

NATIONAL INSTITUTE FOR RESEARCH IN THE AMAZON – INPA
Integrated Graduate Program in Tropical Biology and Natural Resources – PBTRN
Graduate Program in Tropical Forest Science - CFT

**WOOD DENSITY AND TREE ALLOMETRY IN FORESTS OF
BRAZIL'S 'ARC OF DEFORESTATION': IMPLICATIONS FOR
BIOMASS AND EMISSION OF CARBON FROM LAND-USE CHANGE
IN BRAZILIAN AMAZONIA**

EULER MELO NOGUEIRA

Manaus, Amazonas
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IN BRAZILIAN AMAZONIA**

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Synopsis:

This study presents estimates of wood density, wood moisture content, allometry, and biomass stock for the southern and southwestern portions of the 'arc of deforestation', and adjusts the estimates of biomass and of carbon emission for Brazilian Amazonia.

Keywords: Global Warming, Biomass, Wood density, Allometry, Arc of deforestation, Amazonian.

Dedication

To the Lord God, creator of heaven and earth, to my parents José Anísio Nogueira and Lindaura Martins Melo Nogueira, and to my siblings: Georgheton and family, Liliane, Dayana and Maria Adonay.

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“... because the Lord was with Joseph”

Genesis 39:23

RESUMO

Incertezas nas estimativas de biomassa são a principal causa de incertezas nas estimativas de emissão de gases de efeito estufa na Amazônia. Os resultados apresentados neste estudo reduzem as incertezas nas estimativas de biomassa acima do solo, particularmente no sul e sudoeste da Amazônia brasileira (SSWA), regiões inseridas no 'arco do desmatamento'. No Capítulo I novos dados de densidade de madeira obtidos nas florestas da região SSWA (403 árvores identificadas em nível de espécie e gênero) foram combinados com os inventários de volume de madeira produzidos pelo Projeto RadamBrasil (1973-1983). A área de cada unidade de vegetação, definidas pela intersecção entre tipos de florestas mapeados e divisão geopolítica dos estados, foi utilizada para obter a densidade de madeira média ($0,583 \text{ g cm}^{-3}$) para toda a região SSWA. Esta média é 13,6% menor do que o valor utilizado para esta região em estimativas prévias. A média de $0,642 \text{ g cm}^{-3}$ foi obtida para a Amazônia brasileira como um todo, a partir das novas estimativas para as florestas da porção SSWA juntamente com estimativas para as outras regiões da Amazônia, corrigidas para a variação radial (-5,3%). A nova média de densidade é 7% menor que a média anteriormente estimada para a Amazônia brasileira: $0,69 \text{ g cm}^{-3}$. O impacto sobre as estimativas de biomassa e emissão de carbono é substancial porque a redução é maior em tipos de floresta sob maior desmatamento. Para 1990, com $13,8 \times 10^3 \text{ km}^2$ de desmatamento, as emissões para a Amazônia brasileira seriam reduzidas por $23,4\text{-}24,4 \times 10^6 \text{ Mg CO}_2\text{-equivalente C/ano}$ (para cenários de gás-traço alto e baixo), ou 9,4-9,5% da emissão grossa e 10,7% da emissão líquida comprometida, ambas excluindo o solo. No Capítulo II foram avaliadas relações lineares que descrevem a variação radial da densidade para árvores em floresta densa na Amazônia central (CA) e desenvolvidas novas relações para árvores em floresta aberta no sul da Amazônia (SA). A relação linear descrita na CA para a variação da densidade ao longo do fuste é similar para árvores no SA ($p = 0,144$). Também é demonstrado que as árvores no sul da Amazônia possuem conteúdo de umidade no fuste significativamente maior ($0,416 \pm 0,068 \text{ SD}$; $n = 223$) do que em árvores na CA ($0,38$; $n = 50$). O conteúdo de umidade tem uma forte relação inversa com a densidade básica da madeira, o que explica o menor conteúdo de umidade nas árvores na CA comparado ao SA. No Capítulo III é demonstrado que na CA as árvores são mais altas para um dado diâmetro que em florestas abertas dominadas por bambu e densas livres de bambu, no sudoeste da Amazônia (SW), bem como em florestas abertas no sul da Amazônia (SA). O impacto sobre as estimativas de biomassa foram respectivamente -11,0%, -6,2% e -3,6%. Isto sugere que a estimativa da Comunicação Nacional Brasileira no âmbito da Convenção Quadro das Nações Unidas para Mudanças Climáticas requer redução. As relações observadas entre diâmetro e altura foram inconsistentes com a suposição da teoria de ecologia metabólica e reforça o argumento que o expoente escalar alométrico varia em florestas sobre diferentes substratos ou com diferentes níveis de distúrbios naturais. No Capítulo IV é apresentada nova equação alométrica para estimativa de biomassa desenvolvida a partir de árvores diretamente pesadas no SA e equações para estimativas do volume do fuste na CA e no SA. Estas equações foram utilizadas para aperfeiçoar o modelo de biomassa historicamente aplicado na Amazônia, que se baseia em inventários de volume de madeira em larga-escala. Nova estimativa de biomassa foi produzida para a Amazônia brasileira incorporando novos valores de densidade de madeira, correções para incertezas em estimativa de volume de madeira e fatores utilizados para adicionar o volume dos fustes de pequenas árvores e biomassa das copas. Considerando todos os ajustes, o mapa indica estoque de $125,4 \text{ Pg}$ ($=10^{15} \text{ g}$) de biomassa seca (acima e abaixo do solo) para áreas originalmente florestadas na Amazônia Legal Brasileira ($104,2 \text{ Pg}$ somente acima do solo) no período dos inventários do RadamBrasil, portanto antes que intensivos desmatamentos tivessem ocorrido na região. Se as áreas desmatadas até 2006 forem eliminadas do cálculo, excluindo agricultura, pastagens e vegetação de floresta secundária, a estimativa de biomassa seca estocada é reduzida para $113,3$ e $94,2 \text{ Pg}$ (acima e abaixo do solo, e somente acima do solo).

SUMMARY

Uncertainties in biomass estimates are the main source of uncertainty in estimates of greenhouse-gas emissions in Amazonia. The results presented in this study reduce the uncertainties in estimates of above-ground biomass, particularly in the southern and southwestern portions of the Brazilian Amazon (SSWA), which are in the 'arc of deforestation.' In Chapter I new data on wood density obtained in the forests of the SSWA area (403 trees identified to species or genus) are combined with the inventories of wood volume produced by Projeto RadamBrasil (1973-1983). The area of each vegetation unit, defined as the intersection among forest types and the boundaries of the nine states in Brazilian Amazonia, was used to calculate a mean wood density of 0.583 g.cm^{-3} for the SSWA as a whole. This average is 13.6% lower than the value used for this area in previous estimates. An average of 0.642 g.cm^{-3} was obtained for the Brazilian Amazon as a whole, starting from the new estimates for the forests of the SSWA together with estimates for the other areas of Amazonia, corrected for radial variation (-5.3%). The new density average is 7% lower than the average previously used for the Brazilian Amazon (0.69 g.cm^{-3}). The impact on estimates of biomass and carbon emission is substantial because the reduction is largest in the forest types experiencing the most rapid deforestation. For 1990, with $13.8 \times 10^3 \text{ km}^2$ of deforestation, the estimated emission for the Brazilian Amazon would be reduced by $23.4\text{-}24.4 \times 10^6 \text{ CO}_2\text{-equivalent Mg C/year}$ (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 the soil. In Chapter II linear relationships were appraised that describe the radial variation of density for trees in dense forest in the central Amazon (CA) and new relationships are developed for trees in open forest in the southern Amazon (SA). The linear relationship described in CA for the variation of density along the bole is similar for trees in SA ($p = 0.144$). It is also demonstrated that the trees in the southern Amazon have significantly higher humidity content in their boles ($0.416 \pm 0.068 \text{ SD}$; $n = 223$) than do trees in CA (0.38 ; $n = 50$). Moisture content of the bole had a strong inverse relationship with basic wood density and explains the lower moisture content in the trees in CA relative to SA. In Chapter III CA trees are shown to be taller for any given diameter than they are in bamboo-dominated dense forests, bamboo-free dense forests and open forests in the southwestern Amazon (SW), as well as in the open forests of the southern Amazon (SA). The impact on biomass estimates is -11.0%, -6.2% and -3.6%, respectively. This suggests that the estimate of the Brazilian National Communication to the United Nations Framework Convention on Climate Change requires revision. The relationships observed between diameter and height were inconsistent with the assumptions of metabolic ecological theory and the findings reinforce the argument that the scalar allometric exponent varies among forests growing on different substrata or with different levels of natural disturbance. In Chapter IV new allometric equations for biomass are derived starting from trees weighed directly in SA and from equations for estimates of volume of the bole in CA and in SA. These equations were used to improve the biomass model historically applied in Amazonia, which is based on large-scale inventories of wood volume. A new biomass estimate is produced for the Brazilian Amazon incorporating new values of wood density, corrections for uncertainties in estimates of wood volume and new values for factors used to add the volume of the boles of small trees and the biomass of the crowns. Considering all adjustments the biomass map indicates average biomass of 125.4 Pg ($=10^{15} \text{ g}$) dry weight (above-ground + below-ground) for originally forested areas in the Brazilian Legal Amazon as a whole (104.2 Pg for above-ground only) at the time of the RadamBrasil inventories, which was before intensive deforestation had occurred in the region. If areas deforested through 2006 are eliminated, excluding agriculture, pasture and secondary forest vegetation, the estimation of dry biomass storage was reduced to 113.3 and 94.2 Pg (above-ground + below-ground and only above-ground).

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GENERAL INTRODUCTION

Changes in the atmospheric abundance of greenhouse gases and aerosols, in solar radiation and in land-surface properties alter the energy balance of the climate system. Global atmospheric concentrations of carbon dioxide, methane and nitrous oxide have increased markedly as a result of human activities since 1750 and now far exceed pre-industrial values determined from ice cores spanning many thousands of years (IPCC, 2007). Global surface temperature has increased $\sim 0.2^{\circ}\text{C}$ per decade over the past 30 years, similar to the warming rate predicted in the 1980s in initial global climate model simulations with transient greenhouse-gas changes (Hansen et al., 2006). The conclusion that global warming is a real climate change is confirmed by surface temperature change as inferred from borehole temperature profiles at remote locations, the rate of retreat of alpine glaciers around the world, and progressively earlier breakup of ice on rivers and lakes (IPCC, 2001).

The primary source of the increased atmospheric concentration of carbon dioxide since the pre-industrial period results from fossil-fuel use, with land-use change providing another significant but smaller contribution (IPCC, 2007). Globally, the long-term flux of carbon from changes in land use (1850–2000) released 156 PgC (1 Pg is 10^{15} g) to the atmosphere, about 60% of it from the tropics. Average annual fluxes during the 1980s and 1990s were 2.0 and 2.2 PgC yr⁻¹, respectively, dominated by releases of carbon from tropical deforestation (Houghton, 2003a). Because of this, the biomass of tropical forests plays an important role in the global carbon cycle both as a dynamic reservoir of carbon and as a source of carbon dioxide to the atmosphere in areas undergoing deforestation (Malhi et al., 2006; Fearnside, 2000a). Clearly the future state of Brazil's Amazonian forests is of importance to the carbon composition of the atmosphere (Brown and Lugo, 1992).

Uncertainty in forest biomass is responsible for much of the uncertainty in current estimates of the flux of carbon from land-use change (Houghton et al., 2001). Accurate estimation of biomass in Amazonian forest is an essential step in understanding the contribution of deforestation to increase of carbon dioxide in the atmosphere (Brown, 1995).

The goal of this thesis is to reduce uncertainties in estimates of above-ground biomass and of carbon emissions in Brazilian Amazonia, particularly in the 'arc of deforestation' where most of the carbon flux from land-use change takes place. This study focuses on improved estimates of wood density, which is an important variable for conversion of bole volume to biomass of the bole and in converting bole volume to tree biomass. New allometric relationships are developed for this purpose.

The thesis is divided into four chapters. Chapter I presents new wood density estimates for southern and southwestern Brazilian Amazon (SSWA), which encompass most of the ‘arc of deforestation,’ using locally collected species weighted by their volume in large local inventories. The question is examined of whether the average wood density currently used in carbon emissions estimates is suitable for SSWA. Chapter II focuses on the linear regressions for wood density in the ‘arc of deforestation’ along the region’s southern fringe and makes adjustments to the existing equations that are based on studies in central Amazonia (CA). The thesis also shows that in open forests in southern Amazonia (SA) moisture content of the bole is significantly higher than in dense forest in central Amazonia. Chapter III evaluates whether trees in southwestern and southern Amazonia are shorter at any given diameter than those in central Amazonia. This is important because forest biomass values used for estimating carbon emissions from deforestation throughout Brazilian Amazonia have been based on allometric relationships derived in CA. Chapter IV closes this thesis with biomass equations developed from trees directly weighed in SA and allometric equations for bole volume estimates of trees in both dense forests in CA and open forests in SA. Biomass estimates were obtained from these equations and used them to improve the commonly used biomass model based on large-scale wood-volume inventories carried out in Amazonian forest. Finally, a biomass map for Brazilian Amazonia was produced incorporating all corrections for uncertainties in wood density, in wood volume estimates and in the factors used to add the bole volume of small trees and to add the crown biomass.

GENERAL OBJECTIVE

The present thesis aims to improve the estimates of forest biomass and of carbon emissions from land-use change in Brazilian Amazonia, particularly in the 'arc of deforestation,' which has historically been the primary source of carbon emissions from deforestation and burning.

SPECIFIC OBJECTIVES

- 1.) To estimate the mean basic density of the wood of trees in the southern and southwestern portions of Brazilian Amazonia, weighted by the floristic composition of these areas based on existing large-scale inventories (Projeto RadamBrasil), and evaluate the impact of these improved density values on estimates of biomass and of carbon emissions.
- 2.) To compare the open forests in southern Amazonia with the dense forests in central Amazonia for variation in the basic density of wood along the length and the radius of the bole and compare the moisture content of the wood in these forest types.
- 3.) To develop linear models that allow correction of available data on wood density in Amazonia for density values that consider all components of the boles of the trees, thereby making the corrected values appropriate for biomass calculations.
- 4.) To determine whether the trees in the southern and southwestern portions of Brazilian Amazonia are shorter for any given diameter than the trees in central Amazonia and evaluate the implications of such differences for biomass estimates obtained starting from equations developed in central Amazonia corrected for the effect of height difference and/or wood density.
- 5.) To develop an allometric equation for estimating the biomass of trees in southern Amazonia using only the diameter at breast height (DBH) as an independent variable.
- 6.) To estimate, for forests in central and southern Amazonia, the biomass percentage stocked in trees smaller than 100 cm in circumference (DBH < 31.8 cm) as compared to the biomass of trees greater than 100 cm in circumference and evaluate the values currently used in

biomass models to account for the biomass of the trees not inventoried by Projeto RadamBrasil (1973-1983).

7.) To determine the percentage of biomass present in the crowns as compared to the biomass of the boles for trees in central and southern Amazonia and compare these results with the values currently used in biomass models for adding the biomass of the crowns.

8.) To evaluate the influence of irregular and hollow trunks on the estimates of total wood volume per hectare that were published by Projeto RadamBrasil (1973-1983).

9.) To develop allometric equations to allow estimation of the volume of the bole corrected for the effect of irregularities and hollow spaces using only diameter as an independent variable.

10.) To determine the form factor for trees in open forest for different diameter classes.

11.) To obtain new estimates of total biomass stocks in Amazonia using the Projeto RadamBrasil inventories after applying corrections to estimates of wood volume, wood density, the variables used to convert bole biomass to tree biomass and to per-hectare biomass, as well as using new biomass estimates for non-tree components, both alive and dead.

12.) To obtain a biomass map for Brazilian Amazonia and new estimates for carbon emissions from land-use change.

MATERIALS AND METHODS

The present study was carried out based on information obtained at 13 sites in Brazilian Amazonia, distributed in the states of Acre, Amazonas, Mato Grosso and Pará. Of these, six sites were located near Manaus in central Amazonia (Nogueira et al., 2005) and the other seven were distributed over the “arc of deforestation,” which comprises the southern (SA) and southwestern (SW) portions of the Brazilian Amazon: two sites in the state of Acre (SW open forest dominated by bamboo and SW dense forest without bamboo), four sites were in the northwestern portion of the state of Mato Grosso and one site in the southern portion of the state of Pará (all considered together and classified as “open forest of southern Amazonia,” or SA).

Data collection at all sites was authorized by the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA). In the state of Mato Grosso the collections were also authorized by the State Secretariat for the Environment (SEMA).

In each forest type, trees over 5 cm dbh were chosen at random for cutting, and measurements were made of diameter (dbh or diameter above any buttresses), total height and wood density: A total of 310 trees were measured in dense forest in central Amazonia, 92 trees in open forest dominated by bamboo in southwestern Amazonia, 97 trees in dense forest without bamboo in southwestern Amazonia and 320 trees in open forest in southern Amazonia. In this last forest type, 264 trees (5 to 124 cm dbh or diameter above any buttresses) were cut into pieces and weighted completely. Botanical samples of each tree were collected and identified by para-botanical experts at the National Institute for Research in the Amazon-INPA.

Details of each collection site, such as soils and climate, as well as the details of the methods, are described in each chapter.

Chapter I - Wood density in forests of Brazil's 'arc of deforestation': Implications for biomass and flux of carbon from land-use change in Amazonia¹.

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 chapter 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 \pm 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 overestimated. 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 $13.8 \times 10^3 \text{ km}^2$ of deforestation, emissions for the Brazilian Amazon would be reduced by $23.4\text{-}24.4 \times 10^6 \text{ Mg CO}_2\text{-equivalent C/year}$ (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.

¹ Nogueira, E.M., Fearnside, P.M., Nelson, B.W., França, M.B., 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* 248, 119-135.

Introduction

The largest error in carbon balance in the tropical region results from uncertainty in aboveground forest biomass (Houghton, 2003b, 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; Malhi et al., 2006; Nogueira et al., 2005). 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, 1983; 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 km² 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 chapter 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 A and B.

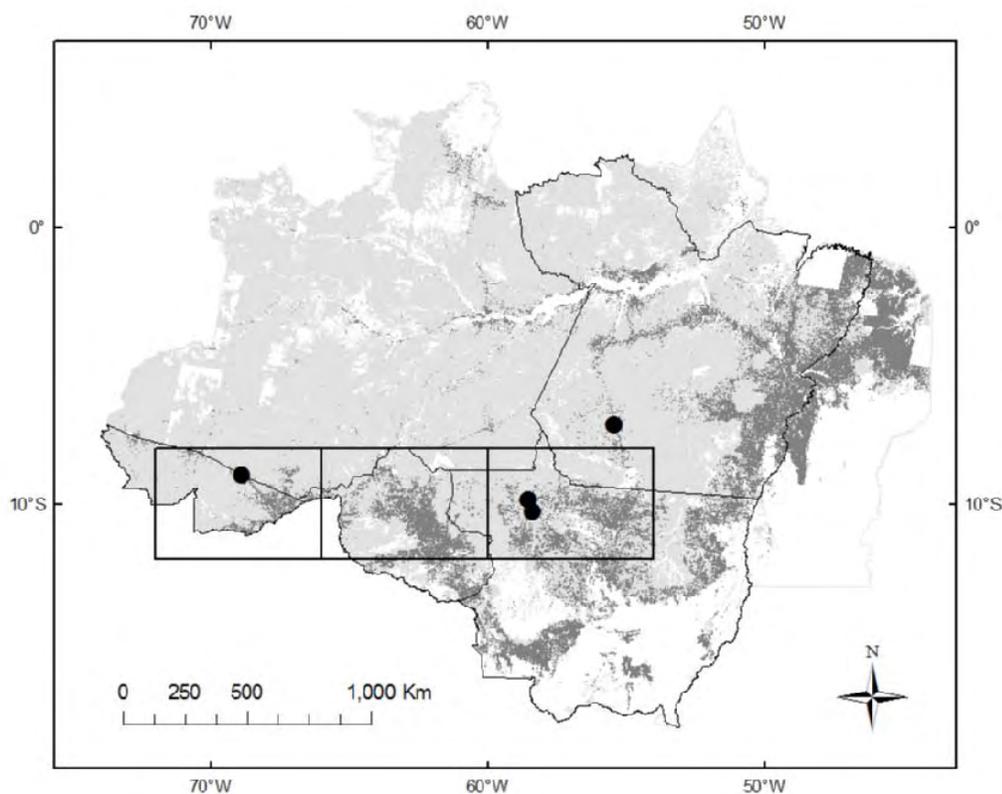


Figure 1. Solid circles show collection sites, from W to E: Sena Madureira, Cotriguaçu, Juruena and Novo Progresso. States mentioned in text are outlined, from W to E: Acre, Rondônia, Mato Grosso and Pará. Rectangles are the RadamBrasil inventories, from W to E: SC.19 Rio Branco, SC.16 Porto Velho and 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 Institute for Space Research (INPE).

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 °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 parobotanists 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 (flutuations) 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 °C (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 \pm 1 s.d.; $n = 44$). 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 angiosperm 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, $p=0.000$).

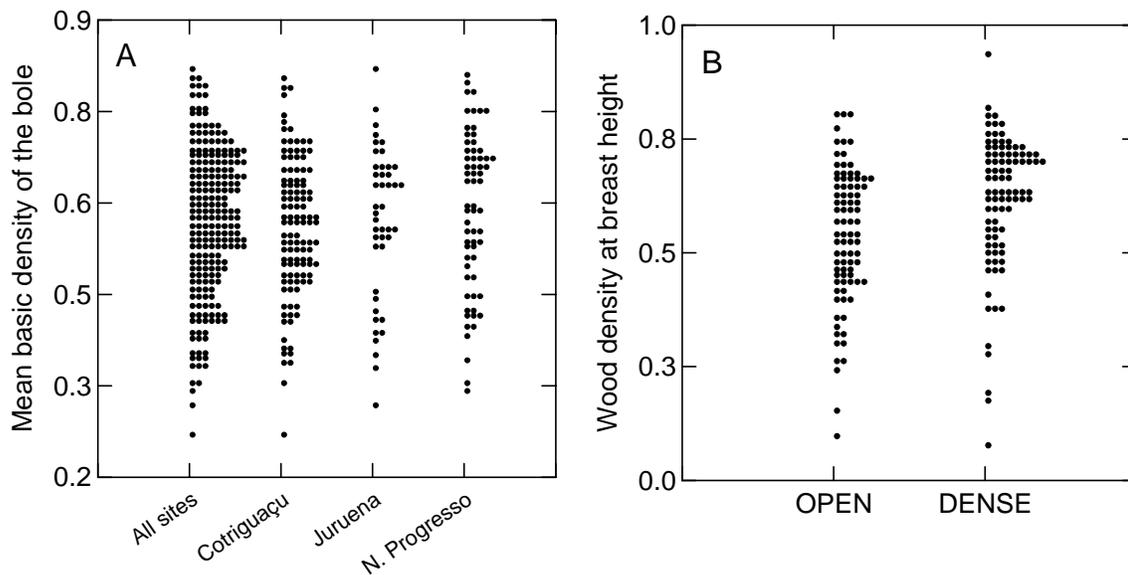


Figure 2. Mean basic density ($\text{g}\cdot\text{cm}^{-3}$) of the bole at the collection sites in southern Amazon, open forest (A) and basic density at breast height in the southwestern Amazon, Acre state (B): open bamboo-dominated forest and dense bamboo-free forest. (A) The mean was obtained from 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.

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.

Table 1. Details of the various mean measures for whole disks and for heartwood at two positions along the bole.

Basic density (whole disks and heartwood)	Juruena			Cotriguaçu			Novo Progresso			All sites together		
	Mean (\pm S.D.)	n	95%	Mean (\pm S.D.)	n	95%	Mean (\pm S.D.)	n	95%	Mean (\pm S.D.)	n	95%
Aritmetic 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: aritmetic 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) ¹	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

All values shown are basic density.

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

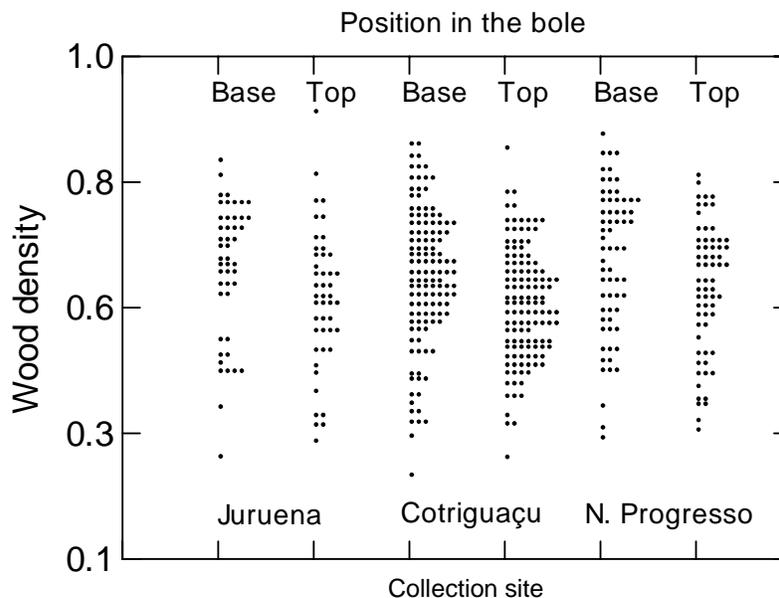


Figure 3. Decrease in the basic wood density ($\text{g}\cdot\text{cm}^{-3}$) from the base to the top of the bole. At the Juruena site 'base' refers to a sample at the top of the stump. At the Cotriguaçu and Novo Progresso sites 'base' refers to a sample at breast height (1.3 m).

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 its diameter or height.

For the southern Amazon trees, wood basic density (mean of the bole) was separated into three classes ($\leq 0.50 \text{ g}\cdot\text{cm}^{-3}$, $0.50\text{-}0.70 \text{ g}\cdot\text{cm}^{-3}$ and $\geq 0.70 \text{ g}\cdot\text{cm}^{-3}$). 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).

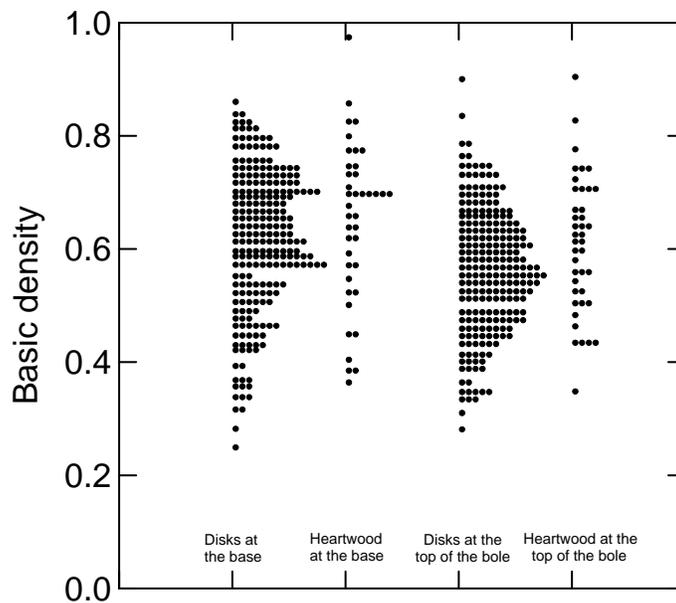


Figure 4. Radial variation between basic density (g cm^3) of whole disks with bark and basic density of heartwood.

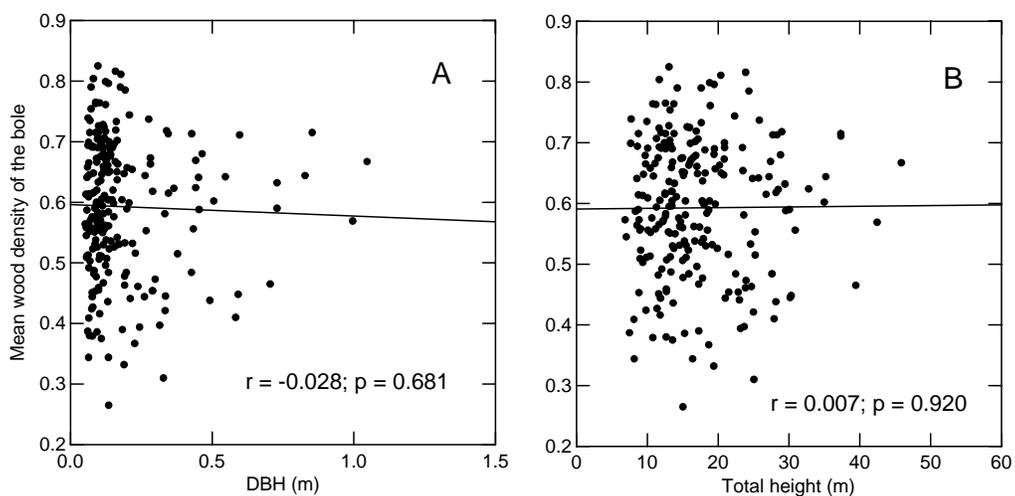


Figure 5. Relationship between mean wood density, **A:** DBH (m) and **B:** total height (m).

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).

