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Wood density in dense forest in central Amazonia, Brazil

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Abstract

Measurements of wood density of trees in Amazonian forests are necessary to reduce uncertainties in estimates of carbon stocks and of greenhouse-gas emissions from deforestation. Based on samples from 310 trees in 186 species or morpho-species collected near Manaus, Brazil, the present study finds that commonly used wood density estimates found in published lists by species need to be adjusted downward by 5.3%. Taking the average bole density from this study as a standard, wood density overestimations in three prior studies of the central Amazon were found to be 6%, 4% and 0%. Estimates of primary forest biomass and of gross emissions from biomass loss through deforestation will have to be reduced by similar percentages. Considering full disks with bark dried at 103 °C, the mean basic density at breast height in the Central Amazon dense forest was 0.704 ± 0.117 (mean $\pm$ 1 standard deviation; $n = 310$; range, 0.27–0.96); at the top of the bole it was 0.647 ± 0.093 ($n = 307$; range, 0.26–0.87). The arithmetic mean of the basic density of the trunk—average of the density at breast height and at the top of the bole—was 0.675 ± 0.101 ($n = 307$; range, 0.27–0.91). The mean basic density of the bole, adjusted for tapering, and using four samples along the bole, was 0.670 ± 0.099 ($n = 71$; range, 0.38–0.86). The arithmetic mean of the basic density for the same trees was 0.675 ± 0.098 (range, 0.39–0.87). The basic density of central heartwood was 0.766 ± 0.158 ($n = 149$; range, 0.34–1.06). Significant differences exist between the various published estimates for Amazonian forest biomass and emissions, but we emphasize that revision of density values based on the present study will not reduce these discrepancies; instead, all estimates will shift in parallel to lower levels. Adjustments to biomass and emissions are sufficiently large to be significant for the global carbon balance. For example, an estimate of net committed emissions of 249×10^6 Mg CO_2-equivalent C/year for Brazilian Amazonia in the 1990, of which 237×10^6 Mg CO_2-equivalent C/year was from net removal of biomass, would be reduced by 14×10^6 Mg CO_2-equivalent C/year (5.7%: larger than the 5.3% adjustment to gross emissions because regrowth estimates remain unchanged). Decrease of similar proportions would apply throughout the tropics. For the 1980s, these downward adjustments total 113×10^6 Mg C/year for CO_2 effects alone, or approximately 132 Mg CO_2-equivalent C/year including trace gases.
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Keywords: Amazon forest; Basic density; Wood density; Basic specific gravity

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1. Introduction

Greenhouse gas emissions from tropical deforestation represent one of the largest uncertainties concerning global climate change (Houghton, 2003). Emissions when forests are cleared are almost directly proportional to the biomass (including both live and dead material) of the forest, which, in turn, depends on the volume of wood and its density. Because such large amounts of biomass are cleared each year, even small alterations in estimates of wood density translate into quantities for forest biomass and greenhouse gas emissions that are significant for global change.

Density is an important physical characteristic of wood in defining technological and commercial use because it is an excellent indicator of the amount of wood present in a sample and of the workability of the material (Silva, 1984; Trugilho et al., 1990; Chimelo, 1992; ASTM, 2002). The density is related to other properties of the wood, such as resistance, porosity, organization of the anatomical components and the number, size, and chemical composition of the cells (Kollmann and Côté, 1968; Trugilho et al., 1990; Simpson and TenWolde, 1999; Ilic et al., 2000; Hacke et al., 2001; ASTM, 2002). In tropical forests, wood density is related to a tree's resistance to impacts caused by wind, to relative growth rate and mortality (Putz et al., 1983; Muller-Landau, 2004). Wood density is also a strong indicator of the stage of ecological succession, with pioneer species being less dense and having greater variation than climax species (Denslow, 1980; Wiemann and Williamson, 1989; Muller-Landau, 2004). There is great variation in density along the bole, among species, and among individuals in any given species due to differences in the age of the tree and in the climatic life zone (Chudnoff, 1976; Wiemann and Williamson, 1989, 2002; Rueda and Williamson, 1992; de Castro et al., 1993; Rocha, 1994; Higuchi et al., 1998; Woodcock, 2000; Baker et al., 2004; Muller-Landau, 2004). Variation has been observed from the heartwood to the bark, along the length of the bole (the trunk below the first large branch), among different compartments in a given tree and between individuals of the same species. This variation reflects the interaction of the plant with environmental factors, such as climatic and edaphic conditions, natural impacts and competition for light (Chudnoff, 1976; Wiemann and Williamson, 1989; Trugilho et al., 1990; Ilic et al., 2000; França, 2002; Muller-Landau, 2004).

Different methodologies have been used for determining the weight and volume measures, the ratio of which represents density, resulting in different concepts (Trugilho et al., 1990; Fearnside, 1997a). Weight has been determined with different moisture contents, with volume either with or without bark, and using volume either of the fresh wood, dry wood, or of wood that has been dried and later re-hydrated. Among the different ways of calculating density are apparent density (the ratio between weight and volume at a given moisture content), green density (green weight/green volume), simple specific gravity (dry weight/dry volume), true density (excluding naturally occurring pores in the wood by compression of the sample), and basic density or basic specific gravity, which is obtained as the ratio between the dry weight and volume of the green wood (Fearnside, 1997a; de Souza et al., 2002). Basic density was used in the present study and is considered to be the most appropriate density measure for biomass estimation (Brown, 1997; Fearnside, 1997a).

Based on 470 samples from tropical American forests, Reyes et al. (1992) found a mean density of 0.60 ± 0.008 g/cm^3 (mean $\pm$ 1 standard error). Brown and Lugo (1992) report a mean of 0.69 for Amazonia, based on a relationship between biomass and bole volume from data (diameter, species and the volume of all trees) reported by Heinsdijk (1958) and Prance et al. (1976) for two areas of Amazonian forest. Muller-Landau (2004) examined 112 trees from dense forest of the Central Amazon. These represented 89 species and their density was either determined directly from thin wood cores of the full xylem radius or was based on published data at the species level. The 89 species constituted 19% of the trees in a nearby large inventory. When weighted for abundance in that inventory, the 89 species had a mean density of 0.71 ± 0.15 g/cm^3 (mean $\pm$ 1 standard deviation).

Using mainly the inventories of RADAMBRASIL (Brazil, Projeto RADAMBRASIL, 1976–1986) and published lists of density by species (Fearnside, 1997a) the mean basic density for Brazilian Amazonia was estimated at 0.69, considering the different vegetation types and their respective areas. For dense lowland forest in the state of Amazonas, the mean

density reported is 0.70 g cm^{-3}. This value contains uncertainty due to doubts concerning the taxonomy of the species (names are usually only reliable to the genus level) and use of density values determined by different methods (Fearnside, 1997a).

A reliable value for mean density for forests in Amazonia is necessary so that volumetric estimates available from extensive inventories can be converted to estimates of biomass stock (Brown et al., 1989; Brown and Lugo, 1992; Fearnside, 1997a; Houghton et al., 2001). Mean density has also been used in adapting allometric models developed for dense forest to make them applicable to other types of forest, correcting for the effect of density differences (França, 2002; Baker et al., 2004). Studies of wood density in Amazonia can contribute to reducing uncertainties in estimates of the stock and emission of carbon, in addition to contributing to studies of nutrient dynamics in Amazonian ecosystems and to quantification of forest resources.

The objective of this study was to determine the basic density of species in dense forest on plateaus with latosol (Oxisol) soils in central Amazonia, and to evaluate the radial variation and variation along the length of the bole. The study also determined the difference between the densities calculated using the volume of re-hydrated samples and using the fresh volume. A second objective was to evaluate possible bias towards high or low wood density in previous studies.

2. Material and methods

2.1. Collection site

The collection area is located about 50 km northwest of Manaus, Amazonas, Brazil, in the Tarumã–Mirim Rural Settlement Project. Plateau locations were selected in six different lots of small rural farmers. The area has annual average precipitation of 2075 mm, rainfall below 100 mm/month from July to September, mean altitude of 100 m, minimum mean monthly temperature of 26 °C and maximum of 27.6 °C (Brazil, INMET, 2003). The vegetation is dense rain forest of *terra firme* (land that is not seasonally flooded), on yellow latosols (Oxisols) that are poor in nutrients (Magnago et al., 1978; Yamazaki

et al., 1978). Random felling of trees was allowed, this being a new colonization front (<5 years) with deforestation for agricultural use already planned and authorized by the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA). The plots selected were under primary forest, without invasion of pioneer trees or mortality associated with edges.

2.2. Collection of wood samples

Samples of wood of 310 trees were collected (DBH = 5–122 cm) at six different sites distributed over an area of 45 km^2, sampling approximately 50 trees/site. The collection locations were at least 100 m from the edge of the forest. Trees were chosen to fill quotas for each size class but otherwise at random. The chain saw operator was not allowed to choose trees since he might exclude species with very hard wood or with high silica content, both of which shorten chain life. For all trees disks of constant thickness were collected at breast height and at the top of the bole using a chainsaw. For 73 trees, two additional disks were collected at intermediate points such that all four disks were equally spaced along the bole. From each of the disks a wedge-shaped sample was removed that was representative of the radial variations (bark, sapwood and heartwood). Each wedge was immediately sealed in a plastic bag kept in the shade to avoid loss of water. Samples of heartwood of 149 trees were also collected at breast height (~1.36 m). Botanical specimens were collected from every tree for identification.

2.3. Determination of basic density

On the day each sample was collected, its volume was determined based on the Archimedes principle by displacement of water (ASTM, 2002). Impaled with a thin needle, each sample was forcibly immersed in water in a container resting on a digital balance. The balance had 2000-g capacity and 1-g precision, and was calibrated daily using a volumetric flask containing water. The dry weight of each sample was determined in an oven at 80 and 103 °C (ASTM, 2002). A vented electric oven was used in an air-conditioned room kept at 25 °C. Samples, which were kept in double paper bags, were considered com-

pletely dry after three consecutive stable weight readings, checked every 24 h. A single tare weight was used for paper bags from each factory bundle, based on weighing a sheaf of 50 bags heated to the drying temperature for 24 h.

2.4. Determination of mean basic density of the bole

Arithmetic mean density of two or four measurements along the bole was determined for all 307 trees. A taper-adjusted mean density was determined for 71 of these trees, which were sampled at four locations along the bole, using the model of Vital (1984; Eq. (1)):

$$D_{mb} = \{\Sigma(D_{ms1} \times V_{seg1}), (D_{ms2} \times V_{seg2}),$$
$$(D_{ms3} \times V_{seg3})\} \times (\Sigma V_{seg1,2\,and\,3})^{-1} \qquad (1)$$

where D_{mb} is the mean density of the bole; D_{ms1} the mean of the density at breast height, and at 33% of the length between breast height and the top of the bole; D_{ms2} the mean of the density at 33% and at 66% of the length between breast height and the top of the bole; D_{ms3} the mean of the density at 66% of the length between breast height and the top of the bole, and the density at the top of the bole; $V_{seg1,2\,and\,3}$ is the volume of the bole segments at the heights 1.36 m—33%, 33–66% and 66% to top, respectively.

