western Brazil, and to determine whether there are differences in TAGB among forest types.

2. Study sites

A total of 18 out of 20 study sites were located in the northwestern portion of the state of Rondônia and two sites were located in the southern extreme of Amazonas state, Brazil (Fig. 1). Rondônia's average annual rainfall is ~2300 mm, falling mostly between November and April (DNPM, 1978). Mean temperature is 25.2 °C (average maximum of 31.1 °C, and average minimum of 20.9 °C), and average relative humidity is 85% (Departamento Nacional de Meterologia, Brasil, 1992). Soils at the individual sites ranged from upland red–yellow and yellow oxisols and red–yellow ultisols, to alluvial soils with hydromorphic lateritic and gley characteristics (DNPM, 1978). The elevation at the sites ranged from 61 to 310 m.

Forests in this part of Amazonia are representative of forests within the crescent of deforestation occurring along the southern and eastern fringe of the Amazon (Fearnside, 1990). Under the Holdridge system, they would be classified as tropical moist forests (Holdridge et al., 1971). Under RADAMBRASIL, these forests were classified as seasonal tropical

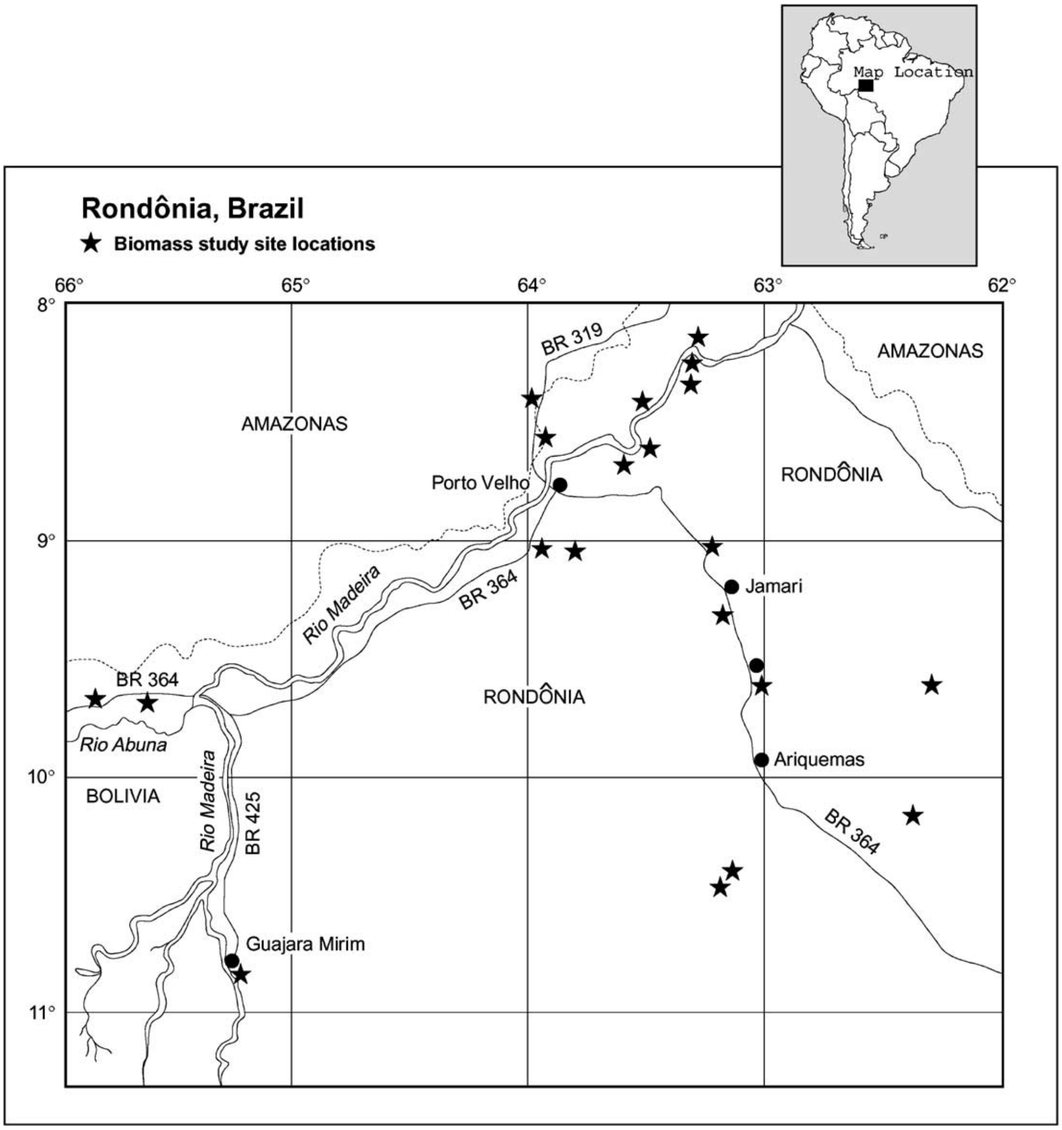

Fig. 1. Study sites were located in southern Amazonas and Rondônia, Brazil.

evergreen forests transitional between evergreen tropical forests and semi-deciduous tropical forests (DNPM, 1978).

Each of our 20 sites had been sampled and partitioned into forest types as part of the RADAM-BRASIL inventory in the early 1970s (Table 1). We labeled study plots with the corresponding original numbers of the forest inventory plots of the RADAM-BRASIL study.

The most coarse resolution of forest classification separated our study sites into forest types: (1) open (characterized by well-spaced individual trees, numerous palms and the presence of vines); (2) dense (normally having three strata; one of large trees, one of small regenerating trees and one of shrubs and herbaceous material); and (3) ecotone (edge forests in contact with savanna and any of the other classes of forest formations) tropical forest (DNPM, 1978).

