Nogueira, E.M., P.M. Fearnside, B.W. Nelson & M.B. França. 2007. Wood density in forests of Brazil's 'arc of deforestation': Implications for biomass and flux of carbon from land-use change in Amazonia. *Forest Ecology and Management* (in press).

DOI: 10.1016/j.foreco.2007.04.047

ISSN: 0378-1127

Wood density in forests of Brazil's 'arc of deforestation': Implications for biomass and flux of carbon from land-use change in Amazonia.

Euler Melo Nogueira[1]
Philip Martin Fearnside[2*]
Bruce Walker Nelson[2]
Mabiane Batista França[1]

[1] Graduate Program in Tropical Forest Science, National Institute for Research in the Amazon - INPA, Av. André Araújo, n° 2936, C.P. 478, CEP 69 011-970, Manaus, Amazonas, Brazil.

[2] Department of Ecology, National Institute for Research in the Amazon - INPA, Av. André Araújo n° 2936, C.P. 478, CEP 69 011-970, Manaus, Amazonas, Brazil.

* Corresponding author: Tel.: +55 92 3643 1822; Fax +55 92 3642 8909
E-mail address: pmfearn@inpa.gov.br

14 February 2007
23 April 2007
25 April 2007
2 June 2007

Abstract

Wood density is an important variable in estimates of forest biomass and greenhouse-gas emissions from land-use change. The mean wood density used in estimates of forest biomass in the Brazilian Amazon has heretofore been based on samples from outside the "arc of deforestation", where most of the carbon flux from land-use change takes place. This paper presents new wood density estimates for the southern and southwest Brazilian Amazon (SSWA) portions of the arc of deforestation, using locally collected species weighted by their volume in large local inventories. Mean wood density was computed for the entire bole, including the bark, and taking into account radial and longitudinal variation. A total of 403 trees were sampled at six sites. In the southern Brazilian Amazon (SBA), 225 trees (119 species or morpho-species) were sampled at four sites. In eastern Acre state 178 trees (128 species or morpho-species) were sampled at breast height in two forest types. Mean basic density in the SBA sites was 0.593 ± 0.113 (mean ± 1 sd; n = 225; range 0.265-0.825). For the trees sampled in Acre the mean wood density at breast height was 0.540 ± 0.149 (n=87) in open bamboo-dominated forest and 0.619 ± 0.149 (n=91) in dense bamboo-free forest. Mean wood density in the SBA sites was significantly higher than in the bamboo dominated forest but not the dense forest at the Acre site. From commercial wood inventories by the RadamBrasil Project in the SSWA portion of the arc of deforestation, the wood volume and wood density of each species or genus were used to estimate average wood density of all wood volume in each vegetation unit. These units were defined by the intersection of mapped forest types and states. The area of each unit was then used to compute a mean wood density of 0.583 g cm^{-3} for all wood volume in the SSWA. This is 13.6% lower than the value applied to this region in previous estimates of mean wood density. When combined with the new estimates for the SSWA, this gave an average wood density of 0.642 g cm^{-3} for all the wood volume in the entire Brazilian Amazon, which is 7% less than a prior estimate of 0.69 g cm^{-3}. These results suggest that current estimates of carbon emissions from land-use change in the Brazilian Amazon are too high. The impact on biomass estimates and carbon emissions is substantial because the downward adjustment is greater in forest types undergoing the most deforestation. For 1990, with 13.8×10^3 km^2 of deforestation, emissions for the Brazilian Amazon would be reduced by $23.4\text{-}24.4 \times 10^6$ Mg CO_2-equivalent C/year (for high- and low-trace gas scenarios), or 9.4-9.5% of the gross emission and 10.7% of the net committed emission, both excluding soils.

Keywords: Amazon forest; Carbon flux, Forest biomass, Global warming; Wood density.

Introduction

The largest error in carbon balance in the tropical region results from uncertainty in aboveground forest biomass (Houghton, 2003a, 2005; Houghton et al., 2001). Wood density is an important variable for improving estimates of carbon stocks and of greenhouse-gas emissions from deforestation or forest converted to other uses (Baker et al., 2004; Chave et al., 2005; Fearnside, 1997; Nogueira et al., 2005; Malhi et al., 2006). This is because wood density is used when inventories of bole volume are converted to biomass (Brown et al., 1989; Brown, 1997; Fearnside, 2000a,b; Houghton et al., 2001). Furthermore, improved estimates of wood density would enhance understanding of changes in carbon stocks before and after land-use change.

Emissions of carbon from Amazon deforestation are determined by the biomass of those forests currently being deforested, not by the average biomass of the region. The portion of the Brazilian Amazon responsible for most of the emission is the ‘arc of deforestation,’ encompassing the southwestern, southern and eastern edges of the basin (Brazil, INPE, 2002). Though numerous forest inventories of wood volume of large trees have been conducted in the southern and southwestern Brazilian Amazon (Brazil, Projeto RadamBrasil, 1980; see Figure 1), data are scarce for wood density directly measured in the arc of deforestation. Consequently, recent studies of the stock and emission of carbon for Amazonia (Achard et al., 2004; Brown, 1997; Fearnside, 2000a,b; Fearnside and Laurance, 2003, 2004; Houghton et al., 2001) have been based on wood density from published lists that were obtained in parts of the Amazon region outside of the arc of deforestation (Brown et al., 1989; Fearnside, 1997).

The use of wood-density data obtained outside the arc of deforestation could result in overestimates because soils are more fertile along the southern and southwestern edges of the basin (Brazil, Projeto RadamBrasil, 1976, 1978, 1980; Brown and Prance, 1987, Fig. 2.1; Sombroek, 2000). Wood density has been shown to vary inversely with soil fertility (Baker et al., 2004; Muller-Landau, 2004; Parolin and Ferreira, 1998; ter Steege et al., 2006). Other factors, such as natural disturbance frequency, understory light availability, humidity and climatic life zones, may affect growth strategies and therefore wood density (Chudnoff, 1976; Wiemann and Williamson, 2002; Woodcock and Shier, 2003). In the southern and southwest Brazilian Amazon (SSWA), open forests naturally disturbed by abundant climbing bamboos or lianas tend to have more fast-growing trees with lighter wood (Nelson et al., 2006). These forests occupied 400,000 km^2 of the SSWA prior to their partial deforestation (Brazil, IBGE, 1997; Nelson, 1994). Open forest types also have fewer stems per hectare, more canopy gaps and consequently higher light penetration as compared with dense forest (Veloso et al., 1991). These forests also have less annual precipitation and a longer dry season than the central and western portions of the Amazon (Brazil, ANA/SIH, 2006).

Another problem with existing wood-density estimates is that many of the wood-density values available for Amazonia were not intended for use in biomass estimates. Methods differ as to the radial and longitudinal position of the sample within the bole and in the way that mass and volume of the wood sample were determined. Most methods lead to an overestimate of mean wood density of the whole tree (Fearnside, 1997; Nogueira et al., 2005). Many of the wood-density datasets used by Fearnside (1997) for biomass estimates lacked a correction for radial variation. This error was calculated to be -5.3% for dense forest in central Amazonia (Nogueira et al., 2005). In addition, some wood-density data also do not account for decreasing density with height along the bole.

The question is examined of whether the average wood density currently used in carbon-emissions estimates is suitable for the SSWA. This paper uses two new datasets of wood density by taxon.

Materials and Methods

Collection sites

The locations of all sites are shown in Figure 1. Felled trees were always from primary forest, or forests without visible signs of disturbance. It should be noted that, while forests like those studied are known as "primary forests," all forests in Amazonia may be affected by past disturbances from indigenous peoples and extreme climatic events (Clark, 2007). Stands with any evidence of past logging were avoided. The dataset representing the southwest Amazon is comprised of 178 trees from open bamboo-dominated and from dense forest in eastern Acre state (França, 2002). The southern Amazon dataset is from four sites in northwestern Mato Grosso and southern Pará, totaling 225 trees. These four sites were located in open rain forest dominated by vines or by large palms. At all sites the altitude is 200 to 300 m above mean sea level. Dense forest and seasonal forest occur in close proximity to the southern Amazon sites, while savannas occur in more elevated areas (Brazil, Projeto RadamBrasil, 1980). Species lists for both regions are provided in the Appendix.

[Figure 1]

The Acre site is 25 km west of the town of Sena Madureira. Approximately equal numbers of trees were sampled from dense forest (91 trees) and from open bamboo-dominated forest (87 trees). Two of the southern Amazon sites were located in the county of Juruena in northwestern Mato Grosso (44 trees sampled). A third site was in the county of Cotriguaçu (116 trees) also in northwestern Mato Grosso. The fourth was in the county of Novo Progresso in southern Pará (65 trees) near the BR-163 Highway.

Soil under both forest types in Acre is relatively fertile vertisol, or vertic latosol with high concentrations of cations (Vidalenc, 2000). The sites in Mato Grosso state are on xanthic or orthic ferralsols and ferralic arenosols. At the site in southern Pará the soils are orthic acrisols and ferralsols on granite-shield uplands (FAO, 1988; Sombroek, 2000).

The climate in eastern Acre state is tropical humid with 2250 mm of annual rainfall and 4 months with less than 100 mm per month. At the Mato Grosso sites the predominant climate is also tropical humid with 2075 mm average annual precipitation and six-months with monthly precipitation below 100 mm (Brazil, ANA/SIH, 2006). At the southern Pará site the average annual precipitation is 2280 mm with three months of precipitation below 100 mm per month (Brazil, ANA/SIH, 2006). At all sites, the mean annual temperature ranges from 19.5 to 31.5 ^{o}C (Brazil, INMET, 2006).

Wood samples and density determination

Samples were taken from trees felled at random within each size class, starting at 5 cm DBH. However, quotas were established for each size class based on the proportion that class contributes to basal area in local forest inventories. Measurements of diameter were made of DBH (1.30 m above the ground or above the buttresses, when present), total height and height of the commercial bole. Botanical samples were collected for all trees and identified by expert parabotanists at the herbarium of the National Institute for Research in the Amazon (INPA).

A wood disk of constant thickness (~3 cm) was taken at breast height or from the top of the stump (at the Juruena site, due to requirements of the logging company), even in the presence of buttresses. At the two Acre sites (França, 2002) disks were taken only at breast height. At the four southern Amazon sites a second disk came from the top of the commercial bole, below the thickening associated with the base of the first large branch. In all cases, possible radial variation in density was compensated by obtaining a full slice of even thickness, including the bark. Basic wood density was determined for the entire disk or for a sector (like a pie slice) obtained from it. If the disk had eccentric growth rings the sector was obtained from a region midway between the areas with the narrowest and the widest rings. If a tree had buttresses and channels (flutations) at breast height, the sector included part of a buttress and part of a channel. The sector was positioned to provide approximate proportional representation of the cross-sectional areas of buttresses and channels in the disk as a whole. The same methodology was applied in studies in central Amazonia (Nogueira et al., 2005), and it is believed to provide an appropriate protocol for future density studies. At the southern Amazon sites, samples of the heartwood were also taken when present. The heartwood samples were taken close to the center of the disks.

In this study, wood density is defined as "basic density" or "basic specific gravity". This is the ratio between the oven dry mass and the fresh volume of the green wood (Fearnside, 1997; Nogueira et al., 2005). To avoid volume shrinkage, fresh disks and sectors were kept in the shade and the green mass and volume were determined on the day of felling. Green mass was obtained with a battery-operated scale with 1% accuracy and 2000 g capacity. The green volume was determined by displacing water in a container placed on the same scale. The specimen was impaled on a thin needle and forced underwater. The increase in weight of the container (grams) corresponds to the volume of the immersed specimen in cm^3 (ASTM 2002). Volume was determined after first wetting the specimen to fill exposed pores. For the dry weight of each sample a vented electric oven was used at 103 ^oC (ASTM, 2002). The samples were considered completely dry when the weight was stable for three consecutive days. For all trees mean basic density of the bole was determined as the arithmetic mean of the density at breast height (or top of the stump for the Juruena site) and at the top of the bole. A taper-adjusted mean density was not used because it did not differ significantly from the arithmetic mean (Nogueira et al., 2005).

Average wood density by forest type in the SSWA

Two regional tables of mean wood density by taxon (species or genus) were developed, one for the southwest and another for the southern Brazilian Amazon. Names were checked using Ribeiro et al. (1999) and/or the Missouri Botanical Garden Tropicos database (http://mobot.mobot.org/W3TSearch/vast.html). All values are means of the bole, including bark, sapwood and heartwood. Because no disk was collected from the top of the bole in Acre, for that dataset a correction of -4.2% was applied to adjust for decrease in density with height along the bole. This was the correction found at the Mato Grosso and Pará sites and is similar to the value of -4.3% reported in Nogueira et al. (2005) for dense forest of the Central Amazon.