The volume of each segment (the frustum of a paraboloid) was obtained using the Smalian formula:

$$V = \{(As_i + As_f) \times 0.5\} \times h \qquad (2)$$

where As_i is the cross sectional area at base of segment; As_f the cross sectional area at top of the segment; h is the length of the segment.

For correct determination of the area of each cross section of the bole, a drawing was traced of the external edge of the entire disk, and of the internal edge if the log was hollow. The drawings were photographed using a digital camera with an 80 mm lens at a distance of 4 m. The area of each section was determined by counting pixels later transformed to cm^2. Scale varied only 0.6% between the center and edge of the tracing paper and this was averaged out by using registration marks at the four corners. When present, the hollow areas were subtracted in determining the total area of each section. This procedure was adopted in order to eliminate errors implicit in the common assumption that the bole is a solid of revolution and that diameter and volume can be inferred from circumference obtained with a measuring tape. The procedure eliminated volume overestimates that are caused by the occurrence of trunks with oval cross-sections, external irregularities above buttresses, or hollow cores; these conditions are common in Amazonian species.

2.5. Density obtained using re-hydrated volume of heartwood

Heartwood samples were always obtained near the center of the disk at breast height, but varied in size and thus in their surface-to-volume ratios. This will affect re-hydration rate so three sub-samples were taken, each measuring approximately 2 cm × 2 cm × 3 cm (volume, 12 cm^3). To reduce bias in density in the radial direction, the sub-samples were obtained along the radial axis and a mean density calculated. The sub-samples were weighed on a digital balance with 0.01 g precision immediately after drying at 103 °C. They were then immersed in water for 14 days under refrigeration to avoid decomposition, and the re-hydrated volumes determined by the Archimedes principle using the same balance.

2.6. Botanical identification

All botanical samples were identified by experts (parabotanists), who are employees of the herbarium of the National Institute for Research in the Amazon (INPA).

3. Results

3.1. Wood density: vertical and radial variation

The 310 trees were identified as 186 different species or morpho-species, with four trees unidentified (Appendices A and B). The values for basic density at breast height and at the upper end of the bole for each species are presented in Appendix A. All density values are based on dry weight obtained at 103 °C, except where noted. Following the classification proposed by Melo et al. (1990), only 5% of the trees in this study have light wood (density, ≤ 0.50 g cm^{-3}),
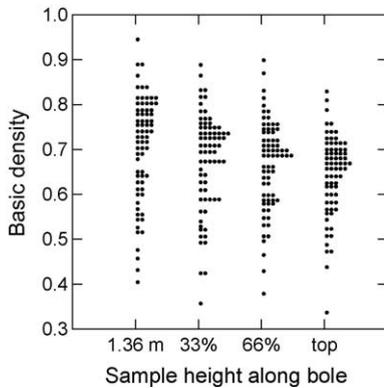
Fig. 1. Variation of the density along the bole ($n = 73$; trees with DBH = 5–122 cm). Where BH = breast height; top = top of the bole; 33% and 66% = intermediate heights.

64% have wood of medium weight (density, 0.50–0.72) and 31% have heavy wood (density, >0.72).

The mean density generally decreases from breast height to the top of the bole (Fig. 1; Table 1). For 87% of the trees, the density decreased with height on the bole, the most extreme case being a 57% decrease. Only 13% of the trees increased in density with height, the most extreme case being a 24% increase. Density at the top of the bole is 8% lower than at breast height, on average.

Using density of the disk at breast height as an indication of average density of the entire bole will

result in a 4.3% overestimate of a stand's average bole wood density. The mean basic density with bark at breast height for all species was 0.704 ± 0.117 (mean $\pm$ 1 standard deviation; $n = 310$; range, 0.27–0.96). The mean basic density with bark at the top of the bole was 0.647 ± 0.093 ($n = 307$; range, 0.26–0.87). The arithmetic mean basic density of the entire bole, based on disks from just two positions, was 0.675 ± 0.101 ($n = 307$; range, 0.27–0.91; Appendix A), significantly lower than the density at breast height (paired t-test; $p < 0.001$; $n = 307$). For the 73 trees sampled at four positions along the length of the bole, a similar arithmetic mean was obtained: 0.675 ± 0.098 ($n = 73$; range, 0.39–0.87). Mean basic density of these trees, adjusted for tapering of the bole, was similar to the arithmetic mean: 0.670 ± 0.099 ($n = 71$; range, 0.38–0.86).

Using heartwood density at breast height will lead to 5.3% overestimate of density of the entire disk at that height (paired t-test; $p < 0.001$; $n = 149$). For the trees from which heartwood was collected separately, the whole-disk basic density at breast height was 0.728 on average, while the average density of just the heartwood at breast height was 0.785 (Fig. 2). Not all trees showed this pattern: for 18% the heartwood density was lower than the full disk by 0–26%. For 80% of the trees the heartwood was 0–20% denser and in 2% of the trees heartwood was 40–56% denser than the whole disk.

Table 1
Test of mean for density values obtained from dry weight determined at 80 and 103 °C, fresh volume and volume obtained through re-hydration

Density (sampling position)	n	Temperature for determination of the dry weight, mean (standard deviation), comparison of means[*]	
		80 °C	103 °C
Breast height (~1.36 m above the ground)	310	0.712 (0.119)[aA]	0.704 (0.117)[aB]
Top of the bole (at location of the first thick branch)	307	0.654 (0.093)[bA]	0.647 (0.093)[bB]
Arithmetic mean of the bole (density at breast height and at the top of the bole)	307	0.683 (0.102)[cA]	0.675 (0.101)[cB]
Arithmetic mean of the bole (breast height, top of the bole and 2 intermediate samples)	73	0.682 (0.099)[cA]	0.675 (0.098)[bcB]
Average adjusted for the volume of the segments of the bole (breast height, top of the bole and 2 intermediate samples)	71	0.678 (0.100)[abcA]	0.670 (0.099)[abcB]
Heartwood at breast height (green volume)	145	0.775 (0.162)[dA]	0.766 (0.158)[dBα]
Heartwood at breast height (re-hydrated volume)	145	–	0.785 (0.167)[dß]

[*] The same lower-case letters appearing in the same column indicate that values do not differ significantly (Tukey test; $p > 0.05$). Different capital letters in the same line differ statistically (paired t-test; $p \leq 0.001$). Different Greek letters in the same column indicate that values differ statistically (paired t-test; $p \leq 0.001$).
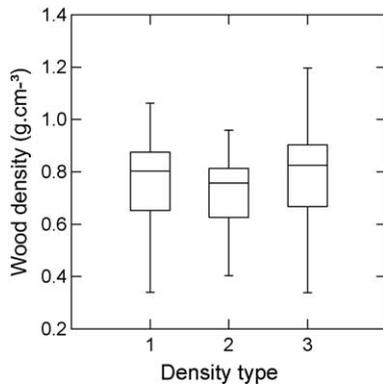
Fig. 2. Different density types at breast height, showing mean, first and third quartiles, and range of the data for trees with DBH ≥5 cm. 1 = basic density of the heartwood; 2 = basic density of the entire disk with bark; 3 = density of the heartwood obtained with re-hydrated volume.

3.2. Effect of re-hydration and drying temperature (80 and 103 °C) on density

Using oven-dried samples that were later re-hydrated to estimate basic density of heartwood led to a 2.5% overestimate (Table 1; paired *t*-test; $p < 0.001$; $n = 145$). The basic density from green volume of the heartwood, for the trees from which heartwood was collected, was 0.766 ± 0.158 (range, 0.34–1.06). But when obtained using re-hydrated volume, the density of the heartwood was 0.785 ± 0.167 (range, 0.17–1.05). Fourteen days were insufficient for the complete recovery of the green volume of small wood blocks

of approximately 12 cm³. The difference was larger with denser wood ($p < 0.001$; $n = 144$), probably because denser wood is more resistant to the penetration of water during immersion. The error in estimating basic density using re-hydrated samples will therefore probably be less than 2.5% in forest types or in parts of a tree with basic density lower than 0.766. The error will also be less if re-hydrating air-dried samples to determine volume prior to oven drying, as is standard procedure. The widepread practice of re-hydration is undoubtedly due to the greater convenience of not being obliged to determine volumes immediately after sample collection.

Density from dry weight at 80 °C was, on average, 1.1% higher than at 103 °C (Table 1; paired *t*-test; $p < 0.001$; $n = 310$), despite the dry weight at each temperature being based on three consecutive stable readings. Although 103 °C is recommended in official protocols for density determination (ASTM, 2002), tests at 80 °C were conducted as well due to the existence of density data for Amazonia that were determined at this temperature.

3.3. Relationship of density to morphometric variables

The arithmetic mean density of the bole showed no significant correlation with bole height, corrected bole volume or DBH (Fig. 3b). But density showed a nearly significant relationship with total tree height (Fig. 3a) ($p = 0.07$; Pearson correlation).
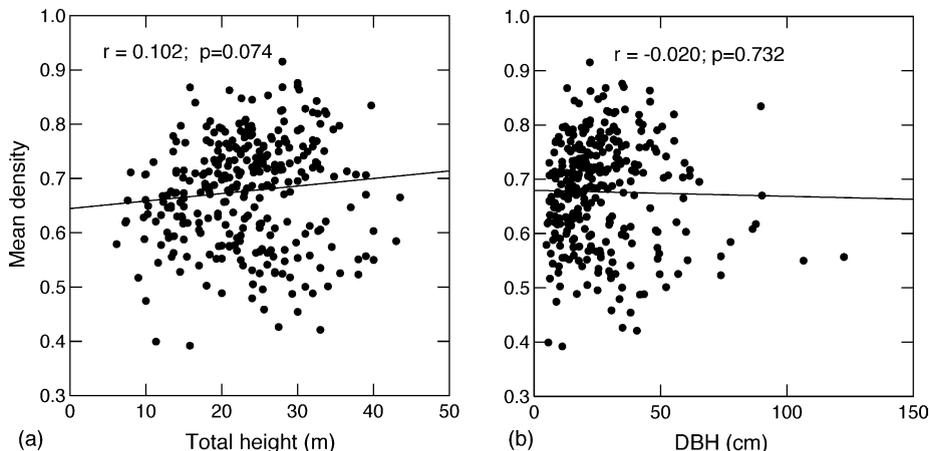

Fig. 3. Total tree height and DBH are not correlated with wood density (Pearson correlations, density is at breast height).