Table 1
Forest classification, plot numbers, location, and total aboveground biomass (TAGB, Mg ha^{-1}) of the forest inventory sites sampled in this study[a]

Forest type-region				TAGB (Mg ha^{-1})	Means		
Geomorphic sub-region	Topographic-formation	Plot	Location		Formation	Sub-region	Region
Open tropical forest							
Amazon alluvial	Alluvial terraces	225	Longitude 63°29′56.1″ latitude 8°26′20.9″	328.8			
		226	Longitude 63°19′36.9″ latitude 8°8′25.5″	288.2		308.5 (20.3)	
Broken surface of the upper Xigu / Tapajos/Madeira	Sub-montane rolling hills	70	Longitude 65°39′0.6″ latitude 9°39′34.9″	345.7			
		74	Longitude 63°15′9.9″ latitude 9°2′30.1″	294.7			
		75	Longitude 63°9′15.1″ latitude 9°18′7.4″	311.5			
		76	Longitude 63°3′16.4″ latitude 9°36′56.0″	310.8, 315.7			
	Sub-montane broken surface	89[b]	Longitude 62°15′36.7″ latitude 9°41′47.6″	299.4			
		113[b]	Longitude 62°20′51.7″ latitude 10°11′2.1″	320.9	310.1 (10.7)	313.8 (12.9)	312.8 (6.7)
Dense tropical forest							
Amazon alluvial	Alluvial plane, periodically flooded	1[b]	Longitude 63°19′38.4″ latitude 8°10′58.1″	407.7			
		2[b]	Longitude 63°20′14.2″ latitude 8°11′23.9″	319.1	363.4 (44.3)		
Low plates of Amazonia	Rolling lowlands	229	Longitude 63°59′47.3″ latitude 9°1′30.9″	299.5			
Low hills of southern Amazonia	Sub-montane low hills	24	Longitude 63°5′9.5″ latitude 10°22′44.7″	533.8			
		25	Longitude 63°7′37.9″ latitude 10°22′51.3″	441.7	487.8 (46.1)		
Precambrian platform cover	Sub-montane broken surface	43[b]	Longitude 65°53′8.8″ latitude 9°41′44.4″	298.1			
		44[b]	Longitude 63°49′49.9″ latitude 9°2′12.4″	336.4	317.3 (19.2)		376.6 (33.4)
Ecotone tropical forest							
Forest/savanna edge (open forest)	Lowland plates	186[b]	Longitude 63°58′45.1″ latitude 8°33′23.0″	348.3			
		188	Longitude 63°57′45.0″ latitude 8°23′53.9″	297.9			
		190[b]	Longitude 63°31′34.5″ latitude 8°35′19.7″	422.1			
		195	Longitude 63°36′38.0″ latitude 8°42′35.8″	332.6			350.2 (26.2)
Areas of human influence (open forests)[c]							
Platform cover above 600 m sub-montane table lands		218	Longitude 65°18′45.5″ latitude 10°47′44.7″	287.3			
Mean TAGB for all 20 plots							341.2 (14.2)

[a] Region, sub-region, and formations are those delineated by RADAMBRASIL. Locations are ±100 m. Standard errors are in parentheses.
[b] Due to difficulty obtaining GPS readings under canopy, these sites are ±200 m. Sites 1, 2 and 190 may be ±2 km from listed location.
[c] The plot was located on a military reserve, there were no stumps present, and the history for its classification by RADAMBRASIL as human influenced was unknown.

Open forests were the most abundant forest type in Rondônia (DNPM, 1978).

2.1. Plot site selection

Selection of RADAMBRASIL plots for re-sampling in this study was based on accessibility and the continued existence of the forest overstory (many sites had been deforested since the 1970s). Twenty plots, with no aprior knowledge of structure and composition, were selected for study. Plots were assumed to be representative of the forests of this region. Geographical locations of the sites were determined from maps and coordinates provided by D. Skole, University of New Hampshire, and were located in the field using a Global Positioning System (GPS) (Table 1). We also used a RADAMBRASIL map and satellite photos of the area to assist in plot location. In cases where portions of the area containing the original RADAMBRASIL sites had likely been deforested (i.e. adjacent to a road), we moved our plots to the closest intact forest still within the same forest type, usually a short distance (100–200 m).

Many of the plots had minor levels of human impact. However, the level of disturbance in sample plots did not appear to be appreciably greater than that reported at the time of the RADAMBRASIL inventory (DNPM, 1978). For example, subsistence palm and tree harvest for local use and trails used for rubber-tapping were reported in the original inventory. Some sites were located near areas of long-term (>100 years), low-density (Euro–American) settlement (e.g. river villages and rubber-tapping sites). Five of the 20 sites had at least one stump indicating past selective tree harvest. The remaining sites had no stumps. All of the stumps appeared to have originated >10 years prior to our study and were the result of local farm use, not commercial harvest.

2.2. Total aboveground biomass components

TAGB was estimated by measuring all organic materials above mineral soil. TAGB was divided into "tree" (broad-leaved trees) and "non-tree" (other components, predominantly palms) components based on structural and ecological significance and practicality of measurement.

Tree diameter was measured at 1.37 m above the ground (dbh) or immediately above the tree buttress or stilt roots when present. Trees were separated into seven diameter classes based on dbh (<10, 10–30, 30–50, 50–70, 70–100, 100–200 and >200 cm dbh). Palms were sampled separately from broadleaf trees. We divided them into three categories (basal palms with no trunks, <10 and $\geq$10 cm dbh). Vines and lianas were placed in two size classes (<10 and $\geq$10 cm dbh). Other components included small dicots (plants <1.37 m in height), litter/rootmat (forest floor), standing dead trees and palms, and dead and downed coarse woody debris (CWD). We divided CWD into two categories: 2.5–7.6 and $\geq$7.6 cm diameter (Kauffman et al., 1988, 1995). The forest floor component was composed of litter, small wood debris (<2.5 cm diameter), and rootmat. Rootmat contained a large amount of decomposing organic matter, as well as live roots, and was not as well developed as that in the Venezuelan Amazon reported by Kauffman et al. (1988).

2.3. Plot layout

At each site, a 75 m $\times$ 105 m (0.79 ha) plot was established. Two 105 m transects divided the plot into three 25 m $\times$ 105 m (0.26 ha) sub-plots. The diameter for all trees $\geq$30 cm dbh was recorded in the entire plot (0.79 ha). All trees and palms 10–30 cm dbh were measured in the center 25 m $\times$ 105 m sub-plot. Along every 15 m of each 105 m transect, we established a planer intersect transect to measure downed CWD ($n = 16$, 8 per transect) (Van Wagner, 1968; Brown and Roussopoulos, 1974). At each of the 15 m points along each transect, a 2 m $\times$ 10 m plot was established to measure small trees, vines, and palms ($\geq$1.37 m in height, but <10 cm dbh), and basal leaf palms. The density of dicot seedlings in a 1 m $\times$ 1 m plot was measured at the same 15 m points along the 105 m transect. The biomass of the forest floor was measured in a 50 cm $\times$ 50 cm microplot.

