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

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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 paper 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. The equations were used 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 aboveground components of 267 trees in open forests of SA were cut and weighed, and the proportion of the biomass stored in the crowns of trees in open forest was found to be higher than in dense-forest. In the case of inventoried wood volume, corrections were applied for indentations and hollow trunks and it was 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 2702 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. Considering all adjustments, the biomass map indicates total biomass of 123.1 Gt (1 Gt = 1 billion tons) dry weight (aboveground + belowground) for originally forested areas in 1976 in the Brazilian Legal Amazon as a whole (102.3 Gt for aboveground only) at the time of the RadamBrasil inventories, which were carried out before intensive deforestation had occurred in the region. Excluded from this estimate are 529,000 km^2 of forest lacking sufficient RadamBrasil inventory data. After forest losses of 676,000 km^2 by 2006 – not counting 175,000 km^2 of this deforested area lacking RadamBrasil data – the estimated dry biomass stock was reduced to 105.4 and 87.6 Gt (aboveground + belowground and only above–ground). Thus, at the 2006 time the carbon storage in forested areas in Brazilian Amazonia as a whole will be around 51.1 Gt (assuming 1 Mg dry biomass = 0.485 Mg C). Biomass estimates by forest type (aggregated into 12 vegetation classes) are provided for each state in the Brazilian Legal Amazon.

Keywords: Allometric relationships; Amazon forest; Biomass stock; Brazil, Carbon; Global warming, Greenhouse gases, Tropical forest.

1. 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 of climate change (Nepstad et al., 1999; Cox et al., 2000, 2004; Houghton, 2005; Malhi et al., 2006; IPCC, 2007). Because the carbon stocks are uncertain (Houghton et al., 2001; Eva et al., 2003; Fearnside and Laurance, 2003), the range of possible emissions of carbon from tropical deforestation and degradation is broad (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, 2000; Houghton et al., 2001). Although uncertainties are inherent in 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 the only database that can be used for estimating forest biomass with an adequate level of representativeness because of the large scale over which the data were collected in the landscape (Brown et al., 1989; Brown and Lugo, 1992). Although large-scale spatial representation is a crucial disadvantage of allometric models that are developed from a small number of directly harvested trees, 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 (Grace, 2004; Chave et al., 2005). 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 (Sheil, 1995; Nogueira et al., 2006), (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 (Heinsdijk, 1958; Pitt, 1961, p. 20; Brazil, RadamBrasil Project, 1973-1983). Any uncertainties in the bole-volume estimates imply proportionate uncertainties in biomass and carbon emission estimates.

The model normally used 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 of crown biomass. The model estimates biomass 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), substantial uncertainty remains in converting bole volume to tree biomass, due to uncertainty in the addition of bole volumes of uninventoried, small trees and the biomass of crowns.

In this paper we seek 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 relatively fertile soils in the southern Amazon and 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 the RadamBrasil plots, and the biomass stocks by forest type were calculated for each of the nine states in the Brazilian Legal Amazon.

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 is subject to inaccuracies due to the practical difficulty of obtaining unbiased height or density measurements for large areas (Overman et al., 1994; Brown et al., 1995). 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 (Overman et al., 1994; Brown, 1997; Higuchi et al., 1998; Chave et al., 2005).

2. Materials and methods

2.1. 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 municipality, the other sites in southern Amazonia (SA) are described by Nogueira et al. (2007). In CA 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 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 Carlinda was not used in biomass equations, but was used in tapering and bole volume equations. All randomly selected trees were felled after authorization by the Brazilian

Institute for the Environment and Renewable Natural Resources (IBAMA). For CA an inventory of 72 ha (de Castilho, 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 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 et al., 2005).

2.2. Data collection

In CA, 302 trees (5 to 106 cm dbh or above buttresses) were collected at six different locations distributed over an area of 45 km^2. Approximately 50 trees per site were sampled in plots measuring 30 × 30 m. In SA, 300 trees were collected (5 to 124 cm dbh or just above any buttresses) 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 parabotanists 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 chainsaw. 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): $\{(Asi + Asf) / 2\} \times h$; where Asi = area of the cross section at breast height, Asf = 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.