The wood density values from the 119 tree species or morpho-species felled in Mato Grosso and Pará were applied to the "SC.21 Juruena" and "SC.20 Porto Velho" RadamBrasil inventory sets (Brazil, Projeto RadamBrasil, 1976, 1978, 1980). The 128 species or morpho-species felled in Acre were used for the "SC.19 Rio Branco" inventory set. When correspondence was not possible at the species level, genus-level wood density was used. The geographic area of these three inventory sets is shown in Figure 1. Each RadamBrasil publication provides wood volumes by taxon (genus or species) within each forest type within a 4 × 6 degree area. The volume of each matched species or genus was used to estimate the average wood density of all the wood volume in vegetation units that are defined by the intersection of forest types and states. These "vegetation units" are similar to the "ecoregions" defined by Fearnside and Ferraz (1995) using a less-detailed vegetation map, and are useful for studies in conjunction with Brazil's deforestation monitoring program, which releases estimates by state. About 36% of the wood volume reported by RadamBrasil could be matched to a genus or species collected in this study for the RadamBrasil map sheets in which the plots were located. If only the vegetation units of our sample plots are considered (i.e., dense and open submontane rain forest in Mato Grosso), the percentage of the volume matched to genus or species increases to 42% (Table 2). The average wood density of each vegetation unit was based on the local volumes of these matched taxa. This same average was applied to the unmatched taxa. The mean wood density for the entire SSWA portion of the arc of deforestation was then calculated by taking an average of the values for all vegetation units, weighted by the relative geographic area of each vegetation unit.

Adjustments to wood density, biomass and carbon emission estimates for the entire Brazilian Amazon

A new average wood density was computed for all the wood volume in the entire Brazilian Amazon using all of the Radam inventory sets. For the three inventories in the SSWA area, the procedure was as described above. The same procedure was used in the remainder of the Brazilian Amazon, but based on other wood densities previously reported by Fearnside (1997). These other density values, applied outside the SSWA, were reduced by 5.3% because, in the majority of these other datasets, samples were taken from or near the heartwood (as in the samples of Brazil, IBDF, 1981; 1983; 1988). No correction for variation along the bole was applied because the majority of the samples (i.e., the IBDF data) were taken at random along the bole with sampling probability at each point on the bole adjusted for the effect of tapering on wood volume.

Other corrections were not applied, such as those for samples whose green volume was estimated after soaking in water. This can result in overestimated density when the samples are re-hydrated after drying and underestimation when hydrated to saturation without prior drying. The Fearnside (1997) wood densities were originally obtained from Amorim (1991), Brazil, IBDF (1981, 1983, 1988), Brazil, INPA (1991), Brazil, INPA/CPPF (unpublished [1981]), Chudnoff (1980), do Nascimento (1993) and Reid, Collins and Associates (1977). Other more recent datasets available for Amazonia were not used because the mean densities currently used in biomass and emissions estimates were based on this Fearnside dataset.

The new and the old adjusted wood densities were obtained for all the volume of wood in each of the mapped forest types in each of the RadamBrasil inventories across all of the Brazilian Amazon. When weighted by the area and deforestation rates of each vegetation unit, this produced corrected estimates of aboveground live biomass and proportional corrections to carbon emissions estimates in the region.

Results

Mean basic density of the bole, vertical and radial variation and relationship of bole density to DBH and total height.

The mean basic density of the bole did not differ significantly between southern Amazon sites (Figure 2A; Table 1). The mean density of the bole at the Juruena site was

0.591 ± 0.118 (mean ± 1 sd.; n = 44). At the Cotriguaçu site it was 0.584 ± 0.106 (n = 116) and at the Novo Progresso site it was 0.610 ± 0.121 (n = 65) (Table 1). In the full southern Amazon dataset, the mean basic density of the bole was 0.593 ± 0.113 for the 225 felled boles. These represent 119 species or morpho-species and 19 taxa identified only to genus-level. These species and genera belong to 41 different angisoperm families.

In the southwestern Amazon sites (Acre state) the wood density differs significantly (Figure 2B; Tukey test, p=0.000). In open bamboo-dominated forest the mean basic density at breast height was 0.540 ± 0.149 (n = 87; 95% CI 0.508 – 0.572). In dense forest mean basic density was 0.610 ± 0.149 (n = 91; 0.588 – 0.650). Only mean basic density in the open bamboo-dominated forest at the Acre site differed from those at the Southern Amazon sites (Tukey test, p=0.000).

[Figure 2]
[Table 1]

At all southern Amazon sites the basic density at the base of the bole was higher than at the top of the bole by 8-10% (Fig. 3). The basic density at the base of the bole at the Juruena site was 0.621 ± 0.121 (n = 47), 9.9% higher than at the top of the bole -- 0.565 ± 0.124 (n=46) -- and 5.1% higher than the mean for the bole. At the Cotriguaçu site the basic density at breast height (0.608 ± 0.122; n = 126) was 9.2% higher than at the top of the bole, 0.557 ± 0.100 (n = 125), and 4.1% higher than the mean for the bole. At the Novo Progresso site the difference between wood density at breast height and at the top of the bole was 8.7%; the value was 0.636 ± 0.131 (n = 65) at breast height and 0.585 ± 0.116 (n = 65) at the top of the bole. The difference between density at breast height and the mean for the bole was similar to the difference at others sites: 4.3%. Considering the arithmetic mean of all trees irrespective of the number of trees at each site, the mean bole density was ~4.2% lower than then mean at breast height. More details concerning variation of the density with height of the bole are given in Table 1 and Figure 3.

[Figure 3]

Heartwood basic density was higher than basic density in whole disks with bark (Figure 4; Table 1). The heartwood density was 0.650 ± 0.141 (n=40) at the base of the bole and 0.610 ± 0.119 (n = 41) at the top of the bole. The mean heartwood basic density of the bole was 0.632 ± 0.125 (n = 38). Considering the same trees (n=30), mean heartwood density of the bole was 3.3% higher than mean basic density of the entire bole; the values for the mean differ statistically (paired t-test; p = 0.036).

Considering all trees in the southern Amazon sites, there was no correlation between mean wood density of the entire bole and DBH (Fig. 5A) or total height (Fig. 5B). At the two sites in Acre, there was no relationship between a tree's basic density at breast height and it's diameter or height.

For the southern Amazon trees, wood basic density (mean of the bole) was separated into three classes (≤0.50 g.cm^{-3}, 0.50 -0.70 g.cm^{-3} and ≥0.70 g.cm^{-3}). Species were predominantly light (21%) and medium (62%), only 17% being heavy. Considering all species and morpho-species, means were 28% light, 59% medium and 13% heavy. If classification of the woods in heavy, medium or light is based on interval limits of ≤0.50, 0.50 - 0.72 and ≥0.72, in accord with the procedures adopted by Ibama (see Brazil, de Souza et al., 2002; Melo et al., 1990; Nogueira et al., 2005); the distribution across all species and morpho-species changed to 63% (medium) and 9% (heavy).

[Figure 4]
[Figure 5]

Wood basic density by forest type in the SSWA portion of the arc of deforestation

Use of the wood-density data described in Fearnside (1997) for estimating mean wood density for the entire Amazon region results in overestimates of the mean wood density for the forest types that occur in the arc of deforestation (Fig. 6 A-C).

Using the new data sampled in Mato Grosso and Pará states as described above, the mean wood densities for all forest types (weighted by species volume based on the two RadamBrasil inventories: Folhas SC.21 Juruena and SC.20 Porto Velho) were lower than the means found by Fearnside (1997, his Tables 6 and 7) by amounts ranging from 8 to 22% (Table 2, Fig. 6A-C). The average difference for all forest types in these two RadamBrasil inventory areas was 12.5% (Table 2). Including the new Acre wood densities with the 4.2% correction for height along the bole applied to the "SC.19 Rio Branco" RadamBrasil inventory, the overall reduction of wood density from the prior estimate of Fearnside (1997) for the three RadamBrasil inventory areas comprising the southern and southwest Amazon was 13.6%. This percentage is the overestimate in wood density for a large portion of the 'arc of deforestation' without weighting by the area of each forest type.

[Figure 6]
[Table 2]

Density and biomass adjustments for the entire Brazilian Amazon

Making the downward correction of 13.6% for density of wood in the SSWA, and the downward adjustment of 5.3% to density values used by Fearnside (1997) for the rest of the Brazilian Amazon, the new mean for Brazilian Amazonia as a whole is 0.642, a value 7% lower than the value of 0.69 found by Fearnside (1997; Table 7). In Table 3 new means for wood density are shown by state and forest type, including all corrections. When weighted by the volume of above-ground live vegetation deforested in 1990 in each forest type (as described in Table 7 in Fearnside, 1997), the mean density is reduced to 0.631, or a further reduction of 1.7%.

Discussion

Environmental conditions and variation in wood density

Studies have generally assumed that variation in wood density is purely driven by variation in species composition. Although there are important environmental influences, mean wood density is conserved phylogenetically (Chave et al., 2006). The range of wood density exhibited by any given species being likely to have genetically determined components associated with intrinsic growth allometry and other architectural features of the species (Meinzer, 2003; Sterck et al., 2006; van Gelder et al., 2006; Wright et al., 2003).

The variation in mean forest wood density has been analysed by tree species composition (ter Steege et al., 2006; Terborgh and Andersen, 1998). Thus, in southern Amazonia one cause of lower wood density in the forests will be the increasing abundance of low wood-density species (ter Steege et al., 2006), with greater frequency of families that have light wood. In regions like southwestern Brazilian Amazonia, abundant gaps in open forest are created by vines or climbing bamboo favoring fast-growing tree species with low wood density (Putz et al., 1983; Nelson et al., 2006). In Acre, wood density in one open bamboo-dominated forest averaged 0.51, versus 0.60 in neighboring forest without bamboo (França, 2002). Bamboo also reduced the number of large trees per hectare. With lower wood density and fewer large trees, the bamboo-dominated forest had half the biomass of the dense forest (França, 2002; Nelson et al., 2006).

It is thought that variation in certain environmental factors may drive these patterns in composition and wood density. Wood density has been demonstrated to vary with different environmental conditions. Such factors as soil fertility (Baker et al., 2004; Muller-Landau, 2004), and light conditions (van Gelder et al., 2006) are recognized as affecting wood density at the stand level. The intensity of solar radiation is higher but more seasonal at the southern margins of Amazonia, where the climate shifts towards non-tropical conditions and there are long dry seasons (Malhi et al., 2004). Due to the long dry period in southern Amazonia, the degree of seasonality and the magnitude of resulting drought stress could affect wood density. This is because wood density determines the variation in a suite of characteristics related to efficiency and integrity of xylem water transport, regulation of leaf water balance, and avoidance of turgor loss (Meinzer, 2003; Hacke et al., 2001). The gain in cavitation resistance with increasing wood density appears to be associated with a cost in terms of reduced hydraulic conductivity. Thus, for plants growing in arid environments it is reasonable to suggest that the increased cavitation resistance is an advantageous feature, but, despite potential environmental influences, a broad range of wood densities co-exist in both arid and humid environments. The accumulating evidence suggests that within the tropics, seasonality and rainfall (Borajas-Morales, 1987; Wiemann and Williamson, 2002) do not explain large-scale regional variation in wood density (Baker et al., 2004; Muller-Landau, 2004), although this feature constrains physiological options related to plant water economy, leading to broad functional convergence (Meinzer, 2003).

Therefore, ideally it is important to sample wood density data in the study area, rather than simply using published values of species averages. The mean wood density at the species level obtained from two datasets with identical sampling methods (dense forest in central Amazonia, Nogueira et al., 2005 and open forest in southern Amazonia, new dataset reported in this study) allows a comparison of the mean wood density of the bole between locations for two species. For *Brosimum lactescens* (S. Moore) C.C. Berg (Moraceae) in central Amazonia the mean wood density of the bole was 0.708 (n = 2) versus 0.620 (n = 8) in southern Amazonia. Wood density of *Pouteria anomala* (Pires) T.D. Penn. (Sapotaceae) was 0.725 (n = 4) in central Amazonia and 0.680 (n = 4) in southern Amazonia. In spite of phylogenetic conservatism in wood density, these instances suggest an important effect of environmental conditions such as soils. They also suggest that comparative studies employing a uniform methodology between various species in different soil and forest types could enhance knowledge of the separate effects of the environmental factors at a finer scale.

Analysis of the responses to the environment in wood density and in patterns of species composition may help define the roles of these two effects in gradients of wood density in Amazonia (Malhi et al., 2006; Baker et al., 2004). The results of this paper provide wood densities specific to southern Amazonia, where the dry period is long (six months with precipitation below 100 mm: Brazil, ANA/SIH, 2006). It is precisely in these portions of Amazonia that there has been a major gap in the datasets used in previous studies that have not found wood density to be correlated with climatic variables (Malhi et al., 2004, 2006).