2.4. Biomass estimations

Individual equations for each forest component were used for calculating the biomass (Tables 2 and 3). Biomass of trees $\geq$5 cm dbh was calculated from equations based on dbh given by Higuchi et al. (1998)

Table 2
Allometric equations used to determine aboveground biomass of tree components and forest structure[a]

Parameter	Equation	Source
Trees <5 cm dbh	$[(\exp(1.0583 \times \ln(D^2) + 4.9375)) \times 1.143]/10^6$, $R^2 = 0.94$, $N = 66$	Hughes et al. (1999)
Trees 5–20 cm dbh	$[(\exp(-1.754 + 2.665 \times \ln(D))) \times 0.604]/10^3$, $R^2 = 0.92$, $N = 244$	Higuchi et al. (1998)
Trees >20 cm dbh	$[(\exp(-0.151 + 2.17 \times \ln(D))) \times 0.604]/10^3$, $R^2 = 0.90$, $N = 71$	Higuchi et al. (1998)
Height trees <20 cm dbh (m)	$[\exp(0.6387 + 0.7988 \times \ln(D))] \times 1.0438$, $R^2 = 0.85$, $N = 40$	This study
Height trees >20 cm dbh (m)	$[-19.5873 + 13.2823 \times \ln(D)] \times 0.9999$, $R^2 = 0.64$, $N = 89$	This study
Quadratic stand diameter (QSD)	$\sqrt{\sum D^2/n}$ or $\sqrt{(\mathrm{BA}/n)} \times (4/\pi)$	
Standing dead trees		
Trees <10 cm dbh	$[(\exp(1.1788 \times \ln(D^2) + 4.4189)) \times 1.0819]/10^6$, $R^2 = 0.96$, $N = 66$	Hughes et al. (1999)
Trees >10 cm dbh	$(\pi r^2 \times H) \times \mathrm{sg}$	
Wood debris 2.5 to 7.60 cm dbh	$\mathrm{sg} \times ((\pi^2 \times N \times S \times C_s \times d^2)/8L) \times 10^2$, $\mathrm{sg} = 0.413\ \mathrm{g\ cm^{-3}}$	Van Wagner (1968), Brown and Roussopoulos (1974)
Wood debris >7.6 cm dbh	$\mathrm{sg} \times ((\pi^2 \times \sum D^2 \times S \times C_s \times d^2)/8L) \times 10^2$; sg sound $= 482\ \mathrm{g\ cm^{-3}}$ sg rotten $= 0.342$; sg palm $= 0.327$	Van Wagner (1968), Brown and Roussopoulos (1974)

[a] Biomass is expressed in Mg on a dry weight basis. D: dbh (cm); H: height (m); BA: basal area (cm^2); sg: specific gravity of wood (g cm^{-3}); N: number of intercepted wood particles; S: secant of wood particles; C_s: slope correction factor ($\sqrt{1 + (\%\mathrm{slope}/100)^2}$); $\sum D^2$: sum of wood particle diameter squared; L: transect length (cm); stem: stem height (m); d^2: quadratic mean diameter of wood particles; r: radius (m).

for Amazonian trees. Biomass of trees <5 cm dbh was calculated from equations based on dbh given by Hughes et al. (1999). Tree height was estimated from a regression equation with tree diameter as the independent variable. Data for the tree height model were collected from 129 trees in Rondônia. Diameter at breast height of the trees ranged from 1.5 to 238 cm.

Biomass of CWD was calculated by using the methods of Van Wagner (1968). Transects to measure mass of CWD ≥7.6 cm in diameter were 15 m long. Pieces of CWD that were 2.5–7.6 cm in diameter were measured along the central 5 m of the 15-m transect. Coarse woody debris was further separated into tree (dicot) wood or palm wood components. The ≥7.6-cm diameter class was also separated into sound or rotten classes following the methods of Kauffman et al. (1988) and Brown (1971).

One hundred samples for each size class of CWD were collected in forests near Jamari, Rondônia, to obtain an average wood density (sg = 0.41 g cm^{-3} for CWD 2.5–7.6 cm, 0.49 g cm^{-3} for sound wood, 0.34 g cm^{-3} for rotten wood, and 0.33 g cm^{-3} for

Table 3
Allometric equations used to determine aboveground biomass of forest components other than trees[a]

Parameter	Equation	Source
Attalea sp. palm >1.78 m H	$\{[(46.1 \times \mathrm{stem}\,H) - 82.1] + [0.375 \times [(46.1 \times \mathrm{stem}\,H) - 82.1]]\}/10^3$ $R^2 = 0.99$, $N = 7$	Anderson (1983)
Palm (not *Attalea*) >10 cm dbh	$(4.5 + (7.7(\mathrm{stem}\,H))/10^3$, $R^2 = 0.90$, $N = 25$	Frangi and Lugo (1985)
Palm <10 cm dbh	$[[(\exp(0.9285 \times \ln(D^2))) + 5.7236] \times 1.050]/10^6$, $R^2 = 0.39$, $N = 15$	This study
Stemless palm	$(\mathrm{Leaves} \times 296.54)/10^6$	This study
Lianas	$(0.12 + 0.91 \log_{10}(\mathrm{BA}))/10^3$, $R^2 = 0.82$, $N = 20$	Putz (1983)
Dicot seedlings	Seedling count × mean wt. (determined from sub-sample)/10^6	This study
Forest floor	Wet wt. × %dry wt./100 (determined from sub-sample)/10^6	This study
Standing dead palm		
Palm <10 cm dbh	$[(\exp(1.5321 \times \ln(D^2) + 3.2758)) \times 1.0931]/10^6$, $R^2 = 0.34$, $N = 15$	This study
Palm >10 cm dbh	$((\pi r^2 \times H) \times \mathrm{sg})/10^6$, $\mathrm{sg} = 0.327\ \mathrm{g\ cm^{-3}}$	

[a] Biomass is expressed in Mg on a dry weight basis. D: dbh (cm); H: height (m); BA: basal area (cm^2); sg: specific gravity of wood (g cm^{-3}); stem: stem height (m); r: radius (m); wt.: weight in gram.

palm wood $\geq$7.6 cm diameter). For the 2.5–7.6 cm diameter classes, the diameter and angle off the horizontal of 65 individual pieces along a 100 m transect were measured to calculate the quadratic mean diameter and wood particle tilt (Brown and Roussopoulos, 1974). Thereafter, we only counted pieces that intersected the line, and we used density, quadratic mean diameter, and wood particle tilt variables to calculate biomass.