2.3. 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 stand balance with 200 Kg capacity and 100-g divisions. The fresh mass of the six boles of large trees harvested in the Rohsamar Fazenda (Juruena municipality) 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 of 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., 2008a). 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_{crown} in CA trees × Mc_{bole} in SA trees) / (Mc_{bole} in CA trees). The crown *Mc* estimated 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 × BA) / (2 - EF), where EF = enlargement factor and BA = 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 × (bole height - BA height)) / ((BA + cross-sectional area at the top of the bole) / 2)] × (bole height - BA 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 × % enlargement between BA and stump height). Also in this case BA is corrected only for irregularities. Therefore, the stump biomass = (mean of the cross-sectional areas at the base and top of the stump × stump height) × 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.

2.4. Biomass allometric equation

Dry mass and diameter were log transformed to satisfy the least-squares linear regression (Magnusson and Mourão, 2005). The studentized residuals were plotted against leverage, including identification of outliers based on calculation of Cook´s distance. 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 allow comparison with published allometric equations that include different numbers of variables (André and Elian, 2000), standardized distribution of residuals, and a low standard error of the estimate or SEE (the √Mean Standard Error (Neter and Wasserman, 1974)). The following results 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.

To assess the performance of the equations developed in this study as compared to previously published models we used 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.

2.5. 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 bole equations the same statistical criteria were adopted as described above for biomass equations.

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

The form factor for each tree 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 in order to compare the results with those obtained by the RadamBrasil Project in which the variable "Asi_n" in the denominator of the formula for form factor was *not corrected* for the effect of indentations and hollow trunks.

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 paper, the mean tapering of boles was analyzed by forest type, reflecting differences in canopy structure and in wood 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.

2.7. 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. The RadamBrasil volume inventories start with trees 31.8 cm in diameter (1 m circumference); the VEF values reported in this study therefore 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).

2.8. 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 the aboveground biomass of the trees to the bole biomass. The aboveground biomass of the trees 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). 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.

2.9. Biomass mapped across the Amazon

A total of 2702 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) and *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 aboveground tree biomass. Nascimento and Laurance (2002; Table 2) found 6.5% (=21.11/325.51) of aboveground 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 aboveground 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 range. Corrections are also not included for bark in wood density values, because linear equations were used for radial variation correction of the disc, including the bark.

[Table 1 here]

From metadata describing each inventory plot these were classified into 12 different forest types. The average biomass (above + below ground) of plots belonging to each type was then used to map biomass classes across the Brazilian Amazon. Within each forest type the variance of inventory plots was ignored and spatial homogeneity was assumed. The extent of each of the 12 forest types as of 1976 was obtained by consolidating the forest classes in a digital map derived from RadamBrasil data (Brazil, IBGE, 1997). Because some of these forest types are contact zones with intermingled open white-sand and natural savanna, the forest portion of each of the 12 types was obtained from a more detailed map with a cell size of 90 meters (Brazil, INPE, 2008). This second map provided the "primitive" extent of Amazon forest and the extent of all accumulated deforestation up to 2006. Finally, two sets of tables were derived as products: one giving the area of the forest biomass classes by state in 1976, the other in 2006. Biomass was not tabulated or mapped in areas deforested prior to 1976, nor in forest types with less than 10 RadamBrasil inventory plots, nor in three land areas in the extreme eastern Amazonia (0.041 x 10^6 km^2) lacking data from INPE on the extent of forest and deforestation. Biomass was tabulated and mapped for 3.378 x 10^6 km^2 of the forested Brazilian Amazon in 1976 and for 2.877 x 10^6 km^2 of the remaining forest in 2006. The difference, an area of 0.501 x 10^6 km^2, was deforested over the 30-year period. Due to insufficient RadamBrasil inventory plots, biomass losses were not estimated for an additional 0.175 x 10^6 km^2 deforested over the same period

3. Results and Discussion

3.1. Allometric biomass equation

In spite of there being several previous allometric equations developed in Amazonian forests (Overman et al., 1994; dos Santos, 1996; Higuchi et al., 1998; Araújo et al., 1999; Chambers et al., 2001), equations have not been developed based on direct measurements in non-dense forest types, which are precisely where deforestation has historically predominated (Brazil, INPE, 2008). This is the case of the southern part of the Brazilian Amazon, where open forest and contact zones (ecotones) on relatively fertile soils prevail (Brazil, IBGE, 1997).