Mean wood density: radial variation and variation along the length of the bole

The changes in density along the bole and in the radial direction for open forest in southern Amazonia are similar to those found in dense forest in central Amazonia (Nogueira et al., 2005). The average radial variation (difference between heartwood and full disk densities) is 3.3% here and 5.3% in central Amazonia. Variation along the length of the bole (difference between full disk at breast height and density of the entire bole) was 4.2% for southern Amazonia, and 4.3% in central Amazonia. Due to these variations, the use of the previously published datasets on wood density obtained by different methodologies can partially explain differences between means reported by various other authors, including the accuracy of recent estimates. The major wood-density datasets available for Amazonia were not designed for estimating tree biomass. Data are scarce for wood density obtained from samples adequately positioned in the bole and with dry weight and volume determined by appropriate methods (see Nogueira et al., 2005, pp. 268-269 and Fearnside, 1997).

Normalization of the wood density data may be performed using linear models as suggest by Reyes et al. (1992). Normalization can also be done using equations for moisture content as proposed by Brotero (1956) and Oliveira (1981), as used in IBAMA lists, or with Sallenave's (1971) equation used by Chave et al. (2006).

Correction for the position of the samples in the bole can be done using linear models developed by Nogueira et al. (2005) or using simple percentage corrections. However, theses models were not tested for open forest in the southern Amazon. Linear models have the convenience of only requiring transformation of the independent variable, in this case the wood density. However, it is not possible to use the model for all corrections. For instance, the model was not tested by direct comparison of cores taken with increment borers with full disks including bark, but a large number of recent studies have used samples obtained using increment borers (DeWalt and Chave, 2004; King et al., 2006; Muller-Landau, 2004; Woodcock, 2000; Woodcock and Shier, 2003). The large wood-density dataset for Brazilian Amazonia (Brazil, IBDF, 1981, 1983, 1988) is difficult to standardize adequately for accurate estimates of the whole bole (*i.e.*, with corrections for radial variation and variation along the bole). It is important to focus attention on methods used for the weight and volume measures, such as time and temperature of drying and proper use of the water-displacement method (Trugilho et al., 1990). While errors from these factors may be ignored for purposes that do not require a high level of accuracy in estimates of mean density, the errors are too large for biomass estimates in tropical forests. This is because a difference of few percent in mean wood density can imply large errors in calculations of the carbon balance.

Wood basic density by forest type in the arc of deforestation, southern and southwestern portions of Brazilian Amazonia: Adjustments for biomass and carbon emission estimates

The estimates of wood density for the Amazon region have been improved by recent studies (Baker et al., 2004; Chave et al., 2006; Nogueira et al., 2005). The recent estimates are significantly different from values reported for specific regions, which were used in previous calculation of the mean wood density for Brazilian Amazonia as a whole. The value of 0.69 g cm^{-3} had been used in a number of carbon emission and biomass estimates (Brown et al., 1989; Brown, 1997; Houghton et al., 2001) and is based on Brown et al. (1989) and Fearnside (1997). In Fearnside (1997) the values that were used in each region were weighted by area of forest type. The comparison of the values used in calculating the 0.69 mean with recent estimates reinforces the suggestion of an overestimate in the mean wood density for Brazilian Amazonia (Nogueira et al., 2005). For instance, the mean estimate for dense forest (0.66) by Chave et al. (2006) is similar to the mean of 0.67 found by Nogueira et al. (2005), and both are lower than the 0.70 value derived by Fearnside (1997) for the same forest type. For southern and southwestern Amazonia, the present study found a mean of ~0.58, similar to the 0.60 found by Chave et al. (2006) for southwestern Amazonia and also lower than the values in Fearnside (1997). The mean wood density for 2456 tree species from Central and South America by Chave et al. (2006) was 0.645 g cm^{-3}. This is similar to the value of 0.642 g cm^{-3} (Table 3) found in this paper for the whole of Brazilian Amazonia obtained by updating the values in Fearnside (1997), using the inventory volume of each taxon and the area of each forest type. The mean wood density reported in this paper was obtained from a substantially smaller list of wood densities by taxon than that of Chave et al. (2006). However, the two new datasets presented here were directly sampled in the southern and southwestern Amazon and represent the entire bole. Furthermore, this paper made adjustments for radial variation to the other data used in Fearnside (1997).

Because of the need for assessing the consistency of the means obtained using the new dataset for SSWA and the França (2002) dataset for Acre, means were compared only for species that were coincident between the Fearnside (1997) dataset and the new southern Amazon or southwest Amazon datasets described here. The column "test" in Table 2 shows that the results are similar, with different percentage reductions at the species level. With the exception a few species, the dataset used by Fearnside (1997) for the large RadamBrasil inventories has a tendency to overestimate wood density (Figure 6 A-C).

A wide range of estimates have been made of carbon emissions from land-cover change in the tropics (Achard et al., 2002, 2004; DeFries et al., 2002; Fearnside, 2000a,b; Houghton, 2003a, b, 2005; McGuire et al., 2001). The results of the present study imply a downward adjustment of all estimates in parallel. Consequently there will be little effect on the relative differences between the various previous biomass and carbon emissions estimates for Amazonia (the effect is not zero because only values for primary forest biomass are affected, not those for the secondary forests whose growth counterbalances part of the gross emission). The reduction in net committed emissions is large because it applies to two major types forest undergoing deforestation in recent years (see Brazil, INPE, 2006; Houghton et al., 2001). The reduction of 23.4-24.4 × 10^6 Mg of CO_2-equivalent C/year for 1990 for low- and high-trace gas scenarios, respectively is sufficiently large to be significant for the global carbon balance. Considering living and dead biomass only (i.e., ignoring soils, cattle, periodic reburning and other emissions sources), this reduction represents 9.4-9.5% of the gross emission, or 10.7% of the net committed emission as calculated by Fearnside (2000a, with corrections for form factor and hollow trees as described in Fearnside and Laurance, 2004). For estimates (Fearnside, 2007) that include wood-density adjustments based on the Central Amazon data of Nogueira et al. (2005), the SSWA dataset in the present paper reduces estimated 1990 emissions by 4.1% for gross emissions and 4.3% for net committed emissions. The corrected gross emission for 1990 is 247.7-257.5 × 10^6 Mg of CO_2-equivalent C/year, while the net committed emission is 218.1-227.8 × 10^6 Mg of CO_2-equivalent C/year for biomass emissions only, and 230.0-239.7 × 10^6 Mg of CO_2-equivalent C/year including soils and other sources. Deforestation in 1990 (the standard base year for national inventories under the United Nations Framework Convention on Climate Change) was 13.8 × 10^3 km^2 (in primary forest only, not counting clearing of savannas or re-clearing of secondary forests).

In spite of this new SSWA dataset and the recent studies with improved estimates, Fearnside's (1997) argument is still valid: there is a need to expand the dataset on wood density so that it is better distributed across the Amazon region. It is particularly important to expand the number of the collections in regions undergoing deforestation.

Conclusions

This study suggests that the mean wood density values for the whole Amazon region that have been widely used in biomass estimates were overestimated, probably because they were obtained using datasets with uncertainties in methodology and that were restricted as to forest type. The absence of a wood-density dataset directly sampled in the forest type undergoing the most rapid deforestation is an important cause of overestimated carbon emission for Brazilian Amazonia. Considering the forest type and species composition for forests in southern and southwestern Amazonia, a downward adjustment by 13.6% is needed relative to the mean used in many previous estimates. For the entire Brazilian Amazon, the mean wood density previously estimated by Fearnside (1997) should be lowered by 7%, to 0.642. For mean wood density weighted by the volume deforested in 1990 in each forest type the value is lowered by 9% to 0.631. The impacts on biomass estimates and on carbon emissions are substantial because the greatest adjustment is necessary exactly in the forest types undergoing the most deforestation. Estimates of net committed emissions for Brazilian Amazonia in 1990 that already include wood density values weighted by the volumes of each species present at the locations undergoing deforestation (*e.g.*, Fearnside, 2000a,b with adjustments described in Fearnside and Laurance, 2004) would be reduced by 10.7%: 23.4-24.4 × 10^6 Mg CO_2-equivalent C/year for high and low trace gas scenarios, respectively. The impact is sufficient to affect the global carbon balance. These new data will help to reduce uncertainties in various previous biomass studies and in the carbon budget for the Amazon.

Acknowledgments

We thank the National Council of Scientific and Technological Development - CNPq (350230/97-8; 465819/00-1; 470765/2001-1; 306031/2004-3; 557152/2005-4; 420199/2005-5), National Institute for Research in the Amazon-INPA (PPI 1-3160; PRJ05.57), and Foundation for the Support for Research of Amazonas State-FAPEAM. We thank J.B. Ferraz for allowing use of a car for field work. We are grateful to the São Nicolau Farm (ONF-Brasil) for access to their area and accommodation and food support. We are grateful to Rohden Indústria Lígnea Ltda for access to their forest and for field support. We thank Vicente DaRiva and Imbrózio for access to their land. We thank the Knidel and Cecílio families for accommodation in Juruena, and Alzelindo Chave Vieira, Leandro José, Joel Rodrigues do Carmo and José Carlos de Lima for work in the field. Two anonymous reviewers contributed helpful comments.

References

Achard, F., Eva, H.D., Mayaux, P., Stibig, H-J., Belward, A., 2004. Improved estimates of net carbon emissions from land cover change in the tropics for the 1990s. Global Biogeochemical Cycles 18, GB2008, DOI: 10.1029/2003GB002142.

Achard, F., Eva, H.D., Stibig H-J., Mayaux, P., Gallego, J., Richards, T., Malingreau, J.-P., 2002. Determination of deforestation rates of the world's humid tropical forests. Science 297, 999-1002.

Amorim, L.C., 1991. Variação da densidade básica no sentido radial em madeiras tropicais da Amazônia. Relatório Final. PIBIC/CNPq. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil. 124 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 Biology 10, 545-562.

Borajas-Morales, J., 1987. Wood density gravity in species from two tropical forests in Mexico. IAWA Journal 8, 143-148.

Brazil, ANA/SIH, 2006. Hidroweb, Sistemas de Informações Hidrológicas. Agência Nacional de Águas (ANA), Brasília, DF, Brazil. (http://www.hidroweb.ana.gov.br/hidroweb/). Accessed 24/02/2006.

Brazil, IBDF, 1981. Madeiras da Amazônia: características e utilização; Brazil, Floresta Nacional do Tapajós/Amazonian Timbers: characteristics and utilization; Tapajós National Forest, Vol. 1. Instituto Brasileiro de Desenvolvimento Florestal (IBDF), Brasília, DF, Brazil. 113 pp.

Brazil, IBDF, 1983. Potencial Madeireiro do Grande Carajás. Instituto Brasileiro de Desenvolvimento Florestal (IBDF), Brasília, DF, Brazil. 134 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, IBGE, 1997. Diagnóstico Ambiental da Amazônia Legal. Instituto Brasileiro de Geografia e Estatística (IBGE), Rio de Janeiro, Brazil. (CD-ROM using Vista-Map GIS, produced by IBGE/DGC/DERNA-DEGEO-DECAR).

Brazil, INMET, 2006. Instituto Nacional de Metereologia (INMET), Brasília, DF, Brazil http://www.inmet.gov.br. Accessed 25/02/2006.

Brazil, INPA, 1991. Catálogo de Madeiras da Amazônia. Instituto Nacional de Pesquisas da Amazônia (INPA), Coordenação de Pesquisas em Produtos Florestais (CPPF), Manaus, Amazonas, Brazil. 163 pp.

Brazil, INPE, 2002. Monitoring of the Brazilian Amazonian Forest by Satellite 2000-2001. Instituto Nacional de Pesquisas Espaciais (INPE), São José dos Campos, São Paulo, Brazil. http://www.inpe/br/informacoes_Eventos/amazonia.htm. Accessed 09/08/2006.

Brazil, INPE, 2006. Monitoramento da Floresta Amazônica Brasileira por satélite, Projeto PRODES. Instituto Nacional de Pesquisas Espaciais (INPE), São José dos Campos, São Paulo, Brazil. http://www.dpi.inpe.br/prodesdigital

Brazil, Projeto RadamBrasil, 1976. Folha SC 19, Rio Branco. Levantamento de Recursos Naturais. Departamento Nacional de Produção Mineral. Rio de Janeiro, Brazil. Vol. 12. 464 pp.

Brazil, Projeto RadamBrasil, 1978. Folha SC.20, Porto Velho. Levantamento de Recursos Naturais. Departamento Nacional de Produção Mineral. Rio de Janeiro, Brazil. Vol. 16. 668 pp.