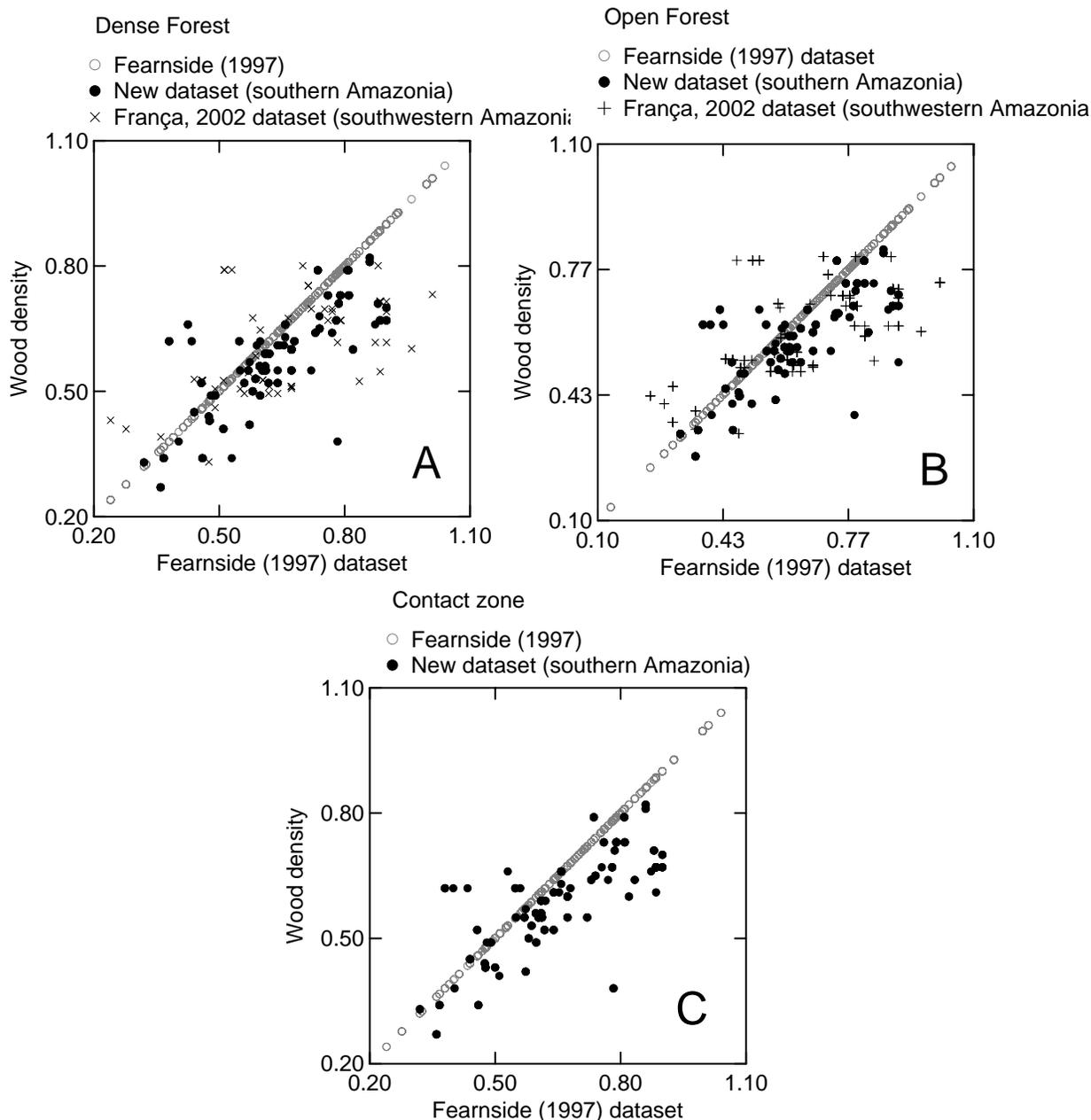


Figure 6. Comparison by forest type between the dataset used in Fearnside (1997), the new dataset obtained in southern Pará and northern Mato Grosso and the França (2002) dataset obtained in Acre. The values for wood density in the figure represent mean species-level or genus-level values. (A and B)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

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.

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%.

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).

State	Vegetation type	Fearnside (1997)	% Wood identified to: genus/species in Fearnside (1997)	New datasets	% Wood identified to: genus/species in New dataset	Test ^a	% 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 ^b	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 ^b	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 ^b	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 ^b	37.7 / 7.0	0.632	28.3 / 16.8	8.08
	Average	0.662		0.583		0.659		12.58

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.

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

^b 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 of 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).

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}).

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)		<i>0.634</i>	0.635		0.609	<i>0.634</i>	0.554	0.635	<i>0.634</i>	0.634
	Dense lowland (Db-0)	0.572	<i>0.634</i>	0.662	<i>0.634</i>		0.701	<i>0.668</i>	0.636		0.668
	Dense montane (Dm-0)		<i>0.646</i>	<i>0.646</i>			<i>0.646</i>		0.646		0.646
	Dense submontane (Ds-0)	<i>0.687</i>	<i>0.687</i>	0.696	<i>0.687</i>	0.582	0.695	0.599	0.670	<i>0.687</i>	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	<i>0.589</i>	<i>0.589</i>	0.589	<i>0.589</i>	0.589
Seasonal forest	Deciduous submontane (Cs-0)				<i>0.602</i>	<i>0.602</i>	<i>0.602</i>			<i>0.602</i>	<i>0.602</i>
	Semideciduous alluvial (Fa-0)					<i>0.602</i>					<i>0.602</i>
	Semideciduous submontane (Fs-0)					<i>0.602</i>		<i>0.602</i>	<i>0.602</i>	<i>0.602</i>	<i>0.602</i>
Woody oligotrophic vegetation of swampy and sandy areas	Open arboreal (La-0)			0.711					<i>0.711</i>		0.711
	Dense arboreal (Ld-0)			<i>0.602</i>					<i>0.602</i>		<i>0.602</i>
	Grassy-woody (Lg-0)			<i>0.602</i>					<i>0.602</i>		<i>0.602</i>
Areas of ecological tension and contact (ecotones)	Woody oligotrophic vegetation of swampy and sandy areas - rain forest (LO-0)			0.642					0.642		0.642
	Rain forest - seasonal forest (ON-0)					0.585	<i>0.587</i>	<i>0.587</i>	0.679		0.587
Areas of pioneer formations (early succession)	Fluvio-marine influence (Pf-0)		<i>0.602</i>		<i>0.602</i>		<i>0.602</i>				0.602
Areas of ecological tension and contact (ecotones)	Savanna-dense rain forest (SM-0)				<i>0.602</i>						0.602
	Savanna-seasonal forest (SN-0)			0.583	<i>0.583</i>	0.582	<i>0.583</i>	<i>0.583</i>	0.714	<i>0.583</i>	0.583
	Savanna-ombrophilous forest (SO-0)		<i>0.672</i>	0.655		<i>0.672</i>	<i>0.679</i>	<i>0.672</i>	<i>0.672</i>	<i>0.672</i>	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 seven 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).

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 (Terborgh and Andersen, 1998; ter Steege et al., 2006). 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 (Nelson et al., 2006; Putz et al., 1983). 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 (Hacke et al., 2001; Meinzer, 2003). 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 location in 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 (Baker et al., 2004; Malhi et al., 2006). The results of this chapter 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 Fearnside, 1997 and Nogueira et al., 2005, pp. 268-269).

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, these 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 chapter 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 chapter 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 study 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 $23.4\text{-}24.4 \times 10^6$ Mg of CO₂-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 study reduces estimated 1990 emissions by 4.1% for gross emissions and 4.3% for net committed emissions. The corrected gross emission for 1990 is $247.7\text{-}257.5 \times 10^6$ Mg of CO₂-equivalent C/year, while the net committed emission is $218.1\text{-}227.8 \times 10^6$ Mg of CO₂-equivalent C/year for biomass emissions only, and $230.0\text{-}239.7 \times 10^6$ Mg of CO₂-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 km² (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%: $23.4\text{--}24.4 \times 10^6$ Mg CO₂-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.

Chapter II - Linear regressions for normalization of wood density in biomass estimates of Amazon forests²

Abstract

Wood density is an important variable needed to obtain accurate estimates of biomass and carbon flux in tropical regions. However, the Amazon region lacks large-scale wood density datasets that employ a sampling methodology adequate for use in estimates of biomass and carbon emissions. Normalization of the available datasets is needed to avoid bias in estimates that combine previous studies of wood density, which used wood sampling at diverse positions in the bole or with various methods of density determination. This chapter examines the question of whether regressions for radial variation and for variation along the bole in wood density, both developed in dense forest in central Amazonia (CA), are suitable for open forest in southern Amazonia (SA) that are currently the target of most of Amazonia's deforestation activity. The wood density of the heartwood and density of full disks or slices (bark, sapwood and heartwood) in each tree (n = 146 trees in CA; 76 in SA) were measured to assess the radial variation. Therefore sampling is not representative at the community level but only for trees with heartwood. For variation along the length of the bole, wood density at breast height and at the top of the bole were used (307 trees in CA; 235 in SA). Moisture content of the bole was measured for 223 trees in SA and compared with values reported by studies from CA in similar dense forest (n = 50 trees). Comparing regressions that predict full disk density from the heartwood density, the pattern of radial variation differs slightly and significantly between the two forest types (ANCOVA p = 0.001); the slopes have similar values but the intercepts differ. The variation along the bole in the two forest types does not differ significantly (p = 0.144). So the CA model for predicting mean bole density from the density of a slice at breast height gives an unbiased estimate of the mean bole density when applied to SA trees. In SA the mean moisture content of the bole was 0.416 (\pm 0.068 SD; n = 223 trees). Moisture content of the bole had a strong inverse relationship with basic wood density (Pearson correlation = -0.77, p=0.000; n=222), which explains the lower moisture content in the trees in CA relative to SA. There was a much weaker inverse relationship between moisture content and green wood density (r = -0.292, p = 0.000; n = 222). These two results are expected if the density of dry wood tissue free of air varies little across all species and if trees with less-dense wood store more water, but not much more air, in the same volume of green wood. The relationship between wood basic density and green ('fresh') density presented in this study provides an alternative means of obtaining basic wood density directly in the field when drying samples is not possible.

Keywords: Amazon forests, basic wood density, global warming, green wood density, linear regression, moisture content.

² Written according to the norms of the journal Forest Ecology and Management.

Introduction

Wood density has been recognized as an important variable for improving biomass estimates in Amazon forests (Baker et al., 2004; Malhi et al., 2006) and estimates of greenhouse gas emissions (Fearnside, 2007; Nogueira et al., 2005, 2007). Recent large scale estimates of wood density across the Amazon have been based on a variety of earlier studies (Baker et al., 2004; Chave et al., 2006; Fearnside, 1997). However, many wood-density datasets sampled in Amazonia were intended for technological and commercial uses rather than for biomass estimates (e.g., Brazil, IBAMA, 1997; Brazil, IBDF, 1981, 1983, 1988; de Souza et al., 2002; Feldalto et al., 1989). Studies differ in collection methodology, such as the position of the sampling in the bole and the way that weight and volume are determined, usually tending to overestimate mean density (Fearnside, 1997; Nogueira et al., 2005). For biomass estimates the best measure is basic wood density (fully dry weight divided by green volume) expressed as a mean of the bole, that is, including appropriate corrections for radial variation and variation along the length of the bole of each tree. In order to use the available datasets one therefore needs accurate corrections to avoid bias in wood density means calculated from diverse measures.

Several previously published equations allow normalization to estimate basic density based on data from diverse methods of wood-density measurement, such as those that report density with 12% moisture content (e.g., Brotero, 1956; Oliveira, 1981; Reyes et al., 1992; Sallenave, 1971) (Table 1). Recent large-scale wood density estimates have adopted normalization for moisture content (Baker et al., 2004; Chave et al., 2006). However, corrections for position of sampling in the bole have not been applied in recent estimates. Different patterns of radial variation in wood density and of variation along the bole have been found in tropical trees, with density declining from the heartwood outwards in mature forest or in late-successional species and the inverse occurring in typical colonizing species, and a decline in density with height in the bole in all species groups (Nogueira et al., 2005, 2007; Suzuki, 1999; Wiemann and Williamson, 1988; 1989; Wittmann et al., 2006; Woodcock and Shier, 2002; 2003).

Table 1. Previously published equations relating wood density at different moisture contents. Equations are only reported if used in previous studies on wood density of tropical or Amazonian species.

<i>Models for moisture content wood density normalization</i>	<i>Model's details</i>	<i>Reference</i>
$[\text{Density}_{(12\% \text{ moisture content})}] = 0.974 \times ((1 + 0.15 \times \text{CVS}) / (1 + 0.12 \times \text{CVS})) \times [\text{Density}_{(15\% \text{ moisture content})}]$	CVS = coefficient of volumetric swelling.	Brotero (1956), equation used by de Souza (2002)
$[\text{Density}_{(n\% \text{ moisture content})}] = [\text{Basic density}] \times ((1 + n/100) \times (1 - \text{CVn}/100)^{-1})$	CVn = volumetric swelling of wood until the wood reaches n% moisture content.	Oliveira (1981), equation used by de Souza (2002)
$[\text{Basic wood density}] = [\text{Density}_{\% \text{ moisture content}}] - (\% \text{ moisture content} \times d) / (1 + v \times (\text{fiber saturation point} - \% \text{ moisture content}))$	d = weight correction factor per 1% change in moisture content; v = variation in volume per 1% change in moisture content.	Sallenave (1971), equation used by Chave et al. (2006)
$[\text{Basic wood density}] = 0.872 \times [\text{Density}_{(12\% \text{ moisture content})}]$	n = 1893; $r^2 = 0.983$. The factor 0.872 was found by Chave et al. (2006) based on Sallenave wood samples from many tropical forests	Chave et al. (2006) from Sallenave (1955, 1964, 1971)
$[\text{Basic wood density}] = 0.0134 + 0.800 \times [\text{Density}_{(12\% \text{ moisture content})}]$	n = 379 trees (using data in Chudnoff, 1984); $r^2 = 0.988$	Reyes et al. (1992)

See Simpson (1993) for other equations and table for determining density from moisture content.

Some compilations of published wood density are based on heartwood samples taken near breast height. Linear regressions are available relating the wood density of a full disk (bark, sapwood and heartwood) to the density of heartwood and for relating the wood density of a full disk at breast height to the mean basic density of the bole (see Table 2), but these relationships have not been tested in the forests of the southern Amazon. It is particularly important to have correction equations for wood density to improve biomass estimates in the open forests that occur at the southern fringe of the Amazon region where most deforestation activity and carbon emissions are taking place (Brazil, INPE, 2006). Environmental conditions in this region are different from those in dense forest of the central Amazon because soils are more fertile, insolation is higher and dry seasons are longer; all of these characteristics affect wood density in some way (Malhi et al., 2004; Sombroek, 2000; ter Steege et al., 2006). Lower wood densities found in open forest with a prolonged dry season in southern Amazonia (Nogueira et al., 2007) suggest a relationship with stem water storage, and hence help explain the phenology and distribution of species (Borchert, 1994; Reich and Borchert, 1984; Schulze et al., 1988).

Table 2. Linear regressions developed in dense forest in central Amazonia (CA) tested in this study.

<i>Models for wood density corrections in sampling position in the bole*</i>	<i>Regression statistics</i>
(1) [Basic density of the disk at breast height] = 0.146 (± 0.014) + 0.765 (± 0.017) \times [Heartwood basic density]	Coefficients \pm Std Error; $r^2 = 0.931$, MSE = 0.033, F = 1945, n = 146.
(2) [Mean basic density of the bole] = 0.219 (± 0.014) + 0.630 (± 0.018) \times [Heartwood basic density]	Coefficients \pm Std Error; $r^2 = 0.893$, MSE=0.034, F = 1199, n = 145.
(3) [Taper-adjusted mean basic density of the bole] = 0.099 (± 0.020) + 0.808 (± 0.028) \times [Basic density of the disk]	Coefficients \pm Std Error; $r^2 = 0.925$, MSE = 0.027, F = 832, n = 69.

*Data source: Nogueira et al. (2005)

In this study three linear regressions developed in dense forest in central Amazonia (Table 2, from Nogueira et al., 2005) were evaluated for bias when accounting for radial and vertical variation in wood density of trees sampled in the open forests of southern Amazonia (Table 2). If the linear relationships in the two forest type are not significantly different, a single pooled regression can be developed for the two forests. A pooled regression would also have greater precision. Finally, for the southern Amazon open forests this study also examined the ratio between green mass and dry mass for each sample. This ratio was

considered to be equivalent to the moisture content of the bole when obtained from samples at the base and at the top of the bole.

Materials and Methods

Collection sites

The samples used in this study were collected at six sites in primary forests in the central Amazon (CA) and five sites in southern portion of the Brazilian Amazon (SA). The CA sites were located near Manaus, Amazonas state (Nogueira et al., 2005). Four of the SA sites were in the northwestern portion of Mato Grosso state in the counties of Juruena (2 sites), Cotriguaçu (1 site) and Carlinda (1 site). The fifth site was located in the southern portion of the state of Pará in the county of Novo Progresso.

At all CA sites the predominant vegetation is dense forest with a mean altitude ~100 m above mean sea level (m.s.l.). In SA the vegetation is open rain forest at ~300 m above m.s.l. with either vines or palms as subdominant life forms. The soils at the CA sites are yellow latosols (acrisols) that are poor in nutrients (Magnago et al., 1978; Yamazaki et al., 1978). The sites in Mato Grosso state are predominantly on xanthic or orthic ferralsols and ferralic arenosols. At the site in southern Pará the soils are predominantly orthic acrisols and ferralsols on granite shield uplands (FAO, 1988; Sombroek, 2000). At the CA sites the average annual rainfall is about 2300 mm. At the Mato Grosso sites the predominant climate is tropical humid with 2075 mm annual precipitation. Rainfall in the CA is below 100 mm/month during three months, from July to September (Marques-Filho et al., 1981). At the Mato Grosso sites there is a six-month dry period from May to September with mean monthly precipitation below 100 mm (Brazil, ANA/SIH, 2006). At the southern Pará site the average annual precipitation is 2280 mm and the dry period extends from June to August (Brazil, ANA/SIH, 2006; Oliveira et al. 2004). In CA the mean monthly temperature is stable throughout the year at around of 26 °C (Marques-Filho et al., 1981). A similar annual average is found at the other sites (Brazil, INMET, 2006).

Collection of samples for wood density determination

The trees felled in each forest type were always chosen randomly but stratified by size class according to the proportion that each class contributes to basal area in local forest inventories. The research plan was authorized by the Brazilian Institute for Environment and

Renewable Natural Resources (IBAMA) and in Mato Grosso state by the Environment Secretariat (SEMA/MT). For density determination, disks of constant thickness (~3 cm) were taken at breast height (even in the presence of buttresses) or at the top of the stump (Juruena site), and at the top of the commercial bole. For variation in wood density along the length of the bole, samples taken at breast height and at the top of the bole were used: 307 trees in CA with dbh 5-122 cm, identified as 186 species or morpho-species and 235 trees in SA, dbh 5-104 cm, in 130 species or morpho species. Any radial variation in density was included by obtaining a full slice of even thickness. Basic wood density was determined for this disk or for a wedge obtained from it. When present, samples of the heartwood were taken close to the center of the disks. In 146 trees of the CA sites (dbh 13-106 cm, 112 species or morpho-species), heartwood samples were taken only at breast height, while in SA sites (n = 76 trees, dbh = 9-124 cm, 40 species or morpho-species) heartwood samples were also taken at the tops of the stump and bole. The green (or 'fresh') mass and volume were determined on the same day. The green volume was determined by displacing water in a container placed on a battery-operated scale, also used in the mass determination. In this study green mass and volume do not mean that the wood is completely saturated with water (Simpson and TenWolde, 1999), but rather refers to wood newly removed from the tree. In SA trees (n = 223; dbh 5-104 cm, 125 species or morpho-species) the ratio between green mass and mass after oven drying was used as a measure of bole water content (e.g., Borchert, 1994; Schulze et al., 1988). This attribute was obtained both at the base and top of the bole. The green mass was not measured in samples from trees from CA sites. For the dry weight of each sample a vented electric oven was used at 103 °C (ASTM, 2002) and samples were considered completely dry after three consecutive stable weight readings at 24-hour intervals. For all trees, the mean basic density of the bole (not taper-adjusted) was determined as the arithmetic mean of the density at breast height (or at the top of the stump for the Juruena site) and at the top of the bole. A taper-adjusted mean density was not determined in the SA trees because it did not differ significantly from the arithmetic mean (Nogueira et al., 2005). However, the model developed in dense forest (CA) tested in this study used taper-adjusted mean density of the bole as the dependent variable. In this study it was assumed that mean taper-adjusted and mean non-taper adjusted measures also did not differ significantly in open forest.

Linear model statistics from trees in southern Amazon (SA)

Higher adjusted r^2 and lower standard error of the estimate constituted the statistical criteria for selecting the best model to predict full disk density from heartwood density and to predict 'green density' (green mass/green volume) from basic density (dry mass/green volume). The relations between the variables were found to be linear and the residuals were uniformly and normally distributed.

Results

Wood density radial variation

The linear relationships between heartwood density and full disk density for dense forest (CA) and for open forest with palms (SA) had similar slopes ($p = 0.441$) but different intercepts ($p = 0.001$) (Figure 1). The intercept for the CA regression was $0.146 (\pm 0.014 \text{ SE})$, Table 2); for SA it was $0.110 (\pm 0.022)$ (Table 3). Despite not having a statistically significant difference, Figure 1 indicates that the lines are not parallel. The values are clearly lower for lower values of heartwood density, but tend to converge for values above approximately 0.75. In this case, the model for CA could be applied in SA, so long as only the slopes of the lines are considered and not the intercept. In a scatterplot of heartwood density against full-disk density, 63% of the SA samples fell below the regression line for the Central Amazon. The average full disk density of all SA samples estimated using the SA model is off by only ~0.4% (difference = $-0.002 \pm 0.149 \text{ SE}$), but is overestimated by 3% using the CA regression (Model 1 in Table 2).

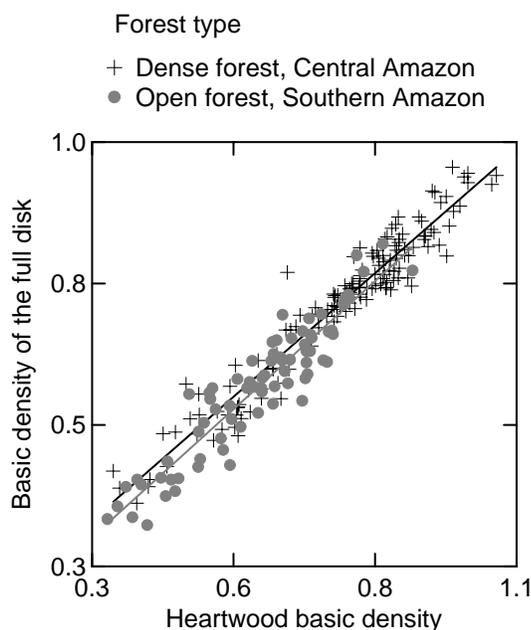


Figure 1. The relationship between basic density of the full disk and basic density of the heartwood in dense forest in central Amazonia (n = 146 trees) and in open forest in southern Amazonia (n = 76 trees).

Table 3. New linear regressions developed in open forest in southern Amazonia (SA) proposed in this study.

<i>Model description</i>	<i>Regression statistics</i>
[Wood density of the full disk] = 0.110 (± 0.022) + 0.793 (± 0.035) \times [Heartwood basic density]	Coefficients \pm Std Error; Adjusted $r^2 = 0.872$, Std error of estimate (SEE) = 0.039, F = 512, n = 76.
[Mean basic density of the bole] = -0.143 (± 0.034) + 0.728 (± 0.033) \times [Mean green wood density of the bole]	Adjusted $r^2 = 0.680$, SEE = 0.064, F = 474, n = 224.
[Mean basic density of the bole] = -0.076 (± 0.036) + 0.654 (± 0.035) \times [Green wood density at breast height]	Adjusted $r^2 = 0.665$, SEE = 0.065, F = 359, n = 181 trees.

Radial variation is denoted %RV, or how much the heartwood density exceeds the full disk density, expressed as a percentage of the latter. A tree with negative %RV has lower wood density in the heartwood than in the whole disk, thus decreasing density toward the center, while positive values are found in trees with increasing density toward the center. In open forest 63% of sampled trees with heartwood had wood density decreasing towards the outside, while in dense forest this was the case for 82% of the trees with heartwood (see Nogueira et al., 2005).

Percent RV was related to $\ln(\text{heartwood density})$ in both forest types ($r^2 = 0.506$ in dense forest and $r^2 = 0.368$ in open forest, both $p = 0.000$). Trees with high density heartwood were lighter toward the outside, while trees with light heartwood tended to increase in density toward the outside (negative values for %RV) (Figure 2). This would seem to be consistent with a tendency for light trees to add denser wood toward the outside as they grow larger. However the relationship between %RV and diameter or height does not support this conclusion. In the SA, trees that *decrease* in density toward the outside do this to a greater degree if they are large, while trees that increase in density toward the outside do not do so to a greater degree if they are large (Table 4, Figure 3A, B). This suggests that trees reinforce the strength of their central core as they grow larger, rather than adding a series of successively denser nested cylinders of wood. No relationship between tree size and %RV was found in the CA region (Figure 3C, D).

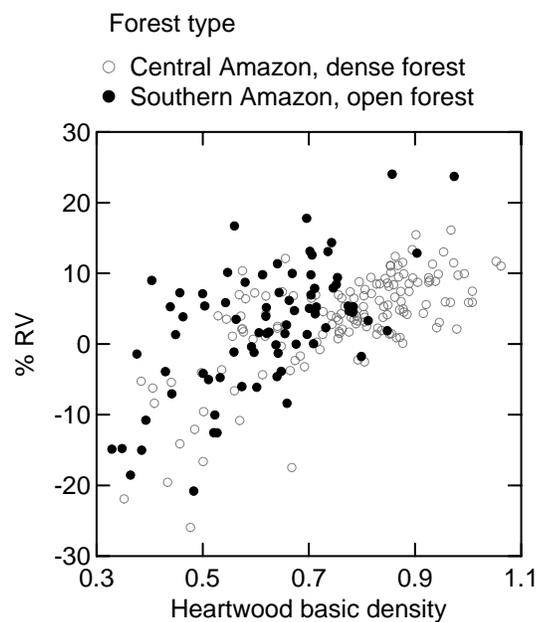


Figure 2. Difference between basic density of heartwood and of the full disk (%RV) in dense and open forest.

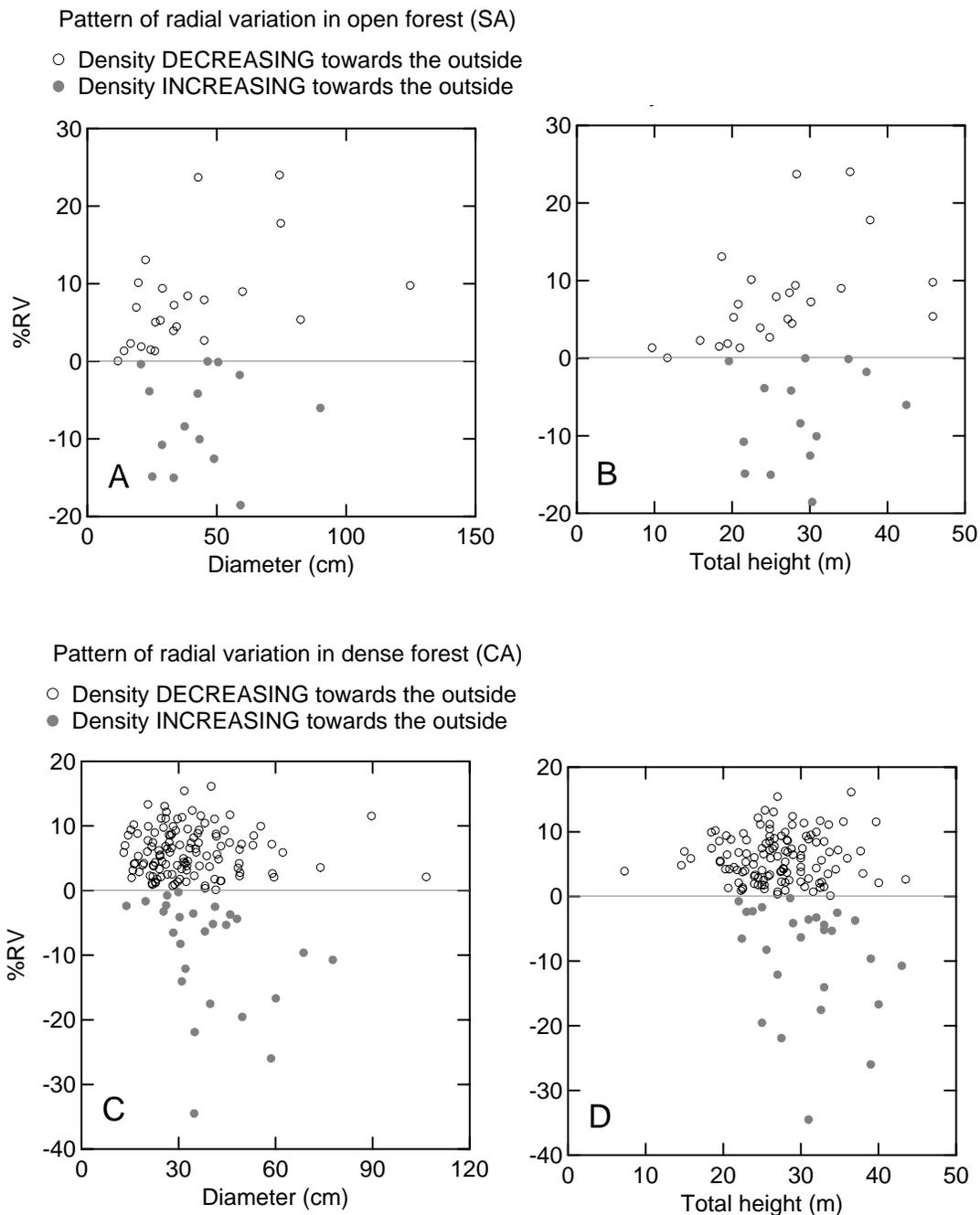


Figure 3. Relationship between diameter (at breast height or above buttresses) and total height of trees with %RV (meaning the difference between basic density of heartwood and that of the full disk) in open forest in southern Amazonia (**A** and **B**) and in dense forest in central Amazonia (**C** and **D**). Positive values of %RV mean that density decreases towards the outside and negative %RV values mean density increases towards the outside. For the significance of Pearson correlation and probability values, see Table 4.