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 A (available in Supplementary Material). Figure 1 shows clearly that the variance about the regression lines increases with dbh. Statistically, such a correlation between mean and variance can be controlled by logging the dependent and independent variables; alternative parameters obtained after excluding the largest tree (the one individual >100 cm diameter above the buttresses, see Figure 1) are presented in Appendix B (available in Supplementary Material). The estimates obtained using these parameters differ only by ~0.1% as compared to biomass estimates obtained from parameters described in Table 2 (both for sampled trees only and for biomass per hectare). Because only one sampled tree had diameter >100 cm, this tree being 124 cm in diameter, the equations should be regarded as unreliable if used for trees in the 100-124 cm dbh range.

[Table 2 here]

[Figure 1 here]

Using only diameter, which is an important advantage for practical use, the equation developed in this study accurately estimated the dry biomass of sampled trees (1% underestimate) and the normalized biomass per hectare (0.05% underestimate). The biomass estimates per hectare were 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).

The results of this study show that biomass estimates obtained from equations developed in central Amazonia result in overestimates if applied to southern Amazonia (e.g., Brazil, MCT, 2004; Cummings et al., 2002). Three previously published allometric equations developed in dense forest in the central Amazon (CA) by Higuchi et al. (1998), Chambers et al. (2001) and da Silva (2007) were tested. All three CA equations tend to overestimate the biomass of smaller trees in SA 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 to the compensating effects of over- and underestimation 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 aboveground components of trees, obtained from the results of da Silva (2007, p. 67, Table 5.8c).

[Figure 2 near here]

Two models that include diameter, height and wood density as independent variables, as published by Chave et al. (2005) and Overman et al. (1994), accurately estimated the biomass of sampled trees and biomass normalized per hectare (both overestimated by about 4%). 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. The quadratic equation published by Brown (1997) that has been used by prior studies in SA forest (Feldpausch et al., 2005, 2006; Jirka et al., 2007) was tested. This equation results in accurate estimates of sampled trees (+1.8%) but when normalized per hectare the error increases to 6.5% (~17 Mg ha^{-1}). 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 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 than estimates using the Brown (1997) linear and quadratic equations or the Chave et al. (2005) and Overman et al. (1994) equations including wood density and height. Despite a better theoretical description of the scaling relationship *Mass α Diameter*, equations including only diameter developed from a dataset that is lumped from several regions may not accurately reflect the true biomass of the trees in any given region (Brown, 2002).

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 of biomass the sampled trees by 13.4%. This suggests errors in biomass maps published by Malhi et al. (2006). Similarly, a recent study (Nogueira et al., 2008b) 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. The biomass underestimates per hectare due to wood density corrections (as in Malhi et al., 2006) will be close to the overestimates that result if the Higuchi et al. (1998) formula is applied without wood density corrections. Although logical, simple corrections to allometric relationships appear to be a risky way to make biomass adjustments.

Considering all trees directly weighed in this study, the dry biomass of the bole 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 in 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 dense forest (CA), where crown biomass is equivalent to 30.8% (n = 121) of the aboveground 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., 2008b) or if the size of crowns in trees in SA tend 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, leading to the conclusion that the crowns in the open forest were not larger than in dense forest (Figure 3). Therefore, higher biomass storage in the crowns in 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 when applied to SA.

[Figure 3 here]

3.2. 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

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. 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 corrected for hollow and irregular trunks based only on conventional diameter measurements (at breast height or above buttresses) and also provide 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 (e.g., RadamBrasil reports), identifying incoherencies between diameter and height measurements.

[Table 3 here]
[Figure 4 here]

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 fenestrated ("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 ± sd; dbh ≥10 cm) occur with very irregularly shaped boles (*Aspidosperma marckgravianum, A. nitidum; Swartzia polyphylla, S. reticulata, S. schomburgkii*) or "fenestrado" (including *Minquartia 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 dbh ≥ 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 (*Minquartia 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 indicating 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.