To calculate forest floor biomass, each sample was initially weighed in the field. Sub-samples were then oven-dried to determine the ratio of wet-to-dry weight. This ratio was then applied to the entire sample to convert from wet-to-dry weight.

To estimate biomass of basal leaf palms, the number of leaves of each individual palm encountered in the 2 m $\times$ 10 m plot was counted and multiplied by a mean weight per leaf derived from a random sample of 30 basal leaves that had been oven-dried and weighed. Three equations were necessary to ascertain biomass of palms: biomass of *Attlea* sp. $\geq$1.78 m high was calculated with the model developed by Anderson (1983); biomass of other palm species $\geq$10 cm dbh was estimated with the model of Frangi and Lugo (1985); and biomass of palms <10 cm dbh was calculated by using a model developed specifically for this study.

Vine biomass estimates were calculated with the model given by Putz (1983). All seedlings (<1.37 m height) were counted in each of the 16 (1 m $\times$ 1 m) plots per site. Seedling biomass was based on sub-sample of 50 randomly collected oven-dried seedlings from which an average weight per seedling had been determined.

Biomass of standing dead trees <10 cm dbh was calculated from an equation developed by Hughes et al. (1999). Biomass of standing dead trees $\geq$10 cm dbh was estimated by first calculating volume, then multiplying volume by the mean value of specific gravity of sound dead wood. Standing dead palm biomass was estimated from an equation developed for this study for palms <10 cm dbh and by multiplying volume by specific gravity (0.327 g cm^{-3}) for palms $\geq$10 cm dbh.

2.5. Forest structure

Tree density and basal area (BA) were calculated for each of the seven diameter classes (Table 2). Quadratic stand diameter (QSD) was calculated for each site based on trees $\geq$10 cm dbh. QSD is the diameter (cm) of the tree with the mean BA of the sampled area (Husch et al., 1972). Density was derived for palm and vine stems <10 and $\geq$10 cm dbh. We used ANOVA and Fishers LSD multiple range test to compare TAGB, the aboveground biomass of all vegetative components and the biomass for trees $\geq$10 cm dbh, for open, dense, and ecotone forest types.

Table 4
Total aboveground biomass (Mg ha^{-1}) partitioned into structural components that comprise each forest type[a]

Component	Open forest ($n = 8$)	Dense forest ($n = 7$)	Ecotone forest ($n = 4$)	20 plots
Seedlings	0.4 (0.1)	0.5 (0.1)	0.4 (0.0)	0.4 (0.0)
All palm	17.5 (11.5)	16.6 (5.3)	37.9 (16.3)	21.6 (6.0)
Vine	0.5 (0.4)	0.6 (0.3)	0.6 (0.5)	0.5 (0.2)
Trees <10 cm dbh	13.7 (1.5)	13.5 (2.4)	11.0 (2.9)	12.4 (1.1)
Trees 10–30 cm dbh	76.0 (4.3)	78.4 (7.5)	68.6 (13.9)	74.7 (4.0)
Trees 30–50 cm dbh	71.4 (5.7)	70.2 (6.9)	64.6 (7.8)	69.2 (3.5)
Trees 50–70 cm dbh	47.1 (6.1)	47.1 (12.9)	22.5 (5.2)	42.0 (5.5)
Trees 70–100 cm dbh	12.3 (3.5)	43.8 (8.8)	31.4 (6.5)	27.5 (4.7)
Trees 100–200 cm dbh	32.6 (8.4)	16.0 (6.0)	45.0 (8.0)	29.0 (5.6)
Trees 200–300 cm dbh	0.0	51.3 (24.8)	38.0 (22.3)	25.5 (10.6)
Dead wood	32.4 (5.2)	30.5 (6.9)	20.8 (6.6)	28.9 (3.4)
Litter/rootmat	10.1 (0.9)	8.3 (1.6)	9.5 (2.3)	9.6 (0.8)
Total aboveground biomass	312.8 (6.7)	376.6 (33.4)	350.2 (26.2)	341.2 (14.2)

[a] Numbers are means with standard errors in parentheses. The open forest plot that was classified as ''human influenced'' was only factored in the 20-plot mean.

3. Results

3.1. Total aboveground biomass

The mean TAGB for the 20 forest sites was 341 Mg ha^{-1} and ranged from 287 to 534 Mg ha^{-1} (Table 1). Mean TAGB of open forest ($n = 8$) was 313 Mg ha^{-1} and ranged from 288 to 346 Mg ha^{-1}. For dense forests ($n = 7$), TAGB ranged from 298 to 534 Mg ha^{-1}, with a mean of 377 Mg ha^{-1}. TAGB differed between open and dense forests at the $P = 0.11$ level of probability. For ecotone forests ($n = 4$), TAGB ranged from 298 to 422 Mg ha^{-1} and averaged 350 Mg ha^{-1}.

Trees ≥10 cm dbh composed a mean of 78% of the TAGB for all plots combined. Biomass of trees ≥10 cm dbh differed between open and dense forests at the $P = 0.13$ level of probability, averaging 238 ± 8 and 307 ± 33 Mg ha^{-1} for the two forest types, respectively. Mean biomass for all trees <50 cm dbh was similar in all three forest types (Table 4).