Table 4. Correlation between pattern of radial variation (%RV) in density with diameter and total height in trees from two forest types: Dense forest, Central Amazonia and Open forest, Southern Amazonia.

% RV in trees from Dense and Open forest		Diameter	Total height
		Pearson correlation and (p value)*	
Density DECREASING towards the outside	Dense (n = 120)	- 0.002 (0.982)	0.053 (0.565)
	Open (n = 24)	0.450 (0.027)	0.490 (0.015)
Density INCREASING towards the outside	Dense (n = 26)	- 0.345 (0.084)	- 0.257 (0.204)
	Open (n = 14)	0.041 (0.890)	0.214 (0.463)

* Numbers in bold type are significantly different at the 5% level.

Variation in wood density along the bole

Two linear regressions (mean density of the bole \times density at breast height) do not differ statistically in paired comparisons between dense (CA) and open forest (SA), ($p = 0.144$; $n = 542$), Figure 4. The linear model for estimating taper-adjusted mean wood density of the bole from disks at breast height (Model 3 in Table 2) resulted in accurate estimates of the mean density of the bole: 0.007 ± 0.157 SE difference between measured and estimated mean, or $\sim 1\%$).

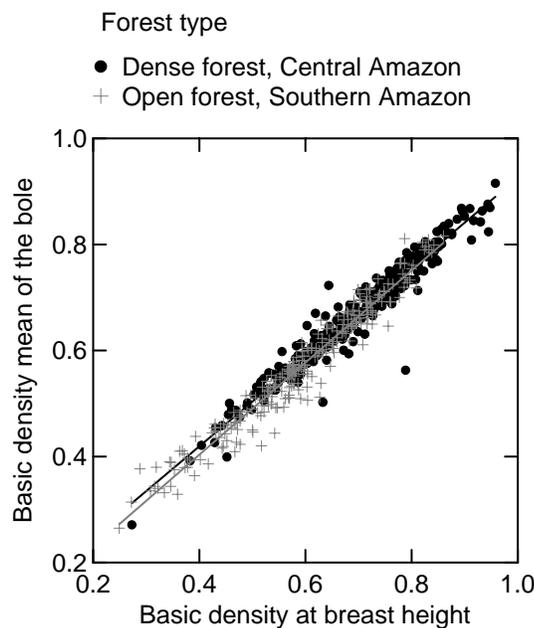


Figure 4. Relationships between the mean basic wood density of the bole and wood density at breast height (full disk) in dense forest in central Amazonia ($n = 307$) and in open forest in southern Amazonia ($n = 235$).

Moisture content

The mean moisture content of the bole in 223 trees in the southern Amazon was 0.416 (± 0.068 SD; 95% CI 0.407 – 0.425; range 0.246 – 0.595). Moisture content of the bole was inversely related to basic wood density (Pearson correlation = -0.77, $p = 0.000$; $n = 222$) (Figure 5A). There was a much weaker inverse relationship between moisture content and green wood density ($r = -0.292$, $p = 0.000$; $n = 222$) (Figure 5B). These two results are expected if the density of dry wood tissue free of air varies little across all species and if trees with less-dense wood store more water, but not much more air, in the same volume of green wood. The moisture content increased with height along the bole (paired t -test, $p = 0.000$; Figure 5C), suggesting more moisture in younger tissues. The percentage moisture content at the base of the bole (top of the stump or at breast height) was 0.399 (± 0.075 SD; $n = 223$, 95% CI 0.389 – 0.408; range 0.22 – 0.67) while at the top of the bole moisture content was 0.433 (± 0.070 SD; $n = 223$, 95% CI 0.442 – 0.423; range 0.18 – 0.65). The moisture content of the entire bole was not significantly related to bole diameter at breast height ($r = 0.020$, $p = 0.766$, $n = 223$). Two linear relations between ‘green density’ and basic wood density using trees sampled only in open forest (SA) are described in Table 3.

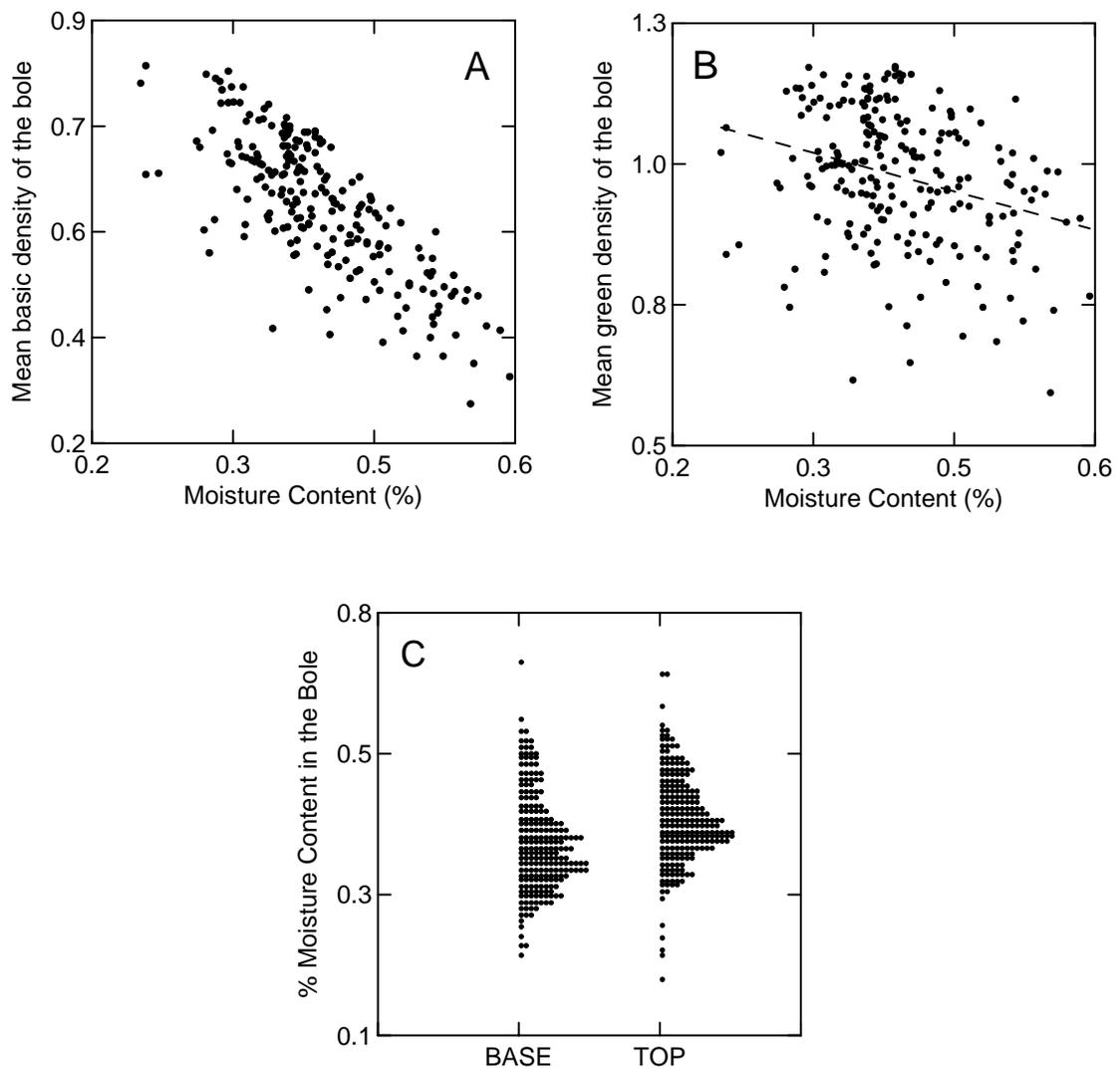


Figure 5. Relationship between moisture content (%) with mean basic wood density of the bole (A) and, mean ‘green density’ of the bole (B). Variation in moisture content (%) along the length of the bole is also presented (C).

Discussion

Wood density normalization for biomass estimates

The relationships reported in this chapter for radial variation and variation along the bole allow a heartwood dataset or a dataset of full-disk densities at breast height sampled in dense and open forest to be converted to basic density of the whole bole that is suitable for

biomass estimates. Dense and open forests are the two main forest types presently undergoing deforestation in Brazilian Amazonia (Brazil, INPE, 2006).

Although radial variation in both dense and open forest has similar patterns, the regression developed in CA (dense forest) does not adequately describe light-density woods (Figure 1). This resulted in overestimated biomass in open forest due to the predominance of trees with light density (Figure 2). The heartwood and full disk densities in open forest tend to be lower than those of dense forest (Figure 1). Although the bias is small (~3%) when the CA linear regression is applied in open forest, this percentage is substantial for carbon balance and can be minimized by use of a region-specific SA regression or by using the CA regression and ignoring the constant. In any case, a separate regression for predicting full disk density from heartwood is described for open forest with palms (Table 3). Furthermore, this chapter examines only one open forest type, which has no intrinsic disturbance. Open forests dominated by climbing bamboo or by dense tangles of lianas have many gaps which favor fast-growing trees with light wood.

The results (Figure 4) show that a single regression developed in dense forest (Table 2, Model 3) also can be applied in open forest to correct for the position of the sampling along the length of the bole. This means that the pattern of variation along the bole is similar between dense forest and open forest and that simple percentage corrections can also be used (about 4.3% on average, see Nogueira et al., 2005, 2007). Bias from variation along the bole has not been corrected in recent large-scale wood-density estimates and can result in substantial overestimation.

Models that predict full-disk density from known heartwood density are needed for biomass estimates because there are regions where only heartwood density is available. For western Amazonia wood density datasets have all been obtained from heartwood (Baker et al. 2004, p. 562, Table A1). These heartwood values without correction were used by Malhi et al. (2006) to produce biomass maps. In Brazilian Amazonia most of the wood density measurements in Amazonian forest were also based on heartwood, such as those of IBDF (Brazil, IBDF, 1981, 1988, 1989) and IBAMA (Brazil, IBAMA, 1997). Although the corrections to current heartwood data help improve biomass estimates, it is important to consider that the patterns of radial density found in this study are not representative at the community level because they were based only on trees with heartwood and therefore do not apply to all species. Moreover, in open forest the use of datasets based only on heartwood can

overestimate density because light species without heartwood will be under-represented, in contrast to dense forest, which is predominantly composed of species with medium or dense wood.

Together with moisture content the corrections for radial variation and variation along the bole allow resolution of almost all bias present in previously published datasets, but there still remains the relation of the density of non-tapered cores to the full-disk density. These relationships are important because core sampling is a practical and non-destructive method and because a number of recent studies have used increment borers (DeWalt and Chave, 2004; King et al., 2006; Muller-Landau, 2004; Woodcock and Shier, 2003; Woodcock, 2000). In spite of several prior studies having obtained wood density from cores sampled with increment borers, no equations exist for estimating density of the full disk using core samples.

Wood density radial variation in trees from dense and open Amazonian forest

The occurrence of trees with dense heartwood is expected to differ between dense and open forest types because the abundance of species with light and medium density wood is higher in open forest (around 91% in open forest with palms versus 67% in dense forest), (Nogueira et al., 2005, 2007). Tropical species with light wood density usually do not have heartwood (e.g. *Cecropia* spp.), and in species with lower central density there is a tendency for wood density to be higher toward the outside, as shown in Figure 2. Moreover a greater percentage of the trees in open forest had %RV in the range -5% to +5% (Figure 2), and thus showed little or no radial tendency. Families such as Bombacaceae, Tiliaceae, Malvaceae, Caricaceae and certain genera of Leguminosae generally have light wood or lack heartwood. Chave et al. (2006) suggest that western Amazonian forests are also dominated by families with low mean wood density. The fast-growing species that are common in liana-dominated and in bamboo-dominated open forests also may not have heartwood.

Although prior studies suggest that substantial radial variation is predominant in species with low wood density, this study shows that the difference between heartwood and full-disk density is also high for species with high heartwood density (Figure 2). Despite heartwood and full-disk density being strongly correlated (Figure 1). Figure 2 indicates that when heartwood is very dense, the sapwood and bark have a lower relative density.

There are four possible strategies as trees grow larger: (1) species with uniformly low density over the course of their development, (2) uniform high density, (3) species that invest

in an increasingly dense heartwood core as they grow and (4) species that initially have lower density overall and invest in higher density wood toward the outside of the bole as they grow. Only the first three patterns were detected in this study. Nonetheless, studies of pioneer and early successional species have found dramatic radial increases from pith to bark (Wiemann and Williamson, 1988; 1989; Woodcock and Shier, 2002, 2003).

In dense forest, species with denser heartwood are more abundant (Figure 2), while in open forest there many species with light heartwood. Also, because of this the stand-level wood density tends to be lower in disturbed forest or in the initial stages of development because of the prevalence of colonizing species (Suzuki, 1999). Thus wood density is an indicator of the changes in primary vegetation in Amazonian forests and is important for studies of biomass loss in standing forests (Laurance et al., 2006). This could be important in assessing changes in biomass of Amazonian forest caused by global warming because the methods used so far are only able to assess increments in diameter over a period of years, but not intrinsic changes in biomass stock, such as those caused by changes in wood density and other wood properties (Bräker, 2001).

Moisture content

The results of this study suggest differences in water storage in the boles of trees in dense forest (CA) and open forest (SA) that could have implications for estimates of biomass in Amazonian forests. In dense forest the moisture content used by Chambers et al. (2001) for converting fresh biomass to dry mass in central Amazonia was 0.38 (± 0.08 SD; $n = 50$ trees) for all above-ground tree components (bole, branches, leaves), similar to the value of 0.39 (bole only) adopted by Higuchi et al. (1998) based on 38 trees and 0.388 found by da Silva (2007) based in 128 trees. The moisture in boles in open forest found in this study (0.416) differs significantly from the value found by Higuchi et al. (1998) and by da Silva (2007) in dense forest in the central Amazon ($t = 5.641$, $df = 222$, p value < 0.0005) and differs from the value of 0.38 reported by Chambers et al. (2001) ($t = 7.847$, p value < 0.0005). This suggests that allometric equations developed in dense forest that estimate fresh mass from diameter only (such as the equations of Chambers et al., 2001 and Higuchi et al., 1998) will lead to two kinds of overestimate when applied to open forest. First, the lower wood density of open forests must be considered. Second, an additional 3-4% overestimate will occur if fresh mass is converted to dry mass using moisture contents typical of dense forest. An example is the

study of Cummings et al. (2002) that used the Higuchi et al. (1998) model. The increase in the percentage moisture content with height of the bole (e.g., Figure 5) indicates that measurements are needed of moisture content along the length of the bole in order to obtain dry mass from tree biomass measures (Nelson et al., 1999).

Moisture content of the bole depends directly on wood properties because when specific gravity is high, lumen volume is low and maximum moisture content is restricted (Simpson, 1993; Simpson and TenWolde, 1999). Species with lower wood density have more parenchyma tissues and hence higher water-storage capacity than denser species (Figure 5A) (Borchert, 1994; Borchert and Pockman, 2005; Roth, 1981; Schulze et al., 1988; Suzuki, 1999). Because of this a higher moisture content is expected in the boles of trees in open forest because there are more light-density species than in dense forest (Nogueira et al., 2005, 2007), which could be caused in part by dry-season length. Although the ecophysiological explanation for differences in moisture content between different forest types is not yet entirely known, it is widely recognized that wood density plays an important role in tree water status because the wood is an important component of the soil-plant-atmosphere continuum (Hinckley et al., 1991). For example, wood density is an important determinant of xylem water transport properties (such as specific hydraulic conductivity and xylem cavitation resistance), thereby determining patterns of regulation of whole-plant water balance (Hacke et al., 2001; Meinzer, 2003).

The lack of a relationship between moisture content and bole diameter shown in this study could help in understanding the partitioning of soil water among species or size-classes of trees in tropical seasonal forest, as well as the presence of deep roots (Dawson, 1996; Goldstein et al., 1998; Meinzer, 2003). Different from several prior studies, the results in this chapter are representative at the community level because they include 125 species or morpho-species distributed over a wide range of diameters (dbh 5 to 104 cm) and because moisture content was obtained from samples of all tissues in the bole (bark, sapwood and heartwood) rather than only from heartwood samples (e.g., Borchert, 1994; Meinzer et al., 1999). Previous studies have developed equations for determining wood density as a function of moisture content (Simpson, 1993). The two new equations developed in the present study are also useful for estimating moisture content in the boles of trees. The new linear models are also useful for converting green (fresh) density to basic density from samples taken at breast height or representative of whole bole (mean of the bole). For Brazilian Amazonia, datasets

are scarce that are obtained as green density, but these relationships are useful for moisture content studies in the boles of trees. These linear regressions allow basic wood density to be obtained directly in the field, without requiring the use of a vented electric oven. This application of the new models can be very important in remote parts of the Amazon forest.

Conclusions

In spite of the importance of corrections for the heartwood density dataset for improved biomass and carbon-flux estimates, linear regressions developed in dense forest do not adequately describe radial variation in trees of open forest, southern Amazonia (SA). Heartwood regressions from dense forest tend to overestimate the mean density of disks or the mean of the bole in open forest. However, for corrections of variation along the bole in open forest, the regression from dense forest provides an accurate correction of the wood-density mean. Two new regressions described in this study allow basic wood density to be obtained from the green density mean of the bole (either from samples taken at breast height or from the mean of the bole). The equations can also be useful in studies of water storage in trees. In open forests in southern Amazonia moisture content of the bole is significantly higher than in dense forest in central Amazonia. For normalization of wood densities from a variety of datasets an equation is needed that directly relates values from cores taken with increment borers to the wood density of disks (heartwood, sapwood and bark).

Chapter III - Tree Height in Brazil's 'Arc of Deforestation':

Shorter trees in south and southwest Amazonia imply lower biomass³

Abstract

This chapter estimates the difference in stand biomass due to shorter and lighter trees in southwest (SW) and southern Amazonia (SA) compared to dense forest in central Amazonia (CA). The official forest biomass values used for estimating carbon emissions from deforestation throughout Brazilian Amazonia have been based on allometric relationships derived in CA. Thus, estimates of carbon emissions will be affected by any differences between CA forests and those in the "arc of deforestation" where clearing activity is concentrated along the southern edge of the Amazon forest. At 12 sites (in the Brazilian states of Amazonas, Acre, Mato Grosso and Pará) 763 trees (dbh = 5 to 124 cm) were felled and measurements were made of total height and of stem diameter. In CA dense forest, trees are taller at any given diameter than are those in SW bamboo-dominated open, SW bamboo-free dense and SA open forests. Compared to CA, the three forest types in the arc of deforestation occur on more-fertile soils, experience a longer dry season and/or are disturbed by climbing bamboos that cause frequent crown damage. Observed relationships between diameter and height were inconsistent with assumptions of metabolic ecology theory. This reinforces the argument that allometric scaling exponents (2/3) between height and diameter vary in forests on different substrates or with different levels of natural disturbance. Reductions in stand biomass due to shorter tree height alone were 11.0%, 6.2% and 3.6%, respectively, in the three forest types in the arc of deforestation. A prior study had shown these forest types to have less-dense wood than CA dense forest. When tree-height and wood-density effects were considered jointly, total downward corrections to estimates of stand biomass were 39%, 22% and 16%, respectively. Downward corrections to biomass in these forests were 76 Mg ha⁻¹ (~ 21.5 Mg ha⁻¹ from the height effect alone), 65 Mg ha⁻¹ (18.5 Mg ha⁻¹ from height), and 45 Mg ha⁻¹ (10.3 Mg ha⁻¹ from height). Hence, biomass stock and carbon emissions are overestimated when allometric relationships from dense forest are applied to SW or SA forest types. Estimates of biomass and carbon emissions in Brazil's National Communication under the United Nations Framework Convention on Climate Change require downward corrections for both wood density and tree height.

keywords: Allometry; Carbon; Global warming; Greenhouse gas emissions; Tropical forest; Wood density.

³ Nogueira, E.M., Nelson, B.W., Fearnside, P.M., França, M.B., de Oliveira, A.C.A., 2008. Tree height in Brazil's 'arc of deforestation': Shorter trees in south and southwest Amazonia imply lower biomass. *Forest Ecology and Management*. doi:10.1016/j.foreco.2008.02.002

Introduction

Large-scale patterns, such as physiognomy of the vegetation, floristic composition, tree turnover and biomass stock have recently been described for Amazonian vegetation (Eva et al., 2004; Houghton et al., 2001; Malhi et al., 2006; Phillips et al., 2004; Terborgh and Andresen, 1998; ter Steege et al., 2000, 2006). Conventional classifications have generally assumed that the Amazon region has two main forest types, identified as “dense” and “open” forest (Veloso et al., 1991). The dense forest is more extensive (Brazil, IBGE, 1997) and has denser wood (Chave et al., 2006; Nogueira et al., 2005, 2007), giving this forest a larger biomass stock than open forest (Malhi et al., 2006). The per-hectare total basal area has been clearly shown to be higher in the central Amazon than at the region’s southern edge, mainly due to the difference in the abundance of small trees (Baker et al., 2004; Malhi et al., 2006). While dense forests are on poor soils, open forests occur on more fertile soils in the southern portion of Brazilian Amazonia (Brazil, RadamBrasil, 1973-1983; Brown and Prance, 1987; Malhi et al., 2004; Sombroek, 2000). Solar radiation is more seasonal and the dry season is longer in open forest, affecting tree species diversity and above-ground net primary productivity (Baker et al., 2004; Chave et al., 2006; Laurance et al., 2006; Malhi et al., 2004; Meinzer et al., 1999, 2001; ter Steege et al., 2003, 2006; Tuomisto et al., 1995).

Two open forest types disturbed by abundant lianas or climbing bamboo cover 366,000 km² of the southern Brazilian Amazon (Brazil, IBGE, 1997). Recent gaps and low-stature patches occupied 40% of a liana-dominated forest in the eastern Amazon (Gerwing and Farias, 2000). Forest dominated by climbing bamboo (*Guadua* spp.) is also largely composed of disturbed patches. These gap-rich forests sustain more fast-growing pioneer tree species. Consequently, wood density is lower than in neighboring dense forest without climbers (Nelson et al., 2006). In open forests disturbed by climbing bamboo or lianas (Putz et al., 1983; Putz, 1984; Schnitzer et al., 2000; Silveira, 1999), smaller trees suffer stem breakage and height loss (Clark and Clark, 2001; Griscom and Ashton, 2006). In the Peruvian Amazon, Griscom and Ashton (2006) found that, in the presence of abundant climbing *Guadua* spp., trees 5-29 cm in diameter attained an average height that was about 50-55% that of trees in the same size classes in nearby bamboo-free plots. Griscom and Ashton (2006) attributed this difference to crown and stem breakage. Trees larger than 30 cm dbh were mostly beyond the reach of bamboo and these showed no difference in average height between neighboring plots with and without bamboo. In a liana-dominated open forest in the

Bolivian Amazon, Alvira et al. (2004) found that a large percentage of trees was infested in all dbh size classes, the largest trees having the highest frequencies and loads. Trees with lianas had more crown damage than trees without lianas.

Differences in the total height of trees are also expected among Amazonian forest types due to differences in ecological interactions, such as tree mortality, development of understory trees, competition and floristic composition, which affect vertical and horizontal structural patterns in forest canopies (Griscom and Ashton, 2003; Latham et al., 1998; Laurance et al., 2006; Lugo and Scatena, 1996; Muller-Landau et al., 2006; Weiner and Thomas, 1992). Thus, allometric relationships (such as the relationships among bole diameter, tree height, crown diameter and wood density) will be useful for understanding the structure and dynamics of tropical forests and the competitive interactions among the tree species (Bohlman and O'Brien, 2006; O'Brien et al., 1995; Perez, 1970; van Gelder et al., 2006; Weiner and Thomas, 1992). Furthermore, knowledge of variation in allometric patterns among Amazonian forests is likely to be useful in improving the theory underlying universal-scaling relationships between diameter and tree size (Enquist, 1999, 2002; Muller-Landau et al., 2006; Niklas and Spatz, 2004).

Variation in the vertical structure of forests could directly affect biomass stock. In transition (open) forest, trees may be shorter at any given diameter as compared to trees in the dense forest in central Amazonia, and obviously the shorter of two stems of the same diameter will have less biomass. Similarly, lighter-density stems with the same volume have less biomass.

Recent Amazonian forest biomass studies applied wood-density corrections and recognized the necessity of adapting allometry to improve biomass estimates, mainly at the southern edge of Amazonia (Baker et al., 2004; Malhi et al., 2004, 2006). However, if no correction is made for the height effect, the biomass will be overestimated by allometric relationships derived from central Amazonian studies. Recent wood-density studies (Nogueira et al., 2007), combined with appropriate understanding of the structure of southern Amazonian forests, could provide substantial insights into the impact of land-cover and land-use change on the global carbon cycle. This is because the southern edge of Amazonia comprises the "arc of deforestation" and constitutes the predominant source of carbon emissions from deforestation in Brazil. This is also the area where the greatest uncertainties

remain in carbon-stock estimates (Houghton et al., 2000, 2001; Nepstad et al., 2001; Nogueira et al., 2007).

In this study evaluated whether trees of southwestern and southern Amazonia forest are shorter at any given diameter than in central Amazonia. The study also assesses whether the scaling of tree stem diameter (D) with total height (L) is consistent with the assumptions of metabolic ecology theory that suggest the universal scaling relationship $\log L \propto \log D^{2/3}$ (Muller-Landau et al., 2006). In addition, the study converts the eventual differences in the total tree height and wood density between forest types into differences in estimates of stand biomass.

Materials and Methods

Study sites

At 12 sites in the Brazilian Amazon (in the states of Amazonas, Acre, Mato Grosso and Pará) 763 trees were measured (“diameter at breast height”, or dbh = 5 to 124 cm). Six sites were close to Manaus in central Amazonia (Nogueira et al., 2005) and the other six sites were distributed in the ‘arc of deforestation’: two sites in Acre state (SW open bamboo-dominated and SW dense forest), three sites in northwestern Mato Grosso state and one site in the southern portion of Pará state (together designated as “SA open forest”) (Nogueira et al., 2007). In each forest type, trees over 5 cm dbh were felled and measurements were made of total height, diameter (dbh or above buttresses) and wood density: 310 trees in CA dense forest, 92 trees in SW open bamboo-dominated forest, 97 trees in SW dense forest without bamboo and 264 trees in SA open forest (in this last forest type, wood-density samples were taken of 72% of the trees).

Detailed descriptions of all sites are available in Nogueira et al. (2005, 2007). These two previous studies address the wood-density effect on biomass and on estimates of carbon emissions based on wood-volume inventories throughout Amazonia. In the present study the effect of the total height of trees, together with the previously published wood-density dataset, are used to adjust allometric equations from well-studied forests in central Amazonia to the forests of southern and southwestern Amazonia. This objective is similar to that of recent studies that applied only wood density adaptations to allometric equations (Baker et al., 2004; Malhi et al., 2006).

Data collection

At all sites, trees to be felled were chosen randomly, but stratified by size classes starting at 5 cm dbh, according to the proportion that each class contributes to basal area in local forest inventories. For each tree, measurements were made of dbh (1.36 m above the ground at the central Amazonia sites and 1.30 m above the ground at the other sites, or above buttresses when present for all sites), and total height. The wood-density datasets used in this study were obtained from Nogueira et al. (2005, 2007), where detailed information is given on botanical specimens and the methodology for wood-density determination.

Adapting allometry

Height \times diameter relationship: effect on biomass

The data from the two southwestern and the combined southern Amazonia forests were compared with those from the central Amazon in paired regressions. Data for each pair were pooled so as to examine the effects on total tree height of $\ln(\text{diameter})$, forest type and the interaction between $\ln(\text{diameter})$ and forest type. If the interaction is significant (different slopes), the two regressions in a pair are different. If the interaction is nonsignificant, the two slopes are homogeneous and an analysis of co-variance is needed to test for a difference between the two intercepts. If the intercepts are different, a height correction can still be applied to the biomass. If neither the slopes nor the intercepts are different, the trees in the test forest and in the central Amazon forest are not distinguishable (Neter and Wasserman, 1974; Sokal and Rohlf, 1995). Only the effect of a shorter trunk is considered, including the portion inside the crown. The trunk is taken to be 66% of total tree biomass in central-Amazonian dense forest (Higuchi et al., 1998). Biomasses of branches, twigs and leaves are assumed to be unaffected by reduced height.