It should be stressed that the volume equations developed in this study could contribute to 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).

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

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).

[Table 4 here]

[Figure 5 here]

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 (dbh ≥ 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).

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, as mentioned above, the form factor was found to be lower for trees in open forest (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 ± 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 form factor from corrected measurements in trees of intermediate size due to hollow trunks. For this reason the 5% difference 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.

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 ± sd; 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 in diameter. 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.

3.4. Volume expansion factor (VEF)

The VEF adopted until now 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, 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 m^3 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. Use of the revised VEF dispenses the separate correction derived by Fearnside (1994) for the missing dbh range. The estimates derived here were calculated from bole volume corrected for indentations and hollow trunks.

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. 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 up to now in biomass models for dense forest will be underestimated by around 25%. This value 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 aboveground 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 aboveground biomass storage in trees 10 to 30 cm dbh was 36.2%, while 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. In the case of the inventories in which trees were sampled starting at 25 cm stem diameter (such as the FAO inventories: Heinsdijk, 1957, 1958; Glerum, 1960; Glerum and Smitt, 1962) the appropriate VEF value will be 1.305.

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.

For open forest in southern Amazonia the bole volume estimated for trees 10 to 31.7 cm dbh 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 used up to now 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 the collecting area.

3.5. 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 BEF (biomass expansion factor) adopted until now in biomass estimates for dense forest (inventoried bole biomass ≥ 190 Mg ha^{-1}) is 1.74, which was obtained by Brown et al. (1989) in plots that were mostly located in Venezuela. The BEF proposed by Brown et al. (1989) exaggerates the biomass that is stored in large trees when applied to forests in central Amazonia, and 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). This suggests that the value of BEF in central Amazonia is 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 has nevertheless continued to be the BEF value used until now for biomass estimates based on inventoried wood volumes.

The relationship between tree biomass estimated by a model developed in central Amazonia (Higuchi et al., 1998) using bole biomass (corrected volume × wood density) results in a BEF value of 1.621 ± 0.415 (mean ± 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 biomass estimates results in a 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 ± 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 ≤ 190 Mg ha^{-1}: BEF = exp(3.213 – 0.506 × ln(bole biomass). The BEF value found was 1.930, approximately 18% higher than the BEF value reported here.

3.6. The adjusted biomass map for Brazilian Amazonia

The previous wood-density dataset reduces uncertainties in converting bole volume to estimated bole biomass for Brazilian Amazonia as a whole (Nogueira et al., 2005, 2007; Fearnside, 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 for crown biomass. 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 as related to tree size that would assure that this effect is expected at large scale, correction for this effect was not applied in biomass estimates. 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 ≥190 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 ≥10 cm dbh. Thus, in non-dense forest types the only BEF value used was 1.58 for forest with bole biomass 156 Mg ha^{-1} ± 5% (148.2 to 163.8 Mg ha^{-1}), and in the remaining forest 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 Figure 6. The total biomass (below- and aboveground) for the Brazilian Amazon using the corrected values is 123.1 Gt (1 Gt = 1 billion tons) dry weight, or 59.7 Gt C assuming 1 Mg dry biomass = 0.485 Mg C (da Silva, 2007). The aboveground biomass alone is 102.3 Gt (49.6 Gt C). The total biomass storage and aboveground biomass were estimated in 12 forest types for the nine states of the Brazilian Legal Amazon (Tables 5 and 6, both available in the Supplementary Material). The average per-hectare biomass of each of the vegetation types is also given in Table 5 and 6. Considering only the 0.501 x 10^6 km^2 of deforestation through 2006 for which we estimate biomass – i.e. excluding non-forest areas, areas deforested prior to 1976 and some forest types with insufficient RadamBrasil inventory data – the stock had been reduced to 105.4 and 87.6 Gt (or 51.1 and 42.5 Gt C), respectively for belowground + aboveground and only aboveground, excluding non-forest areas, areas deforested prior to 1976 and some forest types with insufficient RadamBrasil inventory data.

The biomass map 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 south-central Amazonia (northwestern Mato Grosso and southern Pará) and for the northeastern portion of the region (Amapá and northeastern Pará). The estimates of Saatchi et al. (2007) were obtained from data measured in 280 plots in primary forests distributed throughout Amazonia (approximately half of which were in 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 2702 plots in Brazilian Amazonia together with adjustments for allometry and density obtained in different forests.