Brazil, Projeto RadamBrasil, 1980. Folha SC.21, Juruena. Levantamento de Recursos Naturais. Departamento Nacional de Produção Mineral. Rio de Janeiro, Brazil. Vol. 20. 460 pp.

Brotero, F.A., 1956. Métodos de ensaios adotados no IPT para o estudo de madeiras nacionais. Boletim 31, 2$^{a.}$ edição.Instituto de Pesquisas Tecnológicos (IPT), São Paulo, Brazil. 28 pp.

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

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

Brown, K.S.Jr, Prance, G.T., 1987. Soils and vegetation. In: Biogeography and Quaternary History in Tropical America (eds. Whitmore TC, Prance GT), pp. 19-45, Clarendon Press, Oxford, U.K.

Chave, J., Andalo, C., Brown, S., Cairns, M.A., Chambers, J.Q., Eamus, D., Fölster, H., Fromard, F., Higuchi, N., Kira, T., Lescure, J. –P., Puig, H., Riéra, B., Yamakura, T., 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia 145, 87-99.

Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., ter Steege, H., Webb, C.O., 2006. Regional and phylogenetic variation of wood density across 2,456 neotropical tree species. Ecological Applications 16, 56-2367.

Chudnoff, M., 1976. Density of tropical timbers as influenced by climatic life zones. Commonwealth Forestry Review 55, 203-217.

Chudnoff, M., 1980. Tropical Timbers of the world. US Department of Agriculture, Forest Service, Forest Products Laboratory, Madison, WI, USA. 831 pp.

Clark, D.A., 2007. Detecting tropical forests’ responses to global climatic and atmospheric change: Current challenges and a way forward. Biotropica 39, 4-19.

DeFries, R.S., Houghton, R.A., Hansen, M.C., Field, G.B., Skole, D., Townshend, J., 2002. Carbon emissions from tropical deforestation and regrowth based on satellite observations for the 1980s and 1990s. Proceedings of the National Academy of Sciences of the United States of America 99, 14256-14261.

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.

DeWalt, S.J., Chave, J., 2004. Structure and biomass of four lowland Neotropical forests. Biotropica 36, 7-19.

do Nascimento, C.C., 1993. Variabilidade da Densidade Básica e de Propriedades Mecânicas de Madeiras da Amazônia. Masters Thesis in Forestry Sciences, Universidade de São Paulo, Escola Superior de Agricultura ‘Luiz de Queiroz’, Piracicaba, SP, Brazil. 129 pp.

FAO, 1988. Food and Agriculture Organization of the United Nations, Soil Map of the World 1:5,000,000. Revised Legend. FAO World Soil Resource Report 60, Rome, Italy.

Fearnside, P.M., 1997. Wood density for estimating forest biomass in Brazilian Amazonia. Forest Ecology and Management 90, 59-87.

Fearnside, P.M., 2000a. Greenhouse gas emissions from land-use change in Brazil's Amazon region. In: Global Climate Change and Tropical Ecosystems. (eds. Lal, R; Kimble, J. M.; Stewart, B. A.) pp. 231-249, Advances in Soil Science. CRC Press, Boca Raton, Florida, USA. 438 pp.

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.

Fearnside, P.M., 2007. Uso da terra na Amazônia e as mudanças climáticas globais. Brazilian Journal of Ecology 10, 83-100.

Fearnside, P.M., Ferraz, J., 1995. A conservation gap analysis of Brazil's Amazonian vegetation. Conservation Biology 9, 1134-1147.

Fearnside, P.M., Laurance, W.F., 2003. Comment on "Determination of deforestation rates of the world's humid tropical forests". Science 229, 1015a.

Fearnside, P.M., Laurance, W.F., 2004. Tropical deforestation and greenhouse gas emissions. Ecological Applications 14, 982-986.

França, M.B., 2002. Modelagem de Biomassa Através do Padrão Espectral no Sudoeste da Amazônia. Tese de Mestrado, 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.

Houghton, R.A., 2003a. Why are estimates of the terrestrial carbon balance so different? Global Change Biology 9, 500-509.

Houghton, R.A., 2003b. Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850-2000. Tellus Series B-Chemical and Physical Meteorology 55, 378-390.

Houghton, R.A., 2005. Aboveground forest biomass and the global carbon balance. Global Change Biology 11, 945-958.

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 Biology 7, 731-746.

King, D.A., Davies, S.J., Tan, S., Noor, N.S. MD., 2006. The role of wood density and stem support costs in the growth and mortality of tropical trees. Journal of Ecology 94, 670-680.

Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patiño, S., Pitman, C.A., Quesada, C.A., Salomão, R., Silva, J.N.M., Lezama, A.T., Martinez, R.V., Terborgh, J., Vinceti, B., Lloyd, J., 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. Global Change Biology 10, 563-591.

Malhi, Y., Wood, D., Baker, T.R., Wright, J., Phillips, O.L., Cochrane, T., Meir, P., Chave, J., Almeida, S., Arroyo, L., Higuchi, N., Killeen, T., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Vargas, P.N., Pitman, N.C.A., Quesada, C.A., Salomão, R., Silva, J.N.M., Lezama, A.T., Terborgh, J., Martínez, R.V., Vinceti, B., 2006. The regional variation of aboveground live biomass in old-growth Amazonian forests. Global Change Biology 12, 1107-1138.

McGuire, A.D., Sitch, S., Clein, J.S., Dargaville, R., Esser, G., Foley, J., Heimann, M., Joos, F., Kaplan, J., Kicklighter, D.W., Meier, R.A., Melillo, J.M., Moore III, B., Prentice, I.C., Ramankutty, N., Reichenau, T., Schloss, A., Tian, H., Williams, L.J., Wittenberg, U., 2001. Carbon balance of the terrestrial biosphere in the twentieth century: Analyses of CO_2, climate and land use effects with four process-based 10 ecosystem models. Global Biogeochemical Cycles 15, 183-206.

Meinzer, F.C., 2003. Functional convergence in plant responses to the environment. Oecologia 134, 1-11.

Melo, J.E., Coradin, V.T.R., Mendes, J.C., 1990. Classes de densidade para madeiras da 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 intersite variation in wood density of tropical trees. Biotropica 36, 20-32.

Nelson, B.W., 1994. Natural forest disturbance and change in the Brazilian Amazon. Remote Sensing Reviews 10,105-125.

Nelson, B.W., Oliveira, A.C., Vidalenc, D., Smith, M., Bianchini, M.C., Nogueira, E.M., 2006. Florestas dominadas por tabocas trepadeiras do gênero *Guadua*, no sudoeste da Amazônia. In: Anais do Seminário Nacional de Bambu, Faculdade de Arquitetura e Urbanismo, Universidade de Brasília, Brasília, DF, Brazil. pp. 49-55.

Nogueira, E.M., Nelson, B.W., Fearnside, P.M., 2005. Wood density in dense forest in central Amazonia, Brazil. Forest Ecology and Management 208, 261-286.

Oliveira, L.C.S., 1981. A variação da massa específica aparente da madeira em função do teor de umidade. IPT, n.2. Notas técnicas em secagem de madeiras. São Paulo, SP, Brazil.

Parolin, P., Ferreira, L.V., 1998. Are there differences in specific wood gravities between trees in várzea and igapó (Central Amazonia)? Ecotropica 4, 25-32.

Putz, F. E., Coley, P. D., Lu, K., Montalvo, A., Aiello, A. 1983. Uprooting and snapping of trees: structural determinants and ecological consequences. Canadian Journal of Forest Research 13, 1011-1020.

Reid, Collins and Associates, 1977. Jari Hog Fuel Study: Investigation of Moisture Content, Specific Gravity, Rate of Drying and other related proprieties of Indigenous Hardwood Species at Jari, Brazil. Progress Report, Dry Season Sampling and Results, Vancouver, BC, Canada. 63 pp.

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, U.S.A. 15 pp.

Ribeiro, J.E.L. da S., Hopckins, M.J.C., Vicentini, A., Sothers, C.A., Costa, M.A. da S., Brito, J.M. de, Souza, M.A.D. de, Martins, L.H.P., Lohmann, L.G., Assunção, P.A.C.L., Pereira, E.C., Silva, C. da, 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.

Sallenave, P., 1971. Propriétés Physiques et Mécaniques des Bois Tropicaux. Deuxième Supplément. CTFT, Nogent sur Marne, France.

Sombroek, W.G., 2000. Amazon land forms and soils in relation to biological diversity. Acta Amazonica 30, 81-100.

Sterck, F.J., van Gelder, H.A., Poorter, L., 2006. Mechanical branch constraints contribute to life-history variation across tree species in a Bolivian forest. Journal of Ecology 94, 1192-1200.

ter Steege, H., Pitman, N.C.A., Phillips, O.L., Chave, J., Sabatier, D., Duque, A., Molino, J-F., Prévost, M-F., Spichiger, R., Castellanos, H., von Hildebrand, P., Vásquez, R., 2006. Continental-scale patterns of canopy tree composition and function across Amazonia. Nature 443, 444-447.

Terborgh, J., Andresen, E., 1998. The composition of Amazonian forests: patterns at local and regional scales. Journal of Tropical Ecology 14, 645-664.

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

van Gelder, H.A., Poorter, L., Sterck, F.J., 2006. Wood mechanics, allometry, and life-history variation in a tropical rain forest tree community. New Phytologist 171, 367-378.

Veloso, H.P., Rangel Filho, A.L.R., Lima, J.C.A., 1991 Classificação da Vegetação Brasileira Adaptada a um Sistema Universal. IBGE, Rio de Janeiro, Brazil. 123 pp.

Vidalenc, D., 2000. Distribuição das florestas dominadas pelo bambu Guadua weberbaueri em escala de paisagem no sudoeste da Amazônia e fatores edáficos que afetam sua densidade. Tese de Mestrado, Instituto Nacional de Pesquisas da Amazônia/Fundação Universidade Federal do Amazonas, Manaus, Amazonas, Brazil. 92 pp.

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

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

Woodcock, D.W., Shier, A.D., 2003. Does canopy position affect wood specific gravity in temperate forest trees?. Annals of Botany 91, 529-537.

Wright, S.J., Muller-Landau, H.C., Condit, R., Hubbell, S.P., 2003. Gap-dependent recruitment, realized vital rates, and size distributions of tropical trees. Ecology 84, 3174-3185.

Figure Legends

Figure 1. Solid circles show collecton sites, from W to E: Sena Madureira, Cotriguaçu, Juruena and Novo Progresso. States mentioned in text are outlined, from W to E: Acre, Rondônia, Mato Grosso and Pará. Rectangles are the RadamBrasil inventories, from W to E: SC.19 Rio Branco, SC.16 Porto Velho and SC.21 Juruena. Dark grey is the extent of deforestation as of 2004, light grey is remaining forest, white is natural non-forest or vegetation status undetected due to clouds. Deforestation data from Brazil's National Insitute for Space Research (INPE).

Figure 2. Mean basic density (g cm^3) of the bole at the collection sites in southern Amazon, open forest (2A) and basic density at breast height in the southwestern Amazon, Acre state (2B): open bamboo-dominated forest and dense bamboo-free forest. In Figure 2A the mean was obtained from the arithmetic mean of density at the base (height at breast or top of the stump for Juruena site) and at the top of the bole.

Figure 3. Decrease in the basic wood density (g cm^3) from the base to the top of the bole. At the Juruena site 'base' refers to a sample at the top of the stump. At the Cotriguaçu and Novo Progresso sites 'base' refers to a sample at breast height (1.3 m).

Figure 4. Radial variation between basic density (g cm^3) of whole disks with bark and basic density of heartwood.

Figure 5. Relationship between mean wood density, DBH (m) and total height (m).

Figure 6. Comparison by forest type between the dataset used in Fearnside (1997), the new dataset obtained in southern Pará and northern Mato Grosso and the França (2002) dataset obtained in Acre. The values for wood density in the figure represent mean species-level or genus-level values. Figures 6A and 6B include dense or open alluvial, submontane and lowland rain forests. Figure 6C includes areas of ecological tension and contact between savanna/rain forest, savanna/seasonal forest and rain forest/seasonal forest.

Table 1. Details of the various mean measures for whole disks and for heartwood at two positions along the bole. All values shown are basic density.

Table 2. Average wood density for each vegetation unit in the SSWA based on wood volume in three RadamBrasil publications, and the tables of density by taxon in this study and that of Fearnside (1997). Here the Fearnside data are not corrected for radial variation. Percent of total wood volume identified to genus and to species levels is given for the two studies. The RadamBrasil forest-volume inventories include only trees above 31.8 cm DBH. See text for explanation of "test"column.