It was assumed that shorter total height in a southern or southwestern Amazon tree, as compared with a central Amazon tree with the same diameter, translates into a reduced total tree biomass. A correction factor was applied based on the ratio of the two expected total tree heights at a given diameter. Expected total tree height for any given diameter in each forest type was obtained from the relationship between total height and $\ln(\text{diameter})$ in the felled calibration samples. After testing for significant differences, linear regressions between these two variables were developed for each of the four forest types in this study (Table 1).

Table 1. Parameters of linear regressions for different Amazonian forest types.

Forest type	Parameters* [Total height = $a + b \ln(\text{diameter})$]									
	$a (\pm SE)$	a at CI 95%		$b (\pm SE)$	b at CI 95%		n	dbh range	Adjusted r^2	SEE**
SW Amazon, open bamboo-dominated	-16.223 (1.494)	-19.15	-13.29	11.198 (0.464)	10.29	12.11	91	5 - 85	0.866	3.577
SW Amazon, dense forest	-12.068 (1.883)	-15.81	-8.33	10.672 (0.553)	9.59	11.76	97	5 - 106	0.794	4.185
Central Amazon, dense forest	-11.168 (0.793)	-12.72	-9.61	11.210 (0.254)	10.71	11.71	307	5 - 106	0.864	2.691
Southern Amazon, open forest	-10.678 (0.637)	-11.93	-9.43	10.581 (0.233)	10.12	11.04	264	5 - 124	0.887	2.454

* All parameter values are significant for P-value ($p = 0.0001$). Three outliers were excluded in the central-Amazon forest, two in the southern-Amazon forest and one in the SW Bamboo forest. For identification of outliers, the studentized residuals (to identify outliers in y space) were plotted against leverage (to identify outliers in x space) and Cook's distance was calculated. Cook's distance measures the influence of each sample observation on the coefficient estimates (Cook and Weisberg, 1982; Wilkinson, 1990).

** Standard Error of the Estimate (SEE) = $\sqrt{\text{Residual Mean-Square}}$

Wood density: effect on biomass

Previous analyses of wood-density data of the four forest types (Nogueira et al., 2005, 2007) showed the boles of the trees to be denser in the central Amazon than in the other three forest types ($p = 0.0001$, post-hoc Bonferroni). Wood density is highest in the central-Amazon dense forest, lowest in the southwest Amazon bamboo-dominated forest, and has intermediate values in the southwest-Amazon dense forest without bamboo and southern Amazon open forest. As there was no tendency to increase or decrease density as a function of dbh within any of the four forest types (Nogueira et al., 2005, 2007), a single correction factor can be applied to each forest to calculate the effect of wood density on biomass, independent of dbh, either on a tree-by-tree basis or for the total tree biomass per hectare. The correction factor was multiplied by the dry weight biomass of trees estimated using central Amazon dense-forest allometry (Higuchi et al. 1998), in the same way as described above for the height effect. The correction factor is the ratio $W_s : W_c$; where W_s = forest average wood density at breast height in southern or southwestern Amazonia and W_c = dense-forest average wood density at breast height in central Amazonia.

Results

Height \times diameter relationship: trees in southern and southwestern Amazonia tend to be shorter than trees of the same diameter in central Amazonia

The relationships between total tree height and $\ln(\text{diameter})$ are shown in three paired regressions (Figure 1). In all three pairs the interaction effect was insignificant ($p = 0.922$, $p = 0.438$ and $p = 0.818$), meaning that the slopes are homogeneous within each pair. Analysis of co-variance of total tree height using forest type as the categorical factor and $\ln(\text{diameter})$ as the continuous covariate, showed the intercepts of the three forests in the arc of deforestation to be different from that of the central-Amazon forest (ANCOVA $p < 0.001$). Therefore, in all three forest types of the southern and southwest Amazon, trees of any given diameter tend to be shorter than trees of the same diameter in central Amazonia.

In order to express the effect of total height as a biomass difference between forest types, tree biomass was estimated based only on dbh (or diameter above buttresses when these structures are present) using the regression of Higuchi et al. (1998), which was developed for the central Amazon. This gives the biomass estimate B_1 for each tree. If B_2 is the total tree biomass in another forest type after correcting only for the height effect, and C_m is a

multiplicative correction factor, such that $B_2 = B_1 \times C_m$, then under the assumptions outlined in the methods, it can be shown that $C_m = 0.66 (H_{1d}/H_{2d}) + 0.34$; where H_{1d} = expected height in southern or southwestern Amazon forest, at diameter d ; and H_{2d} = expected height in central Amazon dense forest, at the same diameter d . Expected heights are obtained from the linear regressions in Figure 1. The relationship between $\ln(\text{diameter})$ and C_m is shown in Figure 2 for each SW Amazon forest and for the southern Amazon forest. Downward corrections of biomass are greatest for trees with smaller diameters and for the bamboo-dominated forest. Considering just the effect of lower tree-height for a given diameter, the estimated stand biomass (trees and palms ≥ 5 cm dbh) is lower than in the central Amazon by 11% in SW Amazon open forest with bamboo, 6.2% in SW Amazon dense forest, and 3.6% in the southern Amazon open forests.

Generally, the $2/3$ scaling exponent predicted by metabolic ecology theory was violated by large trees in the four Amazonian forests studied. When considering trees of all sizes, the scaling exponents found between $\log_{10}(\text{diameter})$ and $\log_{10}(\text{total height})$ for three of the forest types were significantly lower than the value of $2/3$ predicted by metabolic ecology theory. The exception was SW bamboo-dominated forest, which includes the value $2/3$ in the 95% confidence interval (Table 2). For small trees (dbh < 20 cm), the scaling exponent was significantly greater than $2/3$ in the SW Amazon dense forest, and not significantly different from $2/3$ in the other forest types. These results reinforce the argument that allometric scaling exponents vary in forests with different environmental resources or disturbance regimes.

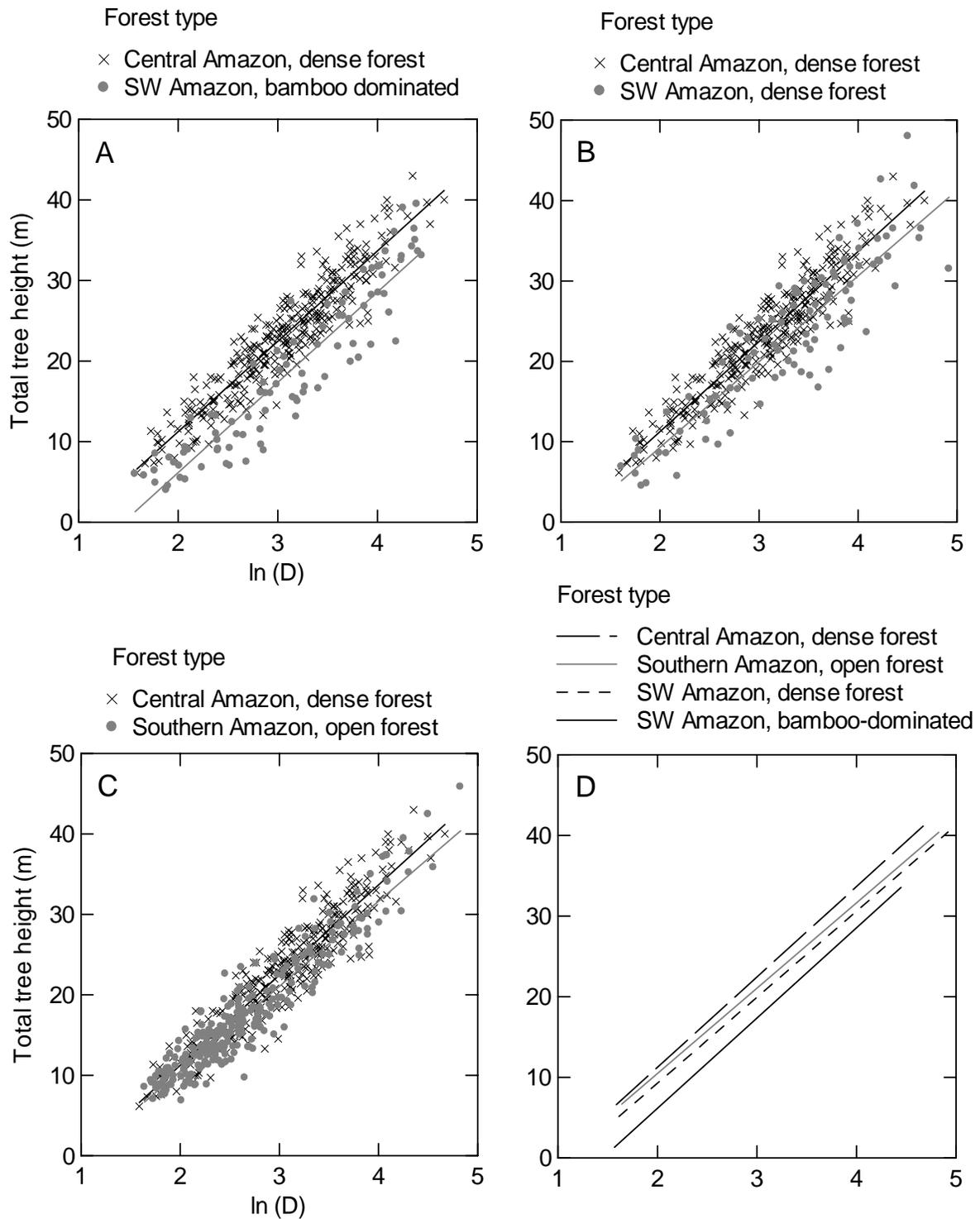


Figure 1. Paired regressions of $\ln(\text{diameter})$ versus total tree height, compared between central Amazon dense forest (\times symbols, dark), two of the southwest Amazon forests and southern Amazon forest (solid circles, gray). **A:** southwest Amazon open, bamboo-dominated forest, **B:** southwest Amazon dense forest, **C:** southern Amazon open forest. **D:** $\ln(\text{Diameter})$ versus total height (m) for all four forest types.

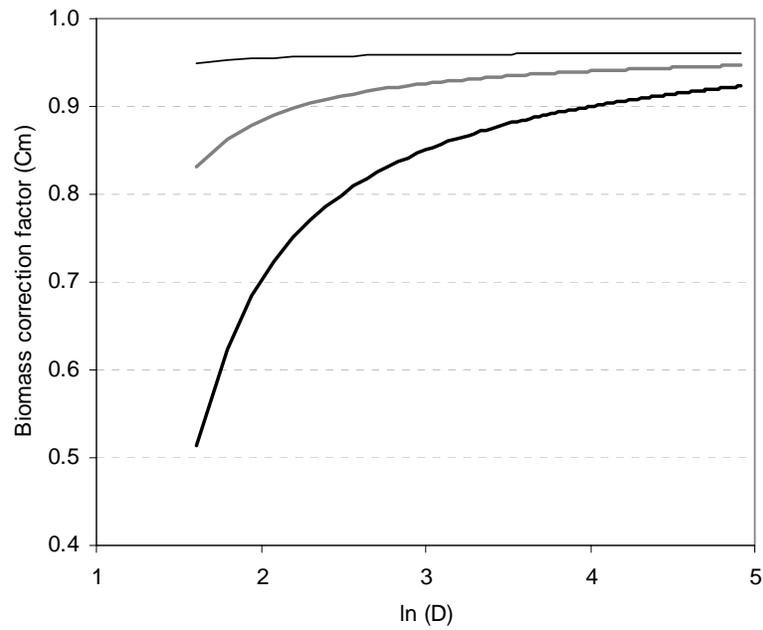


Figure 2. Biomass correction factor (Cm) for the effect of lower stem height in the three test forests compared with the central Amazon dense forest. The upper line gives values for southern Amazon open forest the intermediate line for SW Amazon dense forest and the lower line for open, bamboo-dominated forest. D = diameter in centimeters.

Table 2. Parameters of fitted linear relationships between $\log_{10}(\text{stem diameter})$ with $\log_{10}(\text{tree total height})$ for different Amazonian forest types, including trees of all sizes, diameter < 20 cm and trees with stem diameter ≥ 20 cm. Bold values highlight regression slopes.

Forest type		Parameters [$\log_{10}(\text{Total height}) = a + b \log_{10}(\text{diameter})$]						
		a (\pm SE)	CI 95%	b (\pm SE)	CI 95%	n	Adjusted r^2	SEE*
All trees	Dense forest (Central Amazonia)	0.625 (0.018)	0.590 - 0.661	0.538 (0.013)	0.511 - 0.564	307	0.842	0.061
	Open forest (Southern Amazonia)	0.564 (0.017)	0.530 - 0.597	0.558 (0.014)	0.530 - 0.586	264	0.851	0.066
	Dense forest (SW Amazonia)	0.494 (0.045)	0.404 - 0.584	0.576 (0.031)	0.515 - 0.637	97	0.788	0.101
	Open bamboo-dominated forest (SW Amazonia)	0.276 (0.040)	0.197 - 0.354	0.685 (0.028)	0.628 - 0.741	91	0.867	0.095
Trees < 20 cm in stem diameter								
	Dense forest (Central Amazonia)	0.428 (0.042)	0.346 - 0.510	0.719 (0.038)	0.645 - 0.794	135	0.729	0.067
	Open forest (Southern Amazonia)	0.448 (0.034)	0.381 - 0.515	0.673 (0.033)	0.608 - 0.737	199	0.678	0.068
	Dense forest (SW Amazonia)	0.134 (0.124)**	-0.106 - 0.374	0.919 (0.119)	0.689 - 1.149	30	0.680	0.119
	Open bamboo-dominated forest (SW Amazonia)	0.213 (0.106)***	0.007 - 0.419	0.737 (0.102)	0.538 - 0.935	41	0.573	0.114
Trees ≥ 20 cm in stem diameter								
	Dense forest (Central Amazonia)	0.842 (0.035)	0.774 - 0.911	0.394 (0.023)	0.350 - 0.439	172	0.636	0.046
	Open forest (Southern Amazonia)	0.767 (0.050)	0.671 - 0.863	0.424 (0.032)	0.363 - 0.485	65	0.741	0.047
	Dense forest (SW Amazonia)	0.817 (0.078)	0.663 - 0.971	0.379 (0.048)	0.285 - 0.473	67	0.491	0.074
	Open bamboo-dominated forest (SW Amazonia)	0.547 (0.086)	0.378 - 0.716	0.522 (0.053)	0.419 - 0.625	50	0.672	0.071

*Standard Error of the Estimate (SEE) = $\sqrt{\text{Residual Mean-Square}}$

**Parameter value not significant at the 5% level. Other parameter values (unmarked) are all significant at the 0.1% level.

*** $p = 0.051$.

Effect on biomass due to wood-density differences between trees in southern and southwestern Amazonia and trees in central Amazonia

Based on prior reported mean wood density by forest type (Nogueira et al., 2005, 2007) the wood-density differences expected between central Amazonia and the three other forest types were estimated (Table 3). Average wood density for the entire tree was assumed to vary in direct proportion to the wood density at breast height. The confidence intervals indicate a 23-33% lowering of biomass for trees (≥ 5 cm dbh) in the open bamboo-dominated forest, 11-20% lowering of biomass for trees in dense forest without bamboo and 9-15% lowering of biomass for trees in open forest in southern Amazonia. If only the wood-density correction were applied, the estimated stand biomass reductions for the three forest types would be 28%, 16% and 13%, respectively.

Difference in biomass due to both height and wood density

Due to lower height and lighter wood density, trees and palms (≥ 5 cm dbh) in SW Amazon open bamboo-dominated forest, in SW Amazon dense forest and in southern Amazon open forests, biomass stocks were, respectively, 76, 65 and 45 Mg/ha⁻¹ (dry weight) less than predicted by the uncorrected central Amazon model (Figure 3, Table 4). Considering only the height effect, the estimated biomass reductions for these forests were 21.5, 18.5 and 10.3 Mg ha⁻¹. The effect of lower wood-density on biomass estimates is greater than the effect of tree height in all three forest types in the S and SW Amazon regions (Figure 3). These results suggest that biomass per hectare is substantially overestimated by the central-Amazon model when applied to the southwestern or southern Amazon without corrections. Although the correction applied makes logical sense, it should be emphasized that the corrected biomass estimates have not yet been validated by new allometric relationships determined directly by felling and weighing trees in test plots in southern or southwestern Amazonia.

Table 3. Wood density at breast height (dry weight at 80 °C/green volume with bark) in the four Amazonian forest types^a

Forest type	Sample size (trees \geq 5 cm dbh)	Average basic density at breast height	Std deviation	Biomass correction factor (\pm 2 std errors of the ratio of means) ^b
Central Amazon dense	310	0.712 (0.704)	0.119 (0.117)	---
SW Amazon open bamboo-dominated	92	0.512	0.176	0.718 \pm 0.0534
SW Amazon dense	97	0.600	0.160	0.843 \pm 0.0482
Southern Amazon open	191	(0.618)	(0.125)	0.877 \pm 0.0306

^a Values in parentheses are dry weight at 103 °C. The biomass correction factor is the ratio between the mean wood density in a given forest type and the mean wood density in the central Amazon.

^b Standard error for a ratio of two estimates (Ott and Longnecker, 2001).

Table 4. Effect of total-height and wood-density corrections on estimated per-hectare biomass^a

Forest type	Biomass estimated using central Amazon allometric equation	Biomass corrected for height and wood-density difference	% Difference
SW Amazon bamboo-dominated	194 \pm 36.8	118 \pm 23.4	39%
SW Amazon dense	297 \pm 21.6	232 \pm 17	22%
Southern Amazon open	285	240	16%

^a For the two forest types in the southwestern Amazon means \pm 1 std. dev. (n = 10) are given for trees and palms \geq 5 cm dbh (or above buttresses). In the southern Amazon the biomass estimates were obtained from the mean number of trees for each diameter class (5-cm intervals) estimated from 11 ha where trees \geq 10 cm in diameter were inventoried by Feldpausch et al. (2005) and 30 ha where trees with diameter \geq 5 cm were inventoried by Pereira et al. (2005).

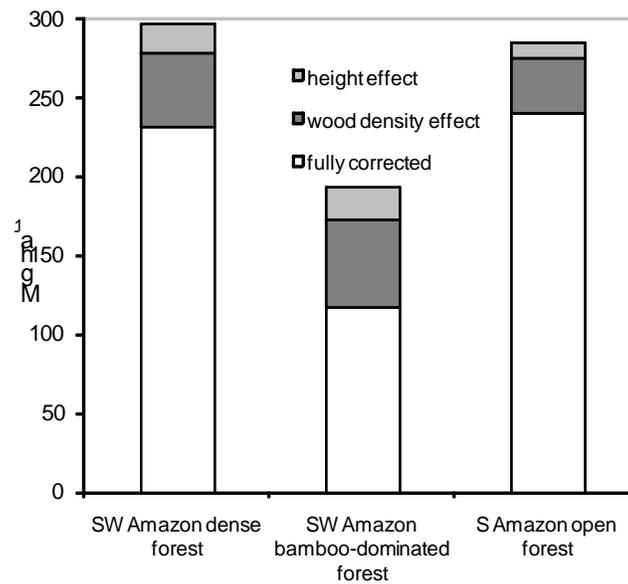


Figure 3. Stand biomass for trees + palms ≥ 5 cm dbh (or above buttresses) in the SW Amazon is adjusted downward by 39% (SW Amazon open, bamboo-dominated forest), 22% (SW Amazon dense forest), and by 16% (southern Amazon open forest) after corrections for lower wood density and shorter tree height as compared with these attributes in central-Amazon dense forest.

Discussion

This study assumes that there is no difference in crown biomass for trees of equal diameter between dense forest in central Amazonia and the three forest types studied in southwestern and southern Amazonia. This may be a conservative assumption. Crown damage was more prevalent in trees infested by abundant climbing bamboos or lianas (Alvira et al., 2004; Griscom and Ashton, 2006) in two widespread open forest types of S and SW Amazonia. On Barro Colorado Island, Panama, Bohlman and O'Brien (2006) found that gap species have smaller crowns than shade species. Gap species are more prevalent in open forests in Amazonia, while shade species are more prevalent in dense forests.

The variation of vegetation structure at the meso scale (i.e. over geographical distances of 1 - 10³ km) and the concurrent changes of tree form are adaptations to the physical, chemical and ecological conditions of each site (Rozendaal et al., 2006). In this sense, the results in this chapter (Figure 1 and Table 2) agree with recent models showing that plant length, diameter, and mass scaling relationships are flexible -- that is, they can vary across species due to species-specific differences in biomass partitioning patterns and ecological

responses to different environmental conditions (Muller-Landau et al., 2006; Niklas and Spatz, 2004). However, knowledge is limited of the main factors affecting allometric relationships in tropical forest under different environmental conditions (Malhi et al., 2006).

Recent universal scaling models have linked constraining functional traits related to water and biomass growth with plant size, architecture and allometry (Meinzer, 2003; Niklas and Enquist, 2001; Niklas and Spatz, 2004; West et al., 1999). For example, it is expected that tree height per unit basal area would be reduced with increasing dry-season length (Malhi et al., 2006; Meinzer, 2003; Meinzer et al., 2001). Because of this, trees will be shorter at any given stem diameter in dry seasonal tropical forest. This may contribute to the lower total height of trees in undisturbed forests in southern Amazonia, where the majority of collection sites in this study have a slightly longer dry period (monthly precipitation < 100 mm) than the dense forest in the central Amazon (Brazil, ANA, 2006).

Southern Amazon forests with their longer dry-season are also expected to have more abundant lianas (which cause crown damage and probably lower tree height). More lianas are expected because lianas may compete better for access to water throughout the dry season (Mascaro et al., 2004; Restom and Nepstad, 2004) and because light intensity increases below seasonally deciduous tree canopies (Gentry, 1991; Rice et al., 2004). Bamboo-dominated Amazon forests may be associated with both drier climate and substrate. At the peak of the dry season in eastern Acre state, climbing *Guadua* remains evergreen at a time when many tree species drop their leaves. *Guadua* may therefore have a competitive advantage in areas with long dry seasons. Within Amazonia, dense populations of climbing *Guadua* mixed in the forest are largely restricted to a lowland *terra firme* landscape peculiar to the headwaters of the muddy Purus and Juruá Rivers. Here modest tectonic uplift and mechanical erosion have exposed seasonally impermeable 2:1 clays rich in cations (Nelson et al., 2006).

While some previous basin-wide estimates of Amazon carbon stocks have made a correction for wood-density, no adjustments have been made for variation in allometric differences such as tree height or crown damage (Baker et al., 2004; Malhi et al., 2006). Available allometric equations for biomass estimates in tropical forest input tree height and wood density as independent variables (Brown et al., 1989; Overman et al., 1994). No models exist that have been validated using tree-biomass data obtained directly from destructive-harvest experiments conducted in southwestern or southern Amazonian forests. Comparing prior biomass estimates from allometric equations with the results of the present study

suggests that biomass and carbon stocks have been overestimated for southern Amazonia (e.g. Alves et al., 1997; Feldspausch et al., 2005). Some estimates of tree biomass within the Amazonian 'arc of deforestation' (Cummings et al., 2002) and at open-forest sites where lianas are a dominant life form (Gerwing and Farias, 2000) have employed allometric relationships designed for dense Amazon forest on infertile soils. These may therefore overestimate above-ground tree biomass and greenhouse-gas emissions in this part of Amazonia where most deforestation is taking place. Brazil's National Communication under the United Nations Framework Convention on Climate Change (Brazil, MCT, 2004) estimates biomass throughout Brazilian Amazonia based on central-Amazonian allometry by Higuchi et al. (1998) applied to tree diameter data from RadamBrasil surveys without correction for either density or tree height.

In spite of recent studies reporting spatial variation in wood density for Amazonia (Baker et al. 2004; Chave et al., 2006; Nogueira et al., 2007), the main environmental factor that explains spatial variation in wood density is still unclear. Environmental and wood-density differences between southern, southwestern and central Amazonia have been discussed by recent studies (Baker et al., 2004; Malhi et al., 2006; Nogueira et al., 2007). Generally, the main causes suggested to explain the lower stand wood density in southwestern and southern Amazonian forests are related to the floristic composition, succession dynamics, edaphic factors and physiological water-use principles. The relationship between wood-density variation and environmental factors has been particularly difficult to assess due to a variety of studies having used different sampling methods (Fearnside, 1997; Nogueira et al., 2005, 2007). The results of this study suggest that the plastic responses of trees to environmental changes are more intense for wood density than for tree height. Assuming that growth rate is inversely proportional to wood density (Enquist et al., 1999; King et al., 2005; Muller-Landau, 2004), the plastic response and hence the resources allocated to tree height will be at least partially dependent on wood-density traits. The effect of environmental conditions on tree height will therefore be weaker than their effect on wood density. As the forests in southern Amazonia are more dynamic than those in central Amazonia (Malhi et al., 2006), shorter trees are logical to expect in spite of lower wood density.

Conclusions

In the southwestern Amazon bamboo-dominated forest, southwestern Amazon dense forest and southern Amazon open forest the trees are shorter than in dense forest in the central Amazon. The height difference was greatest for small trees. Generally the $2/3$ scaling exponent predicted by metabolic ecology theory was violated by large trees in the four Amazonian forests studied. When the Higuchi et al. (1998) equation (which was developed for use in dense forests) is applied to biomass estimates in open forests of south and southwestern Amazonia, the results have to be corrected for tree-height and wood density effects. Together, the two effects represent reductions totaling 39% in southwestern Amazon bamboo-dominated open forest, 22% in southwestern Amazon bamboo-free dense forest and 16% in southern Amazonian open forest (respectively, 76, 65 and 45 Mg ha⁻¹ lower dry biomass than dense forest in the central Amazon). Considering only the height effect, estimated biomass is lowered by 21.5, 18.5 and 10.3 Mg ha⁻¹, respectively, in the southwestern Amazon bamboo-dominated forest, southwestern Amazon dense forest and southern Amazon open forest. Revisions are needed in the estimates of biomass that have been made using allometric equations developed in dense forest in the central Amazon. This implies lower emissions of greenhouse gases than previously thought for deforestation in Brazilian Amazonia, which is concentrated in the “arc of deforestation” in non-dense forest types such as the ones studied here.

Chapter IV - Estimates of forest biomass in the Brazilian Amazon: New allometric equations and adjustments to biomass from wood-volume inventories⁴

Abstract

Uncertainties in biomass estimates in Amazonian forests result in a broad range of possible magnitude for the emissions of carbon from deforestation and other land-use changes. This chapter presents biomass equations developed from trees directly weighed in open forest on fertile soils in the southern Amazon (SA) and allometric equations for bole volume estimates of trees in both dense and open forests. Biomass estimates were obtained from these new equations and used them to improve the commonly used biomass models based on large-scale wood-volume inventories carried out in Amazonian forest. The biomass estimates from the SA allometric equation indicate that equations developed in forests on infertile soils in central Amazonia (CA) result in overestimates if applied to trees in the open forests of SA. All above-ground components of 267 trees in open forests of SA were cut and weighed, and it was found that the proportion of the biomass stored in the crowns of trees in open forest is higher than it is in dense-forest. For wood-volume estimates bole equations were shown to be an alternative way to avoid errors in bole volume due to height estimates, tapering and indentations or hollow trunks. In the case of inventoried wood volume corrections were applied for indentations and hollow trunks and determined that no adjustment is needed for the form factor used in the RadamBrasil volume formula. New values are suggested for use in models to convert wood volume to biomass estimates. A biomass map for Brazilian Amazonia was produced from 2860 plots inventoried by the RadamBrasil Project incorporating all corrections for wood density and wood volume and in factors used to add the bole volume of small trees and the crown biomass. The average biomass values estimated from large-scale inventories of wood volume showed reasonable agreement with biomass estimated by allometric equations. Considering all adjustments the biomass map indicates average biomass of 125.4 Pg ($=10^{15}$ g) dry weight (above-ground + below-ground) for originally forested areas in the Brazilian Legal Amazon as a whole (104.2 Pg for above-ground only) at the time of the RadamBrasil inventories, which were carried out before intensive deforestation had occurred in the region. Savannas and other non-forest vegetation are excluded from the estimate. If areas deforested through 2006 are eliminated, excluding agriculture, pasture and secondary forest vegetation, the estimation of dry biomass storage was reduced to 113.3 and 94.2 Pg (above-ground + below-ground and only above-ground). Thus, at the present time the carbon storage in forested areas in Brazilian Amazonia as a whole will be around 55 Pg (assuming 1 Mg dry biomass = 0.485 Mg C). It is provide the biomass estimated by forest type (aggregated into 15 vegetation classes) for each state in the Brazilian Legal Amazon.

Keywords: Allometric equations, Amazon forest; Biomass estimates; Carbon flux; Global warming; Wood volume.

⁴ Written according to the norms of the journal Forest Ecology and Management.

Introduction

The Amazon forest is a huge and dynamic reservoir of carbon which may be gradually released to the atmosphere through the combined action of deforestation and soil carbon loss due to land-use change and the impact climate change (Cox et al., 2000, 2004; Houghton, 2005; IPCC, 2007; Malhi et al., 2006; Nepstad et al., 1999). Because the carbon stocks are uncertain (Eva et al., 2003; Fearnside and Laurance, 2003; Houghton et al., 2001), the range of possible emissions of carbon from tropical deforestation and degradation is broader than commonly thought (Houghton, 2005). Estimates of the biomass storage are discordant when the same method is applied or when estimates from allometric equations are compared with biomass obtained from large-scale wood-volume inventories (Houghton et al., 2001; Malhi et al., 2006).