The map resulting from the present study shows reasonable coherence in vegetation types and topography across the basin, especially in 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 (Nelson et al., 2006), since these forests were not differentiated from other vegetation classes. The results have a 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 (Baker et al., 2004; Malhi et al., 2006), since a new allometric equation is proposed for southern Amazonia. The adjustments reduce discrepancies between studies developed using different methods and reduce the uncertainties in biomass estimates in Amazonia when they are obtained from either inventoried wood volume or from allometric equations.

[Figure 6 here]

4. 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 and generally available in standard forest inventories. 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. A new allometric equation was needed for SA because applying simple corrections to existing CA allometric equations in order to reflect lower wood density and shorter boles in SA did not produce satisfactory results, as the calculated biomass was underestimated as compared to direct measurements in SA. 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) were underestimated by 25%. For the types of open forest examined 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 2702 RadamBrasil plots. The total carbon stock (below- and aboveground) estimated to be present at the time of the inventories was 59.7 Gt (1 Gt = 1 billion tons) for Brazilian Amazonia as a whole (excluding non-forest areas). Deforestation through 2006 has reduced the stock in forest biomass to 51.1 Gt C. In general, the results reduce the biomass stock estimates for Brazilian Amazonia. They also reduce the discrepancies between previously published estimates and reduce the uncertainties in estimates from allometric equations and wood-volume inventories, as well as the differences when these two methods are compared to each other.

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Figure Legends

Figure 1. Relationship between diameter and the dry weight (in Kg) of the aboveground portion of the 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 weighed. 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 assuming 47.6% moisture content (see section 2.3). See Table 2 for details of equations.

Figure 2. Divergence (%) of biomass estimated by two linear equations [$DW = \exp(-1.754 + 2.665 \times \ln(D)) \times 0.57$; $DW = \exp(-0.151 + 2.17 \times \ln(D)) \times 0.57$] of Higuchi et al. (1998), by the 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 by the 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).

Figure 3. Equation for crown biomass 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).

Figure 4. Relationship between ln(Diameter) and ln(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.

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 points in (A) are trees with accentuated irregularities in bole shape.

Figure 6. Below + aboveground biomass map (dry weight) for Brazilian Legal Amazonia based on 2702 plots inventoried by the RadamBrasil Project (Brazil, Projeto RadamBrasil, 1973-1983). These estimates do not cover non-forest areas (white), areas deforested prior to 1976 (black), and some forest types with insufficient RadamBrasil inventory data (dark grey). For details see Table 7 available in Supplementary Material.

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 liana 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 liana 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 the 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). A value of 2% was adopted based on 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 aboveground biomass was estimated based on equation of Brown et al. (1989). Palms only measured for individuals ≥10 cm dbh, 4% of the biomass in trees ≥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 from Pereira et al. (2005): 102.5 ± 24.5.

Table 2. Parameters of the biomass equations [ln(Dry weight) = α + β ln(Diameter)] in trees sampled in open forest in 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[a]								
		95% CI[b]			*95% CI*[b]				
	α *(±SE)*	*Lower bound*	*Upper bound*	***β*** *(±SE)*	*Lower bound*	*Upper bound*	n	Adjusted r^2	SEE[c]
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

[a]All parameter values are significant ($p \leq 0.0001$).
[b]Confidence Interval
[c]Standard Error of the Estimate (SEE) = √Residual Mean-Square

Table 3. Parameters of bole volume equations [ln(Corrected volume) = α + β ln(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[a]									
	Diameter range	***α*** *(±SE)*	*95% CI*[b] *Lower bound*	*95% CI*[b] *Upper bound*	***β*** *(±SE)*	*95% CI*[b] *Lower bound*	*95% CI*[b] *Upper bound*	n	Adjusted r^2	SEE[c]
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

[a]All parameter values are significant ($p \leq 0.0001$)
[b]Confidence Interval
[c]Standard Error of the Estimate (SEE) = √Residual Mean-Square