Table 3. New mean wood density for Brazilian Amazonia (updated from Fearnside, 1997): volume-weighted means by vegetation zone, vegetation type and state (g cm^{-3}).

Appendix A. Mean basic density of the bole (cross-sectional disk of wood with bark) by species or morpho-species for four sites in the southern portion of Brazilian Amazonia.

Appendix B. Basic density at breast height (cross-sectional disk of wood with bark) in southwestern Amazonia for two forest types: open bamboo-dominated forest and dense bamboo-free forest. The content below is same dataset used by França (2002) after identification of botanical specimens. However, the information in *erratum* notices appended to França (2002, Annex I) was incorporated into the corrected values for Acre used here.

Figure 1.

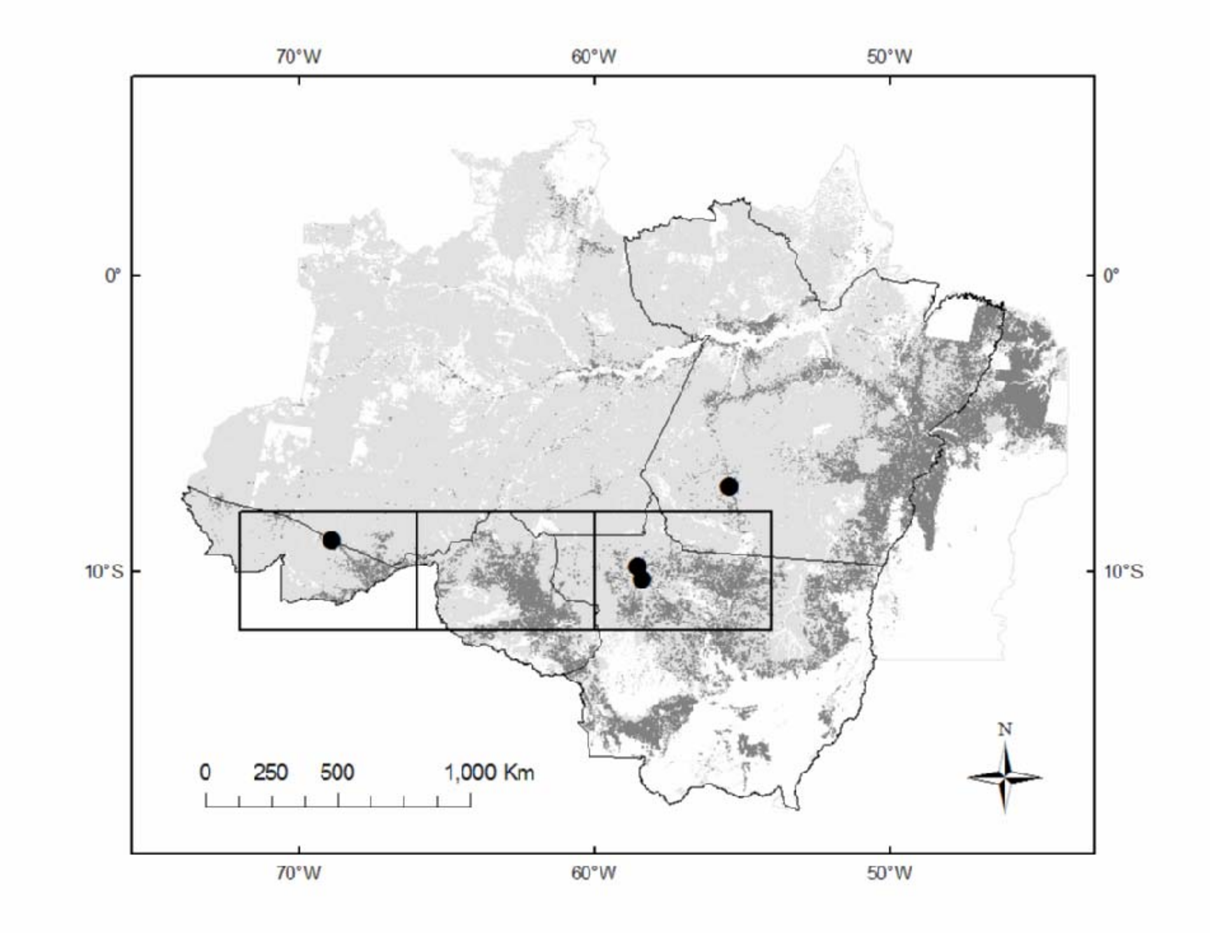


Figure 2.

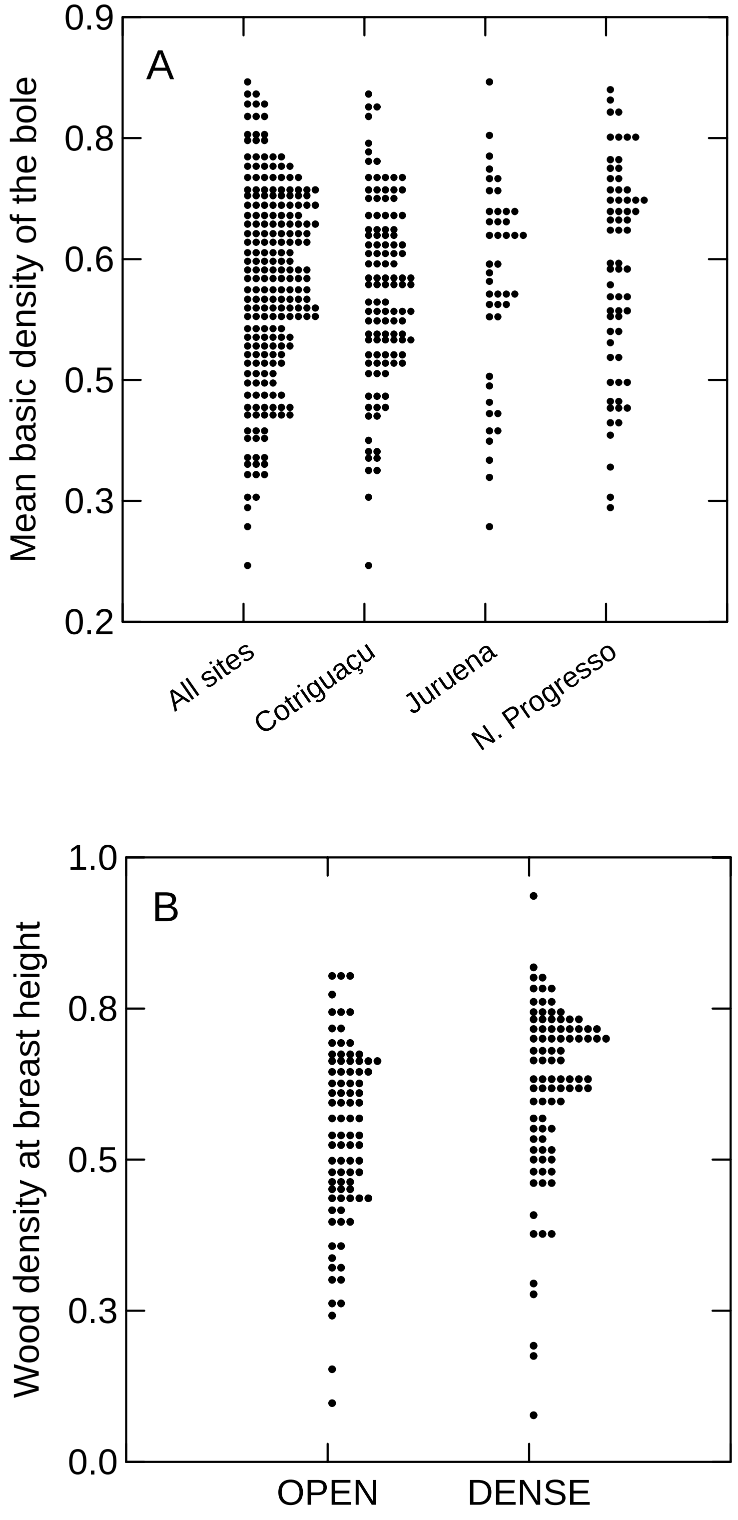

A
Mean basic density of the bole
0.9
0.8
0.6
0.5
0.3
0.2
All sites
Cotriguaçu
Juruena
N. Progresso
B
Wood density at breast height
1.0
0.8
0.5
0.3
0.0
OPEN
DENSE

Figure 3.

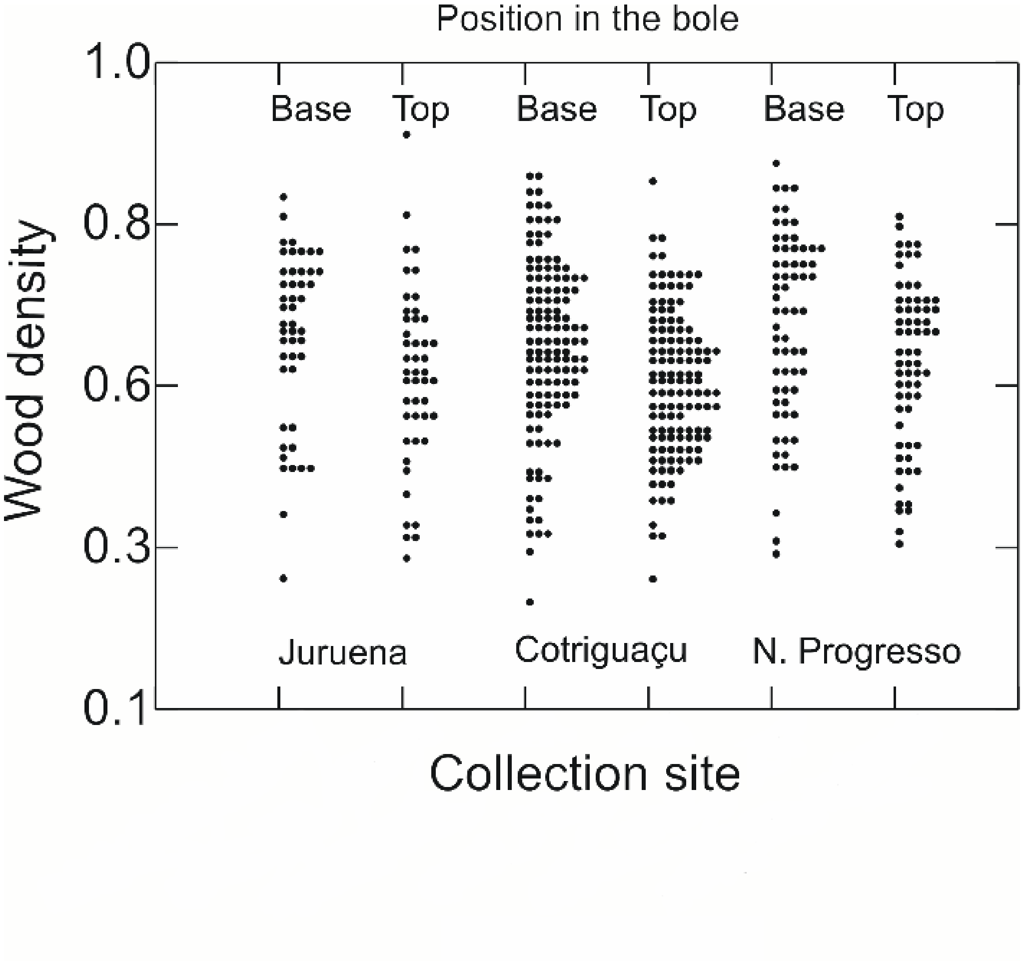

Position in the bole
Base
Top
Base
Top
Base
Top
Wood density
1.0
0.8
0.6
0.3
0.1
Juruena
Cotriguaçu
N. Progresso
Collection site

Figure 4.

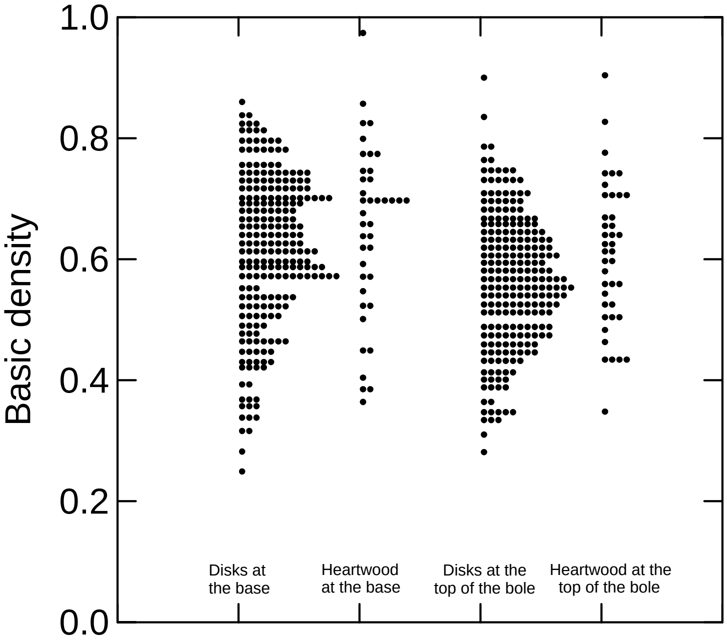

Basic density
1.0
0.8
0.6
0.4
0.2
0.0
Disks at the base
Heartwood at the base
Disks at the top of the bole
Heartwood at the top of the bole

Figure 5.