Table 2

Models to estimate basic density of the disk [BDD][a], arithmetic mean basic density of the bole [MBDB] and taper-adjusted mean basic density of the bole [AMBDB] from heartwood basic density [HBD][a] (green volume), from re-hydrated heartwood density [RHD][a] (re-hydrated volume) and from basic density of the full disk [BDD][a]

Models	Coefficients (standard error)		R^2	MSE	F	n
	α	β				
BDD = α + β (HBD) + ε	0.146 (0.014)	0.765 (0.017)	0.931	0.033	1945	146
BDD = α + β (RHD) + ε	0.167 (0.016)	0.718 (0.020)	0.903	0.040	1291	141
MBDB = α + β (HBD) + ε	0.219 (0.014)	0.630 (0.018)	0.893	0.034	1199	145
MBDB = α + β (RHD) + ε	0.235 (0.015)	0.592 (0.019)	0.873	0.038	947	140
AMBDB = α + β (BDD) + ε	0.099 (0.020)	0.808 (0.028)	0.925	0.027	832	69
AMBDB = α + β (HBD) + ε	0.219 (0.027)	0.611 (0.035)	0.871	0.038	298	46
AMBDB = α + β (RHD) + ε	0.228 (0.029)	0.585 (0.038)	0.847	0.041	243	46

[a] At breast height.

3.4. Density corrections

In Table 2, simple regressions are presented that allow estimation of the mean basic density of the entire bole in dense Amazon forest based on commonly available attributes, such as re-hydrated heartwood density, basic density of heartwood or basic density of the entire disk at breast height. Basic density of the full disk at breast height is also estimated from two types of heartwood density at the same height. All models are highly signi ficant. Residuals are symmetric and non-heteroscedastic.

4. Discussion

4.1. Causes of density variation within the bole and between species and locations

In general, studies that have determined radial and longitudinal variation in density for species in Amazonia (Wiemann and Williamson, 1989; Amorim, 1991; de Macedo, 1991; de Castro et al., 1993; Higuchi and Carvalho, 1994), either present results for few species restricted to certain functional groups or measure either only radial or only longitudinal variation. For 145 trees in central Amazonia, the present study finds patterns of radial variation in the dense *terra firme* forest, with the density usually decreasing from the center to the outside, at breast height. Therefore, the portions of the trunk that are more recent have lower density. This result is in agreement with Fearnside (1997a) (Table 1) and Amorim (1991). However, it is not certain if the same pattern is observed at higher positions on the bole.

Unlike the pattern found here for most of the trees in dense primary forest, in the case of pioneer tropical species, de Castro et al. (1993) affirm that density increases linearly from the center to the outside, a difference that can reach 200–300% in some species. Wiemann and Williamson (1989) demonstrated that for 16 species of tropical trees density increases away from the center, the increase being more accentuated (90–270%) in pioneer species in lowland forest. The same pattern is expected for other colonizing species. Pioneer species probably allocate resources to growth in stature to the detriment of the strength of the trunk, resulting in a bole with lower density and rapid apical growth. In the present study, the density of heartwood was compared with the density of the whole disk including bark, unlike the studies of Wiemann and Williamson (1989) and de Castro et al. (1993), which examined density in 1–2 cm increments along the radius of the disk at breast height, considering the center of the bole and not the heartwood. Among the species in the present study, Amapá (*Brosimum parinarioides* Ducke (Moraceae)), a canopy tree, had the largest decrease in density in the center-bark direction, with the heartwood density being 55% greater than the whole disk with bark. Among the few species that presented the inverse pattern, the greatest difference (18% density increase in the center-bark direction) was detected in *Sclerolobium melanocarpum* Ducke (Caesalpinioideae), a pioneer emergent tree (Ribeiro et al., 1999).

In the present study, density increased with the vertical position of the sample in only 14% of the trees. De Macedo (1991) found that in just 1 of 12 trees collected near Manaus, the density at the base of the bole was smaller than in the upper part. These few cases of lower density at the lower part of the bole may be a consequence of incipient degradation of the wood, which precedes the formation of a hollow core. This process would be more advanced close to the base of the tree, where hollow cores are most common. This could also be responsible for some cases of lower density of the heartwood found in 18% of the trees when compared with the density of the whole disk. *Cupania scrobiculata* L.C. Rich. (Sapindaceae) had a hollow area occupying 7.6% of the cross section at breast height and also had lower density of the intact wood at the same height when compared to the density at the top of the bole. However, no other hollow tree had lower density at breast height when compared to the top of the bole.

Several authors have pointed to different ecophysiological aspects as responsible for variation in the density of the bole, such as structural demands, climatic zone, humidity, age, illumination and rapid growth (DeZeeuw, 1965; Chudnoff, 1976; Denslow, 1980; Wiemann and Williamson, 1988; Rueda and Williamson, 1992; de Castro et al., 1993; Favrichon, 1994; Suzuki, 1999; Ter Steege and Hammond, 2001). Using 56 inventory plots grouped by region, Baker et al. (2004) reported mean stand-level wood density to be 12% higher in the eastern and central Amazon, compared with the northwest Amazon. Muller-Landau (2004), analyzing variation between four widely spread neotropical forest sites, observed that the wood density varies inversely with the fertility of the soil but is independent of rainfall, seasonality and temperature. Woodcock (2000) found different mean wood densities in plots of different successional stages, with lower density in young successional stages, but did not test for differences among soil types. Ter Steege and Hammond (2001), in forests in Guyana, failed to find a relationship between wood density and soil fertility, but did find a relationship between density and the diversity of species and seed size. Several more diverse communities exhibited characteristics of colonizing species, such as lower wood density and smaller seeds. On Barro Colorado Island, Panama, Muller-Landau (2004) also found a

weak negative correlation between the wood density and rate of adult mortality and the rate of relative growth of trees and saplings. In other words, short-lived species with higher rates of growth have lower wood density. Similar results are reported by Favrichon (1994) and Suzuki (1999).

In open forests in the state of Acre, in southwestern Amazonia, low wood density is believed to result from both phytogeographical and ecological factors (França, 2002). For example, trees in the family Bombacaceae, which are typically lightweight, are more abundant in all forest types of this region. A larger number of pioneer tree species and fast-growing species may also be responsible for the low mean density of disks taken at breast height from trees in a bamboo-dominated forest of this region: only 0.51 g cm^{-3} determined at $80\,^{\circ}\text{C}$. Common pioneer taxa here include *Acacia polyphylla*, *Apeiba* sp., *Jacaratia* sp., *Cavanillesia hylogeiton*, *Ceiba* sp. and *Cecropia sciadophylla* (Oliveira, 2000). In these environments, fast-growing species are favored by the occurrence of fertile soils (Cambisols or Inceptisols), by extensive temporary gaps resulting from natural disturbance by bamboo (*Guadua* sp.) and from the periodic and synchronized death of this bamboo. Schnitzer et al. (2000), in a study of 428 treefall gaps in tropical forest on Barro Colorado Island, Panama, found a similar correlation between liana abundance and the abundance of pioneer trees.

4.2. Methodological uncertainties in density determination

An important source of uncertainty in the available density data for Amazonia is species identification in forest inventories. Fearnside (1997a) found that many published inventories are based on common names. When the scientific names are reported, they are not based on formal botanical identification, but rather use tables equating common and scientific designations. According to Pires (1978), more than 90% of the identifications used in the inventories conducted by the Food and Agriculture Organization of the United Nations (FAO) in Amazonia could be in error at the species level because they have been based on common names. The data in the FAO inventory (Heinsdijk, 1958) have been used for calculations of biomass and emissions of carbon in Amazonia

because they are representative of several vegetation types (Brown et al., 1989). These uncertainties demonstrate the importance of studies to determine density with correct identification of the species.

In the present study, a test was conducted on the reliability of the common names supplied by a local woodsman (*mateiro*). These were transformed to scientific names using three guides: Catalog of Trees of Brazil (Camargos et al., 2001), Flora of the Reserva Ducke (Ribeiro et al., 1999) and Common Names of Amazonian Plants (da Silva, 1977); Appendix B. All of the trees also had botanical specimens identified in the herbarium, so the correct scientific names were also known. Only 53% of the scientific names inferred from the common names supplied by the *mateiro* proved to be correct. The common names and scientific names were considered to be equivalent when the common name mentioned by the *mateiro* was similar to one of the common names mentioned in the literature, or to one of the names listed when the common name is a compound word. Mistakes sometimes occurred when the *mateiro* attributed different names for a given species, or when common names were identified in different places. The *mateiro* was sometimes unable to identify the same species that he had identified previously.

Another source of uncertainty is the use of different methods for obtaining density. The following types have been reported (1) apparent densities, with a moisture content of 12% (g water/100 g oven-dry weight), based on the methodology of COPANT (1973); (2) green density, such as the data on 50 species published by IBAMA (de Souza et al., 2002), or for 40 species occurring in the Tapajós National Forest (Fedalto et al., 1989); (3) density based on the volume re-hydrated from green wood samples, such as 75 species collected in the Curuá-Una forest management research area in Pará (Brazil, IBDF, 1988, vol. 2), 23 species sampled in forests in the state of Amapá (Brazil, INPA/CPPF, 1993) and 40 species in the area of the Balbina hydroelectric dam (Brazil, INPA/CPPF, 1991). This has hindered the obtaining of consistent values for basic density using the ratio of dry weight to true green volume in the living tree. In some references, the green volume refers to wood that has been allowed to air dry and is later re-hydrated until saturation, or that has been sampled green and later saturated (Brazil, IBDF, 1988, vol. 2, p. 29).

Time for complete drying of the samples was highly variable; some required more than 20 days at a temperature of $103 \pm 2\,°C$ to achieve a stable weight. Thus, basic density will be overestimated if drying times are limited to a few days and standardized for different species and sample sizes. The density obtained from drying at $80\,°C$ was significantly higher than the density obtained at $103\,°C$ (Table 1). Since the weight obtained at $80\,°C$ was considered dry after stabilization (constant weight for three consecutive measurements), the loss of additional weight when dried at $103\,°C$ could represent water that is chemically bound to the cell wall, as well as organic compounds that are volatilized at the higher temperature.

Presence of hollows means that central heartwood is lost from the disk, causing a bias towards more external wood, which was usually less dense in this study. Hollows were found in 10% of the trees, including 7% at breast height. But hollows accounted for just 0.7% of the total stand bole volume after adjusting for size–class frequencies typical of a large inventory. Our method, in which density is based on a cross-sectional disc instead of small solid wood samples, avoids bias of the density results from the presence of hollows.

4.3. Wood density and biomass estimates

Studies of wood density for species in Amazonia are important for biomass estimates because this information is necessary for conversion of volume data from forest inventories to biomass (Houghton et al., 2001; Brown, 1997; Brown and Lugo, 1992):

$$\text{TAGB} = \text{Inventoried volume} \times \text{VEF}$$
$$\times \text{WD} \times \text{BEF} \qquad (3)$$

where:

TAGB: total above-ground biomass of standing trees (≥ 10 cm DBH; Mg ha^{-1});

Inventoried volume: commercial volume of the boles above the minimum DBH inventoried (m^3 ha^{-1}). Usually, minimum inventoried DBH is between 25 and 30 cm;

VEF: volume expansion factor, to represent the volume of boles between 10 cm and the minimum DBH inventoried;

WD: wood density, stand average of all boles;
BEF: biomass expansion factor (expands bole biomass to all above-ground biomass, for all trees ≥ 10 cm DBH).