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 et al., 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 ± standard deviation; number of trees and comparison of means[1])											
	Trees sampled			Normalized by inventories			Trees sampled			Normalized by inventories		
≥ 5.0	0.721 ± 0.101	303	Aa	0.713 ± 0.099	1334	Aab	0.728 ± 0.090	300	Aa	0.721 ± 0.092	583	Aa
≥ 10.0	0.723 ± 0.101	267	Aa	0.724 ± 0.094	620	Aa	0.719 ± 0.091	200	Aa	0.716 ± 0.093	475	Aa
≥ 31.8	**0.709** ± 0.129	82	Aab*	**0.709** ± 0.129	96	Aab*	**0.687** ± 0.095	30	Aa*	**0.664** ± 0.098	57	Ab
≥ 50.0	0.655 ± 0.205	20	Ab*	0.661 ± 0.205	25	Ab*	0.726 ± 0.090	10	Aa*	0.724 ± 0.084	12	Aab *

[1]The 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).

Figure 1.

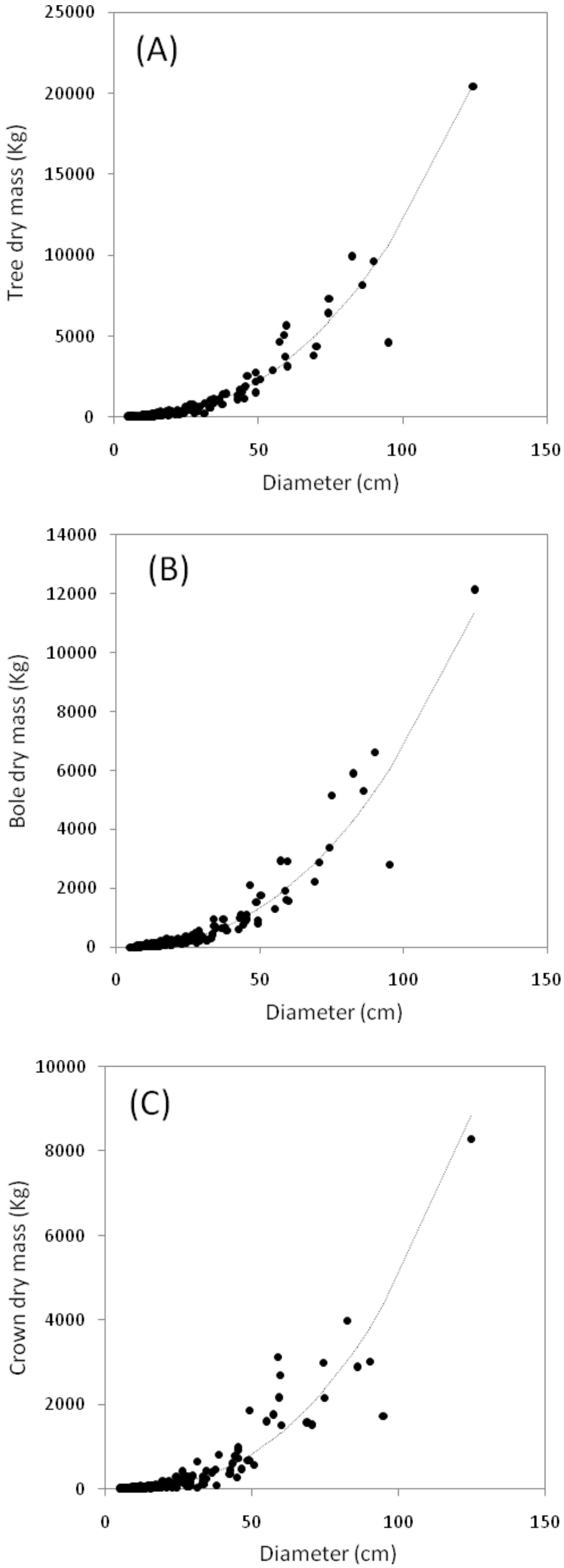

(A)
Tree dry mass (Kg)
25000
20000
15000
10000
5000
0
0
50
100
150
Diameter (cm)
(B)
Bole dry mass (Kg)
14000
12000
10000
8000
6000
4000
2000
0
0
50
100
150
Diameter (cm)
(C)
Crown dry mass (Kg)
10000
8000
6000
4000
2000
0
0
50
100
150
Diameter (cm)

Figure 2.