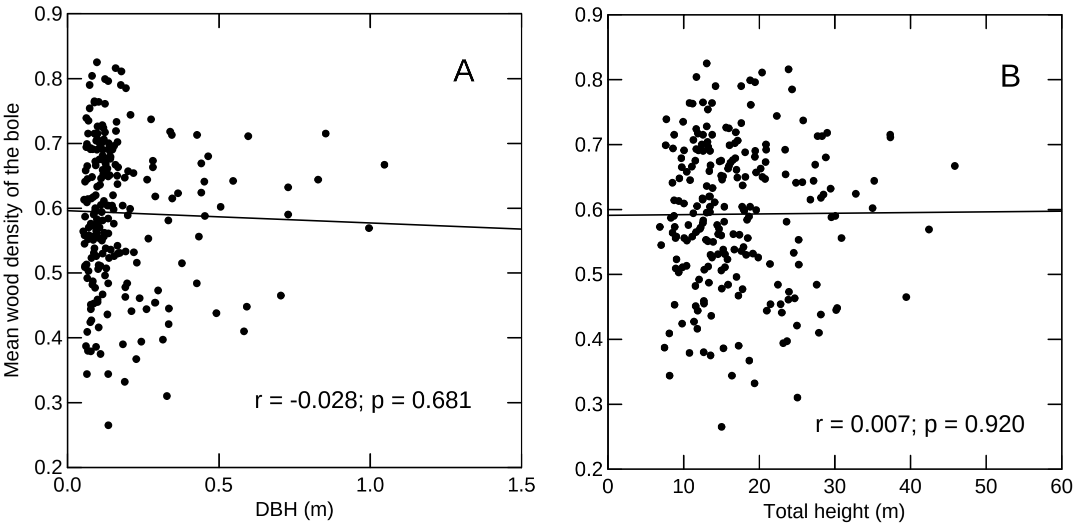
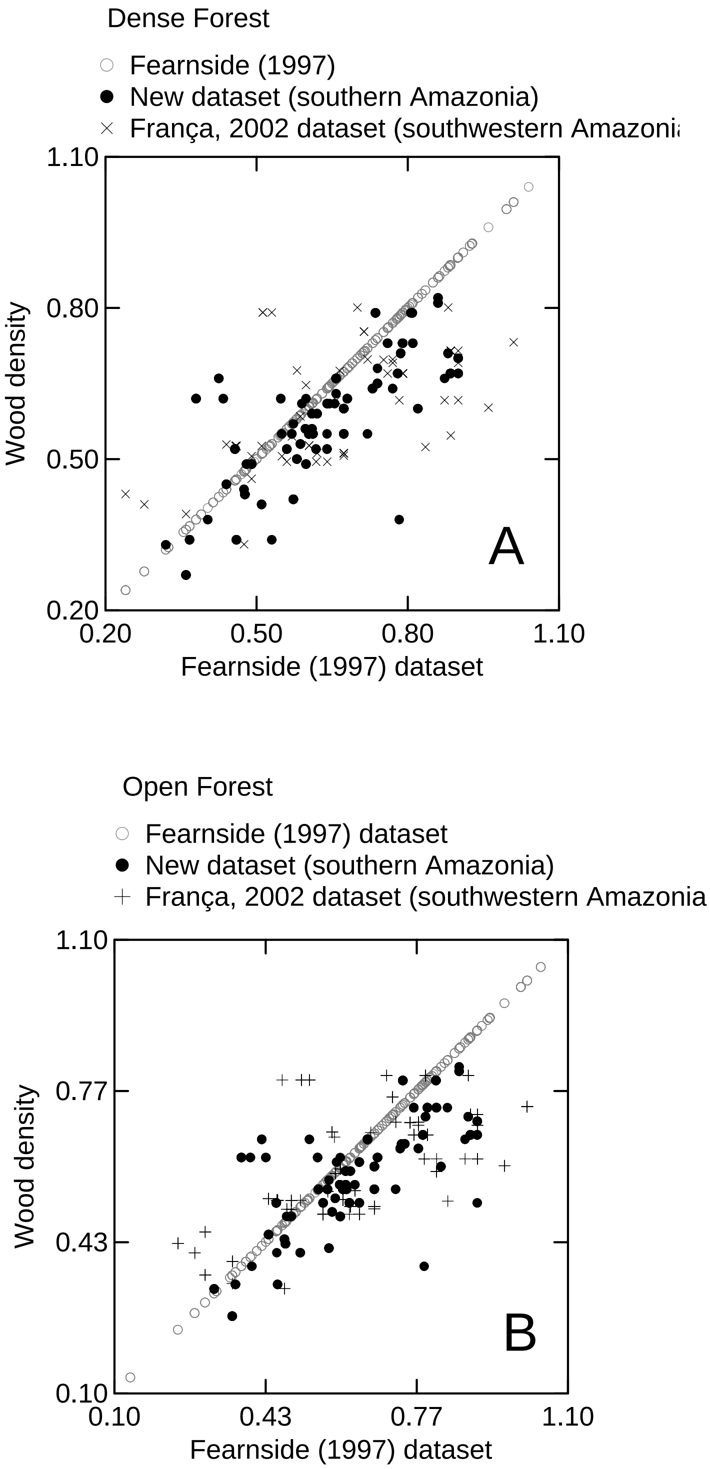

A
B
Mean wood density of the bole
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
0.0
0.5
1.0
1.5
DBH (m)
r = -0.028; p = 0.681
0
10
20
30
40
50
60
Total height (m)
r = 0.007; p = 0.920

Figure 6.


Dense Forest
○ Fearnside (1997)
● New dataset (southern Amazonia)
× França, 2002 dataset (southwestern Amazoni
1.10
0.80
0.50
0.20
Wood density
0.20
0.50
0.80
1.10
Fearnside (1997) dataset
A
Open Forest
○ Fearnside (1997) dataset
● New dataset (southern Amazonia)
+ França, 2002 dataset (southwestern Amazonia
1.10
0.77
0.43
0.10
Wood density
0.10
0.43
0.77
1.10
Fearnside (1997) dataset
B

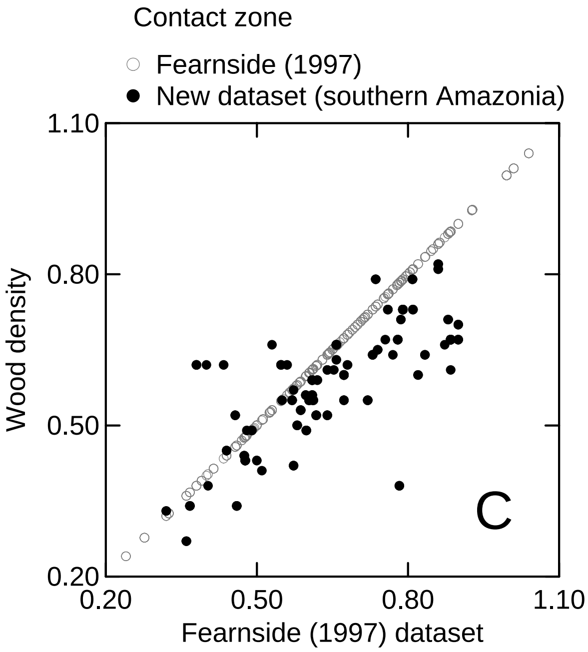

Contact zone
○ Fearnside (1997)
● New dataset (southern Amazonia)
Wood density
1.10
0.80
0.50
0.20
0.20
0.50
0.80
1.10
Fearnside (1997) dataset
C

Table 1.

	Juruena			Cotriguaçu			Novo Progresso			All sites together		
Basic density (whole disks and heartwood)	Mean (±SD)	n	95%	Mean (±SD)	n	95%	Mean (±SD)	n	95%	Mean (±SD)	n	95%
Aritmethic mean density of the bole (disks with bark)	0.591 (0.118)	44	0.55-0.63	0.584 (0.106)	116	0.56-0.60	0.610 (0.121)	65	0.58-0.64	0.593 (0.113)	225	0.58-0.61
Density at the base of the bole (disks with bark)*	0.621 (0.121)	47	0.59-0.66	0.608 (0.122)	126	0.59-0.63	0.636 (0.131)	65	0.60-0.67	0.618 (0.124)	238	0.60-0.63
Density at the top of the bole (disks with bark)	0.565 (0.124)	46	0.53-0.60	0.557 (0.100)	125	0.54-0.57	0.585 (0.116)	65	0.56-0.61	0.566 (0.109)	236	0.55-0.58
Heartwood density: aritmethic mean of the bole	0.650 (0.131)	20	0.59-0.71	0.602 (0.119)	16	0.54-0.66	0.689 (0.084)	2	-	0.632 (0.125)	38	0.59-0.67
Heartwood density at the base of the bole*	0.668 (0.145)	20	0.60-0.73	0.626 (0.143)	18	0.55-0.70	0.701 (0.116)	2	-	0.650 (0.141)	40	0.60-0.70
Heartwood density at the top of the bole	0.633 (0.139)	20	0.57-0.70	0.578 (0.094)	19	0.53-0.62	0.677 (0.052)	2	-	0.610 (0.119)	41	0.57-0.65

* At the Juruena site this value denotes density at the top of the stump. At the other sites density is always at breast height.

Table 2.

State	Vegetation type	Fearnside (1997)	% wood identified to: Genus/Species in Fearnside (1997)	New datasets	% wood identified to: Genus/Species in New dataset	Test**	% wood identified to: Genus/Species in Test	% Fearnside (1997)/New dataset
Rondônia	Dense alluvial rain forest	0.653	80.2 / 58.3	0.554	33.5 / 11.9	0.629	30.2 / 14.2	17.87
Amazonas/Rondônia	Dense submontane rain forest	0.732	80.1 / 51.8	0.599	32.6 / 7.1	0.672	30.3 / 14.1	22.20
Rondônia/Amazonas	Dense submontane rain forest	0.678	72.3 / 45.4	0.604	42.4 / 14.2	0.694	37.2 / 14.2	12.25
Rondônia/Mato Grosso	Dense submontane rain forest	0.666	79.5 / 53.7	0.596	25.8 / 6.9	0.654	23.9 / 6.9	11.74
Rondônia/Amazonas	Open lowland forest	0.691	81.0 / 50.9	0.607	31.2 / 8.1	0.663	30.3 / 7.9	13.84
Rondônia	Open alluvial rain forest	0.637	84.5 / 60.8	0.556	35.6 / 8.7	0.609	32.1 / 8.1	14.57
Rondônia/Mato Grosso/Amazonas	Open submontane rain forest	0.66	76.6 / 51.6	0.594	36.0 / 13.7	0.666	32.9 / 12.9	11.11
Mato Grosso/Rondônia/Amazonas	Open submontane rain forest	0.705	79.1 / 49.2	0.604	32.9 / 8.7	0.685	30.9 / 8.5	16.72
Rondônia/Amazonas	Savanna/rain. forest; Savanna/Dense rain. Forest	0.667	80.4 / 48.7	0.584	35.0 / 12.7	0.646	32.4 / 12.3	14.21
Mato Grosso	Dense alluvial rain forest	0.659	86.9 / 63.4	0.609	36.4 / 15.4	0.673	30.7 / 13.6	8.21
Mato Grosso	Dense submontane rain forest	0.666	85.1 / 63.2	0.582	42.0 / 20.7	0.66	37.4 / 18.6	14.43
Mato Grosso	Open submontane rain forest	0.645	83.4 / 57.0	0.588	42.1 / 16.70	0.635	38.6 / 26.6	9.69
Mato Grosso	Savanna/seasonal forest	0.634	87.5 / 57.3	0.582	39.1 / 12.7	0.651	37.1 / 23.1	8.93
Mato Grosso	Rain Forest/Seasonal Forest	0.651	81.6 / 52.3	0.585	40.4 / 17.8	0.667	36.0 / 21.0	11.28
Acre/Amazonas	Dense lowland rain forest	0.65	80.2 / 51.5	0.572*	30.5 / 5.8	0.647	28.0 / 15.3	8.88
Acre/Amazonas	Open lowland rain forest	0.657	75.0 /50.8	0.550*	39.3 / 7.1	0.69	34.2 / 22.8	14.46
Amazonas/Rondônia	Open submontane rain forest	0.664	94.7 / 50.1	0.589*	38.7 / 3.1	0.697	37.6 / 13.7	7.97
Acre/Amazonas	Open alluvial rain forest	0.602	70.1 / 46.2	0.534*	37.7 / 7.0	0.632	28.3 / 16.8	8.08
	Average	0.662		0.583		0.659		12.58

* Based on the eastern Acre data of Appendix B. Wood density was measured only at breast height, then reduced by 4.2% for longitudinal decrease in density with height along the bole. Without this correction, the values were: 0.597, 0.574, 0.615, and 0.557. All other values in same column were calculated from the southern Amazon dataset (Appendix A).