In Amazonian forests, data from large-scale volume inventories (Brazil, Projeto RadamBrasil, 1973-1983) have been used as the principal basis for estimating biomass and greenhouse-gas emissions from deforestation (Fearnside, 2000b; Houghton et al., 2001). Although uncertainties are inherent at forest-inventory data sampled over extensive areas, these datasets have been preferred for biomass estimation over allometric equations because the inventories are believed to be only data base that can be used for estimating forest biomass at the landscape level because they were collected at the scale of the problem (Brown et al., 1989; Brown and Lugo, 1992). On the other hand, large-scale spatial representativeness is the crucial disadvantage of the allometric models that are developed from a small number of directly harvested trees, but these models have the advantage of being easily applied to a large area for estimating tree biomass (Baker et al., 2004; Chave et al., 2005; Malhi et al., 2006). In spite of seldom being tested directly, allometric equations represent a necessary method for evaluating long-term forest inventories and the magnitude of carbon fluxes between aboveground forest ecosystems and the atmosphere (Chave et al., 2005; Grace, 2004). In addition, it is suggested in this study that directly weighed trees in small-scale samples in specific forest types can be useful for improving values used in models for biomass estimates based on wood-volume data from large-scale inventories.

The uncertainties in the biomass estimates from RadamBrasil volume data (Brazil, Projeto RadamBrasil, 1973-1983) are due to errors in the original wood volume estimates and subsequent conversion to biomass (Brown et al., 1995). In the volume estimates the uncertainties could be (i) in the measurements of basal area because of irregularly shaped or hollow boles (Nogueira et al., 2006; Sheil, 1995), (ii) in the values for commercial height estimated “by eye” without direct measurements, and (iii) due to a single mean form factor

being used for all tree sizes and forest types. The mean tapering (form factor) adopted in the volume estimates was 0.7 for trees with bark and circumference ≥ 100 cm, including all species independent of forest type, diameter class or the length of the bole (Brazil, RadamBrasil Project, 1973-1983; Heinsdijk, 1958; Pitt, 1961, p. 20). Any uncertainties in the bole-volume estimates imply proportionate uncertainties in biomass and carbon emission estimates.

The usual model for Amazonian forest biomass estimates was developed as an alternative way to use datasets on bole volume available from large-scale inventories across Amazonia (see Brown et al., 1989; Brown and Lugo, 1992; Houghton et al., 2001). The bole volume is converted to biomass from wood-density data, together with a ‘volume expansion factor’ for addition of the volume of small trees (generally 10 to 30 cm stem diameter), and a ‘biomass expansion factor’ for addition crown biomass. The model allowing the biomass to be obtained for all trees with boles ≥ 10 cm in diameter at breast height. Although recent studies on wood density have reduced uncertainties in conversions of bole volume to biomass of the bole, particularly in areas undergoing deforestation (Nogueira et al., 2007), uncertainties still remain in converting bole volume to tree biomass. Basically this is due at factors that add the bole volume of uninventoried small trees and the biomass of the crowns.

This chapter seeks to join the two main methods of biomass estimation --allometric equations and inventoried wood volume -- in order to adjust the biomass estimates for Amazonian forests. A new biomass equation is developed from trees harvested on fertile soils in the southern Amazon and two new bole-volume equations are developed from trees in dense and open forests. These allometric relationships are used to assess uncertainties in previous wood-volume and biomass estimates. In the case of the usual biomass model, based on inventoried wood volume, the study evaluated whether the factors currently used to add the bole volume of small trees (volume expansion factor) and the crown biomass (biomass expansion factor) are adequate for the biomass conversion. Finally, all corrections were applied to generate a new biomass map for forests in Brazilian Amazonia from RadamBrasil plots, and the biomass stocks by forest type were calculated for each of the nine states in the Brazilian Legal Amazon.

Materials and Methods

Study sites

Details of the study area in central Amazonia (CA) are described in Nogueira et al. (2005). Except for data from a site located in Carlinda County, the other sites in southern

Amazonia (SA) are described by Nogueira et al. (2007). In CA sites the vegetation is characterized as being dense ombrophilous forest of *terra firme* (land that is not seasonally flooded), on nutrient-poor yellow latosol (Magnago et al., 1978; Yamazaki et al., 1978). In SA sites the vegetation was described as open forest, including the Carlinda site in the northwestern portion of Mato Grosso state. Except for the Carlinda site, where evidence of previous disturbance was observed, all other plots were in primary forest, without invasion of pioneer trees or mortality associated with edges. The dataset sampled at the Carlinda site was not used in biomass equations, only being used in tapering and bole volume equations. All trees were felled randomly after authorization by the Brazilian Institute for the Environment and Renewable Natural Resources (IBAMA). For CA an inventory of 72 ha (de Castilho et al., 2006) was used to adjust the felled samples to a more representative size-class distribution in 5-cm dbh intervals. In SA an inventory of the 11 ha was used for trees ≥ 10 cm dbh (Feldpausch et al., 2005) and an inventory of 30 ha was used for trees 5 to 10 cm dbh (Pereira, 2005).

Data collection

In CA, trees ($n = 302$; dbh or just above any buttresses = 5 to 106 cm) were collected in six different locations distributed over an area of 45 km². Approximately 50 trees per site were sampled in plots measuring 30 × 30 m. In SA, trees were collected ($n = 300$; dbh or just above any buttresses = 5 to 124 cm) in four counties: 30 trees in Juruena (2 sites), 149 trees in Cotriguaçu (1 site), 56 trees in Carlinda (1 site) and 65 trees in Novo Progresso (1 site). Collection sites were located at least 100 m from the nearest forest edge. Botanical samples of all trees were collected and identified by parobotanists who are employees of the herbarium of the National Institute for Research in the Amazon - INPA. A total of 186 species or morpho-species were identified at the sites in CA and 155 in SA.

In both CA and SA regions, disks of constant thickness (~3 cm) were collected after felling from all trees at breast height and at the top of the bole (at the height of the first thick branch), using a chain-saw. For all trees a tape was used to measure total height, height of the bole and circumference at the location where each sample disk was taken. The measurements at breast height were made 1.36 m above the ground at the CA sites and 1.30 m at the SA sites, or just above any buttresses. Each disk was drawn on a poster-board panel by tracing the perimeter and, in cases with hollow trunks, the internal details. The drawings were photographed at a known distance, with the camera placed at a right angle in both the vertical and horizontal planes. The camera, with an 80-mm telephoto lens, was placed at a distance

chosen to minimize the curvature in the photographed plane. A rectangle with known dimensions was drawn on the panels in order to allow corrections for possible distortions in the procedure and also to determine the scale of the digital image (the area of each pixel).

The area of each disk was calculated in pixels using Adobe Photoshop software and was later converted to square centimeters. The bole volume of each tree, corrected for indentations and hollow trunks, was calculated using the Smalian formula (Loetsch et al., 1973): $\{(A_{si} + A_{sf}) / 2\} \times h$; where A_{si} = area of the cross section at breast height, A_{sf} = area of the cross section at the top of the bole; and h = height of the commercial bole. The Smalian formula was applied after correcting the biometric measurements of the sampled trees for the effect of irregular and hollow boles. This is hereafter referred to in this study as the “corrected” volume and is equivalent to the volume that would be obtained by applying the Smalian formula to uncorrected data and then correcting the result for irregular and hollow trunks.

Weighing trees

At the SA sites, 264 trees (5 to 124 cm dbh or above buttresses) were directly harvested and the fresh mass of each tree weighed fully. The bole was cut at the lowest height possible using a chainsaw, which was also used to cut off parts of the bole and the branches in the crown. For large or medium-sized trees a plastic sheet was placed on the ground under the point where the bole or thick branches were cut in order to collect the sawdust, which was also weighed. With the exception of the stump, the entire tree was cut into appropriately sized pieces and weighed using a balance with 200 Kg capacity. The fresh mass of the six boles of large trees harvested in the Rohsamar farm (Jurueña County) were obtained using a different method: each bole was placed on a truck as an intact log, and the loaded truck was driven onto a scale designed for weighing loaded vehicles (capacity >60 metric tons). The crowns these trees were directly weighed in the field using the same balance (200 Kg capacity) used for the other trees. In this study, the crown was considered to be all components above of the top of the commercial bole, weighed together: branches, twigs, leaves, flowers and fruits. In order to obtain the dry mass of the bole, the fresh mass was multiplied by the moisture content (Mc) of the bole of each tree. The mean Mc (0.416 ± 0.068) was used for trees that had no Mc mean of the bole (Nogueira et al., submitted). The Mc of the crown was not measured, but rather estimated using data from the literature. Higuchi et al. (1998) report 42% for moisture in the crown, obtained from 38 trees in central Amazonia (CA). In a recent study, da Silva (2007) reports Mc for roots, boles, branches and leaves obtained from 128 trees, also sampled in CA.

From da Silva (2007), crown $Mc = 44.4\%$. Because bole Mc is significantly higher in the trees of southern Amazonia (SA), the moisture found by da Silva (2007) for crowns was not directly used in this study. Mc was estimated for the crowns of trees in SA from the Mc measured in the boles of trees in SA, assuming the same relationship as was found in CA (from da Silva, 2007) between bole and crown Mc , namely: $(Mc_{\text{crown in CA trees}} \times Mc_{\text{bole in SA trees}}) / (Mc_{\text{bole in CA trees}})$. The crown Mc found for trees in SA was 0.476.

The dry mass of the stump was estimated and later added to the dry mass of the bole. Therefore, dry mass of the bole mentioned in this study also includes the stump and the sawdust produced by cutting the disks (collected for moisture content measurements).

The dry mass of the stump was estimated using volume and wood density of the stump, both of which were estimated. Only stump height was directly measured in the field. The cross-sectional area of the base and top of the stump were estimated and multiplied by the height of the stump. First, the cross-sectional area at the base of the stump (close to the ground) was obtained by $(EF \times BA) / (2 - EF)$, where $EF = \text{enlargement factor}$ and $BA = \text{cross-sectional area at breast height or above any buttresses}$. In this formula the cross-sectional area is corrected for hollow portions or irregularities. The $EF = \{[(BA \times (\text{bole height} - BA \text{ height})) / ((BA + \text{cross-sectional area at the top of the bole}) / 2)] \times (\text{bole height} - BA \text{ height})\}$. In the formula for calculating EF , the cross-sectional areas at breast height or above buttresses and at the top of the bole were only corrected for irregularities, not for hollow trunks, if present. Second, the cross-sectional area at the top of the stump was obtained by: $BA + (BA \times \% \text{ enlargement between BA and stump height})$. Also in this case BA is corrected only for irregularities. Therefore, the stump biomass = $(\text{mean of the cross-sectional areas at the base and top of the stump} \times \text{stump height}) \times \text{mean wood density of the stump}$. The mean density of the stump was obtained from the wood density at the base of the bole corrected for variation along of the length of the bole. The mean wood density of the stump was 1.36% higher (0.626 ± 0.130 ; $n = 233$) than wood density at the base of the bole: 0.618 (at breast height or above buttresses, if present). Stump biomass was found to be equivalent to 1% of the dry biomass of the bole without the stump ($n = 264$ trees) and represents 2.15 Mg/ha^{-1} when normalized for the expected frequency of trees per hectare. This value is useful for adjusting biomass and emissions estimates in deforested areas.

Biomass allometric equation

In this study only diameter (at breast height or above any buttresses, in cm) was adopted as an input variable in a simple model that calculates the aboveground dry biomass

(in Kg). Although it is possible to obtain an appropriate regression model from accurately measured heights and wood densities of trees in this study, the use of a model with height or density as additional parameters can become inaccurate due to the practical difficulty of obtaining unbiased height or density measurements for large areas (Brown et al., 1995; Overman et al., 1994). The priority was to obtain an accurate fit from an equation with only diameter as an independent variable, in order to increase its practical usefulness. In addition, sufficient previously published models exist that include height and wood density. The accuracy of previous models is only discussed here for studies that include diameter, height and wood density together (Brown, 1997; Chave et al., 2005; Higuchi et al., 1998; Overman et al., 1994).

Dry mass and diameter were log transformed to satisfy the least-squares procedure (general linear regression), which assumes that the residuals are normally distributed, that the dependent variable is homogeneously distributed across independent variables, that relationships are linear, that the effects of the factors are additive and that there is no random error in the measurements of the independent variables (Magnusson and Mourão, 2005). The studentized residuals were plotted against leverage and Cook's distance calculated for identification of outliers. Cook's distance measures the influence of each sample observation on the coefficient estimates (Cook and Weisberg, 1982; Wilkinson, 1990).

The statistical criteria used in selecting the best equation were: high adjusted r^2 , to allowing comparison with published allometric equations that include different numbers of variables (André et al., 2000), the standardized distribution of residuals and a lower standard error of the estimate. The standard error of the estimate (SEE) refers to $\sqrt{\text{Mean Standard Error (MSE)}}$ (Neter and Wasserman, 1974). The following measurements were observed for each variable: regression coefficient, standard error of the coefficient, standardized coefficient, tolerance, and a t statistic for measuring the usefulness of the variable in the equation.

Assessing the performance of the equations developed in this study as compared to previously published models was based on the deviation (%) between sum of mass of trees directly measured and the mass as estimated by each of the previous equations; both for sampled trees and as an extrapolation per hectare.

Bole volume equations for trees in dense and open forest

Starting from volumes of the boles corrected for indentations and hollow trunks (dependent variable), and conventional diameter measured as dbh or just above any buttresses (input variable), bole allometric equations were developed for dense and open forest types. In

the select bole equations the same statistical criterion was adopted as mentioned above for biomass equations.

Form factor: mean tapering of the bole for trees in dense and open forest

The form factor was calculated as the ratio between the “corrected” volume of the bole and the volume of the bole if the trunk is assumed to be a cylinder, according to the formula: $ff = \{((Asi_c + Asf_c) / 2) \times h\} / (Asi_n \times h)$; where: Asi_c = corrected area of the cross section at breast height, Asf_c = corrected area of the cross section at the top of the bole; and h = height of the commercial bole. This was done so that it would be possible to compare the results with those obtained with the form factor used by the RadamBrasil Project: the variable " Asi_n " in the denominator of the formula for form factor was *not corrected* for the effect of indentations and hollow trunks. The form factor was obtained in this way for each tree.

For biomass estimates of Amazonian forests previous studies have used a single mean form factor for the whole of Amazonia, independent of forest type. In this chapter, the mean tapering of boles was analyzed considering forest type, reflecting differences in canopy structure and in the density of the stem. Subsequently, the mean form factor was calculated adjusting the felled samples to the distribution of tree diameters in each forest type.

Volume expansion factor (VEF): addition of the bole volume of trees with dbh 10 to 31.7 cm

The VEF reported in this study follows the definition of Brown (1997): ratio of inventoried volume for all trees with a minimum diameter ≥ 10 cm to inventory volume for all trees with a minimum diameter, in this study stems ≥ 31.8 cm in diameter. The VEF was obtained from “corrected” bole volume and therefore does not have an overestimate due to indentations and hollow trunks. It should be stressed that the VEF values reported in this study include trees between 10 and 31.7 cm stem diameter, which could contrast with previous VEF values that did not include trees 25-31.7 or 30-31.7 cm stem diameter (Brown and Lugo, 1992; Brown, 1997). The trees sampled in dense and open forest types were also normalized by the distribution of diameter classes and the proportional volume in the size classes from 10 to 31.7 cm diameter was obtained based on the total bole volume inventoried per hectare for trees ≥ 31.8 cm stem diameter (see item 2.1 for details of inventories).

Biomass expansion factor (BEF): addition of crown biomass to inventoried bole volume

In dense forest in CA the BEF reported in this study was obtained from the ratio of biomass of the trees to the bole biomass. The tree's biomass was estimated using a model

developed in a similar forest type in CA (Higuchi et al., 1998): $\ln(\text{fresh mass}) = -1.754 + 2.665 \times \ln(\text{diameter})$ and $\ln(\text{fresh mass}) = -0.151 + 2.17 \times \ln(\text{diameter})$, respectively for stems 5 – 20 cm and ≥ 20 cm in diameter. The bole biomass was calculated from “corrected” volume of the bole of each tree to avoid overestimates caused by irregularities or hollow trunks multiplied by the mean wood density of each bole (see Nogueira et al., 2005, 2006). A detailed description of the wood-density sampling is given in Nogueira et al. (2005). The large-scale inventories were also used to obtain the BEF normalized by the diameter-class distribution.

In open forest in SA the BEF was estimated from a ratio similar to that used for trees in CA. However, the biomass of trees was obtained directly by weighing each tree. In addition to a BEF value, which can be used when measurements of each tree are unavailable, an allometric equation was developed for crown biomass estimates from conventional diameter measurements.

Biomass mapped across the Amazon

A total of 2860 plots (1 hectare size) were assembled with inventoried wood volume for the entire Brazilian Amazon from 25 reports published by the RadamBrasil Project (Brazil, Projeto RadamBrasil, 1973-1983). Plots were excluded that were less than 1 ha in area or that were in non-forest ecosystems such as savannas (forested, treed parkland and grassy-woody), *campinas* (white sand vegetation); however, contact zones between non-forest and forest formations were included in the analysis. In each plot it was possible to obtain species inventories, the number of trees and a description of the ecosystem. Bole volume was converted to bole biomass based on a large dataset on wood density that includes data published by Fearnside (1997) with some sources corrected for radial variation based on linear equations (Nogueira et al., 2005), other sources by Chave et al. (2006) and recent data by Nogueira et al. (2007). The stand biomass for all trees ≥ 10 cm dbh was obtained using bole biomass and new VEF and BEF values reported in this study. Estimates for the other aboveground live and dead components and belowground components were obtained by addition of percentages to the biomass of trees ≥ 10 cm dbh based on several studies conducted in Brazilian Amazonia, as shown in Table 1. In order to include trees < 10 cm dbh an adjustment of 6.5% has been used for dense forest based on the finding of de Castilho et al. (2006) in a study of 72 ha near Manaus where trees 1 to 10 cm dbh comprise 6.4% (around 19 Mg/ha⁻¹) of the total tree biomass. Nascimento and Laurance (2002; Table 2) found 6.5% (=21.11/325.51) of tree biomass in trees in the 5-9.9 cm dbh range as a percentage of the

biomass of trees ≥ 10 cm dbh. In open forest this percentage is expected to be lower due to the smaller number of young trees as compared to dense forest. Based on 30 ha inventoried in the southwest Amazon (Pereira et al., 2005) there are 102.5 ± 24.5 trees/ha 5-10 cm dbh, while in central Amazonia there are around 715 trees/ha (de Castilho et al., 2006). A value of 4% was used as the mean for non-dense forest to add the biomass of all trees 1-10 cm dbh (Table 1). For the biomass of palms 1.9% was added in dense forests and 8.6% for non-dense forests, see Table 1. For vines 3.1% was used for both dense and open forest, based on several studies across in the Amazon (Table 1). For adding dead aboveground biomass a value of 13.7% is used for both dense and non-dense forests (Table 1). Also, 0.21% was added for other non-tree forest components, according to Fearnside (1997, 2000). Finally, for belowground biomass a value of 25.8% was used for all forest types (Table 1). In this study corrections were not included for trees 30-31.7 cm dbh because the VEF values reported here include this gap. Corrections are also not included for bark in wood density values, because linear equations were used for radial variation correction.

Table 1. Measurements of forest biomass and non-tree components from studies conducted in Brazilian Amazonia (dry weight in Mg/ha⁻¹ and % relative to stand biomass of trees ≥10 cm dbh).

Forest	State	Biomass all trees ≥10 cm	Palms	%	Vines	%	Under-story; seedlings (wood+ leaves)	%	Dead wood (fallen + standing)	%	Litter/Root mat*	%	Below-ground	%	Source	Notes
Dense	Amazonas										7.3				Klinge and Rodrigues (1968)	(01)
	Amazonas	357.0			23.0	6.4			25.8	7.2	7.2	2.0	115.8	32.4	Klinge et al. (1975); Klinge and Rodrigues (1973)	(02)
	Pará										9.9				Klinge (1977)	
	Amazonas										6.4				Franken et al. (1979)	
	Pará										7.3				Silva and Lobo (1982)	
	Pará	392.6	5.0	1.3	3.5	0.9	9.6	2.4	7.1	1.8	18.2	4.6	103.5	26.4	Russel (1983)	(03)
	Pará										6.7				Silva (1984)	
	Rondônia	387.9			4.6	1.2	13.0	3.3	1.7	0.4	15.5	4.0			Revilla Cardenas (1986)	(04)
	Pará	186.1			2.8	1.5	5.6	3.0	11.2	6.0	11.6	6.2			Revilla Cardenas (1987)	(05)
	Pará	297.4			9.7	3.3	9.6	3.2	12.3	4.1	10.5	3.5			Revilla Cardenas (1988)	(06)
	Pará	198.3			9.0	4.5	9.2	4.6	8.9	4.5	13.7	6.9			Revilla Cardenas (1988)	(07)
	Amazonas										7.8				Luizão (1989)	(08)
	Pará										8.0				Dantas and Phillipson (1989)	
	Amazonas	244.0			8.1	3.3			12.0	4.9	9.0	3.7			Fearnside et al. (1993)	
	Amazonas										6.5				Luizão (1995)	
	Roraima										9.2				Barbosa and Fearnside (1996)	
	Amazonas								29.7						Summers (1998)	(09)
	Roraima										8.5				Villela and Proctor (1999)	(10)
	Pará		10.6		32.2										Fearnside et al. (1999)	
	Amazonas	325.5	3.5	1.1	10.8	3.3									Fearnside et al. (2001)	(11)
	Amazonas	325.5	1.3	0.4	8.3	2.5	21.1	6.5	31.0	9.5	10.5	3.2			Nascimento and Laurance (2002)	(12)
	Rondônia/ Amazonas	306.8	16.6	5.4	0.6	0.2	14.0	4.6	30.5	9.9	8.3	2.7			Cummings et al. (2002)	(13)
	Pará	258.0			35.0	13.6	16.0	6.2	55.0	21.3					Gerwing (2002)	(14)
	Pará	287.4							96.1	33.4					Rice et al. (2004)	(15)
	Pará								58.4						Keller et al. (2004)	(16)
	Pará								63.5						Keller et al. (2004)	(17)
	Amazonas										5.9				Luizão et al. (2004)	(18)
	Amazonas										5.8				Monteiro (2005)	
	Amazonas	306.1	2.1	0.7			19.5	6.4							de Castilho et al. (2006)	(19)
	Amazonas	306.1			6.3	2.1									Nogueira (2006)	(20)
	Amazonas	306.1		2.3		1.8		2.9					104.9	34.3	da Silva (2007)	(21)
	Pará								58.4						Palace et al. (2007)	(22)

Non-dense	Pará	126.1			2.9	2.3	6.0	4.8	7.5	5.9	13.1	10.4			Revilla Cardenas (1986)	(23)
	Rondônia	362.5			10.8	3.0	2.6	0.7	5.5	1.5	16.0	4.4			Revilla Cardenas (1987)	(24)
	Rondônia	303.0							27.0	8.9	10.0	3.3			Martinelli et al. (1988)	
	Roraima								5.8		4.6				Scott et al. (1992)	
	Acre	320.0	12.8	4.0					35.0	10.9	38.0	11.9	32.0	10.0	Brown et al. (1992)	(25)
	Rondônia	285.0							34.5	12.1	10.0	3.5			Brown et al. (1995)	(26)
	Rondônia	239.4	21.6	9.0	11.9	5.0			9.7	4.1					Graça et al. (1999)	(27)
	Rondônia/ Amazonas	239.4	17.5	7.3	0.5	0.2	14.1	5.9	32.4	13.5	10.1	4.2			Cummings et al. (2002)	(28)
	Mato Grosso								38.8						Pauletto (2006)	(29)
	Mato Grosso								50.2						Palace et al. (2007)	(30)
	Rondônia/ Amazonas	270.1	37.9	14.0	0.6	0.2	11.4	4.2	20.8	7.7	9.5	3.5			Cummings et al. (2002)	(31)
	Mato Grosso/ Pará	253.8					3.1								This study	(32)
	All data	286.8	12.9	4.6	10.0	3.1	11.0	4.2	29.6	8.8	10.5	4.9	89.0	25.8		
	Dense	299.0	6.5	1.9	11.8	3.4	13.1	4.3	33.4	9.4	9.2	4.1	108.1	31.0		
Non-dense	266.6	22.5	8.6	5.3	2.1	7.4	3.9	24.3	8.1	13.9	5.9	32.0	10.0			

Notes:

* Some of the results reported refer to the annual production of litter, which can differ from the stock per unit area.

(1): Averages of the years 1963 and 1964; (2): Dry weight for lianas was obtained assuming 50% of the fresh weight (see Klinge et al. 1975, Table 9-1). The fresh weight of the roots (255 Mg ha⁻¹) given by Klinge et al. (1975) was converted to dry mass assuming 45.4% humidity, based on the results of da Silva (2007); (3): Vegetation described by the author as submontane broadleaf dense. The biomass of trees ≥10 cm dbh was calculated starting from Table 3.3, year 1982. In the same way, the mean biomass was estimated for trees < 10 cm (9.35) which were added to broadleaved herbs (0.26) mentioned in Table 3.4; (4), (5), (7), (23), (24): the litter and the root mat were added together; (6): From Fearnside et al. (1993); (8), (10): Average of the sites studied by the authors; (9): These estimates only refer to coarse woody litter ≥20 cm dbh (p. 37); (11): The value used for the biomass of trees ≥ 10 cm dbh was that used by Nascimento and Laurance (2002); (12): The biomass of palms does not include individuals ≥10 cm dbh, which accounts for less than 1% of the stems ≥ 10 cm dbh (p. 312); (12), (13), (28), (31): the lianas biomass was estimated by the equation of Putz (1983). The values for understory include the seedlings + trees < 10 cm dbh; (14): For the estimate of biomass of trees (≥10 cm) the equation of Overman et al. (1994) was used and for the lianas biomass the equation of Gerwing and Farias (2000) was used; (15): Rice et al., 2004 report 48 Mg C ha⁻¹ and not the biomass ha⁻¹. This was converted to biomass considering our wood density and 50% C content for biomass (see Table 3). The equation of Chambers et al. (2001) was used for the biomass of trees; (16), (17), (22), (29), (30): Fallen dead woody material with diameter ≥ 2 cm; (18): Averages of the stocks among plateau, slope and valley (Table 3); (3), (16), (17), (26), (29): 15% was added for standing dead trees, based on Palace et al., 2007 (12-17%); Nascimento and Laurance, 2002 (11-14%). Other authors consider a larger percentage, such as 19-20% by Summers, 1998, 18-25% according to Keller et al., 2004; and Rice et al., 2004, and 42-76% according to Delaney et al., 1998; (19): The biomass of trees (excluding palms) ≥10cm = 306.11 Mg ha⁻¹. See Appendix A (325.7 - 6% of the trees (19.5 Mg ha⁻¹) between 1 and 10 cm dbh = 306.11). Palms = 2.1 Mg ha⁻¹. The Higuchi et al. (1998) equation was used for biomass of trees ≥5 cm dbh and palms from Saldarriaga et al. (1988) equation. Trees < 5 cm from the equation by Nascimento and Laurance (2002); (20): Estimates of Nogueira (2006) varied from 6.3, 12.3 and 3.9 in central Amazonia (respectively obtained by the equations of Putz, 1983; Gerwing and Farias, 2000; Gehring et al., 2004). These values vary from 2 to 4% of the biomass of the trees ≥10 cm (= 306.11) estimated by de Castilho et al. (2006). It was adopted 2%, regarding the value obtained using the equation of Putz (1983); (=6.3/306.11); (21): For palms and lianas the same percentage was used as reported by the author for the biomass of the trees ≥5 cm dbh. For the understory the percentage does not include stems 5-10 cm dbh. The fresh weight of the roots reported per hectare was converted to dry biomass assuming 45.4% humidity; calculations were made starting from the information in Table 5.8c, pp. 66, 67. The percentage for roots refers to roots ≥2 mm diameter at the base. The estimate of de Castilho et al. (2006) was used for the biomass of trees ≥10 cm dbh, obtained starting from a similar forest and at large scale (72 ha); (24): Open upland forest on poorly drained terrain ("sandbank" forest); (25): Standing live above-ground biomass was estimated based on equation of Brown et al. (1989). Palms only measured for individuals ≥10 cm dbh, found 4% of the biomass in tree ≥10 cm dbh (Table 1). Belowground biomass obtained from Nepstad (1989), who suggests 10% of tree biomass ≥10 cm. Data for standing dead trunks were obtained from Uhl et al. (1988) in Paragominas, Pará state; (26): Estimate refers to fallen dead trunks and litter; (27): For the biomass of all trees ≥10 cm the values used for calculations were from Cummings et al. (2002) for open forest, because Graça et al. (1999) did not estimate the biomass of the trees with leaves. Also litter data were excluded because they include many leaves that had fallen after the trees were felled and dried; (32): 91 trees with 5-10 cm dbh were completely weighted and replicated for an expected frequency per hectare: 102.5 ± 24.5.