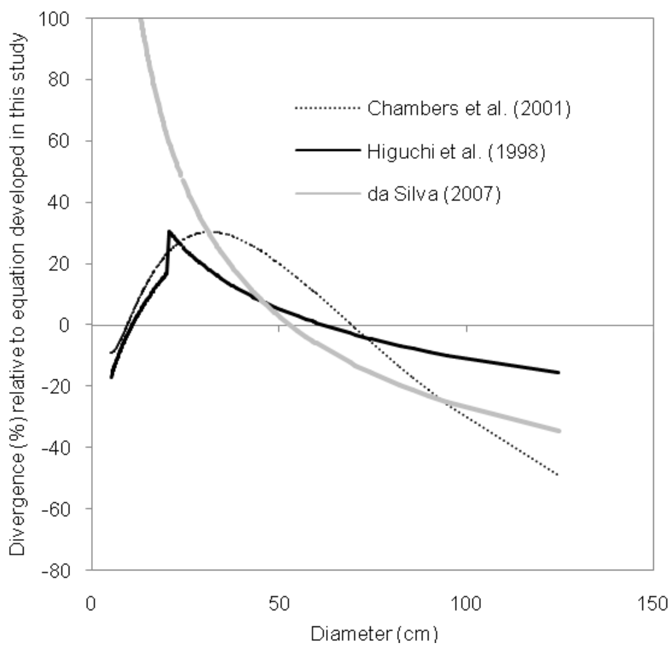


Figure 3.

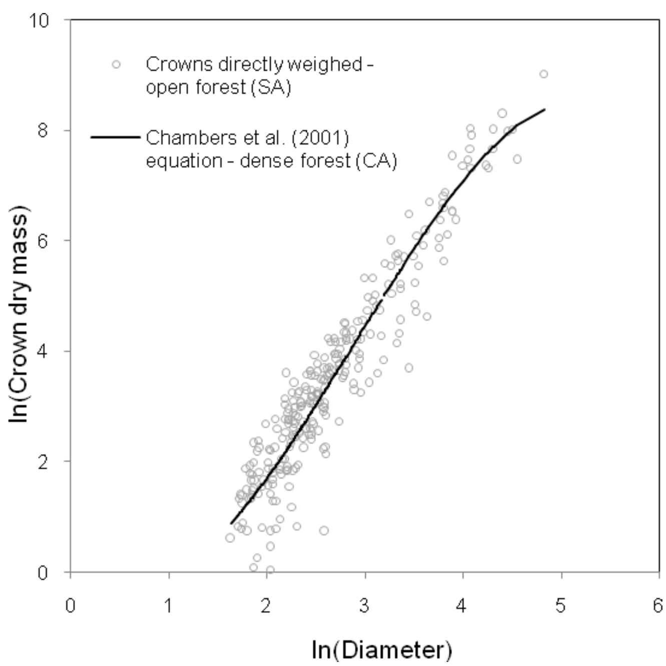


Figure 4.