** Test column provides the mean wood density for each landscape unit using the Fearnside (1997) table of density by taxon, but only using those taxa found in the new datasets of this paper. The test shows that the reduction in density is little affected by the fraction of identifications made to the species level.

Table 3.

Forest vegetation type: Group, Subgroup and class (code)		Acre	Amapa	Amazonas	Maranhão	Mato Grosso	Pará	Rondônia	Roraima	Tocantins/Goiás	Area-weighted mean
Rain (ombrophilous) forest	Dense alluvial (Da-0)		*0.634*	0.635		0.609	*0.634*	0.554	0.635	*0.634*	0.634
	Dense lowland (Db-0)	0.572	*0.634*	0.662	*0.634*		0.701	*0.668*	0.636		0.668
	Dense montane (Dm-0)		*0.646*	*0.646*			*0.646*		0.646		0.646
	Dense submontane (Ds-0)	*0.687*	*0.687*	0.696	*0.687*	0.582	0.695	0.599	0.670	*0.687*	0.687
	Mean dense forests										0.672
Rain (ombrophilous) forest	Open alluvial (Aa-0)	0.534		0.534			0.534	0.534			0.534
	Open lowland (Ab-0)	0.550		0.620				0.595			0.595
	Open submontane (As-0)			0.589		0.588	*0.589*	0.589	0.589	*0.589*	0.589
Seasonal forest	Deciduous submontane (Cs-0)				*0.602*	*0.602*	*0.602*			*0.602*	*0.602*
	Semideciduous alluvial (Fa-0)					*0.602*					*0.602*
	Semideciduous submontane (Fs-0)					*0.602*		*0.602*	*0.602*	*0.602*	*0.602*
Woody oligotrophic vegetation of swampy and sandy areas	Open arboreal (La-0)			0.711					*0.711*		0.711
	Dense arboreal (Ld-0)			*0.602*					*0.602*		*0.602*
	Grassy-woody (Lg-0)			*0.602*					*0.602*		*0.602*
Areas of ecological tension and contact (ecotones)	Woody oligotrophic vegetation of swampy & sandy areas - rain forest (LO-0)			0.642					0.642		0.642
	Rain forest - seasonal forest (ON-0)					0.585	*0.587*	*0.587*	0.679		0.587
Areas of pioneer formations (early succession)	Fluvio-marine influence (Pf-0)		*0.602*		*0.602*		*0.602*				0.602
Areas of ecological tension and contact (ecotones)	Savanna-dense rain forest (SM-0)				*0.602*						0.602
	Savanna-seasonal forest (SN-0)			*0.583*	*0.583*	0.582	*0.583*	*0.583*	0.714	*0.583*	0.583
	Savanna-rain forest (SO-0)		*0.672*	0.655		*0.672*	0.679	*0.672*	*0.672*	*0.672*	0.672
	Mean non-dense forests										0.602
	Mean all forests										0.642

* Values in italics are for ecoregions without species-specific data; the area-weighted mean for the same vegetation type in other states has been substituted. For the 7 non-dense forest types with no data from any state, the area-weighted mean for all non-dense forests has been used. For detailed information about forest types , see Fearnside (1997).

Appendix A.

Family	Scientific name	Mean of the bole (st. deviation)	n
Anacardiaceae	*Anacardium giganteum* W. Hancock ex Engl.	0.445	1
Fabaceae	*Andira inermis* (W. Wright) Kunth ex. DC.	0.650	1
Annonaceae	*Annona ambotay* Aubl.	0.605	1
Tiliaceae	*Apeiba echinata* Gaertner	0.265	1
Apocynaceae	*Aspidosperma* cf. *spruceanum* Mull. Arg.	0.726 (0.010)	2
Anacardiaceae	*Astronium le-cointei* Ducke	0.638 (0.062)	7
Moraceae	*Batocarpus amazonicus* (Ducke) Fosberg	0.604	1
Bixaceae	*Bixa arborea* Huber	0.332	1
Moraceae	*Brosimum acutifolium* Huber ssp. *interjectum* C.C. Berg	0.511	1
Moraceae	*Brosimum gaudichaudii* Trécul	0.644	1
Moraceae	*Brosimum guianense* (Aubl.) Huber	0.766 (0.065)	3
Moraceae	*Brosimum lactescens* (S. Moore) C.C.Berg.	0.627 (0.048)	6
Urticaceae	*Castilloa ulei* Warb	0.410	1
Cecropiaceae	*Cecropia sciadophylla* Mart.	0.310	1
Ulmaceae	*Celtis schippii* Standl.	0.669	1
Hippocrateaceae	*Cheiloclinium cognatum* (Miers) A.C. Smith	0.703 (0.025)	11
Sapotaceae	*Chrysophyllum lucentifolium* Cronquist ssp. *pachicardium* Pires T. D. Pen	0.737	1
Sapotaceae	*Chrysophyllum* sp.	0.728	1
Moraceae	*Clarisia racemosa* Ruiz & Pav.	0.526	1
Cochlospermaceae	*Cochlospermum orinocense* (Kunth) Steud.	0.394	1
Euphorbiaceae	*Conceveiba guianensis* Aubl.	0.556	1
Caesalpinioideae	*Copaifera multijuga* Hayne	0.563 (0.009)	2
Boraginaceae	*Cordia ecalyculata* Vell.	0.467	1
Boraginaceae	*Cordia* sp.	0.550	1
Boraginaceae	*Cordia sprucei* Mez	0.467 (0.022)	2
Euphorbiaceae	*Croton palanostigma* Klotzsch	0.454	1
Fabaceae	*Diplotropis purpurea* var. *leptophylla* (Kleinhoonte) Amshoff	0.674 (0.053)	2
Sapotaceae	*Ecclinusa guianensis* Eyma	0.613 (0.124)	4
Mimosoideae	*Enterolobium* sp.	0.379	1
Bombacaceae	*Eriotheca globosa* (Aubl.) Robyns	0.590	1
Myrtaceae	*Eugenia anastomosans* DC.	0.594	1
Annonaceae	*Fusaea longifolia* (Aubl.) Saff.	0.657 (0.035)	4
Nyctaginaceae	*Guapira noxia* (Netto) Lundell	0.533	1
Meliaceae	*Guarea* cf. *humaitensis* T.D. Penn.	0.513	1
Meliaceae	*Guarea grandifolia* DC.	0.623	1
Meliaceae	*Guarea kunthiana* A.Juss.	0.492	1
Meliaceae	*Guarea* sp.	0.613	1
Meliaceae	*Guarea trunciflora* C. DC.	0.607 (0.016)	2
Annonaceae	*Guatteria citriodora* Ducke	0.516	1
Annonaceae	*Guatteria* sp.	0.487	1
Sterculiaceae	*Guazuma* sp.	0.484	1
Lecythidaceae	*Gustavia augusta* L.	0.604	1
Chrysobalanaceae	*Hirtella* cf. *racemosa* Lam.	0.761	1
Chrysobalanaceae	*Hirtella* sp.	0.699	1
Caesalpinioideae	*Hymenaea courbaril* L.	0.785	1
Fabaceae	*Hymenolobium* cf. *pulcherrimum* Ducke	0.586 (0.023)	2
Fabaceae	*Hymenolobium modestum* Ducke	0.538	1
Fabaceae	*Hymenolobium nitidum* Benth.	0.632	1
Fabaceae	*Hymenolobium sericeum* Ducke	0.715	1
Mimosoideae	*Inga alba* (Swartz.) Willd.	0.588	1

Appendix A. (continued)

Family	Scientific name	Mean of the bole (standard deviation)	n
Mimosoideae	*Inga flagelliformis* (Vell.) Mart.	0.496	1
Mimosoideae	*Inga stipularis* DC.	0.676	1
Mimosoideae	*Inga thibaudiana* DC. ssp. *thibaudiana*	0.657	1
Myristicaceae	*Iryanthera sagotiana* Warb.	0.551	1
Rubiaceae	*Isertia hypoleuca* Benth.	0.484	1
Flacourtiaceae	*Laetia procera* (Poepp.) Eichler	0.615	1
Tiliaceae	*Lueheopsis duckeana* Burret	0.546 (0.022)	2
Moraceae	*Maquira calophylla* (Planch. & Endl.) C.C. Berg	0.617 (0.095)	3
Moraceae	*Maquira sclerophylla* (Ducke) C.C. Berg	0.416	1
Sapindaceae	*Matayba cf. purgans* (Poepp. & Endl.) Radlk.	0.565	1
Rutaceae	*Metrodorea flavida* K. Krause	0.693 (0.046)	5
Melastomataceae	*Miconia holosericea* (L.) DC.	0.587	1
Memecylaceae	*Mouriri duckeanoides* Morley	0.704	1
Moraceae	*Naucleopsis caloneura* (Huber) Ducke	0.453	1
Nyctaginaceae	*Neea* cf. *oppositifolia* Ruiz & Pav.	0.454	1
Lauraceae	*Ocotea aciphylla* (Nees) Mez	0.466 (0.112)	2
Lauraceae	*Ocotea longifolia* H.B.K.	0.558	1
Lauraceae	*Ocotea nitida* (Meissn.) Rohwer	0.536	1
Lauraceae	*Ocotea* sp.	0.702	1
Mimosoideae	*Parkia* sp.	0.624	1
Violaceae	*Paypayrola grandiflora* Tul.	0.492 (0.021)	2
Fabaceae	*Poeppigia procera* C. Presl	0.531	1
Cecropiaceae	*Pourouma* cf. *tomentosa* Miq. ssp. *apiculata* (Bem.) C.C. Berg. & van Heus.	0.379 (0.016)	2
Cecropiaceae	*Pourouma minor* Benoist	0.423 (0.046)	4
Sapotaceae	*Pouteria anomala* (Pires) T.D. Penn.	0.680 (0.011)	4
Sapotaceae	*Pouteria* cf. *campanulata* Baehni	0.690 (0.069)	3
Sapotaceae	*Pouteria* cf. *cladantha* Sandwith	0.615	1
Sapotaceae	*Pouteria* cf. *glomerata* (Miq.) Radlk.	0.643 (0.088)	4
Sapotaceae	*Pouteria reticulata* (Engl.) Eyma	0.682 (0.034)	2
Sapotaceae	*Pouteria* sp.	0.681	1
Burseraceae	*Protium* cf. *decandrum* (Aubl.) March.	0.562 (0.028)	2
Burseraceae	*Protium* cf. *spruceanum* (Benth.) Engl.	0.568 (0.008)	2
Burseraceae	*Protium guianensis* (Aubl.) Marchand	0.665	1
Burseraceae	*Protium* sp.	0.620	1
Burseraceae	*Protium tenuifolium* (Engl.) Engl.	0.553	1
Moraceae	*Pseudolmedia laevis* (Ruiz & Pav.) Macbr.	0.593 (0.041)	7
Moraceae	*Pseudolmedia macrophylla* Trécul	0.588 (0.049)	4
Annonaceae	*Pseudoxandra obscurinervis* Maas	0.691	1
Vochysiaceae	*Qualea* cf. *paraensis* Ducke	0.553	1
Bombacaceae	*Quararibea ochrocalyx* (K. Schum.) Vischer	0.563 (0.024)	5
Violaceae	*Rinoreocarpus ulei* (Melch.) Ducke	0.589	1
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	0.441	1
Sapotaceae	*Sarcaulus* sp.	0.680	1
Araliaceae	*Schefflera morototoni* (Aubl.) Frodin	0.423 (0.036)	2
Caesalpinioideae	*Sclerolobium* cf. *micropetalum* Ducke	0.553 (0.123)	3
Caesalpinioideae	*Sclerolobium* cf. *setiferum* Ducke	0.438	1
Caesalpinioideae	*Sclerolobium* sp.	0.576	1
Caesalpinioideae	*Sclerolobium* sp.	0.645	1
Caesalpinioideae	*Sclerolobium* sp.	0.511	1
Caesalpinioideae	*Sclerolobium* sp.	0.380	1

Appendix A. (continued)