The following values are assumed for Amazonia, in accordance with Houghton et al. (2001), (citing Brown and Lugo, 1992):

VEF = 1.25 for dense forests, or 1.5 for other Amazonian forests; WD = 0.69;
BEF = exp{3.213–0.506 ln SB},
for SB < 190 Mg ha^{-1};
BEF = 1.74, for SB > 190 Mg ha^{-1};
SB = stand biomass (biomass of the boles) ≥ 10 cm;
DBH = inventoried volume $\times$ VEF $\times$ WD.

For estimates based on volumetric data, wood density of 0.69 g cm^{-3} has been used as mean value for Brazilian Amazonia (Houghton et al., 2001; Fearnside, 1997a; Brown, 1997; Brown and Lugo, 1992; Brown et al., 1989). This value may be subject to the overestimation biases reported in this paper.

For dense forest of Central Amazonia, the density difference between heartwood and whole disk will lead to an overestimate of 5.3%, the difference between the whole disk at breast height and the average total bole density is 4.3%, while the effect of re-hydrating oven-dried heartwood is an overestimate of 2.5%. So, if average bole density of a stand is based on re-hydrating oven-dried samples of heartwood taken near the center of a disk at breast height, there will be ~12.1% overestimate of both density and biomass (Eq. (3)). A fourth tendency for over-estimation is the exclusion of bark from most samples used in prior studies. A fifth tendency in the same direction will result from using standard drying times. Re-hydration times of 14 days or less are a sixth source of overestimate, as shown in this study. Re-hydration of samples larger than the small (12 cm^3) blocks used in this study will mean even greater overestimates than those reported here, but re-hydration of wood, more porous than the heartwood used here, or re-hydrating air-dried samples will reduce or eliminate the bias.

To what extent do previously published lists of wood density by species include all these biases towards overestimate? In the case of data on wood density of Amazonian trees published by the Coordination of Research on Forest Products of the National Institute for Research in Amazonia, the Laboratory of Forestry Research of the Brazilian Institute for the Environment and Renewable Natural Resources and the Center for Wood Technology of the Superintendency for Development of Amazonia (SUDAM), samples were taken at random from different sections of the bole, based on the norms of COPANT (Brazil, IBDF, 1981,1988; Brazil, INPA/CPPF, 1991, pp. 5 and 7; Brazil, INPA/CPPF, 1993, p. 8; Brazil, IBAMA, 1997). Sampling protocols for basic density followed by the Brazilian Institute for Forest Development (IBDF, 1981,1988) are random with respect to height along the bole, but the center of each specimen was, on average, just 5.3 cm from center of the disk. Re-hydration protocols used by Brazil, IBDF (1981,1988) called for immersing green wood "for a long period" then drying at 103 °C, and so will be more efficient at regaining fresh volume than re-hydration that begins from dried samples.

The net effect of biases in the estimate of stand density and biomass using published wood density data can be better examined by comparing the results of this study with three previous estimates for the Central Amazon, which matched forest inventories to published lists of wood density by taxon. In those studies, overestimates of average density of the entire bole—here presumed to be 0.67 g cm^{-3}—were 6%, 4% and 0% (Fearnside, 1997a; Baker et al., 2004; Muller-Landau, 2004). Based on samples collected without bark and at breast height, plus published data at the species level, Muller-Landau (2004) found an inventory-adjusted average basic density of 0.71 for 112 trees from Central Amazon dense forest. Fearnside (1997a) reported an average density of 0.70 g cm^{-3} for this same region, using published density data and inventories. His number is identical to the value found in the present study at breast height, but is higher than the 0.67 g cm^{-3} mean basic density of the entire bole with bark. Baker et al. (2004) found 0.67 g cm^{-3} to be the stand level average for wood density in the Central Amazon based on 11 ha of dense forest inventory and lists of wood density covering 584 species of Amazonian trees. Their matches were made mostly at the genus or family level, i.e., were matched to related species or related genera. This may introduce a bias towards the more workable (less dense) commercial timbers and towards trees har-

vested on more fertile soil than the Central Amazon. In the case of Baker et al. (2004), these two biases towards lower wood density appear to have fully compensated the density overestimation biases reported in this paper.

5. Significance for global change estimates

The adjustments to wood density values used for calculating the biomass of Amazonian forests and the greenhouse gas emissions that result when these forests are cleared have important implications for global change. For example, an estimate of net committed emissions of 249×10^6 Mg CO_2-equivalent C/year for Brazilian Amazonia in 1990 (midpoint of high- and low-trace gas scenarios, including effects of CO_2, CH_4 and N_2O), of which 237×10^6 Mg CO_2-equivalent C/year was from net removal of biomass (updated from Fearnside, 2000a), would be reduced by 14×10^6 Mg CO_2-equivalent C/year, or 5.7%. The percentage reduction in net emissions is greater than the 5.3% reduction in gross emissions because the estimates for biomass accumulation in regenerating secondary forest are unaffected by the wood density adjustments.

Decreases of similar proportion would apply throughout the tropics. An annual gross emission of 2.0×10^9 Mg of carbon (without considering trace-gas effects) from biomass in the tropics during the 1980s (Fearnside, 2000b, p. 128) would be reduced by

113×10^6 Mg C annually, assuming the same adjustment applies to all tropical forests.

This adjustment would be increased to approximately 132 Mg CO_2-equivalent C/year if the effect of trace gases is considered (15.5% $\pm$ 9.5%, based on Fearnside, 1997b).

6. Conclusions

Wood density estimates that have been widely used as the basis of estimating Amazon forest biomass need to be adjusted downward by 5.3% for density variation in the cross-sectional disk. Some studies will require an additional 4.3% downward adjustment for density variation along the length of the bole.

The present study's results for wood density imply a 5.3% downward adjustment for estimates of primary forest biomass in Amazonia, and adjustment by the same amount of estimates of gross emissions of greenhouse gases from deforestation. Because regrowth estimates are unaffected by the adjustments, net committed emissions would be lowered by a slightly greater percentage: 5.7% in the case of Amazonian deforestation. However, these adjustments do not resolve differences among the various estimates that exist for biomass and emissions, since all estimates have been based on nearly identical assumptions regarding wood density in tropical forests.

Appendix A

Basic density (cross-sectional disk of wood with bark) of trees (DBH $\geq$5 cm) in Central Amazonia (dense *terra firme* forest)

Family	Scientific name	n	Basic density at breast height ~1.36 m, mean (standard deviation)	Basic density at the top of the bole, mean (standard deviation)	Arithmetic mean of the bole (breast height and top of the bole)
Anacardiaceae	*Anacardium parvifolium* Ducke	1	0.508	0.554	0.531
Fabaceae	*Andira* sp.	1	0.813	0.727	0.770
	Andira unifoliolata Ducke	1	0.760	0.663	0.711
Lauraceae	*Aniba cylindriflora* kosterm.	1	0.629	0.569	0.599
	Aniba hostmanniana (Nees) Mez.	1	0.766	0.671	0.718

Appendix A. *(Continued)*

	Aniba panurensis (Meissn.) Mez.	1	0.747	0.713	0.730
	Aniba williamsii O.C. Schmidt	1	0.741	0.678	0.709
Annonaceae	*Annona foetida* Mart.	1	0.572	0.517	0.544
Apocynaceae	*Aspidosperma discolon* A.D.C.	2	0.758 (0.016)	0.689 (0.034)	0.724 (0.025)
Anacardiaceae	*Astronium le-cointei* Ducke	1	0.812	0.614	0.713
Myrtaceae	*Blepharocalyx eggersii* (Kiaersk.) Landrum	1	0.726	0.693	0.710
Annonaceae	*Bocageopsis multiflora* (Mart.) R.E. Fr.	1	0.674	0.585	0.629
	Bocageopsis sp.	1	0.696	0.632	0.664
Papilionoideae	*Bocoa viridiflora* (Ducke) R.S. Cowan	1	0.835	0.745	0.790
Rubiaceae	*Botryarrhena pendula* Ducke	1	0.734	0.678	0.706
Moraceae	*Brosimum guianense* (Aubl.) Huber	1	0.780	0.736	0.758
	Brosimum lactescens (S. Moore) C.C. Berg.	2	0.703 (0.001)	0.715 (0.006)	0.709 (0.003)
	Brosimum parinarioides Ducke	2	0.610 (0.042)	0.522 (0.002)	0.566 (0.022)
	Brosimum rubescens Taub.	1	0.776	0.684	0.730
	Brosimum utile (H.B.K.) Pittier ssp. ovatifolium (Ducke) C.C. Berg.	1	0.540	0.510	0.525
Malpighiaceae	*Byrsonima* sp.	1	0.601	0.594	0.598
Lecythidaceae	*Cariniana decandra* Ducke	1	0.559	0.554	0.557
	Cariniana micrantha Ducke	1	0.563	0.536	0.550
Caryocaraceae	*Caryocar* sp.	1	0.712	0.712	0.712
Olacaceae	*Chaunochiton kappleri* (Sagot ex Engl.) Ducke	1	0.529	0.519	0.524
Rubiaceae	*Chimarrhis turbinata* D.C.	1	0.650	0.000	0.325
Sapotaceae	*Chrysophyllum amazonicum* T.D. Penn.	1	0.826	0.784	0.805
	Chrysophyllum lucentifolium Cronquist ssp. *pachycarpum* Pires & T.D. Penn.	1	0.787	0.712	0.749
	Chrysophyllum sanguinolentum (Pierre) Baehni ssp. *sanguinolentum*	1	0.624	0.618	0.621
	Chrysophyllum sanguinolentum (Pierre) Baehni ssp. *spurium* (Ducke) T.D. Penn.	4	0.660 (0.094)	0.625 (0.075)	0.642 (0.084)

Appendix A. *(Continued)*

	Chrysophyllum ucuquirana-branca (Aubrév. & Pellegrin) T.D. Penn.	1	0.733	0.636	0.684
Clusiaceae	*Clusia* sp.	1	0.821	0.760	0.791
Lecythidaceae	*Corythophora alta* Kunth	3	0.724 (0.026)	0.680 (0.019)	0.702 (0.019)
	Corythophora rimosa W.A. Rodrigues ssp. *rimosa*	1	0.683	0.630	0.656
	Corythophora rimosa W.A. Rodrigues	1	0.712	0.638	0.675
Chrysobalanaceae	*Couepia* sp.	1	0.720	0.632	0.676
	Couepia ulei Pilg.	2	0.816 (0.007)	0.714 (0.038)	0.765 (0.022)
Rubiaceae	*Coussarea ampla* Mull. Arg.	1	0.476	0.472	0.474
	Coussarea hirticalix Standl.	1	0.645	0.646	0.646
Sapindaceae	*Cupania scrobiculata* L.C. Rich.	3	0.506 (0.066)	0.567 (0.083)	0.537 (0.074)
Caesalpiniaceae	*Dipterix* sp.	1	0.917	0.772	0.845
Annonaceae	*Duguetia chysea* Maas	1	0.845	0.700	0.773
	Duguetia megalocarpa Maas	1	0.910	0.825	0.867
	Duguetia stelechantha (Diels) R.E. Fr.	1	0.849	0.687	0.768
	Duguetia surinamensis R.E. Fr.	1	0.780	0.654	0.717
Sapotaceae	*Ecclinusa guianensis* Eyma	1	0.549	0.529	0.539
Humiriaceae	*Endopleura uchi* (Huber) Cuatrec.	2	0.786 (0.002)	0.706 (0.033)	0.746 (0.018)
Caesalpiniaceae	*Eperua duckeana* R.S. Cowan	3	0.791 (0.050)	0.737 (0.024)	0.764 (0.037)
	Eperua glabriflora (Ducke) R.S. Cowan	1	0.759	0.727	0.743
Annonaceae	*Ephedrantus amazonicus* R.E. Fr.	1	0.816	0.771	0.794
Lecythidaceae	*Eschweilera amazoniciformis* S.A. Mori	3	0.823 (0.018)	0.718 (0.017)	0.770 (0.016)
	Eschweilera atropetiolata S.A. Mori	3	0.753 (0.022)	0.636 (0.010)	0.694 (0.014)
	Eschweilera carinata S.A. Mori	2	0.782 (0.013)	0.705 (0.062)	0.744 (0.038)
	Eschweilera collina Eyma	3	0.735 (0.025)	0.623 (0.026)	0.679 (0.012)
	Eschweilera coriaceae (D.C.) Mart. ex Berg.	6	0.699 (0.156)	0.642 (0.126)	0.671 (0.140)