The geographical coordinates of each plot inventoried were obtained with ruler measurements from phyto-physiognomic maps available in the original RadamBrasil Project reports (Brazil, Projeto RadamBrasil, 1973-1983) at a scale of 1:1,000,000. An updated version of this phyto-physiognomic map, or simply a vegetation map, produced in 2007 (IBGE/SIPAM) at a scale of 1:250,000, has been related to the average corrected biomass value for each vegetation class. The vegetation classification system is based on Veloso et al. (1991).

Using GIS software (ARCGIS version 9.0, ESRI), a number of geo-processing steps have been run to recover original vegetation classes over deforested and degraded areas in order to calculate the original biomass at the moment of the vegetation inventory and secondly to aggregate vegetation classes to the classification level used for the biomass calculations. The total area of each vegetation class (ha) has been derived from the map. The total biomass of each vegetation type in the region has been calculated by simply multiplying the area for each type (ha) times the average biomass per hectare. The vegetation classes included cover 344,867,575 ha, or 67.5% of the Brazilian Legal Amazon (510,468,420 ha); the vegetation classes used do not include savannas or *campina* vegetation types.

Fourteen percent of the area is classified as human altered land cover. The original vegetation classes have been recovered for this area from the RadamBrasil dataset, which includes information on the original vegetation classes before the land cover alterations. Around 11% of the altered area has been reclassified. For a large part of the dataset the original vegetation type up to phyto group classification level (e.g. Da = Dense alluvial ombrophilous forest) were recovered. The additional areas were classified up to the general formation level (e.g. Dense ombrophilous forest) or were maintained as altered areas. For the areas with vegetation classified at the formation level, the biomass values for the different phyto groups were averaged.

Results

Allometric biomass equation

Table 2 presents biomass allometric equations developed from trees sampled in open forest in southern Amazonia (SA), which allows the dry weight (in Kg) of the whole tree, bole or crown to be obtained based only on diameter measurements (Figure 1A - C). The dry masses of all trees are available in Appendix C.

Table 2. Parameters of the biomass equations [$\ln(\text{Dry weight}) = a + b \ln(\text{Diameter})$] in trees sampled in open forest in the southern Amazonia (SA) (diameter range 5-124 cm). The diameter measurements were taken at breast height (1.30 m above the ground) or just above any buttresses. Measurements of diameter are in cm and those of mass are in Kg.

Model	Parameters*						n	Adjusted r^2	SEE**
	a ($\pm SE$)	<i>Lower</i> <95%>	<i>Upper</i>	b ($\pm SE$)	<i>Lower</i> <95%>	<i>Upper</i>			
Whole tree	- 1.716 (0.079)	- 1.872	- 1.560	2.413 (0.029)	2.357	2.470	262	0.964	0.306
Bole	- 1.929 (0.093)	- 2.111	- 1.746	2.335 (0.034)	2.269	2.402	262	0.949	0.359
Crown	- 3.355 (0.146)	- 3.642	- 3.069	2.578 (0.053)	2.474	2.682	261	0.901	0.564

*All parameter values are significant ($p \leq 0.0001$).

**Standard Error of the Estimate (SEE) = $\sqrt{\text{Residual Mean-Square}}$

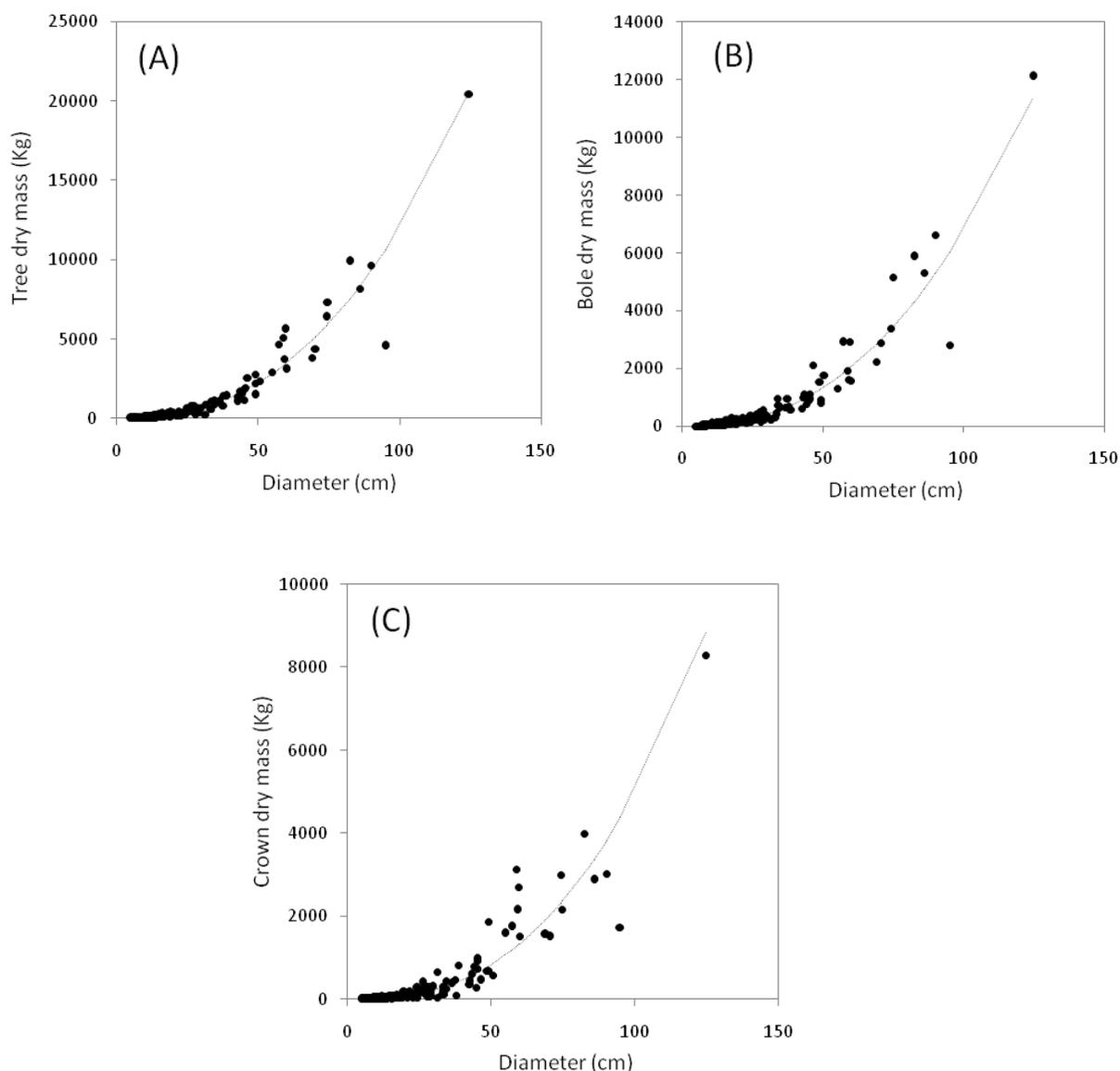


Figure 1. Relationship between diameter and the dry weight (in Kg) of whole tree (A), bole (B) and crown (C). The diameter measurements (in cm) were taken at breast height (1.30 m above the ground) or just above any buttresses. Each tree was directly weighted. The dry weight was obtained from individual moisture content measurements from samples taken at the base and at the top of the bole in each tree. The dry weight of the crown was determined considering a 47.6% moisture content (see section 2.3). See Table 2 for details about equations.

The linear equation developed in this study accurately estimated the dry biomass of sampled trees (-1%) and the normalized biomass per hectare (-0.05%). The biomass estimates per hectare was obtained after normalization of sampled trees for the number of trees in each diameter class (5-cm intervals) estimated from large inventories (for details see section 2.1).

Three previously published allometric equations developed in dense forest in the central Amazon (CA) by Higuchi et al. (1998), Chambers et al. (2001) and by da Silva (2007) were tested. All three CA equations tend to overestimate the biomass of smaller trees while underestimating the biomass of larger trees. Nevertheless, the total biomass estimated for sampled trees from CA equations was similar to that obtained in the field (respectively -0.8%, -2.2% and 1.6% for equations by Higuchi et al., 1998; Chambers et al., 2001 and da Silva, 2007), due the compensating effects of over- and underestimates of small and large trees (Figure 2). However, when the biomass per hectare is estimated using CA equations the estimates were found to be 6% higher for the equations published by Higuchi et al. (1998), 8.3% for the cubic equation of Chambers et al. (2001) and 18.7% for the power equation of da Silva (2007). The higher estimates per hectare from da Silva's equation are explained by the overestimates of smaller trees (Figure 2), since in CA dense forest there are many smaller trees (see Table 4 in de Castilho et al., 2006). For converting fresh to dry mass estimated with the Higuchi and da Silva equations a value of 0.57 was used, assuming a moisture content of 43% in the above-ground components of trees, obtained from the results of da Silva (2007, p. 67, Table 5.8c).

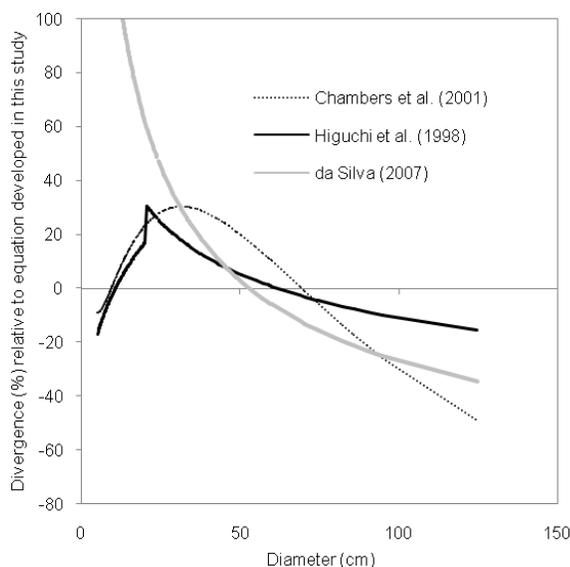


Figure 2. Divergence (%) of biomass estimated for the two linear equations [$DW = \exp(-1.754 + 2.665 \times \ln(D)) \times 0.57$; $DW = \exp(-0.151 + 2.17 \times \ln(D)) \times 0.57$] by Higuchi et al. (1998), for Chambers et al. (2001) cubic equation [$DW = \exp(-0.37 + 0.333 \times \ln(D) + 0.933 \times \ln(D)^2 - 0.122 \times \ln(D)^3)$], and recent power equation [$\exp = (2.2737 \times D^{1.9156}) \times 0.57$] developed by da Silva (2007), relative to the linear equation developed in this study. The Higuchi and da Silva equations relate diameter to fresh mass. In this study 43% moisture content was used to obtain dry mass, based on a recent dataset by da Silva (2007).

Two models that include diameter, height and wood density as independent variables, as published by Chave et al. (2005) and Overman et al. (1994), estimated with accuracy the biomass of sampled trees or when normalized per hectare (both overestimating about 4%). The quadratic equation published by Brown (1997) that has been used by prior studies in SA forest was tested. This equation results in accurate estimates of sampled trees (+1.8%) but when normalized per hectare the error increases to 6.5%. This differs from the linear equation also published by Brown (1997), which overestimated the biomass of sampled trees by 4.6% but overestimated by only in 2% when normalized per hectare.

Other previously published equations (Brown et al., 1989; linear and quadratic equations by Chambers et al., 2001; Chave et al., 2001; cubic equation by Chave et al., 2005; da Silva, 2007 with diameter and height; dos Santos, 1996 and Saldarriaga et al., 1988) were also tested, but all resulted in larger errors.

The correction for lower wood density (ratio = 0.593/0.67) was applied to biomass estimated from the Chambers et al. (2001) equation as proposed by Baker et al. (2004) and Malhi et al. (2006). The results underestimated the biomass per hectare by 4.7%. This suggests similar errors in biomass maps published by Malhi et al. (2006). Similarly, a recent study (Nogueira et al., 2008) that adds corrections for shorter stems to the Higuchi et al. (1998) equation implies a greater error in underestimates of biomass for SA open forests. Although logical, simple corrections to allometric relationships appear to be a risky way to make biomass adjustments.

The bole dry biomass was 60.6% of the biomass of the whole tree. This relation is 57.9% when the comparison is based on fresh mass due to higher moisture content in the tissues of the crown, such as leaves and fine branches. These two results indicate that, as compared to the bole, the biomass stored in the crowns of trees in open forest (39.4%) is significantly higher than in trees in the dense forest (CA), where crown biomass is equivalent to 30.8% (n = 121) of the biomass of the whole tree (da Silva, 2007, p. 57) or 34.4% (n = 38) according to Higuchi et al. (1998).

An assessment was made of whether this difference could to be explained by a shorter bole at any given diameter in SA trees (Nogueira et al., 2008) or because the size of crowns in trees in SA trend to be larger than in CA. Results from the crown biomass model developed in dense forest (Chambers et al., 2001) were plotted against data on crowns directly weighed in open forest and concluded that the crowns in the open forest were not larger than in dense forest (Figure 3). Therefore, higher biomass storage in the crowns in the SA as compared to

bole mass is due only to shorter boles in open forest as compared to dense forest. Using the equation for boles in dense forest also developed by Chambers et al. (2001) resulted in a 13% overestimate of bole biomass per hectare.

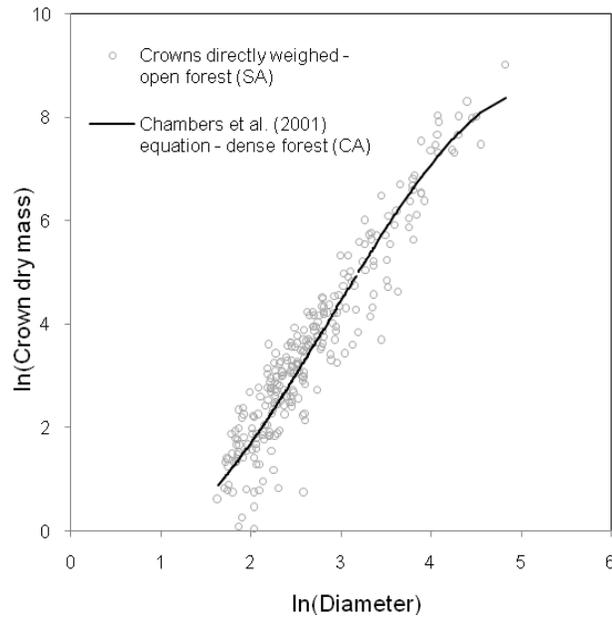


Figure 3. Equation for crown biomass estimates developed in dense forest, central Amazonia (CA) by Chambers et al. (2001) plotted against crown mass directly weighed in open forest, southern Amazonia (SA). Measurements of diameter are in cm; crown mass is in Kg (dry weight).

Allometric equations for bole-volume estimates

Equations for bole-volume estimates were developed for dense forest in CA and for open forest in SA (Table 3 and Figure 4A-C). All equations allow bole volume to be obtained corrected for hollow and irregular trunks based only on conventional diameter measurements (at breast height or above buttresses) and are also an alternative way to avoid errors due to height estimates and tapering. The equations also allow inclusion of trees with stem diameter <31.8 cm, which were not inventoried by the RadamBrasil Project. The equations can also adjust for errors in published tree measurements in large-scale inventories, identifying incoherencies between diameter and height measurements.

Table 3. Parameters of bole volume equations [$\ln(\text{Corrected volume}) = a + b \ln(\text{Diameter})$] in central (CA) and southern Amazonia (SA). The diameter measurements were taken at breast height (1.36 m above the ground in CA or 1.30 m in SA) or just above any buttresses. Measurements of the diameter are in cm and of those of volume are in m^3 .

Forest type	Parameters*								Adjusted r^2	SEE**
	Diameter range	a ($\pm SE$)	Lower <95%>	Upper	b ($\pm SE$)	Lower <95%>	Upper	n		
Dense forest, CA	5 – 39.9	- 9.008 (0.091)	- 9.186	- 8.830	2.579 (0.031)	2.640	2.518	253	0.965	0.245
	40 – 106	- 6.860 (0.565)	- 7.996	- 5.723	1.994 (0.143)	2.281	1.706	48	0.805	0.228
Open forest, SA	5 – 82	- 8.939 (0.068)	- 9.072	- 8.806	2.507 (0.025)	2.458	2.557	298	0.971	0.251

*All parameter values are significant ($p \leq 0.0001$)

**Standard Error of the Estimate (SEE) = $\sqrt{\text{Residual Mean-Square}}$

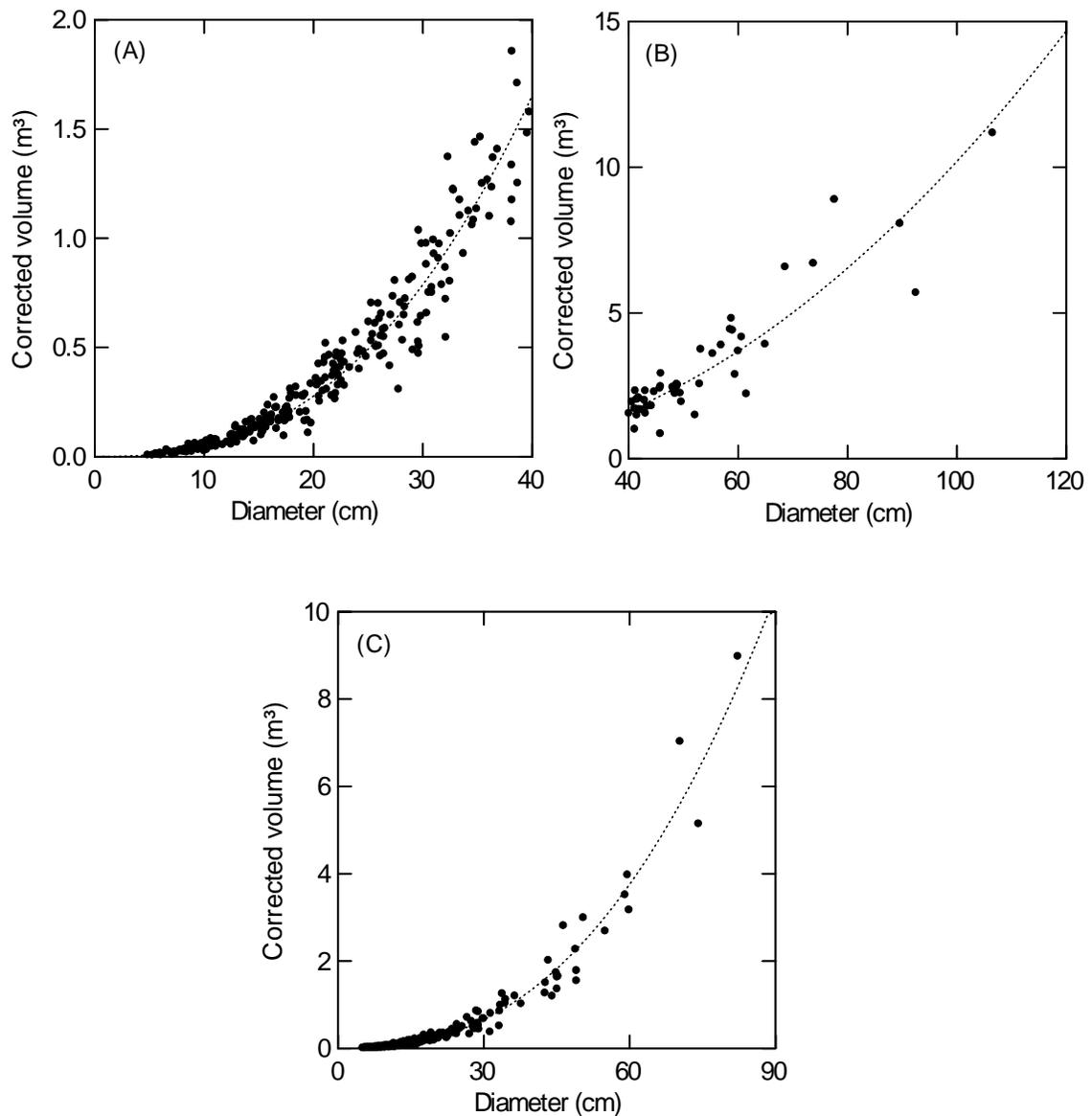


Figure 4. Relationship between $\ln(\text{Diameter})$ and $\ln(\text{Corrected volume})$ considering trees dbh 5-39.9 cm (A) and dbh 40-106 cm (B), both in dense forest, and trees dbh 5-82 cm (C) in open forest. The diameter measurements were taken at breast height (1.36 m above the ground in central Amazonia or 1.30 m in southern Amazonia) or just above any buttresses. Measurements of diameter are in cm and those of bole volume in m^3 . See Table 3 for details of equations.

Form factor: mean tapering of the boles in dense and open Amazonian forests

In general, the mean form factor considering trees of all sizes (starting diameter ≥ 5 cm) is similar between dense forest in CA and open forest in SA (Tukey test; $p > 0.05$). In dense forest the tapering increases (lower form factor) with increasing tree size, while in open forest the tapering of trees of intermediate size is higher than in dense forest (Figure 5A-B).

Because of this, the form factor found considering only trees ≥ 31.8 cm in diameter (minimum diameter inventoried by RadamBrasil) and normalized by the diameter distribution per hectare was lower in open forest (Table 4).

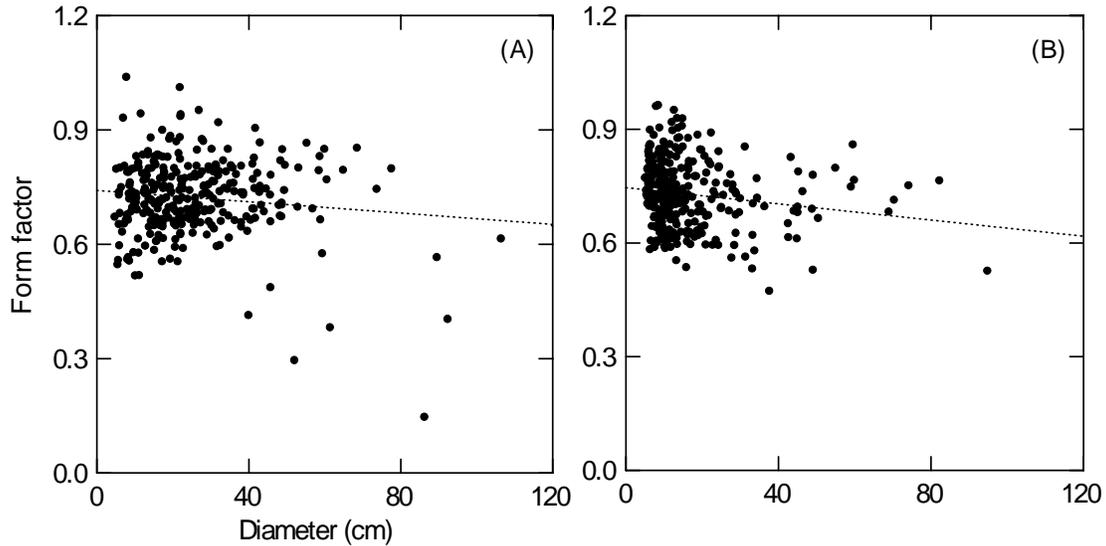


Figure 5. Tapering of the bole (form factor) by tree size in two forest types: **(A)** Dense forest, central Amazonia (CA) ($n = 299$) and **(B)** Open forest, southern Amazonia (SA) ($n = 300$). The diameter measurements were taken at breast height (1.36 m above the ground in CA or 1.30 m in SA) or just above any buttresses. Disperse cases in **(A)** are trees with accentuated irregularities in bole shape (see section 4.3).

The form factor found for trees ≥ 31.8 cm stem diameter in dense forest did not differ significantly from the value adopted in the RadamBrasil volume estimates (0.7) (one-sample t test, $p > 0.05$; Table 4). Considering only the mean form factor of sampled trees ($\text{dbh} \geq 31.8$ cm) in SA open forest, there is no significant difference from 0.7 (one-sample t test, $p = 0.459$), but when normalized to the expected frequency per hectare, a statistical difference was detected (Table 4). In this case, the RadamBrasil wood-volume inventories in open forest types were overestimated by around 5% in the open forest in southern Amazonia where the mean form factor is around 0.66 (Table 4).

Table 4. Mean tapering of the bole (form factor) in dense forest in central Amazonia (CA) and in open forest in the southern Amazonia (SA). The table presents means of trees sampled and means normalized by the diameter distribution expected per hectare. An inventory of 72 ha (de Castilho et al., 2006) was used in CA in adjusting the diameter classes. In SA 11 ha (Feldpausch et al., 2005) were used for trees ≥ 10 cm diameter and 30 ha (Pereira, 2005) for trees 5-10 cm in diameter. The diameter measurements were taken at breast height (1.36 m above the ground in CA or 1.30 m in SA) or just above any buttresses.

Tree size (diameter in cm):	Dense forest, CA						Open forest, SA					
	(mean \pm standard deviation; number of trees and comparison of means ¹)											
	Trees sampled			Normalized by inventories			Trees sampled			Normalized by inventories		
≥ 5.0	0.721 \pm 0.101	303	Aa	0.713 \pm 0.099	1334	Aab	0.728 \pm 0.090	300	Aa	0.721 \pm 0.092	583	Aa
≥ 10.0	0.723 \pm 0.101	267	Aa	0.724 \pm 0.094	620	Aa	0.719 \pm 0.091	200	Aa	0.716 \pm 0.093	475	Aa
≥ 31.8	0.709 \pm 0.129	82	Aab*	0.709 \pm 0.129	96	Aab*	0.687 \pm 0.095	30	Aa*	0.664 \pm 0.098	57	Ab
≥ 50.0	0.655 \pm 0.205	20	Ab*	0.661 \pm 0.205	25	Ab*	0.726 \pm 0.090	10	Aa*	0.724 \pm 0.084	12	Aab*

¹The same lower-case letters appearing in the same column or capital letters in the same line indicate that values do not differ significantly (Tukey test; $p > 0.05$).

*Indicates that values do not differ significantly from the form factor (0.7) used in RadamBrasil volume estimates (one-sample t test; p -value > 0.05).

Volume expansion factor (VEF)

The VEF currently adopted in biomass estimates is 1.25 for dense forest and 1.5 for non-dense forest. These values are used to add the bole volume of trees 10 to 30 cm in diameter (Brown and Lugo, 1992). Therefore, since the RadamBrasil volume inventories start with trees 31.8 cm in diameter (1 m circumference), there is a gap for trees 30 to 31.7 cm in diameter. This means that the bole volume of around 11 trees was not counted, according to the 72-ha inventory in dense forest in central Amazonia (de Castilho et al., 2006), which is equivalent at $9.5 \text{ m}^3 \cdot \text{ha}^{-1}$. In this study the bole volume of the trees 10 to 31.7 cm in diameter was estimated in dense and open forest; because of this the VEF values reported here are obviously expected to be higher than values in the literature that do not include trees with dbh 30 to 31.7 cm. The estimates were calculated from bole volume corrected for indentations and hollow trunks.

In dense forest in CA, trees 10 to 31.7 cm in diameter represent 53.7% of the bole volume of the trees ≥ 31.8 cm diameter. Therefore, the VEF estimated from corrected bole volume was 1.537 when normalized by the diameter distribution expected per hectare. In this case, the VEF (1.25) adopted currently in biomass models for dense forest will be underestimated by around 25%. In the case of the inventories in which trees were sampled starting at 25 cm stem diameter (such as the FAO inventories: Glerum, 1960; Glerum and Smitt, 1962; Heinsdijk, 1957, 1958) the appropriate VEF value will be 1.305.

For open forest in southern Amazonia the bole volume estimated for trees 10 to 31.7 cm was equivalent to 50.6 % of the bole volume of all trees ≥ 31.8 cm diameter (when normalized by the diameter distribution per hectare). Therefore the appropriate VEF value is 1.506, similar to the value currently used in biomass estimates. In the case of inventories of trees ≥ 25 cm in diameter, the VEF value found was 1.283. In this forest type, for 6.7% of the sampled trees the bole volume was not corrected for indentations and hollow trunks because of operational demands of the logging company that owns of the collecting area.

Biomass expansion factor (BEF)

The BEF (biomass expansion factor) currently adopted in biomass estimates for dense forest (inventoried bole biomass $\geq 190 \text{ Mg ha}^{-1}$) is 1.74, which was obtained by Brown et al. (1989) in plots that were mostly located in Venezuela.

The relationship between tree biomass estimated by a model developed in central Amazonia (Higuchi et al., 1998) using bole biomass (corrected volume \times wood density) results in a BEF value of 1.621 ± 0.415 (mean \pm sd; $n = 267$ trees). Normalized by the

diameter distribution per hectare the BEF is 1.635 ± 0.441 . The two BEF values differ statistically from the 1.74 value (one-sample t test, $p < 0.001$). The BEF value obtained from 267 trees sampled in this study is similar to the mean ratio between the total weight of the tree and the weight of the bole (~ 1.64) reported for 315 trees sampled by Higuchi et al. (1998, p. 157). Considering these results, the BEF currently adopted in the biomass estimates results in 6% overestimate of the crown biomass of trees in dense forest in central Amazonia.