Family	Scientific name	Mean of the bole (standard deviation)	n
Caesalpinioideae	*Sclerolobium* sp.	0.463	1
Simaroubaceae	*Simarouba amara* Aubl.	0.344	1
Siparunaceae	*Siparuna* sp.	0.436	1
Sterculiaceae	*Sterculia excelsa* Mart.	0.455 (0.015)	2
Sterculiaceae	*Sterculia pruriens* (Aubl.) K. Schum.	0.344	1
Sterculiaceae	*Sterculia* sp.	0.387	1
Bignoniaceae	*Tabebuia* sp.	0.713	1
Sapindaceae	*Talisia cerasina* (Benth.) Radlk.	0.825	1
Burseraceae	*Tetragastris altissima* (Aubl.) Swart	0.646 (0.033)	8
Burseraceae	*Tetragastris panamensis* (Engl.) Kuntze	0.666	1
Sterculiaceae	*Theobroma microcarpum* Mart.	0.476 (0.031)	5
Sterculiaceae	*Theobroma speciosum* Willd. ex Spreng	0.495 (0.029)	6
Sapindaceae	*Toulicia guianensis* Aubl.	0.671 (0.029)	2
Clusiaceae	*Tovomita* sp.	0.713	1
Burseraceae	*Trattinnickia* cf. *peruviana* Loes.	0.515	1
Meliaceae	*Trichilia* cf. *rubra* C. DC.	0.790	1
Meliaceae	*Trichilia guianensis* Klotzsch ex C. DC.	0.804	1
Meliaceae	*Trichilia micrantha* Benth.	0.683 (0.064)	8
Meliaceae	*Trichilia quadrijuga* Kunth	0.620	1
Meliaceae	*Trichilia* sp.	0.765	1
Meliaceae	*Trichilia* sp.	0.558	1
Meliaceae	*Trichilia* sp.	0.764	1
Humiriaceae	*Vantanea guianensis* Aubl.	0.816	1
Humiriaceae	*Vantanea* sp.	0.799	1
Myristicaceae	*Virola* cf. *venosa* (Benth.) Warb.	0.427	1

Appendix B.

Family	Scientific name	Basic density at breast height	n
Mimosaceae	*Acacia paniculata* Willd.	0.472	1
Mimosaceae	*Acacia paraensis* Ducke	0.554	2
Fabaceae	*Alexa* sp.	0.665	1
Sapindaceae	*Allophylus pilosus* (J.F. Macbr.) A.H. Gentry	0.614	5
Ulmaceae	*Ampelocera edentula* Kuhl	0.804	1
Fabaceae	*Andira multistipula* Ducke	0.675	1
Tiliaceae	*Apeiba echinata* Gaertner	0.391	2
Tiliaceae	*Apeiba tibourbou* Aubl.	0.242	1
Olacaceae	*Aptandra tubicina* (Poepp.) Benth. ex Miers	0.605	1
Apocynaceae	*Aspidosperma ulei* Markgr.	0.670	1
Anacardiaceae	*Astronium le-cointei* Ducke	0.691	2
Sterculiaceae	*Basiloxylon* sp.	0.175	1
Moraceae	*Batocarpus* cf. *amazonicus* (Ducke) Fosberg	0.605	1
Fabaceae	*Bocoa alterna* (Benth.) R. S. Cowan	0.747	1
Bombacaceae	*Bombacopsis macrocalyx* (Ducke) Robyns	0.362	2
Monimiaceae	*Bracteanthus glycycarpus* Ducke	0.677	1
Moraceae	*Brosimum alicastrum* subsp. *bolivarense* (Pittier) C.C. Berg	0.618	1
Moraceae	*Brosimum guianense* (Aubl.) Huber	0.602	1
Moraceae	*Brosimum lactescens* (S. Moore) C.C.Berg.	0.632	2
Combretaceae	*Buchenavia grandis* Ducke	0.753	1
Myrtaceae	*Calyptranthes* sp.	0.480	1
Myrtaceae	*Calyptranthes* sp.	0.818	1
Euphorbiaceae	*Caryodendron grandifolium* (Mull. Arg.) Pax	0.644	5
Flacourtiaceae	*Casearia javintensis* H.B.K.	0.571	1
Flacourtiaceae	*Casearia pitumba* Sleumer	0.519	1
Flacourtiaceae	*Casearia* sp.	0.621	1
Flacourtiaceae	*Casearia* sp.	0.723	1
Olacaceae	*Cathedra acuminata* (Benth.) Miers	0.658	1
Bombacaceae	*Cavanillesia* sp.	0.153	1
Bombacaceae	*Cavanillesia* sp.	0.192	1
Cecropiaceae	*Cecropia distachya* Huber	0.438	1
Cecropiaceae	*Cecropia ficifolia* Warb. ex Snethl.	0.277	1
Cecropiaceae	*Cecropia latiloba* Miq.	0.271	1
Cecropiaceae	*Cecropia sciadophylla* Mart.	0.456	1
Bombacaceae	*Ceiba insignis* (Kunth) P.E. Gibbs & Semir	0.410	3
Cochlospermaceae	cf. *Cochlospermum* sp.	0.790	1
Sapotaceae	*Chrysophyllum* sp.	0.589	1
Verbenaceae	*Citharexylum macrophyllum* Poir.	0.538	1
Moraceae	Clarisia biflora Ruiz & Pav.	0.498	1
Moraceae	*Clarisia ilicifolia* (Spreng.) Lanj. & Rossb.	0.672	1
Fabaceae	*Clathrotropis macrocarpa* Ducke	0.675	1
Caesalpinioideae	*Copaifera multijuga* Hayne	0.547	1
Boraginaceae	*Cordia alliodora* (Ruiz & Pav.) Oken	0.372	1
Boraginaceae	*Cordia* sp.	0.640	1
Euphorbiaceae	*Drypetes variabilis* Uittien	0.713	5
Annonaceae	*Duguetia quitarensis* Benth.	0.754	2
Annonaceae	*Duguetia spixiana* Mart.	0.613	1
Fabaceae	*Dypterix alata* Vogel	0.936	1
Lecythidaceae	*Eschweilera* aff. *coriacea* (DC.) Mart. ex Berg.	0.615	1

Appendix B. (continued)

Family	Scientific name	Basic density at breast height	n
Lecythidaceae	*Eschweilera ovalifolia* (DC.) Nied.	0.618	1
Rutaceae	*Esenbeckia* sp.	0.446	1
Moraceae	*Ficus gomelleira* Kunth & Bouché	0.387	1
Moraceae	*Ficus paraensis* (Miq.) Miq.	0.480	1
Rubiaceae	*Genipa* sp.	0.545	1
Meliaceae	*Guarea kunthiana* A. Juss.	0.595	1
Meliaceae	*Guarea pubescens* (Rich.) A. Juss.	0.617	1
Meliaceae	*Guarea* sp.	0.684	1
Meliaceae	*Guarea* sp.	0.695	1
Annonaceae	*Guatteria* cf. *schomburgkiana* Mart.	0.676	1
Euphorbiaceae	*Hevea* cf. *brasiliensis* (Kunth) Mull. Arg.	0.525	2
Euphorbiaceae	*Hevea* sp.	0.262	1
Euphorbiaceae	*Hevea spruceana* (Benth.) Mull. Arg.	0.530	1
Chrysobalanaceae	*Hirtella excelsa* Standl. ex Prance	0.712	3
Chrysobalanaceae	*Hirtella* cf. *racemosa* Lam.	0.720	1
Aquifoliaceae	*Ilex inundata* Poepp. ex Reissek	0.649	3
Mimosaceae	*Inga* cf. *disticha* Benth.	0.483	1
Mimosaceae	*Inga* cf. *laurina* Willd.	0.696	1
Mimosaceae	*Inga edulis* Mart.	0.507	1
Mimosaceae	*Inga ingoides* (Rich.) Willd.	0.463	2
Mimosaceae	*Inga marginata* Willd.	0.468	3
Mimosoideae	*Inga nobilis* Willd.	0.591	1
Rubiaceae	*Ixora peruviana* (Spruce ex K. Schum.) Standl.	0.664	1
Caricaceae	*Jacaratia digitata* (Poepp.& Endl.) Solms	0.087	2
Lecythidaceae	*Lecythis* sp.	0.628	1
Violaceae	*Leonia crassa* L.B. Sm. & A. Fernández	0.695	1
Fabaceae	*Lonchocarpus* sp.	0.535	1
Flacourtiaceae	*Lunania parviflora* Spruce ex Benth.	0.537	1
Moraceae	*Maclura tinctoria* ssp. *tinctoria*	0.668	1
Annonaceae	*Malmea* sp.	0.445	1
Fabaceae	*Martiodendron elatum* var. *occidentale* (Ducke) R. Koeppen	0.805	1
Sapindaceae	*Matayba arborescens* (Aubl.) Radlk.	0.737	1
Bombacaceae	*Matisia* sp.	0.571	1
Lauraceae	*Mezilaurus micrantha* van der Werff	0.801	1
Lauraceae	*Ocotea longifolia* H.B.K.	0.497	2
Lauraceae	*Ocotea oblonga* (Meissn.) Mez	0.556	2
Annonaceae	*Oxandra espintana* (Spruce ex Benth.) Baill.	0.749	1
Annonaceae	*Oxandra polyantha* R. E. Fr.	0.778	1
Annonaceae	*Oxandra* sp.	0.729	1
Moraceae	*Perebea guianensis* Aubl.	0.734	3
Moraceae	*Perebea mollis* (Planch. & Endl.) Huber ssp. *mollis*	0.613	1
Moraceae	*Perebea* sp.	0.676	1
Fabaceae	*Platymiscium* sp.	0.524	1
Anacardiaceae	*Poupartia amazonica* Ducke	0.392	1
Sapotaceae	*Pouteria* cf. *campanulata* Baehni	0.715	1
Moraceae	*Pseudolmedia laevis* (Ruiz & Pav.) Macbr.	0.702	4
Moraceae	*Pseudolmedia macrophylla* Trécul	0.542	2
Fabaceae	*Pterocarpus* aff. *rohrii* Vahl	0.481	1
Fabaceae	*Pterocarpus* cf. *officinalis* Jacq.	0.578	1
Bombacaceae	*Quararibea* cf. *guianensis* Aubl.	0.451	7

Appendix B. (continued)

Family	Scientific name	Basic density at breast height	n
Clusiaceae	*Rheedia acuminata* (Ruiz & Pav.) Planch. & Triana	0.698	1
Violaceae	*Rinorea amapensis* Hekking	0.616	1
Violaceae	*Rinorea lindeniana* (Tul.) Kuntze	0.675	1
Humiriaceae	*Sacoglottis* sp.	0.698	1
Euphorbiaceae	*Sapium glandulosum* (L.) Morong	0.479	1
Euphorbiaceae	*Sapium marmieri* Huber	0.331	3
Euphorbiaceae	*Sapium obovatum* Klotzsch ex Mull. Arg.	0.435	2
Euphorbiaceae	*Sapium* sp.	0.331	1
Fabaceae	*Schizolobium amazonicum* Huber ex Ducke	0.431	1
Caesalpinioideae	*Sclerolobium* sp.	0.495	1
Elaeocarpaceae	*Sloanea porphyrocarpa* Ducke	0.732	1
Moraceae	*Sorocea briquetii* J.F. Macbr.	0.625	1
Moraceae	*Sorocea hirtella* Mildbr.	0.648	1
Sterculiaceae	*Sterculia excelsa* Mart.	0.526	1
Myrsinaceae	*Stylogyne micrantha* (Kunth) Mez	0.510	1
Bignoniaceae	*Tabebuia* sp.	0.803	1
Bignoniaceae	*Tabebuia* sp.	0.799	1
Dichapetalaceae	*Tapura peruviana* K. Krause	0.711	1
Combretaceae	*Terminalia argentea* Mart.	0.697	2
Sterculiaceae	*Theobroma speciosum* Willd. ex Spreng	0.607	1
Meliaceae	*Trichilia* aff. *cipo* (A. Juss.) C. DC.	0.712	1
Meliaceae	*Trichilia catigua* A. Juss.	0.673	1
Meliaceae	*Trichilia guianensis* Klotzsch ex C. DC.	0.654	3
Meliaceae	*Trichilia quadrijuga* subsp. *quadrijuga*	0.747	2
Vochysiaceae	*Vochysia guianensis* Aubl.	0.791	1
Rutaceae	*Zanthoxylum* cf. *riedelianum* Engl.	0.321	1
Fabaceae	*Zollernia* cf. *grandifolia* Schery	0.744	1
Fabaceae	*Zygia latifolia* (L.) Fawc. & Rendle	0.621	1
Fabaceae	*Zygia* sp.	0.686	1