Appendix A. *(Continued)*

	Eschweilera grandiflora (Aubl.) Sandwith	2	0.752 (0.018)	0.674 (0.016)	0.713 (0.001)
	Eschweilera rodriguesiana Mori	12	0.762 (0.053)	0.688 (0.041)	0.725 (0.041)
	Eschweilera sp.	7	0.734 (0.079)	0.687 (0.027)	0.710 (0.049)
	Eschweilera tessmannii Knuth	3	0.789 (0.023)	0.713 (0.040)	0.751 (0.029)
	Eschweilera wachenheimii (Benoist) Sandwith	9	0.750 (0.027)	-	-
Myrtaceae	*Eugenia* aff. *citrifolia* Poir.	1	0.664	0.663	0.663
	Eugenia cf. *illepida* McVaugh	1	0.690	0.658	0.674
	Eugenia diplocampta Diels	1	0.789	0.744	0.766
Arecaceae	*Euterpe precatoria* Mart.	1	0.273	0.269	0.271
Rubiaceae	*Ferdinandusa elliptica* Pohl.	1	0.650	0.590	0.620
Annonaceae	*Fusaea longifolia* (Aubl.) Saff.	1	0.653	0.615	0.634
Celastraceae	*Goupia glabra* Aubl.	1	0.747	0.677	0.712
Meliaceae	*Guarea scabra* A. Juss.	1	0.740	0.672	0.706
	Guarea sp.	1	0.691	0.605	0.648
Lecythidaceae	*Gustavia elliptica* S.A. Mori	13	0.669 (0.026)	0.627 (0.028)	0.648 (0.026)
Moraceae	*Helianthostylis sprucei* Baill.	3	0.585 (0.045)	0.597 (0.027)	0.591 (0.036)
	Helicostylis sp.	2	0.709 (0.036)	0.713 (0.035)	0.711 (0.035)
Euphorbiaceae	*Hevea brasiliensis* (Willd ex Adr. Juss.) Muell. Arg.	1	0.533	0.522	0.528
	Hevea guianensis Aubl.	1	0.514	0.556	0.535
Apocynaceae	*Himatanthus* cf. *sucuuba* (Spruce) Woodson.	1	0.404	0.438	0.421
Chrysobalanaceae	*Hirtella* cf. *pimichina* Lass. & Mag.	1	0.824	0.759	0.791
	Hirtella sp.	1	0.828	0.765	0.797
Humiriaceae	*Humiriastrum cuspidatum* (Benth.) Cuatr.	1	0.721	0.666	0.693
Mimosaceae	*Inga* sp.	1	0.503	0.530	0.517
Myristicaceae	*Iryanthera juruensis* Warb.	3	0.672 (0.059)	0.556 (0.013)	0.614 (0.033)
	Iryanthera ulei Warb.	1	0.587	0.549	0.568

Appendix A. *(Continued)*

Bignoniaceae	*Jacaranda* sp.	1	0.457	0.543	0.500
Quiinaceae	*Lacunaria crenata* (Tul.) A.C. Sm.	1	0.773	0.725	0.749
Lecythidaceae	*Lecythis parvifructa* S.A. Mori	2	0.741 (0.023)	0.710 (0.046)	0.726 (0.034)
	Lecythis poiteaui Berg.	1	0.763	0.632	0.697
	Lecythis prancei S.A. Mori	2	0.875 (0.015)	0.791 (0.025)	0.833 (0.020)
	Lecythis sp.	2	0.705 (0.175)	0.668 (0.114)	0.686 (0.145)
Chrysobalanaceae	*Licania* cf. *rodriguesii* Prance	1	0.844	0.757	0.800
	Licania impressa Prance	2	0.921 (0.030)	0.403 (0.570)	0.662 (0.270)
	Licania micrantha Miq.	1	0.811	0.746	0.779
	Licania prismatocarpa Spruce ex Hook.f.	1	0.857	0.744	0.801
	Licania sothersae Prance	1	0.839	0.736	0.788
	Licania sp.	5	0.817 (0.062)	0.763 (0.053)	0.790 (0.057)
Lauraceae	*Licaria guianensis* Aubl.	1	0.749	0.677	0.713
Euphorbiaceae	*Mabea caudata* Pax & K. Hoffm	1	0.670	0.573	0.621
	Mabea piriri Aubl.	1	0.644	0.801	0.723
Sapotaceae	*Manilkara bidentata* (A.D.C.) A. Chev.	1	0.813	0.702	0.758
	Manilkara cavalcantei Pires & W.A. Rodrigues	1	0.834	0.759	0.797
Moraceae	*Maquira sclerophylla* (Ducke) C.C. Berg.	2	0.504 (0.020)	0.509 (0.011)	0.506 (0.016)
Sapidaceae	*Matayba* sp.	1	0.823	0.677	0.750
Lauraceae	*Mezilaurus duckei* van der Werff	1	0.716	0.685	0.700
	Mezilaurus itauba (Meissn.) Taubert ex. Mez	1	0.659	0.654	0.657
Euphorbiaceae	*Micrandra rossiana* R.E. Schult	1	0.678	0.596	0.637
	Micrandra siphonioides Benth.	1	0.584	0.570	0.577
Sapotaceae	*Micropholis guyanensis* (A. D.C.) Pierre ssp. *duckeana* (Baehni) T.D. Penn.	2	0.719 (0.015)	0.641 (0.003)	0.680 (0.009)
	Micropholis guyanensis (A. D.C.) Pierre ssp. guyanensis	1	0.663	0.588	0.626

Appendix A. *(Continued)*

	Micropholis mensalis (Baehni) Aubrév.	2	0.717 (0.180)	0.639 (0.155)	0.678 (0.168)
	Micropholis venulosa (Mart. & Eichler) Pierre	2	0.608 (0.044)	0.565 (0.009)	0.587 (0.027)
	Micropholis williamii Aubrév. & Pellegrin	1	0.718	0.650	0.684
Olacaceae	*Minquartia guianensis* Aubl.	1	0.777	0.756	0.766
Memecylaceae	*Mouriri brevipes* Hook	1	0.775	0.714	0.744
Nyctaginaceae	*Neea* sp.	2	0.571 (0.017)	0.594 (0.058)	0.582 (0.037)
Lauraceae	*Ocotea amazonica* (Meissn.) Mez.	1	0.443	0.473	0.458
	Ocotea canaliculata (Rich) Mez.	1	0.455	0.503	0.479
	Ocotea fragantissima Ducke	2	0.582 (0.021)	0.568 (0.006)	0.575 (0.014)
	Ocotea myriantha (Meissn.) Mez.	1	0.611	0.599	0.605
	Ocotea percurrens Vicentini	1	0.519	0.531	0.525
Arecaceae	*Oenocarpus* sp.	1	0.789	0.337	0.563
Papilionoideae	*Ormosia smithii* Rudd.	1	0.714	0.725	0.720
Myristicaceae	*Osteophloeum platyspermum* (A.D.C.) Warb.	1	0.469	0.505	0.487
Ochnaceae	*Ouratea discophora* Ducke	1	0.791	0.778	0.785
Mimosoideae	*Parkia pendula* (Willd.) Walp.	1	0.544	0.507	0.525
Mimosaceae	*Parkia* sp.	1	0.617	0.589	0.603
Violaceae	*Paypayrola grandiflora* Tul.	1	0.630	0.611	0.620
Caesalpiniaceae	*Peltogyne* sp.	1	0.944	0.807	0.876
Icacinaceae	*Poraqueiba guianensis* Aubl.	1	0.751	0.688	0.719
Sapotaceae	*Pouteria anomala* (Pires) T.D. Penn.	4	0.760 (0.031)	0.691 (0.039)	0.726 (0.034)
	Pouteria caimito (Ruiz & Pav.) Radlk.	2	0.897 (0.051)	0.800 (0.010)	0.849 (0.020)
	Pouteria cf. *stipulifera* T.D. Penn.	1	0.741	0.640	0.690
	Pouteria cladantha Sandwith	1	0.894	0.842	0.868
	Pouteria flavilatex T.D. Penn.	1	0.665	0.588	0.627
	Pouteria macrophylla (Lam.) Eyma	2	0.858 (0.026)	0.727 (0.056)	0.792 (0.041)
	Pouteria reticulata (Engl.) Eyma	1	0.930	0.755	0.842
	Pouteria spp.	9	0.695 (0.128)	0.618 (0.059)	0.656 (0.092)
	Pouteria vernicosa T.D. Penn.	1	0.737	0.693	0.715
Burseraceae	*Protium altsonii* Sandwith	2	0.684 (0.272)	0.636 (0.177)	0.660 (0.224)
	Protium fimbriatum Swart.	1	0.599	0.554	0.577
	Protium grandifolium Engl.	1	0.638	0.594	0.616