3.2. Distribution of TAGB among forest components

Live trees made up most of the TAGB, averaging 252, 320, and 281 Mg ha^{-1} in open, dense, and ecotone forest types, respectively (Table 4). For all sites combined, aboveground biomass of live trees (all size classes) was 280 Mg ha^{-1} or 82% of TAGB. Open and dense forests were similar in average biomass for trees <10 cm dbh (~14 Mg ha^{-1}), trees 10–30 cm dbh (76 and 78 Mg ha^{-1}), trees 30–50 cm dbh (71 and 70 Mg ha^{-1}), and trees 50–70 cm dbh (47 Mg ha^{-1}) (Table 4). The ecotone forests had slightly lower values than did open or dense forests for biomass of trees <50 cm dbh (144 Mg ha^{-1} compared with ~162 Mg ha^{-1} in open and dense forests). Differences in tree biomass distribution emerged in the 50–70 cm dbh class; biomass of this tree size class was similar in open and dense forests (~47 Mg ha^{-1}), but was half as much (~22 Mg ha^{-1}) in ecotone forests. In open forests, aboveground biomass of trees ≥70 cm dbh was much lower than in both dense and ecotone forests, 45 Mg ha^{-1} compared to 111 and 114 Mg ha^{-1}, respectively (Table 4).

Trees with a dbh of 10–50 cm composed 47, 42, and 38% of the TAGB in open, dense, and ecotone forests, respectively. Trees with dbh 50–70 cm composed 15, 12, and 6% of TAGB in open, dense, and ecotone forest, respectively. Trees with dbh ≥70 cm dbh composed 15, 26, and 32% of TAGB in open, dense, and ecotone forests, respectively.

Mean biomass of palms, vines, and seedlings (live non-tree components) was ~18 Mg ha^{-1} in both open and dense forest types, but was 39 Mg ha^{-1} in ecotone forests (Table 4). However, variation of the components was high among stands with a range of 4–95 Mg ha^{-1} in open, and 1–74 Mg ha^{-1} ecotone forests. Dense forest sites had a narrower range of 3–39 Mg ha^{-1}. Large palms composed the majority of the live non-tree biomass while vines and seedlings contributing minimally to the TAGB (a range of 0–3 Mg ha^{-1} over all forest types).

In general, standing dead plants (palms, vines, and trees), CWD, and the litter/rootmat (forest floor) composed an equal or larger proportion of the TAGB than did live non-tree vegetation (Table 4). For all 20 plots combined, this dead component composed an average of 12% of TAGB. CWD and standing dead trees, averaged 32 Mg ha^{-1} in open forests, 30 Mg ha^{-1} in dense forests, and 28 Mg ha^{-1} in ecotone forests (Table 4). CWD comprised a mean of 29 Mg ha^{-1} or 9% of TAGB for the 20 plots combined. The aboveground biomass of the forest floor was 9 Mg ha^{-1}. The remaining components of standing dead ranged from 0 to 1 Mg ha^{-1}.

3.3. Biomass structure as a proportion of the overstory tree biomass

Because many studies use constant proportions of overstory tree biomass (OTB = aboveground biomass of live trees ≥10 cm dbh) to estimate TAGB (Brown and Lugo, 1992; Fearnside, 1992a,b; Laurence et al., 1998) it is useful to examine biomass components from this study in the same way. The aboveground biomass of trees >30 cm dbh composed 68, 72, and 75% of the OTB in open, dense, and ecotone forests, respectively. However, there were notable differences among the forest types in the distribution of the biomass of large trees (trees ≥70 cm dbh) as a proportion of OTB. For all sites combined, large trees composed 28% of OTB. In open forests, large trees composed 18% of OTB, while in dense forest, they were 32%, and in ecotone forests, they were 41%.

Palm biomass composed an additional 9% of OTB for all 20 sites and was highest in ecotone forests (average, 18%). Palm biomass was lower in open and dense forests, composing 8 and 6% of OTB, respectively. The biomass of CWD was equivalent to an additional 13.2, 11.0, and 9.4% of the OTB for open, dense, and ecotone forests, respectively, with a mean of 11.6% for all plots combined. The biomass of the forest floor was equivalent to an additional 4.3, 2.9, and 3.6% of the OTB in open, dense, and ecotone forests, respectively, and 3.4% for the 20 plots combined.

3.4. Density

Tree density (trees ≥10 cm dbh) within forest types averaged 429 individuals per hectare (range, 291–527 individuals per hectare) in open forest and 377 individuals per hectare (range, 223–487 individuals per hectare) in ecotone forests, while dense forests averaged 450 individuals per hectare (with a narrower range, 402–533 individuals per hectare Table 5). Average density of small trees (<10 cm dbh) was highest in open forest and differed by 25% between open forest (~7500 ha^{-1}), dense forest (~5800 ha^{-1}), and ecotone forests (~4900 ha^{-1}). However, plots within a given forest type varied widely (~2000–9000 ha^{-1} in each forest type; Table 5).

The mean density of large trees was lower in open forests than in dense or ecotone forests (3.8, 7.1, and 7.0 individuals per hectare, respectively). Densities of largest tree size class (those ≥200 cm dbh) were 0.0, 0.7, and 0.6 individuals per hectare for open, dense, and ecotone forest types, respectively.

The average density for trees 10–30 and 30–50 cm dbh was similar for open, dense, and ecotone forests (359 and 52, 379 and 51, and 315 and 48 individuals per hectare Table 5). The pattern changed with the 50–70 cm dbh trees, which had similar densities in open and dense forest, but had approximately half the density in ecotone forests (open and dense forests, 13 individuals per hectare ecotone forests seven individuals per hectare Table 5).

Density of standing dead trees 10–30 cm dbh varied slightly among forest types with 27, 19, and 13 individuals per hectare for open, dense, and ecotone forests, respectively. Density of standing dead trees ≥30 cm dbh was similar in dense and ecotone forests at 6 and 5 individuals per hectare, whereas open forest had 10 individuals per hectare (Table 5).