In open forest the crown biomass of 262 trees was directly weighed and a linear model was developed to obtain crown biomass from diameter measures alone (Table 2). Although an allometric equation is preferred, the BEF value of 1.580 ± 0.357 (mean \pm sd; normalized by the diameter distribution per hectare) could be used in cases where individual tree diameters are not available. A value of the BEF was estimated for the plots in this study using the allometric equation developed by Brown and Lugo (1992) for use where the bole biomass is $\leq 190 \text{ Mg ha}^{-1}$: $\text{BEF} = \exp(3.213 - 0.506 \times \ln(\text{bole biomass}))$. The BEF value found was 1.930, around 18% higher than the BEF value reported here.

The adjusted biomass map for Brazilian Amazonia

The new wood-density dataset reduces uncertainties in converting bole volume to estimated bole biomass for Brazilian Amazonia as a whole. In the case of uncertainties in the volume reported in the inventories, corrections were not applied for lower form factor in open forest because this is related to hollow trunks in the intermediate-sized trees sampled (Figure 5B). As there are no data on occurrence of hollow trunks that relate to tree size that would assure that this effect is expected at large scale, this effect was not applied in biomass estimates (see discussion section). However, overestimates in bole volume (4.4% found in dense forest and 3.3% in open forest) by the formula adopted in the RadamBrasil inventories, which includes a form factor of 0.7, was applied in biomass adjustments because new BEF values were used in this study. This error has not been transferred to the biomass estimates because it is assumed to be compensated by the variables that add the crown biomass (BEF) when the volume data are converted to biomass (see Nogueira et al., 2006, p. 19). The new VEF values were applied to all forest types and the BEF value for dense forest (1.635) was applied to forest types with bole biomass $\geq 190 \text{ Mg ha}^{-1}$. In the non-dense forest type a BEF value of 1.58 was found for a forest with a biomass stock of 156 Mg ha^{-1} (dry weight) in all boles $\geq 10 \text{ cm dbh}$. Thus, in non-dense forest types the only BEF value used was 1.58 for forest with bole biomass $156 \text{ Mg ha}^{-1} \pm 5\%$ (148.2 to 163.8 Mg ha^{-1}), and in the remaining forest applied the equation proposed by Brown and Lugo (1992) that relates BEF to the

corresponding biomass of the inventoried volume was applied. This was adopted because other work in the tropics and later work on US forests has shown that the magnitude of the BEF varies with the merchantable volume of the stand, with high values of BEF at low values of volume, and values generally *decreasing exponentially* to a constant BEF at high volume (Brown, 2002). If the BEF value of 1.58 is applied to plots with a stock in bole biomass lower than 156 Mg ha^{-1} , the biomass would be systematically underestimated.

The distribution of biomass over the Brazilian Amazon is presented in Figures 6. The total biomass (below- and above-ground) for the Brazilian Amazon using the corrected values is 125.4 Pg ($=10^{15} \text{ g}$) dry weight, or 60.8 PgC assuming $1 \text{ Mg dry biomass} = 0.485 \text{ Mg C}$ (da Silva, 2007). The above-ground biomass alone is 104.2 Pg (50.5 PgC). The total biomass storage and above-ground biomass were estimated in 15 forest type for the nine states of the Brazilian Legal Amazon (Tables 5 and 6). The average per-hectare biomass of each of the vegetation types is also given in Table 5. Considering the cumulative deforestation in Brazilian Amazonia through 2006 (Brazil, INPE, 2007), the dry biomass stock had been reduced to 113.3 and 94.2 Pg (or 54.9 and 45.6 PgC), respectively for below-ground + above-ground and only above-ground, excluded non-forest areas or secondary formations. These results have implications for biomass and carbon emissions because they directly affect the estimates of carbon stock and emission in all forest types when compared with previous estimates.

Table 5. Average total biomass (below + above-ground) and above-ground biomass by forest type (dry weight in Mg ha⁻¹) and total stock by state ($\times 10^6$ Mg) in Brazilian Legal Amazonia at the time of the RadamBrasil inventory, therefore before intensive deforestation had occurred. Values in brackets [value] denote only above-ground biomass. All other values denote below + above-ground biomass. Secondary formations and non-forest vegetation were not considered.

Forest type (IBGE code)	Average DW Biomass (Mg ha ⁻¹)	Acre	Amazonas	Amapá	Maranhão	Mato Grosso	Pará	Rondônia	Roraima	Tocantins	Total
Open alluvial rain forest (Aa)	357.8 [298.4]	453.878 [378.527]	2628.872 [2192.441]	29.953 [24.980]		10.425 [8.695]	3.068 [2.559]	179.527 [149.723]		10.739 [8.956]	3316.462 [2765.881]
Open lowland rain forest (Ab)	363.4 [303.1]	4230.781 [3528.755]	8244.753 [6876.677]		2.680 [2.235]		29.563 [24.657]	1516.546 [1264.901]	9.952 [8.301]		14034.274 [11705.526]
Open submontane rain forest (As)	336 [280.2]		1688.396 [1408.002]	18.651 [15.554]	43.295 [36.105]	3370.779 [2810.989]	8995.234 [7501.383]	2954.668 [2463.982]	340.164 [283.672]	513.068 [427.862]	17924.254 [14947.548]
Seasonal Deciduous submontane (Cs)	290.1 [241.9]					259.290 [216.209]	100.996 [84.216]			43.249 [36.064]	403.536 [336.488]
Dense alluvial rain forest (Da)	360.8 [299.3]	21.282 [17.654]	4427.041 [3672.432]	217.135 [180.124]	29.309 [24.313]	177.148 [146.952]	2079.974 [1725.433]	71.020 [58.914]	108.029 [89.615]	9.829 [8.153]	7140.766 [5923.590]
Dense lowland rain forest (Db)	384.5 [318.9]	611.706 [507.342]	25590.142 [21224.177]	796.717 [660.788]	336.086 [278.746]		6215.557 [5155.113]	69.043 [57.263]	381.177 [316.144]		34000.426 [28199.573]
Dense montane rain forest (Dm)	361.3 [299.7]		414.986 [344.233]				32.419 [26.892]		922.239 [765.002]		1369.644 [1136.126]
Dense submontane rain forest (Ds)	385.3 [319.6]	30.798 [25.547]	7694.882 [6382.778]	3132.182 [2598.093]	633.965 [525.864]	1994.164 [1654.127]	17294.611 [14345.595]	435.885 [361.560]	3133.542 [2599.221]	39.105 [32.437]	34389.134 [28525.220]
Seasonal Semideciduous alluvial (Fa)	283.4 [236.4]				0.474 [0.395]	565.080 [471.365]	24.166 [20.158]	9.578 [7.990]	19.671 [16.409]	150.606 [125.629]	769.574 [641.946]
Seasonal Semideciduous in lowland areas (Fb)	309.3 [258]					327.601 [273.265]		46.747 [38.993]			374.347 [312.259]
Seasonal semideciduous submontane (Fs)	315.7 [263.3]				177.145 [147.743]	5298.019 [4418.652]	317.448 [264.758]	252.242 [210.375]	438.728 [365.908]	8.973 [7.484]	6492.555 [5414.918]
Contact Woody oligotrophic vegetation (<i>Campinarana</i>) of swampy and sandy areas / Rain forest (LO)	384.6 [320.8]		468.644 [390.903]			0.260 [0.217]	3.857 [3.217]		246.608 [205.699]		719.370 [600.036]
Contact Rain forest/Seasonal forest (ON)	310.6 [259.1]					1142.401 [952.981]	10.584 [8.829]	99.742 [83.204]	30.902 [25.778]		1283.629 [1070.793]
Contact Savanna / Seasonal forest (SN)	302.7 [252.4]				738.387 [615.689]	1244.575 [1037.762]	28.094 [23.425]	27.929 [23.288]	0.492 [0.410]	261.612 [218.139]	2301.089 [1918.714]
Contact Savanna / Rain forest (SO)	314.3 [262.1]		75.873 [63.272]	8.750 [7.296]	3.460 [2.886]	173.921 [145.035]	223.638 [186.495]	301.178 [251.157]		119.260 [99.453]	906.079 [755.594]
Total only Above-ground		[4457.825]	[42554.913]	[3486.835]	[1633.975]	[12136.249]	[29372.729]	[4971.350]	[4676.158]	[964.177]	[104254.211]
Total (Below- and Above-ground)		5348.444	51233.588	4203.387	1964.801	14563.662	35359.207	5964.104	5631.504	1156.440	125425.138

Table 6. Stock estimate of dry biomass ($\times 10^6$ Mg) by state and forest type in Brazilian Legal Amazonia, excluding areas deforested through 2006 (Brazil, INPE, 2007). Values in brackets [value] denote only above-ground biomass. All other values denote below + above-ground biomass. Secondary formations and non-forest vegetation were not considered. The forest type is in the column headed “IBGE code” (see Table 5 for correspondence).

IBGE code	Acre	Amapá	Amazonas	Maranhão	Mato grosso	Pará	Rondônia	Roraima	Tocantins	Total
Aa	394.288	27.180	2573.827		10.149	2.466	172.890		7.350	3188.151
	[328.830]	[22.668]	[2146.534]		[8.464]	[2.057]	[144.188]		[6.130]	[2658.872]
Ab	4105.243		8172.446	0.500		23.820	1312.795	9.903		13624.707
	[3424.048]		[6816.369]	[0.417]		[19.867]	[1094.959]	[8.260]		[11363.920]
As		17.994	1658.517	20.518	2911.118	8237.571	2299.615	323.842	264.490	15733.665
		[15.006]	[1383.084]	[17.110]	[2427.664]	[6869.546]	[1917.715]	[270.061]	[220.566]	[13120.753]
Cs					163.691	96.389			43.249	303.330
					[136.494]	[80.374]			[36.063]	[252.932]
Da	20.524	212.723	4332.541	21.446	162.814	1994.710	66.093	107.652	8.667	6927.170
	[17.026]	[176.463]	[3594.039]	[17.791]	[135.062]	[1654.702]	[54.827]	[89.303]	[7.190]	[5746.402]
Db	494.833	778.474	24093.628	297.693		5459.001	64.967	380.815		31569.409
	[410.409]	[645.657]	[19982.985]	[246.903]		[4527.635]	[53.883]	[315.844]		[26183.315]
Dm			414.784			32.418		920.949		1368.151
			[344.065]			[26.891]		[763.931]		[1134.887]
Ds	30.777	3124.909	7639.255	453.528	1295.669	15898.043	300.742	3049.585	9.092	31801.601
	[25.529]	[2592.060]	[6336.636]	[376.194]	[1074.736]	[13187.165]	[249.461]	[2529.581]	[7.541]	[26378.904]
Fa				0.138	525.633	20.590	8.086	19.301	146.288	720.035
				[0.115]	[438.460]	[17.175]	[6.745]	[16.100]	[122.027]	[600.622]
Fb					253.719		32.892			286.610
					[211.637]		[27.436]			[239.073]
Fs				152.774	4227.746	308.664	204.652	381.344	8.338	5283.518
				[127.417]	[3526.023]	[257.432]	[170.684]	[318.049]	6.954	[4406.558]
LO			442.504		0.244	1.820		244.811		689.379
			[369.098]		[0.204]	[1.518]		[204.200]		[575.020]
ON					110.917	0.468	7.654	7.192		126.232
					[92.526]	[0.390]	[6.385]	[6.000]		[105.301]
SN				694.400	477.601	18.100	12.035	0.492	242.215	1444.844
				[579.011]	[398.238]	[15.093]	[10.035]	[0.410]	[201.966]	[1204.753]
SO		7.860	46.762	2.686	47.273	52.652	125.757		12.727	295.717
		[6.555]	[38.996]	[2.240]	[39.422]	[43.908]	[104.871]		[10.613]	[246.604]
Total	5045.664	4169.139	49374.264	1643.682	10186.575	32146.713	4608.178	5445.887	742.417	113362.519
	[4205.842]	3458.409	[41011.808]	[1367.197]	[8488.931]	[26703.753]	[3841.188]	[4521.738]	[619.051]	[94217.917]

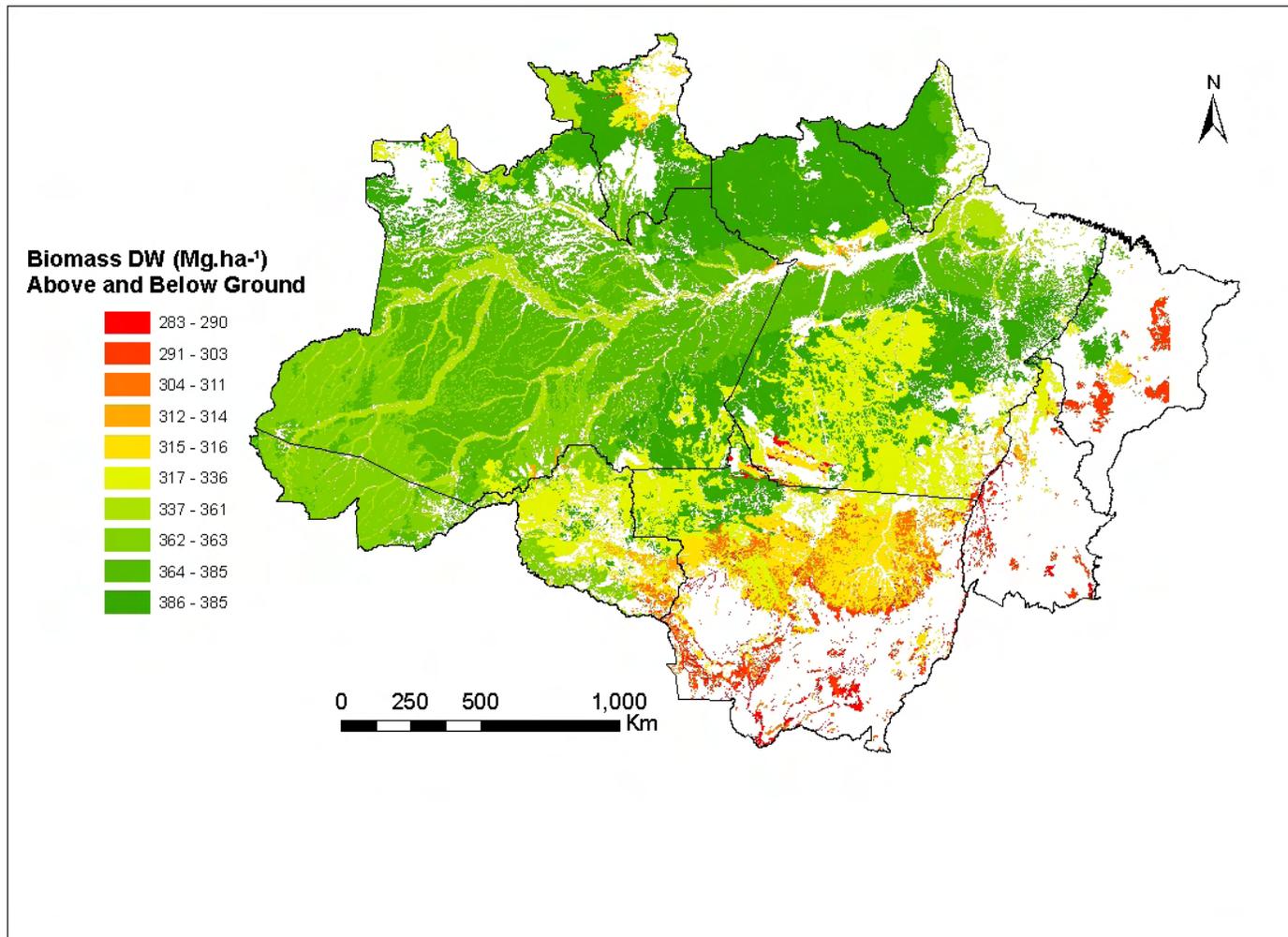


Figure 6. Below and aboveground biomass map (dry weight) for Brazilian Legal Amazonia based on 2860 plots inventoried by the RadamBrasil Project (Brazil, Projeto RadamBrasil, 1973-1983). These estimates do not include savanna, *campinarana*, secondary formations or pioneers. The color scaling of the biomass map is according to Jenks natural breaks classification.

Discussion

Allometric biomass equation developed in the southern Amazon

In spite of there being several previous allometric equations developed in Amazonian forests (Araújo et al., 1999; Chambers et al., 2001; Higuchi et al., 1998; Overman et al., 1994; dos Santos, 1996), equations have not been developed based on direct measurements in non-dense forest types, which are precisely where deforestation has historically predominated (Brazil, INPE, 2007). This is the case of the southern part of the Brazilian Amazon, where open forest and contact zones (ecotones) on fertile soils prevail (Brazil, IBGE, 1997). The new equation proposed by this study is the first equation developed from trees directly weighed in southern Amazon forests. This equation makes it possible to obtain accurate tree biomass estimates using only diameter. This is an important advantage for practical use. In addition, the previously published models that theoretically allow estimation of tree biomass for any forest type, due to their use of height and wood density as input variables, produced larger errors than the equation developed in this study.

The results of this study show that biomass estimates obtained from equations developed in central Amazonia result in overestimates if applied in southern Amazonia (Cummings et al., 2002). However, if downward corrections due to lower wood density and height are applied, the biomass would be underestimated (see Baker et al., 2004; Malhi et al., 2006; Nogueira et al., 2008). The biomass underestimates per hectare due to wood density corrections (as in Malhi et al., 2006) will be close to the overestimates if the Higuchi et al. (1998) formula is applied without wood density corrections. The results also indicate that biomass estimates from quadratic allometric equations developed by Brown (1997) will imply an overestimate of 17 Mg ha⁻¹ in open forest in the southern Amazon (Feldpausch et al., 2005). A linear equation with only diameter as an input variable, published by Brown (1997) for moist forest, and the equations developed by Overman et al. (1994) and Chave et al. (2005) that need diameter, height and wood density, resulted in reasonable biomass estimates per hectare. Surprisingly, the equations developed by Chave et al. (2005) and Overman et al. (1994) provide very similar fits and hence biomass estimates, although the Chave et al. equation was developed from 2410 trees while the Overman et al. equation used only 54 trees. These two equations resulted in very small differences, basically due to smaller trees. This appears to reinforce the argument that it is more reasonable to develop regional allometric equations (Brown, 2002) than to fit tree biomass to large datasets (Chave et al., 2005), because, despite a better theoretical description of the scaling relationship $Mass \propto Diameter$,

fitting from a dataset that is lumped from several regions may not accurately reflect the true biomass of the trees in any given region.

Allometric equations for bole-volume estimates in dense and open Amazonian forest: an alternative way to avoid errors due to height estimates, tapering, indentations and hollow trunks

The volume equations developed in Amazonia for estimating the commercial bole of trees generally ignore non-commercial trees or those with hollow trunks or with irregular boles (indentations, non-circular forms or protuberances), which are also denominated as slitted (“fenestrado”) and channeled (“acanalado”) boles according Ribeiro et al. (1999, p. 27). A large inventory in central Amazonia (72 ha; de Castilho et al., 2006) has shown that 9.7 ± 0.7 trees/ha (mean \pm sd; $\text{dbh} \geq 10$ cm) occur with very irregularly shaped boles (*Aspidosperma marckgravianum*, *A. nitidum*; *Swartzia polyphylla*, *S. reticulata*, *S. schomburgkii*) or “fenestrado” (including *Miquartia guianensis*; *Geissospermum argenteum*, *G. urceolatum*). These trees could imply a substantial bias in volume estimates, especially when large trees are included (Nogueira et al., 2006). Considering the species cited above, the mean number of individuals with $\text{dbh} \geq 40$ cm was 1.6/ha (s.d. = 1.8). These arguments are reinforced if these or other species are hollow and/or have irregular trunks. According to Ribeiro et al. (1999), very irregular bole shapes occur in several families in Amazonia, such as Apocynaceae (*Aspidosperma nitidum* Benth.), Olacaceae (*Miquartia guianensis* Aubl.), Leguminosae (*Swartzia* sp.), Euphorbiaceae (*Pausandra macropetala* Ducke), Melastomataceae (*Miconia splendens* Griseb) and Rubiaceae (*Amaioua guianensis* Aubl.).

Previous bole-volume models developed in central Amazonia might have overestimated the dependent variable if they did not exclude trees with indentations and hollow trunks. The errors would be present in the estimates of the cross-sectional area of the bole, which is frequently treated as the “real” volume and has traditionally been obtained using the Smalian formula without corrections for irregular and hollow boles. The Smalian formula is used as a baseline in developing and validating models (Fernandes et al., 1983, p. 539; Higuchi and Ramm, 1985, p. 35; Moura, 1994, p. 29; Ribeiro, 1996, p. 23). These errors might have been eliminated or minimized in the models that were developed or tested using trees that were free of defects such as hollow trunks and protuberances, as assumed by Fernandes et al. (1983, p. 539). Possibly, errors will be small when using these models in estimates of commercial timber, which use species with boles that are more regular than average. Studies that estimate the biomass of all trees in a forest type starting from volume

equations developed for commercial trees will result in overestimation. Because many of the existing datasets were compiled for purposes of commercial timber exploitation, this bias could be present in studies that fit biomass models to these datasets.

Allometric equations for bole volume that include corrections for irregular and hollow trunks and improved estimates of average wood density (Nogueira et al., 2005) can help reduce uncertainties regarding the magnitude of greenhouse-gas emissions from deforestation and other land-use changes in Amazonia. These equations allow estimates to be based on the full sequence of calculation steps, starting from tree measurements to estimate bole volume, then applying appropriate corrections for hollow trunks and irregularities, converting to bole biomass with properly adjusted density values, and adding estimates for trees below the minimum diameter surveyed, for tree components other than the bole and for non-tree forest components. In addition, in datasets from large-scale inventories the use of allometric equations for bole volume that include corrections for irregular and hollow trunks could help resolve discrepancies in diameter and bole height given in RadamBrasil reports. It should be stressed that these methods are needed for assessing carbon stocks and emissions from deforestation and that the task of detecting biomass changes in standing forest requires different methods based on detailed monitoring of individual trees (see Fearnside, 2004).

Form factor: mean tapering of the boles in dense and open Amazonian forest and implications for biomass estimates

The method adopted in this study for calculating form factor allows an adequate estimate of the mean tapering of the bole to be obtained. If conventional measurements are used, the mean form factor is found to be higher than form factors derived from the relationship between corrected bole volume and the volume of a cylinder calculated from conventional diameter measurements. While with the method adopted here the form factor tends to decrease with tree size, non-corrected measures of form factor tend to increase with tree size. This is expected because errors in biometric characters tend to increase with tree size (Nogueira et al., 2006) due to indentations and greater frequency of hollow trunks. For dense forest in central Amazonia the form factor presented in this study (0.709), based on the relationship between “corrected” volume and volume from conventional measurements, agrees with the form factor used by the RadamBrasil Project (0.70). However, form factor was found to be lower in trees in the open forest because it is lower in trees of intermediate size (Table 4; Figure 5B). In analyzing the trees in open forest, it was noted that around 36% of trees with stem diameter ≥ 31.8 cm have hollow spaces in the trunk, which suggests that

occurrence of hollow trunks explains a lower form factor in trees of intermediate size, particularly those 31.8 to 49 cm dbh. The form factor found in open forest using non-corrected measurements was 0.760 ± 0.075 (mean \pm sd, $n=38$; trees ≥ 31.8 cm dbh); the form factor increases with tree size (0.745 and 0.781 for trees ≥ 10 and ≥ 50 cm, respectively). These data confirm the decreases in the form factor from corrected measurements in trees of intermediate size due to hollow trunks. For this reason the difference of 5% between mean form factor in open forest and the value of 0.7 used by the RadamBrasil Project was not applied in biomass adjustments. The difference is substantial and its effect on biomass therefore has important implications for carbon emission, but there is no information about distribution of hollow trunks by tree size that would allow consistent adjustments to biomass. These results also reinforce the necessity of assessing whether a single form factor is adequate for use with all trees across the Amazon basin.

A previous study in central Amazonia reported 0.75 as the mean form factor (Moura, 1994; dbh ≥ 45 cm, $n = 752$ trees), obtained from conventional measurements. Using the same methodology as Moura (1994), a mean value of 0.789 ± 0.090 (mean \pm s.d.; $n = 33$; dbh ≥ 45 cm) was found for trees sampled in this study, while using the “corrected” measurement methodology the mean was 0.680 ± 0.170 . The results, together with values reported in Table 4, suggest that for large trees in central Amazonia, the effect of irregularities of the bole and hollow trunks will have a strong influence on the estimate of the mean form factor. In spite of large trees storing a substantial portion of the biomass, they have little influence on the mean form factor, which is strongly influenced by the large number of small trees. Eliminating the large trees (dbh ≥ 50 cm; $n = 20$), the mean form factor is increased by only 2.5%, while considering only trees ≥ 31.8 cm dbh raises mean form factor from 0.709 to 0.727(2.5%). These same trees are equivalent to 37% of the bole volume of all trees ≥ 10 cm stem diameter. Considering only the form factor of trees with dbh ≥ 50 cm, there is an overestimate of at least 6% with respect to the form factor of 0.7 used in the RadamBrasil Project formula. The use of a mean form factor without weighting by the proportional volume of the large trees will result in errors in the estimated volume per hectare.

In the case of the estimates published by the RadamBrasil Project, it is possible that the error in the form factor for large trees is being offset by underestimation of the volume of the trees 31.8 to 49 cm. Similarly, in open forest the higher form factor of the large trees could offset the lower form factor of intermediate sized trees. For all of these reasons, in the biomass adjustments in this study the mean form factor used in dense forest by the RadamBrasil Project was considered unbiased.

Volume expansion factor (VEF)

Underestimation of the Volume expansion factor (VEF) value proposed by Brown et al. (1989) and Brown and Lugo (1992) was found only in the dense-forest type. This is confirmed by the results for biomass stock in 20 1-ha plots in central Amazonia (Nascimento and Laurance, 2002; Table 3), where trees with dbh ≥ 30 cm stock only 65.25% of the biomass of trees with dbh ≥ 10 cm. In this case, the VEF ($34.75/65.25 = 0.532$) will be 1.532, similar to the 1.537 value found in this study. Another large (72 ha) biomass study in central Amazonia (de Castilho et al., 2006) similarly indicates that the biomass storage in trees 10 to 30 cm dbh was 36.2%, while in trees ≥ 30 cm dbh contained 63.8% of the biomass in all trees ≥ 10 cm dbh. The VEF in this case will be 1.567. Together, the results reinforce the fact that adjustments are necessary in biomass estimates in dense forest due to underestimates in the commonly used value of VEF.

Biomass expansion factor (BEF)

The biomass expansion factor (BEF) value is related to structural variables of the forest because BEF varies as a function of stem-wood biomass (Brown and Lugo, 1992). The regional variation in Amazonian forest biomass could directly affect the BEF value. The variable BEF takes into account the observation that large trees have relatively more biomass in stems than small trees (Houghton et al., 2001). The BEF proposed by Brown et al. (1989) was estimated assuming that a large part of the biomass is stored in large trees. The biomass estimates for large trees is the main difference between the models of Brown et al. (1989) and those developed in central Amazonia by Chambers et al. (2001) and Higuchi et al. (1998). The large-scale inventories in central Amazonia indicate that trees with dbh ≥ 60 cm stock around 13-18% of the biomass of all trees ≥ 10 cm dbh (Nascimento and Laurance, 2002; de Castilho et al., 2006), while in other Amazonian regions there is a higher biomass stock in larger trees. For example, Chave et al. (2001; Table 3) found 39% of the biomass in only 12 trees ≥ 70 cm dbh, which represents only about 2.3% of the trees ≥ 19 cm dbh. The biomass in large trees in central Amazonia would instead be found in intermediate-sized trees, which would explain the value of BEF being lower than in the plots used by Brown et al. (1989). In addition, Brown (1997) proposed a new equation to replace the earlier one (i.e., Brown et al., 1989) that had been used in deriving the estimate of BEF, which nevertheless continues to be the BEF value in current use for in biomass estimates based on inventoried wood volumes.

Significance for biomass in Brazilian Amazonia

Recent studies have indicated downward adjustments to biomass and carbon emissions in Brazilian Amazonia due to corrections in the conversions of inventoried bole volume to bole biomass (Fearnside, 2007; Nogueira et al., 2005, 2007). In the case of the results reported in this study, corrections are derived for the inventoried wood-volume dataset, and for factors used to account for smaller trees and crown biomass. The biomass map presented in this study from large-scale inventories of wood volume shows lower biomass stock, in general, as compared to previous studies. The spatial pattern of biomass distribution reported in this study is similar to the distributions reported by Saatchi et al. (2007) for forests in the center-south region (northwestern Mato Grosso and southern Pará) and for the northeastern portion of Brazilian Amazonia (Amapá and northeastern Pará). The estimates of Saatchi et al. (2007) were obtained from data measured in 544 plots distributed throughout Amazonia (including the portion outside of Brazil), together with calibrations based on classification of forests by remote sensing. The methodology is therefore different from that adopted in the present study, which is based on 2860 plots in Brazilian Amazonia together with adjustments for allometry and density obtained in different forests.

The map resulting from the study shows reasonable coherence in vegetation types and topography across the basin, especially at the critical area for deforestation at the forest's southern edge. In higher altitude areas in the southern and southwestern Amazon (in the states of Pará, Mato Grosso, Rondônia and part of Acre), where deforestation is concentrated, the results clearly show lower biomass. In Acre state, biomass is possibly overestimated for the bamboo-dominated forests, since they were not differentiated from other vegetation classes. The results cause substantial impact on biomass and carbon-emissions estimates obtained from large-scale inventories of forest volume in Brazilian Amazonia; the results also imply changes in biomass estimates derived from allometric equations, since a new allometric equation is proposed for southern Amazonia (Baker et al., 2004; Malhi et al., 2006). The adjustments reduce discrepancies between studies developed using different methods and reduce the uncertainties in biomass estimates in Amazonia when they are obtained from inventoried wood volume or from allometric equations.