Appendix A. *(Continued)*

	Protium guianense (Aubl.) March. ssp. *guianense*	1	0.711	0.701	0.706
	Protium sp.	6	0.567 (0.058)	0.520 (0.088)	0.543 (0.073)
	Protium tenuifolium (Engl.) Engl.	2	0.556 (0.008)	0.581 (0.013)	0.568 (0.002)
	Protium trifoliolatum Engl.	1	0.640	0.624	0.632
Moraceae	*Pseudolmedia laevis* (Ruiz & Pavan) Macbr.	1	0.598	0.552	0.575
	Pseudolmedia murure standl.	1	0.756	0.693	0.725
Papilionoideae	*Pterocarpus amazonicus* Hub.	1	0.528	0.527	0.527
Quiinaceae	*Quiina obovata* Tul.	1	0.851	0.760	0.805
Violaceae	*Rinorea guianensis* Aubl. var. *subintegrifolia*	1	0.780	0.700	0.740
	Rinorea racemosa (Mart.) Kuntze	2	0.682 (0.053)	0.647 (0.079)	0.664 (0.066)
Hippograteaceae	*Salacia* sp.	1	0.713	0.679	0.696
Sapotaceae	*Sarcaulus brasiliensis* ssp. *brasiliensis* (A.D.C.) Eyma	1	0.615	0.543	0.579
Caesalpinioideae	*Sclerolobium* cf. *micropetalum* Ducke	1	0.690	0.603	0.647
	Sclerolobium melanocarpum Ducke	2	0.524 (0.134)	0.572 (0.211)	0.548 (0.172)
	Sclerolobium paraense Hub.	1	0.802	0.723	0.763
Bombacaceae	*Scleronema micranthum* Ducke	4	0.552 (0.032)	0.563 (0.007)	0.558 (0.014)
	Without botanical sample	2	0.773 (0.095)	0.656 (0.058)	0.714 (0.077)
Combretaceae	Unidentified	1	0.848	0.800	0.824
Simaroubaceae	*Simaba* sp.	1	0.617	0.646	0.632
Siparunaceae	*Siparuna argyrochysea* Pert.	1	0.617	0.620	0.618
	Siparuna cuspidata (Tul.) A.D.C.	1	0.632	0.605	0.618
	Siparuna decipiens (Tul.) A.D.C.	1	0.591	0.519	0.555
Elaeocarpaceae	*Sloanea guianensis* (Aubl.) Benth.	1	0.856	0.801	0.828
	Sloanea schomburgkii Benth.	1	0.870	0.808	0.839
	Sloanea synandra Spruce ex Benth.	1	0.653	0.581	0.617
Mimosaceae	*Stryphnodendron racemiferum* (Duke) Rodr.	1	0.752	0.679	0.715
Rubiaceae	*Duroia fusifera* Hook. Fex. K. Schum.	1	0.672	0.529	0.600
Papilionoideae	*Swartzia corrugata* Benth.	1	0.913	0.703	0.808

Appendix A. *(Continued)*

	Swartzia cuspidata Spruce ex. Benth.	1	0.678	0.640	0.659
	Swartzia ingifolia Ducke	2	0.815 (0.002)	0.721 (0.047)	0.768 (0.025)
	Swartzia polyphylla D.C.	1	0.643	0.573	0.608
Sapindaceae	*Talisia* cf. *microphylla* Uitt.	2	0.773 (0.017)	0.681 (0.016)	0.727 (0.001)
Burseraceae	*Tetragastris panamensis* (Engl.) Kuntze	1	0.783	0.726	0.754
Sterculiaceae	*Theobroma sylvestre* Mart.	3	0.668 (0.031)	0.473 (0.090)	0.571 (0.060)
Leguminoseae	Tintarana	1	0.638	0.692	0.665
Clusiaceae	*Tovomita* sp.	1	0.764	0.693	0.729
Burseraceae	*Trattinnickia peruviana* Loes.	2	0.560 (0.054)	0.561 (0.016)	0.561 (0.019)
Moraceae	*Trymatococcus amazonicus* Poepp. & Endl.	1	0.548	0.555	0.552
Annonaceae	*Unonopsis* sp.	1	0.727	0.651	0.689
	Unonopsis stipitata Diels	1	0.686	0.627	0.656
Humiriaceae	*Vantanea macrocarpa* Ducke	2	0.953 (0.007)	0.831 (0.058)	0.892 (0.032)
Myristicaceae	*Virola caducifolia* W.A. Rodrigues	1	0.461	0.515	0.488
	Virola michelli Heck	1	0.586	0.492	0.539
	Virola sp.	2	0.511 (0.017)	0.483 (0.007)	0.497 (0.012)
	Virola venosa (Benth.) Warb.	1	0.622	0.559	0.590
Vochysiaceae	*Vochysia* cf. *melinonii* Bechmann	1	0.591	0.634	0.612
Annonaceae	*Xylopia amazonica* R.E. Fr.	1	0.787	0.657	0.722
Mimosoideae	*Zygia juruana* (Harms) L. Rico	1	0.851	0.740	0.796
Mimosaceae	*Zygia racemosa* (Ducke) Barneby & J.W. Grimes	3	0.748 (0.022)	0.701 (0.032)	0.725 (0.026)

Appendix B

Common names for species for which wood density was determined[a]

Scientific name	Common names
Anacardium parvifolium Ducke	Cajuí. cajuí-folha-miúda
Andira sp.	Sucupira
Andira unifoliolata Ducke	Acapurana
Aniba cylindriflora kosterm.	
Aniba hostmanniana (Nees) Mez.	Louro-amarelo. louro-capitiu
Aniba panurensis (Meissn.) Mez.	
Aniba williamsii O.C. Schmidt	Louro-amarelo
Annona foetida Mart.	Envira-alta. graviola-da-mata
Aspidosperma discolon A.D.C.	Araruába. cabo-de-machado. canela-de-veado
Astronium le-cointei Ducke	Muiraquatiara. aroeira
Blepharocalyx eggersii (Kiaersk.) Landrum	
Bocageopsis multiflora (Mart.) R.E. Fr.	Envira-preta. envira-surucucu. envira-surucucu-folha-miúda
Bocageopsis sp.	Envira
Bocoa viridiflora (Ducke) R.S. Cowan	Muirajibóia-preta
Botryarrhena pendula Ducke	
Brosimum guianense (Aubl.) Huber	Pau-rainha-roxo
Brosimum lactescens (S. Moore) C.C. Berg.	Leiteira. muiratinga
Brosimum parinarioides Ducke	Amapá. amapá-roxo. amaparana
Brosimum rubescens Taub.	Garrote. pau-rainha. muirapiranga. pau-brasil. rainha
Brosimum utile (H.B.K.) Pittier ssp. *ovatifolium* (Ducke) C.C. Berg.	Garrote. leiteira
Byrsonima sp.	Murici. murixi
Cariniana decandra Ducke	Tauarí. castanha-de-macaco
Cariniana micrantha Ducke	Taurí. castanha-de-macaco
Caryocar sp.	Piquiarana
Chaunochiton kappleri (Sagot ex Engl.) Ducke	Capoteiro. pau-branco
Chimarrhis turbinata D.C.	Pau-de-remo
Chrysophyllum amazonicum T.D. Penn.	Abiurana
Chrysophyllum lucentifolium Cronquist ssp. *pachycarpum* Pires & T.D. Penn.	Vaca
Chrysophyllum prieurii A.D.C.	Massaranduba. castanha-vermelha. abiurana vermelha. abiurana maçaranduba. maçarandubarana
Chrysophyllum sanguinolentum (Pierre) Baehni ssp. *sanguinolentum*	Coquirana. pau-de-porco. ucuquirana
Chrysophyllum sanguinolentum (Pierre) Baehni ssp. *spurium* (Ducke) T.D. Penn.	Balata-brava. ucuquirana
Chrysophyllum ucuquirana-branca (Aubrév. & Pellegrin) T.D. Penn.	Coquirana-branca

Appendix B. *(Continued)*

Clusia sp.	Bacupari. criúva. clúsia. guanandi-de-areia. pororoca
Corythophora alta Kunth	Ripeiro. ripeiro-vermelho
Corythophora rimosa W.A. Rodrigues ssp. *rimosa*	Castanha-jacaré. casca-jacaré
Corythophora rimosa W.A. Rodrigues	Castanha-jacaré. casca-jacaré
Couepia sp.	Amescla. bom-nome-preto. cabatã-cega-machado. carrapeta. carrapeta-tataburá
Couepia ulei Pilg.	
Coussarea ampla Mull. Arg.	
Coussarea hirticalix Standl.	
Cupania scrobiculata L.C. Rich.	Espeturana
Dipterix sp.	
Duguetia chysea Maas	
Duguetia megalocarpa Maas	Envira-cajú
Duguetia stelechantha (Diels) R.E. Fr.	
Duguetia surinamensis R.E. Fr.	Envira-amargosa
Ecclinusa guianensis Eyma	Abiurana-caju. abiurana-bacuri. cauchorana
Endopleura uchi (Huber) Cuatrec.	Uchi. uxi-amarelo. uxi-liso. uxi-pucu
Eperua duckeana R.S. Cowan	Muirapiranga-folha-grande
Eperua glabriflora (Ducke) R.S. Cowan	Muirapiranga-folha-miúda
Ephedrantus amazonicus R.E. Fr.	Envira-dura. envira-taia. envira-dura
Eschweilera amazoniciformis S.A. Mori	Matamatá
Eschweilera atropetiolata S.A. Mori	Castanha-vermelha
Eschweilera carinata S.A. Mori	
Eschweilera collina Eyma	Ripeiro-branco
Eschweilera coriaceae (D.C.) Mart. ex Berg.	Matamatá-verdadeira
Eschweilera grandiflora (Aubl.) Sandwith	Matamatá-rósea
Eschweilera pseudodecolorans S.A. Mori	Matamatá
Eschweilera rodriguesiana Mori	
Eschweilera sp.	Burangica. cuia-de-macaco. embiribaçu. jatereu. mangue. quiriba. macaco-de-cuia. tiriba
Eschweilera tessmannii Knuth	Ripeiro-vermelho
Eschweilera wachenheimii (Benoist) Sandwith	Matamatá-mirim
Eugenia aff. *citrifolia* Poir.	
Eugenia cf. *illepida* McVaugh	
Eugenia diplocampta Diels	
Euterpe precatoria Mart.	Açaí-da-mata
Ferdinandusa elliptica Pohl.	Café-bravo
Fusaea longifolia (Aubl.) Saff.	Envira-preta. envira-surucucu
Goupia glabra Aubl.	Cupiúba