Large palm density was 60 individuals per hectare in open forests, but was 97 and 107 individuals per hectare in dense and ecotone forests, respectively (Table 5). Small palms (<10 cm dbh) were much more abundant in ecotone forests (633 individuals per hectare) than in open and dense forests (203 and 196

Table 5
Density (individuals per hectare) of forest components separated by forest type[a]

Component	Open forest ($n = 8$)	Dense forest ($n = 7$)	Ecotone forest ($n = 4$)	All forests combined ($n = 20$)
Seedlings × 1000	174 (23)	205 (27)	151 (19)	180 (14)
Basal leaf palm	754 (170)	442 (93)	758 (304)	630 (97)
Palm <10 cm dbh	203 (60)	196 (58)	633 (423)	286 (90)
Palm ≥10 cm dbh	60 (19)	97 (28)	107 (37)	82 (14)
Vine <10 cm dbh	2379 (557)	2500 (345)	1195 (181)	2242 (278)
Vine ≥10 cm dbh	1 (1.4)	5 (1.5)	5 (3.5)	3 (1.1)
Trees ≤10 cm dbh	7500 (800)	5800 (900)	4900 (100)	6300 (600)
Trees 10–30 cm dbh	359.5 (25.8)	378.8 (25.2)	315.2 (56.8)	350.7 (18.5)
Trees 30–50 cm dbh	51.90 (3.82)	50.98 (4.65)	48.25 (6.24)	50.70 (2.42)
Trees 50–70 cm dbh	13.49 (1.50)	13.42 (3.64)	6.67 (1.41)	12.0 (1.5)
Trees 70–100 cm dbh	1.75 (0.41)	5.62 (1.10)	4.44 (0.82)	3.7 (0.6)
Trees 100–200 cm dbh	2.06 (0.63)	0.73 (0.38)	1.90 (0.36)	1.5 (0.3)
Trees 200–300 cm dbh	0.00	0.73 (0.38)	0.63 (0.36)	0.4 (0.2)
Dead trees ≥30 cm dbh	10 (2)	5 (2)	6 (2)	7 (1)

[a] Numbers are means with standard errors in parentheses. The open forest plot that was classified as ''human influenced'' was only factored in the 20-plot mean.

Table 6
Basal area ($m^2\ ha^{-1}$) of live trees in plots of each forest type[a]

Trees (cm dbh)	Open forest ($n = 8$)	Dense forest ($n = 7$)	Ecotone forest ($n = 4$)	All forests combined ($n = 20$)
<10	3.38 (0.38)	3.37 (0.55)	2.81 (0.66)	3.22 (0.27)
10–30	7.92 (0.46)	8.32 (0.71)	7.13 (1.39)	7.78 (0.40)
30–50	5.81 (0.46)	5.70 (0.55)	5.26 (0.63)	5.63 (0.28)
50–70	3.56 (0.45)	3.56 (0.97)	1.71 (0.39)	3.18 (0.41)
70–100	0.88 (0.24)	3.11 (0.62)	2.25 (0.46)	1.96 (0.33)
100–200	2.09 (0.57)	1.40 (0.68)	2.93 (0.52)	1.92 (0.36)
200–300	0.00 (0.00)	3.06 (1.49)	2.30 (1.34)	1.53 (0.51)
Total	23.74 (0.79)	28.08 (1.90)	24.39 (3.85)	25.21 (1.12)

[a] Values are means with standard error in parentheses. Numbers are means with standard errors in parentheses. The open forest plot that was classified as "human influenced" was only factored in the 20-plot mean.

individuals per hectare, respectively). Densities of seedlings and small vines (<10 cm dbh) were similar among forest types. Density of basal leaf palms was similar in open and ecotone forests (∼750 individuals per hectare), but lower in dense forests (443 individuals per hectare).

3.5. Basal area and quadratic stand diameter

The total BA ranged from 19 to 26 $m^2\ ha^{-1}$ in open, 23–37 $m^2\ ha^{-1}$ in dense, and 15–34 $m^2\ ha^{-1}$ in ecotone forests. The average total BA the forest types did not differ by >4 $m^2\ ha^{-1}$ (average 24, 28, and 24 $m^2\ ha^{-1}$ for open, dense, and ecotone forests, respectively; Table 6). These differences in average BA are equivalent to that of one very large tree per hectare (>200 cm dbh). Likewise, QSD differed only slightly between forest types. The mean QSD for trees ≥10 cm dbh) in open forests was 25 cm, and was 27 cm in dense and ecotone forests. The mean QSD of trees ≥30 cm dbh was slightly higher for dense and ecotone forests than for open forests (48, 54, and 55 cm in open, dense, and ecotone forests, respectively).

4. Discussion

4.1. Total aboveground biomass differences among forest types

Previous direct measurements of TAGB from dense forests in the Legal Amazon have ranged from 206 to 403 Mg ha^{-1} (Revilla Cardinas, 1986, 1987 in Fearnside et al., 1993) and averaged 321 Mg ha^{-1} (Fearnside et al., 1993). Those measurements were lower (by 56 Mg ha^{-1}, a difference of 15%) than our average for dense forests (i.e. a mean of 377 Mg ha^{-1} and a range of 298–533 Mg ha^{-1}). The average for open forests from direct measurement was 258 Mg ha^{-1} (Revilla Cardinas, 1986, 1987 in Fearnside et al., 1993), which was also lower (by 55 Mg ha^{-1}, a difference of 18%) than our average for open forests (313 Mg ha^{-1}, range 288–346 Mg ha^{-1}). Whether differences among studies reflect true differences in TAGB among Amazonian forests or are differences in sample design and analysis is unknown.

The TAGB of the 20 sampled forest stands fell within the range reported for many other studies of the Brazilian Amazon. The live aboveground biomass of open forests was 270 Mg ha^{-1}, which is similar to a Rondônian open forest with a standing alive aboveground biomass of 285 Mg ha^{-1} measured by Brown et al. (1995) and one measured by Graça et al. (1999) with a value of 311 Mg ha^{-1} TAGB. TAGB of the dense forests in our study averaged 376 Mg ha^{-1}, which is comparable to estimates of 361 Mg ha^{-1} given by Fearnside (1985), 352 Mg ha^{-1} reported in Brown et al. (1995), and 356 Mg ha^{-1} (for aboveground biomass of live trees and palm) reported by Laurance et al. (1999). Correction multiplier factors, from Fearnside (1992a), for belowground biomass were used to convert from total biomass estimates (above- and belowground, reported in Fearnside, 1997) to mean TAGB for each forest type, open, dense, and ecotone, in Rondônia. The derived means were comparable to ours for open forests (313 Mg ha^{-1}), but were 6% lower in ecotone forest (332 Mg ha^{-1}) and 13% lower for dense forests (328 Mg ha^{-1}).

Brown et al. (1989) and Brown and Lugo (1992) suggested that field studies resulted in higher TAGB estimates because of a bias by researchers and/or foresters in site selection. In contrast, Brown et al. (1995) found that biomass from a site selected on the basis of its appearance yielded a lower biomass than sites selected without regard to forest structure. They suggested that subjective selection did not result in biased high biomass estimates because of the inability to see >30–40 m into a forest. We found it was impossible to determine structure from one side of our 105 m plots to the other because we could see no farther than 15 m into the forest.