Conclusions

The new allometric equations developed in this study allow accurate biomass and volume estimates to be obtained from diameter alone, which is the variable that is most easily measured in the field. The results indicate higher biomass storage in the crowns of trees (as

compared to the bole of the same trees) in southern Amazonia (SA) than in central Amazonia (CA), due to shorter boles at any given diameter in the SA trees. The results confirm that previous equations developed in CA overestimate biomass if applied to SA trees. Simple corrections to CA allometric equations were found to reflect lower wood density or shorter boles resulted in biomass underestimates. The SA and CA allometric relationships were used to adjust regional biomass estimates from large-scale wood-volume inventories. Current values for adding crown biomass (biomass expansion factor) in dense forest were found to result in a 6% overestimate and values adopted for adding small trees (volume expansion factor) are underestimated by 25%. For the types of open forest studied in this study, the equations that have been used in the past for adding crown biomass overestimate this component by around 18%, and a new allometric equation is proposed. Finally, all corrections were applied to adjust the estimates and produce a biomass map for Brazilian Amazonia from 2860 RadamBrasil plots. The total carbon stock (below- and above-ground) estimated to be present at the time of the inventories was 60.8 Pg ($=10^{15}$ g) for Brazilian Amazonia as a whole (excluding non-forest areas). Deforestation through 2006 has reduced the stock in forest biomass to 54.9 PgC.

GENERAL CONCLUSION

Chapter I concludes that the mean wood density values that have been widely used in biomass estimates for the Amazon region as a whole 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%: $23.4\text{--}24.4 \times 10^6$ Mg CO₂-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.

Chapter II shows that, spite of the importance of corrections for the heartwood density dataset for improved biomass and carbon-flux estimates, linear regressions developed in dense forest do not adequately describe radial variation in trees of open forest, southern Amazonia (SA). Heartwood regressions from dense forest tend to overestimate the mean density of disks or the mean of the bole in open forest. However, for corrections of variation along the bole in open forest, the regression from dense forest provides an accurate correction of the wood-density mean. Two new regressions described in this study allow basic wood density to be obtained from the green density mean of the bole (either from samples taken at breast height or from the mean of the bole). The equations can also be useful in studies of water storage in trees. In open forests in southern Amazonia moisture content of the bole is significantly higher than in dense forest in central Amazonia. For normalization of wood densities from a variety of datasets an equation is needed that directly relates values from

cores taken with increment borers to the wood density of disks (heartwood, sapwood and bark).

Chapter III concludes that in southwestern Amazon bamboo-dominated forest, southwestern Amazon dense forest and southern Amazon open forest the trees are shorter than in dense forest in the central Amazon. The height difference was greatest for small trees. Generally the $2/3$ scaling exponent predicted by metabolic ecology theory was violated by large trees in the four Amazonian forests studied. When the Higuchi et al. (1998) equation (which was developed for use in dense forests) is applied to biomass estimates in open forests of south and southwestern Amazonia, the results have to be corrected for tree-height and wood density effects. Together, the two effects represent reductions totaling 39% in southwestern Amazon bamboo-dominated open forest, 22% in southwestern Amazon bamboo-free dense forest and 16% in southern Amazonian open forest (respectively, 76, 65 and 45 Mg ha⁻¹ lower dry biomass than dense forest in the central Amazon). Considering only the height effect, estimated biomass is lowered by 21.5, 18.5 and 10.3 Mg ha⁻¹, respectively, in the southwestern Amazon bamboo-dominated forest, southwestern Amazon dense forest and southern Amazon open forest. Revisions are needed in the estimates of biomass that have been made using allometric equations developed in dense forest in the central Amazon. This implies lower emissions of greenhouse gases than previously thought for deforestation in Brazilian Amazonia, which is concentrated in the “arc of deforestation” in non-dense forest types such as the ones studied here.

Finally, Chapter IV provides adjustments to biomass estimates for Amazonian forests. A new allometric equations developed in this chapter allow accurate biomass and volume estimates to be obtained from diameter alone, which is the variable that is most easily measured in the field. The results indicate higher biomass storage in the crowns of trees (as compared to the bole of the same trees) in southern Amazonia (SA) than in central Amazonia (CA), due to shorter boles at any given diameter in the SA trees. The results confirm that previous equations developed in CA overestimate biomass if applied to SA trees. Simple corrections to CA allometric equations were found to reflect lower wood density or shorter boles resulted in biomass underestimates. The SA and CA allometric relationships were used to adjust regional biomass estimates from large-scale wood-volume inventories. Current values for adding crown biomass (biomass expansion factor) in dense forest result in a 6% overestimate and values adopted for adding small trees (volume expansion factor) are underestimated by 25%. For the types of open forest studied here, the equations that have been used in the past for adding crown biomass overestimate this component by around 18%,

and a new allometric equation is proposed. Finally, all corrections were applied to adjust the estimates and produce a biomass map for Brazilian Amazonia from 2860 RadamBrasil plots. The total carbon stock (below- and above-ground) estimated to be present at the time of the inventories was 60.8 Pg ($=10^{15}$ g) for Brazilian Amazonia as a whole (excluding non-forest areas). Deforestation through 2006 has reduced the stock in forest biomass to 54.9 PgC.

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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.

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

Appendix A. (continued)

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

Appendix A. (continued)

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

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.

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

Appendix B (continued)

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

Appendix B (continued)

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

Appendix C. Dry mass of trees directly sampled in open forest in southern Amazonia. Measurements of diameter (in cm) were taken at breast height or just above buttresses. Bole dry mass (in Kg), obtained considering moisture content in each tree (or mean value when absent) and including the mass of the stump. Crown dry mass was obtained considering 47.6 % as moisture content (see section 2.3).

Scientific name	Diameter	Bole	Crown	Scientific name	Diameter	Bole	Crown
<i>Pseudolmedia macrophylla</i> Trécul	5.157	4.931	1.834	<i>Trichilia</i> cf. <i>rubra</i> C. DC.	7.321	44.979	14.882
<i>Guarea</i> sp.	5.507	14.309	2.306	<i>Pourouma minor</i> Benoist	7.480	6.918	7.284
<i>Ocotea longifolia</i> H.B.K.	5.570	5.662	3.825	<i>Protium</i> cf. <i>spruceanum</i> (Benth.) Engl.	7.480	6.998	4.873
<i>Ocotea</i> cf. <i>aciphylla</i> (Nees) Mez	5.634	5.320	4.035	<i>Fusaea longifolia</i> (Aubl.) Saff.	7.576	21.878	9.327
<i>Maquira calophylla</i> (Planch. & Endl.) C.C. Berg	5.730	7.388	2.201	<i>Brosimum guianense</i> (Aubl.) Huber	7.639	15.072	6.550
<i>Sclerolobium</i> sp.	5.793	8.279	2.463	<i>Sclerolobium</i> cf. <i>micropetalum</i> Ducke	7.703	11.359	9.170
<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	5.825	7.507	3.458	<i>Theobroma speciosum</i> Willd. ex Spreng	7.703	15.206	2.096
<i>Miconia holosericea</i> (L.) DC.	5.825	7.986	4.087	<i>Theobroma speciosum</i> Willd. ex Spreng	7.703	25.019	1.048
<i>Pouteria reticulata</i> (Engl.) Eyma	5.984	14.236	4.402	<i>Enterolobium</i> sp.	7.703	21.409	4.192
<i>Naucleopsis glabra</i> Spruce ex Pittier	6.048	11.658	6.550	<i>Cordia sprucei</i> Mez	7.703	33.942	1.572
<i>Sterculia</i> sp.	6.112	4.646	2.096	<i>Brosimum guianense</i> (Aubl.) Huber	7.830	25.049	4.978
<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	6.207	6.577	6.812	<i>Pseudolmedia laevis</i> (Ruiz & Pav.) Macbr.	7.862	17.512	6.550
<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	6.207	8.036	6.026	<i>Pouteria</i> cf. <i>cladantha</i> Sandwith	7.862	23.474	5.974
<i>Swartzia polyphylla</i> DC.	6.271	10.106	3.825	<i>Quararibea ochrocalyx</i> (K. Schum.) Vischer	7.862	15.776	5.450
<i>Guarea</i> cf. <i>humaitensis</i> T.D. Penn.	6.303	9.360	3.773	<i>Virola</i> cf. <i>venosa</i> (Benth.) Warb.	7.894	14.932	3.668
<i>Protium</i> cf. <i>spruceanum</i> (Benth.) Engl.	6.303	9.555	5.240	<i>Trichilia guianensis</i> Klotzsch ex C. DC.	8.085	79.689	16.244
<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	6.366	7.216	4.454	<i>Maquira calophylla</i> (Planch. & Endl.) C.C. Berg	8.117	13.955	9.432
<i>Simarouba amara</i> Aubl.	6.366	4.145	4.087	<i>Astronium le-cointei</i> Ducke	8.212	15.780	3.668
<i>Fusaea longifolia</i> (Aubl.) Saff.	6.398	9.725	5.869	<i>Cordia sprucei</i> Mez	8.212	42.586	2.201
<i>Pourouma minor</i> Benoist	6.462	4.008	7.336	<i>Pseudoxandra obscurinervis</i> Maas	8.308	24.409	13.467
<i>Guarea kunthiana</i> A.Juss.	6.462	11.011	4.611	<i>Guatteria</i> sp.	8.435	22.126	2.620
<i>Pseudima frutescens</i> (Aubl.) Radlk.	6.462	13.676	1.100	<i>Iryanthera sagotiana</i> Warb.	8.499	24.144	6.393
<i>Protium guianensis</i> (Aubl.) Marchand	6.462	12.001	10.270	<i>Pouteria</i> cf. <i>campanulata</i> Baehni	8.531	28.203	6.812
<i>Sclerolobium</i> sp.	6.589	13.446	5.240	<i>Trichilia micrantha</i> Benth.	8.594	28.856	5.869
<i>Trichilia micrantha</i> Benth.	6.685	10.369	8.856	<i>Naucleopsis caloneura</i> (Huber) Ducke	8.658	17.148	11.423
<i>Sclerolobium</i> sp.	6.685	9.414	1.310	<i>Poeppigia procera</i> C. Presl	8.722	23.343	7.860
<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	6.780	11.575	10.847	<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	8.881	18.416	16.087
<i>Brosimum lactescens</i> (S. Moore) C.C.Berg.	6.780	10.354	4.192	<i>Pseudolmedia macrophylla</i> Trécul	8.881	30.032	7.860
<i>Theobroma speciosum</i> Willd. ex Spreng	6.907	10.288	6.131	<i>Metrodorea flavida</i> K. Krause	8.913	22.789	23.318
<i>Trichilia micrantha</i> Benth.	6.907	44.145	9.432	<i>Trichilia</i> sp.	8.913	33.617	20.960
<i>Astronium le-cointei</i> Ducke	7.035	14.187	2.253	<i>Trichilia</i> sp.	9.040	26.189	36.575
<i>Trichilia</i> sp.	7.066	13.747	4.716	<i>Pseudolmedia laevis</i> (Ruiz & Pav.) Macbr.	9.072	18.547	12.576
<i>Pouteria</i> cf. <i>campanulata</i> Baehni	7.257	27.261	5.240	<i>Pseudolmedia laevis</i> (Ruiz & Pav.) Macbr.	9.104	29.287	6.655

Appendix C (continued)

Scientific name	Diameter	Bole	Crown	Scientific name	Diameter	Bole	Crown
<i>Theobroma speciosum</i> Willd. ex Spreng	9.135	29.970	6.393	<i>Pouteria</i> cf. <i>anomala</i> (Pires) T.D. Penn.	10.472	47.156	21.694
<i>Pseudolmedia laevis</i> (Ruiz & Pav.) Macbr.	9.167	37.902	6.288	<i>Pouteria</i> cf. <i>campanulata</i> Baehni	10.568	99.734	20.646
<i>Metrodorea flavida</i> K. Krause	9.231	33.512	14.567	<i>Copaifera multijuga</i> Hayne	10.632	35.680	21.222
<i>Trichilia quadrijuga</i> Kunth	9.263	24.457	19.021	<i>Qualea</i> cf. <i>paraensis</i> Ducke	10.663	26.821	14.934
<i>Protium</i> cf. <i>spruceanum</i> (Benth.) Engl.	9.263	19.991	15.982	<i>Diploptropis purpurea</i> var. <i>leptophylla</i> (Kleinhoonte) Amshoff	10.663	38.699	11.266
<i>Tetragastris panamensis</i> (Engl.) Kuntze	9.263	33.426	15.720	<i>Brosimum acutifolium</i> Huber ssp. <i>interjectum</i> C.C. Berg	10.886	30.572	9.432
<i>Guarea trunciflora</i> C. DC.	9.295	25.526	18.078	<i>Pourouma minor</i> Benoist	10.918	24.165	13.362
<i>Swartzia tessmannii</i> Harms	9.326	30.627	9.799	<i>Annona ambotay</i> Aubl.	10.982	44.464	29.239
<i>Ocotea aciphylla</i> (Nees) Mez	9.390	22.049	4.716	<i>Hirtella</i> sp.	11.141	56.516	27.405
<i>Mouriri duckeanoides</i> Morley	9.454	45.959	10.270	<i>Astronium le-cointei</i> Ducke	11.141	42.647	13.624
<i>Matayba</i> cf. <i>purgans</i> (Poepp. & Endl.) Radlk.	9.549	17.283	25.938	<i>Eugenia anastomosans</i> DC.	11.300	28.068	36.313
<i>Theobroma speciosum</i> Willd. ex Spreng	9.549	22.850	11.842	<i>Cordia</i> sp.	11.364	40.127	12.052
<i>Quararibea ochrocalyx</i> (K. Schum.) Vischer	9.645	39.932	3.249	<i>Chrysophyllum</i> sp.	11.459	59.860	38.566
<i>Talisia cerasina</i> (Benth.) Radlk.	9.708	38.083	15.301	<i>Fusaea longifolia</i> (Aubl.) Saff.	11.555	53.173	38.671
<i>Brosimum lactescens</i> (S. Moore) C.C.Berg.	9.708	23.635	13.834	<i>Pouteria</i> sp.	11.555	85.989	13.624
<i>Pseudolmedia laevis</i> (Ruiz & Pav.) Macbr.	9.708	24.438	17.868	<i>Trichilia micrantha</i> Benth.	11.555	69.757	22.532
<i>Pouteria anomala</i> (Pires) T.D. Penn.	9.708	46.525	22.532	<i>Quararibea ochrocalyx</i> (K. Schum.) Vischer	11.555	58.342	21.274
<i>Rinoreocarpus ulei</i> (Melch.) Ducke	9.740	25.732	6.236	<i>Lueheopsis duckeana</i> Burret	11.618	36.176	11.004
<i>Trichilia micrantha</i> Benth.	9.804	28.180	19.440	<i>Cordia ecalyculata</i> Vell.	11.618	52.188	12.157
<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	9.804	26.823	14.672	<i>Tetragastris altissima</i> (Aubl.) Swart	11.650	40.990	24.418
<i>Metrodorea flavida</i> K. Krause	9.868	24.767	30.759	<i>Diploptropis triloba</i> Gleason	11.650	63.497	35.003
<i>Theobroma microcarpum</i> Mart.	9.868	26.561	11.528	<i>Tetragastris altissima</i> (Aubl.) Swart	11.682	34.688	27.248
<i>Quararibea ochrocalyx</i> (K. Schum.) Vischer	9.931	27.591	11.633	<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	11.777	37.882	24.261
<i>Trichilia micrantha</i> Benth.	9.931	40.849	17.292	<i>Pseudolmedia macrophylla</i> Trécul	11.777	57.620	15.353
<i>Theobroma microcarpum</i> Mart.	9.931	28.921	6.498	<i>Brosimum lactescens</i> (S. Moore) C.C.Berg.	11.937	53.812	20.698
<i>Theobroma speciosum</i> Willd. ex Spreng	10.090	77.325	2.306	<i>Astronium le-cointei</i> Ducke	12.000	56.867	14.724
<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	10.186	27.599	16.925	<i>Pouteria reticulata</i> (Engl.) Eyma	12.000	97.335	21.274
<i>Protium</i> cf. <i>spruceanum</i> (Benth.) Engl.	10.186	32.008	25.152	<i>Conceveiba guianensis</i> Aubl.	12.032	41.190	35.632
<i>Tocoyena</i> sp.	10.186	30.453	7.074	<i>Protium</i> cf. <i>spruceanum</i> (Benth.) Engl.	12.159	37.099	51.562
<i>Theobroma speciosum</i> Willd. ex Spreng	10.281	31.993	0.943	<i>Drypetes variabilis</i> Uittien	12.191	50.897	25.414
<i>Trichilia micrantha</i> Benth.	10.281	34.766	26.514	<i>Brosimum lactescens</i> (S. Moore) C.C.Berg.	12.350	45.826	25.833
<i>Maquira sclerophylla</i> (Ducke) C.C. Berg	10.345	25.243	12.262	<i>Vantanea</i> sp.	12.414	87.154	24.890
<i>Leonia glycyarpa</i> Ruiz & Pav.	10.441	29.244	20.017	<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	12.414	39.775	25.676

Anexo C (continuação)

Nome Científico	Diâmetro	Tronco	Copa	Nome Científico	Diâmetro	Tronco	Copa
<i>Inga flagelliformis</i> (Vell.) Mart.	12,414	40,466	44,278	<i>Sclerolobium sp.</i>	15,279	60,103	52,505
<i>Hirtella cf. racemosa</i> Lam.	12,414	95,553	37,309	<i>Couratari sp.</i>	15,438	67,562	15,353
<i>Naucleopsis glabra</i> Spruce ex Pittier	12,541	51,467	25,414	<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	15,438	69,035	42,968
<i>Hymenolobium modestum</i> Ducke	12,573	51,999	12,838	<i>Clarisia racemosa</i> Ruiz & Pav.	15,438	88,251	38,200
<i>Pouteria anomala</i> (Pires) T.D. Penn.	12,637	71,110	22,008	<i>Theobroma microcarpum</i> Mart.	15,756	75,427	44,121
<i>Paypayrola grandiflora</i> Tul.	12,796	28,728	33,117	<i>Fusaea longifolia</i> (Aubl.) Saff.	15,756	103,081	57,064
<i>Brosimum lactescens</i> (S. Moore) C.C.Berg.	13,178	62,120	32,488	<i>Vantanea guianensis</i> Aubl.	15,915	226,887	65,186
<i>Batocarpus amazonicus</i> (Ducke) Fosberg	13,210	74,652	18,235	<i>Aspidosperma cf. spruceanum</i> Mull. Arg.	15,979	72,794	33,588
<i>Siparuna sp.</i>	13,210	40,584	9,222	<i>Aspidosperma cf. spruceanum</i> Mull. Arg.	16,234	99,764	35,422
<i>Toulicia guianensis</i> Aubl.	13,242	98,592	20,122	<i>Leonia glycyarpa</i> Ruiz & Pav.	16,297	70,984	77,028
<i>Tetragastris altissima</i> (Aubl.) Swart	13,369	51,973	33,274	<i>Andira inermis</i> (W. Wright) Kunth ex. DC.	16,393	96,919	37,466
<i>Brosimum lactescens</i> (S. Moore) C.C.Berg.	13,369	77,545	48,732	<i>Protium decandrum</i> (Aubl.) March.	16,457	102,970	47,684
<i>Hymenolobium cf. pulcherrimum</i> Ducke	13,369	80,773	28,558	<i>Ocotea sp.</i>	16,488	94,238	90,862
<i>Isertia hypoleuca</i> Benth.	13,369	53,783	21,117	<i>Tetragastris altissima</i> (Aubl.) Swart	16,520	91,451	92,434
<i>Pseudolmedia laevis</i> (Ruiz & Pav.) Macbr.	13,433	82,510	19,388	<i>Tetragastris altissima</i> (Aubl.) Swart	16,616	63,586	70,111
<i>Brosimum guianense</i> (Aubl.) Huber	13,433	97,291	39,824	<i>Pouteria cf. glomerata</i> (Miq.) Radlk.	16,648	93,245	66,653
<i>Sterculia pruriens</i> (Aubl.) K. Schum.	13,433	37,535	2,096	<i>Heisteria aff. spruceana</i> Engl.	16,648	132,944	43,387
<i>Apeiba echinata</i> Gaertner	13,496	27,077	8,489	<i>Metrodorea flavida</i> K. Krause	16,679	117,125	75,142
<i>Lueheopsis duckeana</i> Burret	13,496	110,742	17,292	<i>Theobroma microcarpum</i> Mart.	17,316	80,148	67,229
<i>Astronium le-cointei</i> Ducke	13,592	115,360	9,746	<i>Ecclinusa guianensis</i> Eyma	17,603	148,523	78,390
<i>Ecclinusa guianensis</i> Eyma	13,687	61,279	35,108	<i>Brosimum guianense</i> (Aubl.) Huber	17,825	253,099	30,025
<i>Toulicia guianensis</i> Aubl.	13,687	110,562	40,348	<i>Ecclinusa guianensis</i> Eyma	18,239	154,452	26,934
<i>Metrodorea flavida</i> K. Krause	13,878	55,304	69,063	<i>Pourouma cf. tomentosa</i> Miq. <i>ssp. apiculata</i> (Benoist) C.C. Berg. & van Heusden	18,335	96,571	55,544
<i>Pseudolmedia laevis</i> (Ruiz & Pav.) Macbr.	13,942	87,073	41,448	<i>Sclerolobium sp.</i>	18,621	98,250	67,910
<i>Pouteria cf. anomala</i> (Pires) T.D. Penn.	14,006	106,683	35,842	<i>Bixa arborea</i> Huber	18,876	80,080	39,824
<i>Inga stipularis</i> DC.	14,069	100,868	37,204	<i>Tetragastris altissima</i> (Aubl.) Swart	18,939	179,786	94,530
<i>Trichilia micrantha</i> Benth.	14,165	59,181	65,081	<i>Sclerolobium sp.</i>	19,099	145,187	47,789
<i>Ocotea nitida</i> (Meissn.) Rohwer	14,324	83,112	38,147	<i>Paypayrola grandiflora</i> Tul.	19,099	88,087	52,295
<i>Gustavia augusta</i> L.	14,706	63,104	69,325	<i>Guapira noxia</i> (Netto) Lundell	19,226	166,992	26,200
<i>Cheiloclinium cognatum</i> (Miers) A.C. Smith	14,833	50,764	52,767	<i>Hymenaea courbaril</i> L.	19,290	280,987	67,491
<i>Maquira calophylla</i> (Planch. & Endl.) C.C. Berg	14,897	151,936	64,871	<i>Guazuma sp.</i>	19,735	157,565	77,552
<i>Protium sp.</i>	14,961	51,163	52,505	<i>Rinoreocarpus ulei</i> (Melch.) Ducke	19,894	137,729	97,097
<i>Pseudolmedia macrophylla</i> Trécul	15,183	98,427	47,422	<i>Inga thibaudiana</i> DC. <i>ssp. thibaudiana</i>	19,990	162,424	207,399

Anexo C (continuação)

Nome Científico	Diâmetro	Tronco	Copa	Nome Científico	Diâmetro	Tronco	Copa
<i>Tetragastris altissima</i> (Aubl.) Swart	20,690	161,175	145,672	<i>Laetia procera</i> (Poepp.) Eichler	34,600	647,936	256,026
<i>Pouteria</i> cf. <i>glomerata</i> (Miq.) Radlk.	20,849	221,429	115,804	<i>Guarea grandifolia</i> DC.	36,478	671,551	376,337
<i>Sapium glandulosum</i> (L.) Morong	21,072	168,438	30,654	<i>Sarcaulus</i> sp.	37,561	958,266	481,084
<i>Pouteria</i> cf. <i>glomerata</i> (Miq.) Radlk.	21,231	167,727	73,412	<i>Trattinnickia</i> cf. <i>peruviana</i> Loes.	37,847	701,722	103,752
<i>Pouteria</i> cf. <i>glomerata</i> (Miq.) Radlk.	21,804	253,713	205,722	<i>Celtis schippii</i> Standl.	38,834	578,894	826,610
<i>Ecclinusa guianensis</i> Eyma	21,868	179,692	137,183	<i>Pourouma minor</i> Benoist	42,654	624,374	429,360
<i>Batocarpus amazonicus</i> (Ducke) Fosberg	22,377	145,583	151,960	<i>Tabebuia</i> sp.	42,813	1001,629	360,040
<i>Pourouma</i> cf. <i>tomentosa</i> Miq. ssp. <i>apiculata</i> (Benoist) C.C. Berg. & van Heusden	22,695	103,069	125,655	<i>Copaifera multijuga</i> Hayne	43,386	1112,924	594,897
<i>Guatteria citriodora</i> Ducke	22,855	160,868	36,942	<i>Parkia</i> sp.	44,245	772,062	803,816
<i>Celtis schippii</i> Standl.	23,619	255,082	113,446	<i>Castilloa ulei</i> Warb	44,977	870,831	280,445
<i>Theobroma microcarpum</i> Mart.	23,810	204,364	72,312	<i>Pouteria</i> cf. <i>glomerata</i> (Miq.) Radlk.	45,200	1123,773	741,612
<i>Cochlospermum orinocense</i> (Kunth) Steud.	24,414	159,851	47,160	<i>Tetragastris altissima</i> (Aubl.) Swart	45,200	959,248	918,504
<i>Dialium guianense</i> Steud.	24,605	388,684	270,541	<i>Inga alba</i> (Swartz.) Willd.	45,391	971,430	970,710
<i>Chrysophyllum prieurii</i> A.DC.	25,656	346,993	179,627	<i>Hymenolobium nitidum</i> Benth.	46,473	2116,318	455,508
<i>Sterculia excelsa</i> Mart.	26,101	230,296	256,021	<i>Eriotheca globosa</i> (Aubl.) Robyns	49,020	1537,381	690,417
<i>Brosimum lactescens</i> (S. Moore) C.C.Berg.	26,261	430,842	403,637	<i>Sclerolobium</i> cf. <i>setiferum</i> Ducke	49,179	797,432	682,248
<i>Protium tenuifolium</i> (Engl.) Engl.	26,674	414,925	154,842	<i>Pouteria engleri</i> Eyma	49,179	929,378	1861,405
<i>Chrysophyllum lucentifolium</i> Cronquist ssp. <i>pachicardium</i> Pires T. D. Pen	27,566	493,789	304,654	<i>Hymenolobium</i> cf. <i>pulcherrimum</i> Ducke	50,611	1783,359	586,560
<i>Cecropia sciadophylla</i> Mart.	27,852	162,585	63,771	<i>Anacardium giganteum</i> W. Hancock ex Engl.	55,068	1304,826	1588,244
<i>Tetragastris altissima</i> (Aubl.) Swart	28,170	347,705	318,435	<i>Bowdichia nitida</i> Spruce ex Benth.	57,296	2908,971	1748,850
<i>Sclerolobium</i> cf. <i>micropetalum</i> Ducke	28,234	279,991	278,034	<i>Hymenolobium sericeum</i> Ducke	58,887	1934,341	3133,447
<i>Hymenolobium modestum</i> Ducke	28,648	525,526	75,980	<i>Schefflera morototoni</i> (Aubl.) Frodin	59,206	1606,274	2154,636
<i>Croton palanostigma</i> Klotzsch	28,903	272,170	184,553	<i>Diplotropis purpurea</i> var. <i>leptophylla</i> (Kleinhoonte) Amshoff	59,683	2921,665	2696,195
<i>Neea</i> cf. <i>oppositifolia</i> Ruiz & Pav.	28,966	229,555	170,090	<i>Anacardium giganteum</i> W. Hancock ex Engl.	60,001	1568,175	1521,329
<i>Guarea trunciflora</i> C. DC.	28,966	425,689	95,473	<i>Abarema jupunba</i> (Willd.) Britton & Killip	69,073	2244,257	1560,210
<i>Theobroma microcarpum</i> Mart.	29,921	376,574	297,265	<i>Sterculia excelsa</i> Mart.	70,506	2899,104	1506,469
<i>Inga thibaudiana</i> DC. ssp. <i>thibaudiana</i>	31,417	236,848	657,096	<i>Brosimum gaudichaudii</i> Trécul	74,262	3383,978	3001,760
<i>Schefflera morototoni</i> (Aubl.) Frodin	31,513	218,053	39,981	<i>Goupia glabra</i> Aubl.	74,803	5151,810	2158,932
<i>Protium</i> cf. <i>decandrum</i> (Aubl.) March.	33,295	316,394	308,112	<i>Astronium le-cointei</i> Ducke	82,442	5879,339	3999,676
<i>Sclerolobium</i> cf. <i>micropetalum</i> Ducke	33,423	406,630	189,478	<i>Torresia acreana</i> Ducke	85,944	5309,510	2877,274
<i>Anacardium giganteum</i> W. Hancock ex Engl.	33,486	453,887	128,223	<i>Hymenolobium pulcherrimum</i> Ducke	90,082	6629,034	3026,289
<i>Astronium le-cointei</i> Ducke	33,900	954,535	112,765	<i>Spondias lutea</i> L.	95,016	2825,135	1741,252
<i>Tovomita</i> sp.	34,473	738,246	446,553	<i>Bagassa guianensis</i> Aubl.	124,777	12118,577	8297,383