Appendix B. *(Continued)*

Guarea scabra A. Juss.	
Guarea sp.	Gito-vermelho. café-branco. cajarana. cedro-baio
Gustavia elliptica S.A. Mori	Mucurão
Helianthostylis sprucei Baill.	Falsa-rainha
Helicostylis sp.	Inharé
Hevea brasiliensis (Willd ex Adr. Juss.) Muell. Arg.	Seringueira. seringa-verdadeira
Hevea guianensis Aubl.	Seringueira. seringa-itaúba. seringa-vermelha
Himatanthus cf. *sucuuba* (Spruce) Woodson.	Sucuúba. sucuba. janaguba
Hirtella cf. *pimichina* Lass. & Mag.	
Hirtella sp.	Amescla-seca. carrapeta-amarela. casca-dura. cega-machado. estalador. oitizinho
Humiriastrum cuspidatum (Benth.) Cuatr.	
Inga sp.	Ingá. alho-bravo. cedro-amarelo. cega-machado. favinha
Iryanthera juruensis Warb.	Lacre-da-mata
Iryanthera ulei Warb.	Ucuuba-branca
Jacaranda sp.	Tamanqueira. falsa-caroba
Lacunaria crenata (Tul.) A.C. Sm.	
Lecythis parvifructa S.A. Mori	Jarana-de-folha-pequena
Lecythis poiteaui Berg.	Jarana-amarela
Lecythis prancei S.A. Mori	Castanha-jarana
Lecythis sp.	Embiratã. pininga. sapucaia-de-pilão. sapucarana. Sapucarana-verdadeira
Licania cf. *rodriguesii* Prance	
Licania impressa Prance	Macucu
Licania micrantha Miq.	Pintadinha
Licania prismatocarpa Spruce ex Hook.f.	
Licania sothersae Prance	
Licania sp.	Caraipé. caripé. cariperana. uxí-do-igapó. uchirana
Licaria guianensis Aubl.	Louro-mangarataia
Mabea caudata Pax & K. Hoffm	Taquari. seringaí
Mabea piriri Aubl.	
Manilkara bidentata (A.D.C.) A. Chev.	Massaranduba
Manilkara cavalcantei Pires & W.A. Rodrigues	Massaranduba-de-folha-miúda
Maquira sclerophylla (Duke) C.C. Berg.	Muiratinga. pau-tanino
Matayba sp.	Breu-pitomba
Mezilaurus duckei van der Werff	Itaúba-abacate
Mezilaurus itauba (Meissn.) Taubert ex Mez	Itaúba. louro-itaúba
Micrandra rossiana R.E. Schult	Cauchorana
Micrandra siphonioides Benth.	Seringarana. cauchorana
Micropholis guyanensis (A.D.C.) Pierre ssp. *duckeana* (Baehni) T.D. Penn.	Balata-rosadinha. chile-bravo. abiurana-bacuri. cauchorana

Appendix B. *(Continued)*

Micropholis guyanensis (A.D.C.) Pierre ssp. *guyanensis*	Balata-brava. maparajuba. abiurana-bacuri. cauchorana
Micropholis mensalis (Baehni) Aubrév.	Abiurana-goiabinha. abiurana-roxa
Micropholis venulosa (Mart. & Eichler) Pierre	Abiurana-branca. Mulungu. rosada-verde
Micropholis williamii Aubrév. & Pellegrin	Abiurana. balata-brava
Minquartia guianensis Aubl.	Acariquara. aquariquara-roxa. acariúba
Mouriri brevipes Hook	Muiraúba
Neea sp.	João-mole
Ocotea amazonica (Meissn.) Mez.	Canela-mamelada
Ocotea canaliculata (Rich) Mez.	Louro-branco. louro-pimenta
Ocotea fragantissima Ducke	Louro-preto
Ocotea myriantha (Meissn.) Mez.	Louro-abacate
Ocotea percurrens Vicentini	
Oenocarpus sp.	
Ormosia smithii Rudd.	
Osteophloeum platyspermum (A.D.C.) Warb.	Ucuuba-chico-de-assis. lacre-da-mata. ucuúba-amarela. ucuúba-branca. ucuubarana
Ouratea discophora Ducke	Uxi-de-morcego
Parkia pendula (Willd.) Walp.	Visgueiro. arara-tucupi. faveira-arara-tucupi. faveira-parquia
Parkia sp.	Faveira
Paypayrola grandiflora Tul.	Manacarana. paparola
Peltogyne sp.	
Poraqueiba guianensis Aubl.	Marirana. umari-amarelo. umari-bravo. umarirana
Pouteria anomala (Pires) T.D. Penn.	Abiurana-balatinha. abiurana-rosadinha. mangabarana. rosadinha. rosadinho
Pouteria caimito (Ruiz & Pav.) Radlk.	Abiurana-aquariquara
Pouteria cf. *stipulifera* T.D. Penn.	
Pouteria cladantha Sandwith	Abiurana-seca
Pouteria flavilatex T.D. Penn.	
Pouteria macrophylla (Lam.) Eyma	Acará-uba
Pouteria reticulata (Engl.) Eyma	Abiurana-cascuda
Pouteria sp.	Abiurana
Pouteria vernicosa T.D. Penn.	Abiurana
Protium altsonii Sandwith	
Protium fimbriatum Swart.	
Protium grandifolium Engl.	
Protium guianense (Aubl.) March. ssp. *guianense*	Pau-de-incenso
Protium sp.	Breu

Appendix B. *(Continued)*

Protium tenuifolium (Engl.) Engl.	Breu. breu-preto
Protium trifoliolatum Engl.	Breu-branco
Pseudolmedia laevis (Ruiz & Pavan) Macbr.	Inharé-folha-miúda. muiratinga
Pseudolmedia murure standl.	
Pterocarpus amazonicus Hub.	Mututi. mututi-da-várzea. pau-sangue
Quiina obovata Tul.	
Rinorea guianensis Aubl. var. *subintegrifolia*	Falsa-cupiúba
Rinorea paniculata (Mart.) Kuntze	
Salacia sp.	Chichuasca
Sarcaulus brasiliensis ssp. *brasiliensis* (A.D.C.) Eyma	Guajará
Sclerolobium cf. *micropetalum* Ducke	
Sclerolobium melanocarpum Ducke	Taxi-vermelho
Sclerolobium paraense Hub.	Pau-de-formiga. pau-ponga. taxi-branco. taxi-preto. taxirana
Scleronema micranthum Ducke	Cardeiro. cedro-bravo. cedrorana
Without botanical sample	Envireira (anonaceae)
Without botanical sample	Pajurá
Unidentified	Tanibuca
Simaba sp.	Calunga
Siparuna argyrochysea Pert.	
Siparuna cuspidata (Tul.) A.D.C.	
Siparuna decipiens (Tul.) A.D.C.	Limão-do-mato. louro-capitiú
Sloanea guianensis (Aubl.) Benth.	Urucurana
Sloanea schomburgkii Benth.	
Sloanea synandra Spruce ex Benth.	
Stryphnodendron racemiferum (Ducke) Rodr.	Ingarana
Suroia fusifera Hook. Fex. K. Schum.	
Swartzia corrugata Benth.	Coração-de-negro
Swartzia cuspidata Spruce ex Benth.	Muirapiranga-folha-miúda
Swartzia ingifolia Ducke	Acapú-amarelo. carrapatinho
Swartzia polyphylla D.C.	Paracutaca. jabelona
Talisia cf. *microphylla* Uitt.	
Tetragastris panamensis (Engl.) Kuntze	Barrote. breu-areu-areu. breu-preto
Theobroma sylvestre Mart.	Cacau-do-mato. cacauí. cacau-azul
Tintarana	Tintarana
Tovomita sp.	Mangue. mangue-branco. mangue-preto. mangue-vermelho
Trattinnickia peruviana Loes.	
Trymatococcus amazonicus Poepp. & Endl.	Pãima
Unonopsis sp.	
Unonopsis stipitata Diels	Envira. envireira. envira-preta. envira-surucucu

Appendix B. *(Continued)*

Vantanea macrocarpa Ducke	Uchirana. quebra-machado. macucu-murici.uxi-quebra-machado
Virola caducifolia W.A. Rodrigues	Ucuuba-peluda
Virola michelli Heck	Ucuuba-preta
Virola sp.	
Virola venosa (Benth.) Warb.	Ucuuba-branca. ucuúba-da-mata
Vochysia cf. *melinonii* Bechmann	Quaruba. quaruba-branca. quarubatinga
Xylopia amazonica R.E. Fr.	Louro-bosta. envira-sarassará. envireira-vermelha. envirataia-vermelha. envirataia-sarassará
Zygia juruana (Harms) L. Rico	Inga-cauliflora
Zygia racemosa (Ducke) Barneby & J.W. Grimes	Angelim-rajado

[a] Names from Pinto et al. (2003), Camargos et al. (2001), Ribeiro et al. (1999) and da Silva (1977).

References

Amorim, L.C., 1991.Variação da densidade básica no sentido radial em madeiras tropicais da Amazônia. Relatório Final, Período abril-90/março-91 (Iniciação Científica/Conselho Nacional de Desenvolvimento Científico e Tecnológico), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil 24 pp.

ASTM, 2002. Standard Test Methods for Specific Gravity of Wood and Wood-Based Materials. Designation: D 2395-02. ASTM International, West Conshohocken, PA, USA, 8 pp.

Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patiño, S., Pitman, N.C.A., Silva, N., Martínez, R.V., 2004. Variation in wood density determines spatial patterns in Amazonian forest biomass. Global Change Biol. 10, 545–562.

Brazil, IBAMA, 1997. Madeiras da Amazônia: Características e Utilização, vol. 3. Amazônia Oriental. Instituto Brasilerio do Meio Ambiente e dois Recursos Naturais (IBAMA), Brasília, DF, Brazil, 141 pp.

Brazil, IBDF, 1981. Madeiras da Amazônia: Características e Utilização: Floresta Nacional do Tapajós. Instituto Brasileiro do Desenvolvimento Florestal (IBDF), Conselho Nacional do Desenvolvimento Científico e Tecnológico (CNPq), Brasília, DF, Brazil, 113 pp.

Brazil, IBDF, 1988. Madeiras da Amazônia, características e utilização; Estação experimental de Curuá-Una (Amazonian Timbers, characteristics and utilization; Curuá-Una Experimental Forest Station), vol. 2. Instituto Brasileiro de Desenvolvimento Florestal (IBDF), Brasília, DF, Brazil, 236 pp.

Brazil, INMET, 2003. Instituto Nacional de Meteorologia. www.inmet.gov.br (accessed 12 August 2003).

Brazil, INPA/CPPF, 1991. Catálogo de madeiras da Amazônia. Coordenação de Pesquisa de Produtos Florestais, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil, 153 pp.

Brazil, INPA/CPPF, 1993. Catálogo de madeiras do Amapá: características tecnológicas. Coordenação de Pesquisas em Produtos Florestais, Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil, 58 pp.

Brazil, Projeto RADAMBRASIL, 1978. Folha SA.20, Levantamento de Recursos Naturais, Manaus, vol. 18. Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil, 747 pp.

Brown, S., 1997. Estimating biomass and biomass change of tropical forest: a primer, Forestry Paper 134. Food and Agriculture Organization of the United Nations (FAO), Rome, Italy, 55 pp.

Brown, S., Lugo, A.E., 1992. Aboveground biomass estimates for tropical moist forests of the Brazilian Amazon. Interciencia 17, 8–18.

Brown, S., Gillespie, A.J.R., Lugo, A.E., 1989. Biomass estimation methods for tropical forest with applications to forest inventory data. Forest Sci. 35, 881–902.

Camargos, J.A.A., Coradin, V.T.R., Czarneski, C.M., de Oliveira, D., Meguerditchian, I., 2001. Catálogo de árvores do Brasil. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, Laboratório de Produtos Florestais, Edições IBAMA, Brasília, DF, Brazil, 896 pp.

Chimelo, J.P., 1992. Relacionamento da anatomia da madeira com suas propriedades físicas e mecânicas. Escola Superior de Agricultura "Luis de Queiroz", Escola Superior de Agricultura "Luis de Queirroz", Universidade de São Paulo (ESALQ/USP), Piracicaba, São Paulo, Brazil, 25 pp. (mimeographed).

Chudnoff, M., 1976. Density of tropical timbers as influenced by climatic life zones. Commonwealth Forest Rev. 55, 203–217.