4.2. Biomass partitioning among forest components

We found that trees from 10 to 30 cm dbh class composed 15–49% of OTB (mean, 29%) over all 20 sites. Similarly, Gillespie et al. (1992) estimated that trees in the 10–35 cm dbh class composed 23–40% of OTB in Venezuela. Trees in the 10–30 cm dbh class comprised a significant proportion of OTB, but were not included in the RADAMBRASIL inventory. Due to the large quantity of biomass components not measured in the RADAMBRASIL forest inventory, caution should be applied when using it to calculate the biomass.

Although total tree biomass differed among forest types, the proportion contributed by trees $\geq$30 cm dbh was similar (means, 68, 72, and 75% of OTB in open, dense, and ecotone forests, respectively). In contrast, Brown and Lugo (1992) assumed that the fraction of the tree volume (and presumably biomass) for those trees $\geq$30 cm dbh was lower in open forests (67%) than in dense forests (80%). The assumption that trees $\geq$30 cm dbh make up a higher proportion of volume in dense forests would result in an underestimation of the volume contained in trees <30 cm dbh and, consequently, in the biomass of those trees. Inasmuch as their biomass estimate is based on volume, this indicates a significant shortcoming in using the RADAMBRASIL inventory to estimate biomass, since we did not find large variation in the proportion of the biomass in the trees $\geq$30 cm dbh component.

Even though densities of large trees ($\geq$70 cm dbh) were low, their biomass made up an average of 18, 32, and 41% of OTB, in open, dense, and ecotone forests, respectively, or 23% of OTB for all 20 sites combined. Brown and Lugo (1992) also found that large trees composed <40% of OTB in Amazon forests.

Mean density of the largest trees ($\geq$200 cm dbh) in the dense and ecotone forest averaged <1 ha^{-1}, but still comprised a mean of 14 and 13% of OTB, respectively. The contribution of these largest trees to the OTB in individual plots was quite variable, ranging from 0 to 42% in the dense forest and 0 to 32% in ecotone forests sites.

The low-density of these large trees underscores the need for large plot sizes. It is possible that even our plot size of 0.79 ha was insufficient to properly quantify density and biomass of this size class. Brown et al. (1995) suggested that a minimum plot size of 0.25 ha would be necessary to reduce the transect uncertainty below that caused by measurements in their open forest sites near Samuel Reservoir in Rondônia, Brazil.

The absence of the largest trees (>200 cm dbh) in eight sampled open forest stands (a total sample area of 6.30 ha) was a notable difference in forest structure compared with dense and ecotone forests. In contrast, 45% of the 11 sites in dense or ecotone forests (total sample area, 8.65 ha) had trees >200 cm dbh.

Palms were a major component of non-tree biomass (Table 7). Palms composed a higher proportion of the TAGB ($\sim$6%) in our western Amazon study than in tierra firme forests of the Venezuelan Amazon (1.3%), as calculated from Jordan and Uhl (1978). Graça et al. (1999) found palms composed 7% of felled TAGB in forest near Ariquemes Rondônia, Brazil. Fearnside (1992a,b) used a factor of 3.5% of OTB to estimate palm biomass in Amazonian forests. Based upon our results, that would underestimate palm biomass in Rondônia forests. Palm biomass averaged 6% of TAGB (range, 0.2–28.8%) and 9.3% (range, 0.2–73.3%) of OTB across all 20 sites. We assumed that large palms ($\geq$10 cm dbh) would have a greater density and biomass in open than in dense forests because RADAMBRASIL (DNPM, 1978) described open forests as having ‘‘enclaves of palms’’. Large palm biomass in open forest sites was highly variable,

Table 7
Palm biomass structure (>10 cm dbh) at sites sampled in this study[a]

Forest type-region	Plot no.	Palm biomass (Mg ha^{-1})	Height (m)	Density (palm per hectare)	Diameter at breast height (cm)		*Attalea* sp. dominant (yes/no)?
					Affalea sp.	Other sp.	
Open tropical forest	225	92.3	11.2	171	30	24	Yes
	226	1.9	8.5	15	33	19	No
	70	5.6	7.8	107	30	13	Yes
	74	2.5	16.0	27	N.D.	N.D.	No
	75	0.0	N.D.	11	N.D.	13	No
	76	7.3	7.9	65	38	14	Yes
	89	6.8	6.7	23	40	0	Yes
	113	8.3	8.0	61	37	19	Yes
Mean		15.6 (11.0)	9.4 (1.2)	60 (20)	35 (6)	14 (3)	
Dense tropical forest	1	10.4	8.9	114	34	27	No
	2	7.3	5.4	160	0	26	No
	229	0.4	13.0	4	0	10	No
	24	22.7	10.6	42	22	0	Yes
	25	24.5	10.0	130	35	18	No
	43	36.4	8.4	202	28	14	No
	44	5.5	15.9	30	28	13	No
		15.3 (4.9)	10.3 (1.3)	97 (28)	29 (5)	18 (4)	
Ecotone	186	46.0	9.3	130	31	11	Yes
	188	71.5	7.9	187	32	29	Yes
	190	0.8	13.5	8	0	17	No
	195	23.8	7.5	103	31	26	Yes
Mean		35.5 (15.1)	9.5 (1.4)	107 (37)	31 (7)	20 (4)	
Others-anthropogenic	218	21.2	9.0	57	26	16	
Grand mean		19.8 (5.6)	9.8 (0.7)	82 (14)	31 (3)	18 (2)	

[a] Values are means for each site, with standard errors in parentheses.

ranging from 0.1 to 92 Mg ha^{-1}. In dense forests, palm biomass was less variable, ranging from 0.0 to 36 Mg ha^{-1}, yet both forests averaged approximately the same biomass (15 Mg ha^{-1}) (Table 7). Ecotone forests averaged twice the palm biomass of open and dense forests (35 Mg ha^{-1}), but it was also highly variable (ranging from 0.8 to 72 Mg ha^{-1}) Density of palms was lower in open forests than in dense and ecotone forests (Table 7).