COPANT, 1973. Descrição macroscópica. microscópica e geral da madeira; esquema de recomendação, 30, 1–019. Comisión Panamericana de Normas Técnicas (COPANT), Bogotá, Colombia.

da Silva, M.F., 1977. Nomes vulgares de plantas amazônicas, Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil, 222 pp.

De Castro, F., Williamson, G.B., Jesus, R.M., 1993. Radial variation in wood specific gravity of *Joannesia princeps*: the roles of age and diameter. Biotropica 25, 176–182.

De Macedo, C.S.M., 1991. Variação longitudinal da densidade básica e da composição química de madeiras e sua avaliação energética. Relatório Final, abril/1990-março/1991 (Iniciação Científica/Conselho Nacional de Desenvolvimento Científico e Tecnológico), Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil, 18 pp.

De Souza, M.H., Magliano, M.M., Camargos, J.A.A., de Souza, M.R., 2002. Madeiras tropicais brasileiras (Brazilian tropical woods), second ed. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, edições IBAMA, Brasília, DF, Brazil, 152 pp.

Denslow, J.S., 1980. Gap partitioning among tropical rain forest trees. Biotropica 12 (Suppl.), 23–30.

DeZeeuw, C., 1965. Variability in wood. In: Côté, W.A. (Ed.), Cellular Ultrastructure of Woody Plants. Syracuse University Press, Syracuse, NY, USA, pp. 457–471.

Favrichon, V., 1994. Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt Guyannaise. Revue d'Ecologie Terre et Vie 49, 379–402.

Fearnside, P.M., 1997a. Wood density for estimating forest biomass in Brazilian Amazonia. Forest Ecol. Manage. 90, 59–87.

Fearnside, P.M., 1997b. Greenhouse gases from deforestation in Brazilian Amazonia: net committed emissions. Climatic Change 35, 321–360.

Fearnside, P.M., 2000a. Greenhouse gas emissions from land-use change in Brazil's Amazon region. In: Lal, R., Kimble, J.M., Stewart, B.A. (Eds.), Global Climate Change and Tropical Ecosystems: Advances in Soil Science. CRC Press, Boca Raton, FL, USA, pp. 231–249.

Fearnside, P.M., 2000b. Global warming and tropical land-use change: greenhouse gas emissions from biomass burning, decomposition and soils in forest conversion, shifting cultivation and secondary vegetation. Climatic Change 46, 115–158.

Fedalto, L.C., Mendes, I.C.A., Coradin, V.T.R., 1989. Madeiras da Amazônia: descrição do lenho de 40 espécies ocorrentes na Floresta Nacional do Tapajós. Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis (IBAMA), Brasília, DF, Brazil, 156 pp.

França, M.B., 2002. Modelagem de biomassa através do padrão espectral no Sudoeste da Amazônia. Masters Thesis in Tropical Forest Science, Instituto Nacional de Pesquisas da Amazônia-Fundação Universidade Federal do Amazonas, Manaus, Amazonas, Brazil, 106 pp.

Hacke, U.G., Sperry, J.S., Pockman, W.T., Davis, S.D., McCulloh, K.A., 2001. Trends in wood density and structure are linked to prevention of xylem implosion by negative pressure. Oecologia 126, 457–461.

Heinsdijk, D., 1958. Report to the Government of Brazil on a forest inventory in the Amazon Valley, Part 3: Region between Rio Tapajós and Rio Madeira. FAO Report No. 969 and Part 4: Region between Rio Tocatins and Rios Guama and Capim. FAO Report No. 992. Expanded Technical Assistance Program (FAO/58/10/8131), Food and Agriculture Organization (FAO), Rome, Italy.

Higuchi, N., Carvalho Jr., J.A., 1994. Fitomassa e Conteúdo de Carbono de Espécies Arbóreas da Amazônia: Anais do seminário "Emissão x Sequestro de CO_2–Uma Nova Oportunidade para o Brasil," Companhia Vale do Rio Doce (CVRD), Rio de Janeiro, Brazil, pp. 127–153.

Higuchi, N., Santos, J., Ribeiro, R.J., Minette, L., Biot, Y., 1998. Biomassa da parte aérea da vegetação da floresta tropical úmida de terra-firme da Amazônia Brasileira. Acta Amazonica 28, 153–166.

Houghton, R.A., 2003. Why are estimates of terrestrial carbon balance so different? Global Change Biol. 9, 500–509.

Houghton, R.A., Lawrence, K.T., Hackler, J.L., Brown, S., 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. Global Change Biol. 7, 731–746.

Ilic, J., Boland, D., McDonald, M., Downes, G., Blakemore, P., 2000. Woody Density Phase 1—State of Knowledge. National Carbon Accounting System Technical Report 18, Australian Greenhouse Office, Canberra, Australia, 228 pp.

Kollmann, F.F.P., Côté Jr., W.A., 1968. Principles of wood science and technology solid wood, vol. 1. Springer-Verlag, New York, USA, 592 pp.

Magnago, H., Barreto, R.A.A., Pastore, U., 1978. Projeto RADAM-BRASIL. Folha SA.20. Parte IV–Vegetação, Departamento Nacional de Produção Mineral, Rio de Janeiro, Brazil, pp. 413–530.

Melo, J.E., Coradin, V.T.R., Mendes, J.C., 1990. Classes de densidade de madeira para a Amazônia Brasileira. Anais do Congresso Florestal Brasileiro 6, vol. 3, Campos do Jordão, São Paulo, Sociedade Brasileira de Silvicultura, São Paulo, SP, Brazil, pp. 695–699.

Muller-Landau, H.C., 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. Biotropica 36 (1), 20–32.

Oliveira, A.C.A., 2000. Efeitos do Bambu *Guadua weberbaueri* Pilger sobre a Fisionomia e Estrutura de uma Floresta no Sudoeste da Amazônia. Masters Thesis in Ecology, Instituto Nacional de Pesquisas da Amazônia–Fundação Universidade Federal do Amazonas, Manaus, Amazonas, Brazil, 103 pp.

Pinto, A.C.M., Higuchi, N., Iida, S., dos Santos, J., Ribeiro, R.J., Rocha, R.M., da Silva, R.P., 2003. Padrão de distribuição espacial de espécies florestais que ocorrem na região de

Manaus-AM. In: Higuchi, N., dos Santos, J., Sampaio, P.T.B., Marenco, R.A., Ferraz, J., de Sales, P.C., Saito, M., Matsumoto, S. (Eds.), Projeto Jacarandá, Fase II: Pesquisas florestais na Amazônia Central. CPST/INPA, Manaus Amazonas, Brazil 252 pp.

Pires J.M., 1978. The forest ecosystems of the Brazilian Amazon: description, functioning and research needs. In: United Nations Educational. Scientific and Cultural Organization (UNESCO)/ United Nations Environmental Programme (UNEP)/Food and Agriculture Organization of the United Nations (FAO), Tropical Forest Ecosystems: A State of Knowledge Report, UNESCO, Paris, France, pp. 607–627.

Prance, G.T., Rodrigues, W.A., da Silva, M.F., 1976. Inventário florestal de um hectare de mata de terra-firme, Km 30 da Estrada Manaus-Itacoatiara. Acta Amazonica 6, 9–35.

Putz, F.E., Coley, P.D., Lu, K., Montalvo, A., Aiello, A., 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Can. J. Forest Res. 13, 1011–1020.

Reyes, G., Brown, S., Chapman, J.C., Lugo, A.E., 1992. Wood densities of tropical tree species. USDA Forest Service. General Technical Report S0-88. Southern Forest Experiment Station, New Orleans, LA, USA, 15 pp.

Ribeiro, J.E.L. da S., Hopkins, M.J.C., Vicentini, A., Sothers, C.A., Costa, M.A. da S., de Brito, J.M., de Souza, M.A.D., Martins, L.H.P., Lohmann, L.G., Assunção, P.A. C.L., Pereira, E. da C., da Silva, C.F., Mesquita, M.R., Procópio, L.C., 1999. Flora da Reserva Ducke: guia de identificação das plantas vasculares de uma floresta de terra-firme na Amazônia Central. INPA/DfID, Manaus, Amazonas, Brazil, 816 pp.

Rocha, J.S., 1994. A segurança de estruturas de madeira determinada a partir da variabilidade da densidade básica e de propriedades mecânicas de madeiras amazônicas. Masters Thesis in Forest Sciences. Escola Superior de Agricultura "Luis de Queirroz", Universidade de São Paulo (ESALQ/USP), Piracicaba, São Paulo, Brazil, 141 pp.

Rueda, R., Williamson, G.B., 1992. Radial and vertical wood specific gravity in *Ochroma pyramidale* (Cav. ex Lam.) Urb. (Bombacaceae). Biotropica 24, 512–518.

Schnitzer, S., Dalling, J., Carson, W.P., 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. J. Ecol. 88, 655–666.

Silva, J.C., 1984. Parâmetros da densidade na qualidade da Madeira. Escola Superior de Agricultura "Luis de Queirroz", Universidade de São Paulo (ESALQ/USP), Piracicaba, São Paulo, Brazil, 82 pp.

Simpson, W., TenWolde, A., 1999. Physical properties and moisture relations of wood. Chapter. 3. In: Forest Products Laboratory. Wood Handbook-wood as an engineering material. Gen. Tech. Re FPL-GTR-113. U.S. Department of Agriculture, Forest Service. Forest Products Laboratory, Madison, WI, USA, 463 pp.

Suzuki, E., 1999. Diversity in specific gravity and water content of wood among Bornean tropical rainforest trees. Ecol. Res. 14, 211–224.

Ter Steege, H., Hammond, D.S., 2001. Character convergence, diversity, and disturbance in tropical rain forest in Guyana. Ecology 82, 3197–3212.

Trugilho, P.F., Silva, D.A., Frazão, F.J.L., Matos, J.L.M., 1990. Comparação de métodos de determinação de densidade básica em Madeira. Acta Amazonica 20, 307–319.

Vital, B.R., 1984. Métodos de determinação da densidade da Madeira, Boletim Técnico, 2, Sociedade de Investigações Florestais (SIF), Viçosa, Minas Gerais, Brazil, 21 pp.

Yamazaki, D.R., Costa, A.M.R., Azevedo, W.P., 1978. Projeto RADAMBRASIL, Folha SA.20, Parte III-Pedologia, Departamento Nacional de Produção Mineral, Rio de Janeiro, RJ, Brazil, pp. 247–410.

Wiemann, M.C., Williamson, G.B., 1988. Extreme radial changes in wood specific gravity in some tropical pioneers. Wood Fiber Sci. 20, 344–349.

Wiemann, M.C., Williamson, G.B., 1989. Radial gradients in the specific gravity of wood in some tropical and temperate trees. Forest Sci. 35, 197–210.

Wiemann, M.C., Williamson, G.B., 2002. Geographic variation in wood specific gravity: effects of latitude, temperature and precipitation. Wood Fiber Sci. 34, 96–107.

Woodcock, D.W., 2000. Wood specific gravity of trees and forest types in the southern Peruvian Amazon. Acta Amazonica 30, 589–599.