Although palm biomass was greater in open forests than dense forests, the density was lower (60 individuals per hectare) in open forests than in dense (97 individuals per hectare) and ecotone (107 individuals) forests (Table 7). In general, palms in open forests were larger and had more biomass per individual than did those in dense forests. *Attelea* sp., a robust palm with a thick stem and a high biomass-to-height ratio, was dominant in 63% of sampled sites in open forests, 75% of sampled sites in ecotone forests, and only 14% of sampled sites in dense forests. Other palm species may have been taller, but tended to have less robust stems (mean dbh, 18 cm) than did *Attelea* sp. (mean dbh, 31 cm).

Seedlings and vines were a minor proportion of TAGB, comprising a mean of <0.4% of OTB and never exceeding 1.27%. Fearnside (1992a) assumed that vine mass was equivalent to 4.25% of OTB. In contrast, vines were found to be 12% of the felled TAGB in two studies in Amazonian forests (Graça et al., 1999 and Fearnside et al., 1999).

The mass of CWD and forest floor in our study averaged 38 Mg ha^{-1} and ranged from 17 to 72 Mg ha^{-1} (Table 4). This is similar to the mass of dead wood and litter reported for other Amazon rainforests. Brown et al. (1995) estimated that fallen dead trunks and litter composed 30 and 10 Mg ha^{-1}, respectively, or 14% of aboveground biomass in open forest near Samuel Reservoir, Rondônia, Brazil. Uhl and Kauffman (1990) reported litter and CWD to be 56 Mg ha^{-1} for a dense forest in Para, Brazil. In the Venezuelan Amazon, Kauffman et al. (1988) found the mass of forest floor and CWD combined to range from 64 to 107 Mg ha^{-1}. Delaney et al. (1998) found total dead wood in tropical moist and lower montain forests to be 33.3 and 42.3 Mg ha^{-1} or 9.6 and 12.4% of aboveground biomass, respectively for forests in Venezuela. From a number of studies, Fearnside (1992b) reported that the surface layer (litter and/or rootmat) composed a mean of 5% of TAGB. Litter and rootmat comprised 4–8% of the TAGB in four slashed forests from Para and Rondônia (Kauffman et al., 1995). These are comparable to the contribution of litter/rootmat to TAGB (range, 1–6% of TAGB) for forests in this study.

4.3. Density

The mean density for trees $\geq$10 cm dbh was 419 individuals per hectare, and ranged from 233 individuals per hectare in an ecotone forest site to 528 individuals per hectare in a dense forest site (Table 5). Density of these forests was similar to that reported for other Amazon forests. Klinge et al. (1975) reported 400 individuals per hectare for forests near Manaus, Brazil. Jordan and Uhl (1978) found trees $\geq$10 cm dbh at densities of 786 individuals per hectare in a tierra firme forest of the Venezuelan Amazon. Brown et al. (1995) measured a density of 475 individuals per hectare (trees $\geq$10 cm dbh) for an open forest near Samuel Hydroelectric Reservoir in Rondônia, Brazil. In this study, site 74, which was in the same forest type and area (Samuel Hydroelectric Reservoir) as the site sampled by Brown et al. (1995), had a similar density, 458 individuals per hectare.

Using data on trees $\geq$25 cm dbh from several Amazonian forest inventories, Brown and Lugo (1992) found trees >70 cm dbh composed no >3% (6–10 individuals per hectare) of the total number of trees. We found that densities of trees $\geq$70 cm dbh were 2.6, 2.7, and 3.5% of the density for trees $\geq$30 cm dbh in open, dense, and ecotone forests, respectively (Table 5).

4.4. Basal area and QSD

Basal area for all trees combined ranged from a mean of 28 m^2 ha^{-1} in dense forest to 24 m^2 ha^{-1} in open forests (Table 6). These ranges were similar to those measured in other moist tropical forests. Basal area of dense forests in Rorima and Para, Brazil ranged from 24 to 32 m^2 ha^{-1} (Higuchi et al., 1994). Lieberman and Lieberman (1987) found a BA ranging from 27 to 31 m^2 ha^{-1} for stems $\geq$10 cm dbh at La Selva in Costa Rica, and Jordan and Uhl (1978) reported an average BA of 33 m^2 ha^{-1} in tierra firme forests in Venezuela. Although total BA was similar among forests, we found the distribution among sites varied. For example, in the Venezuelan tierra firme forest, BA of the small size trees (<10 cm dbh) was 11 m^2 ha^{-1}, whereas in our study, range for the same size class was only 1–5 m^2 ha^{-1}. An open forest site at Samuel Hydroelectric Reservoir in Rondônia had BA of 25 m^2 ha^{-1} for trees $\geq$10 cm dbh and a mean BA per tree of 0.052 m^2 (Brown et al., 1995), whereas in our study, BA was 20 m^2 ha^{-1} for open forests, and 0.047 m^2 per tree.

The QSD, which is calculated from BA, is used in some forest biomass models to derive a "volume expansion factor" (VEF) for extrapolating from forest tree volumes that are reported in the inventory to the volume of trees in size classes that are not reported in the inventory (Brown et al., 1989; Brown and Lugo, 1992; Brown, 1997). We found QSD for open and dense forest types to be very similar for trees $\geq$10 cm dbh: 25 cm in open forest and 27 cm for dense forests.

5. Conclusion

This study provides information on the TAGB and structure of forests that are located in the arc of deforestation described by Fearnside (1990) and are representative of those associated with deforestation in this region. TAGB and structure was measured on 20 different forest stands and included components not often measured in forest inventories. Estimates of tree density, BA, QSD, and biomass of non-tree components are often used to formulate TAGB models based on forest inventories (Brown and Lugo, 1992). The results from this study explain some discrepancies between estimates of TAGB derived from field studies and those from forest inventories. For example, forest inventories rarely measure palms and trees <10 cm dbh, yet these components comprised an average of 12% of TAGB. The RADAMBRASIL forest inventory was limited to quantification of trees >31.8 cm dbh. In this study, live trees $\geq$30 cm dbh only comprised 56% of TAGB (range, 47–72%). The non-tree, dead components and smaller wood particles of TAGB are important because they most likely will completely burn during slash fires following deforestation and, therefore, contribute significantly to CO_2 and trace gas flux to the atmosphere (Kauffman et al., 1995; Guild et al., 1998). Underestimating these components could lead to errors in estimating C pools of standing forests as well as emissions arising from forest conversion. The results from this study, by clarifying forest structure, could be useful to improve TAGB estimates based on other data sets.

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