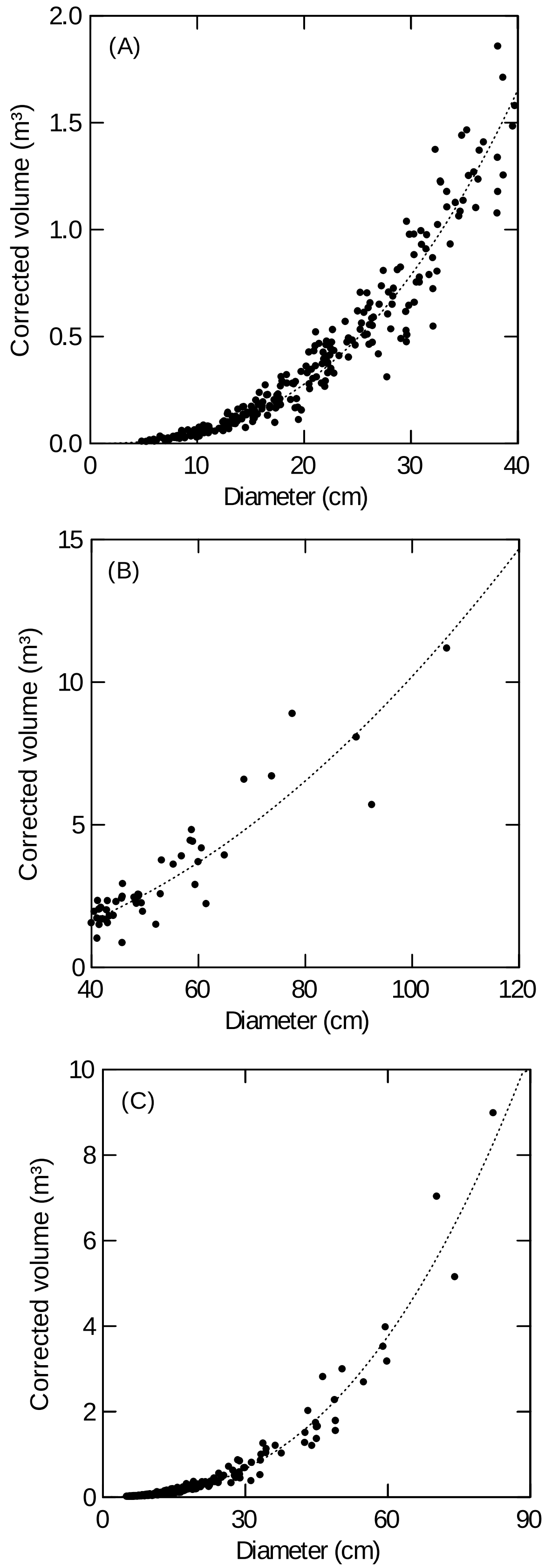

(A)
Corrected volume (m³)
Diameter (cm)
2.0
1.5
1.0
0.5
0.0
0
10
20
30
40
(B)
Corrected volume (m³)
Diameter (cm)
15
10
5
0
40
60
80
100
120
(C)
Corrected volume (m³)
Diameter (cm)
10
8
6
4
2
0
0
30
60
90

Figure 5.

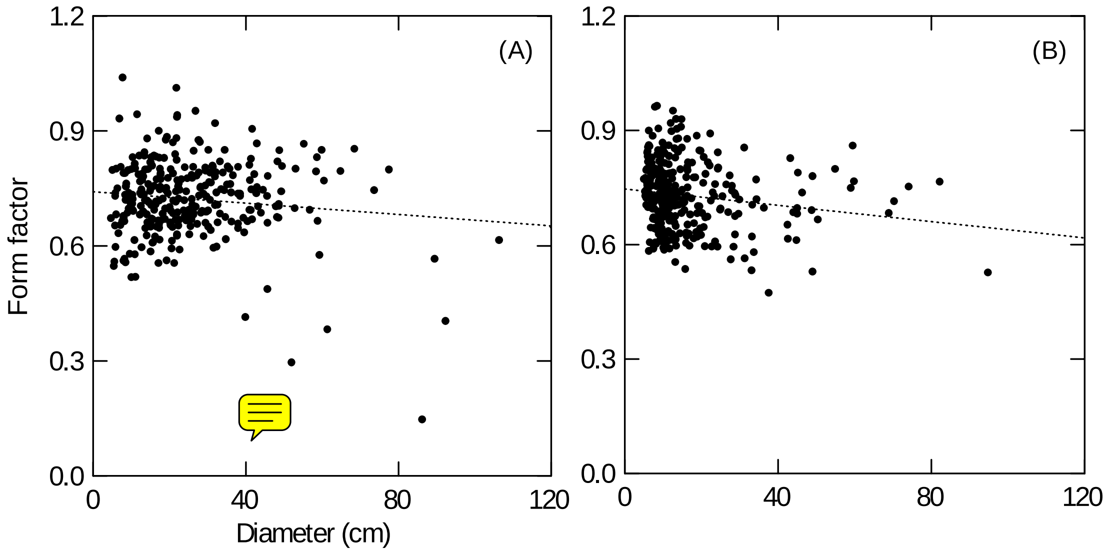
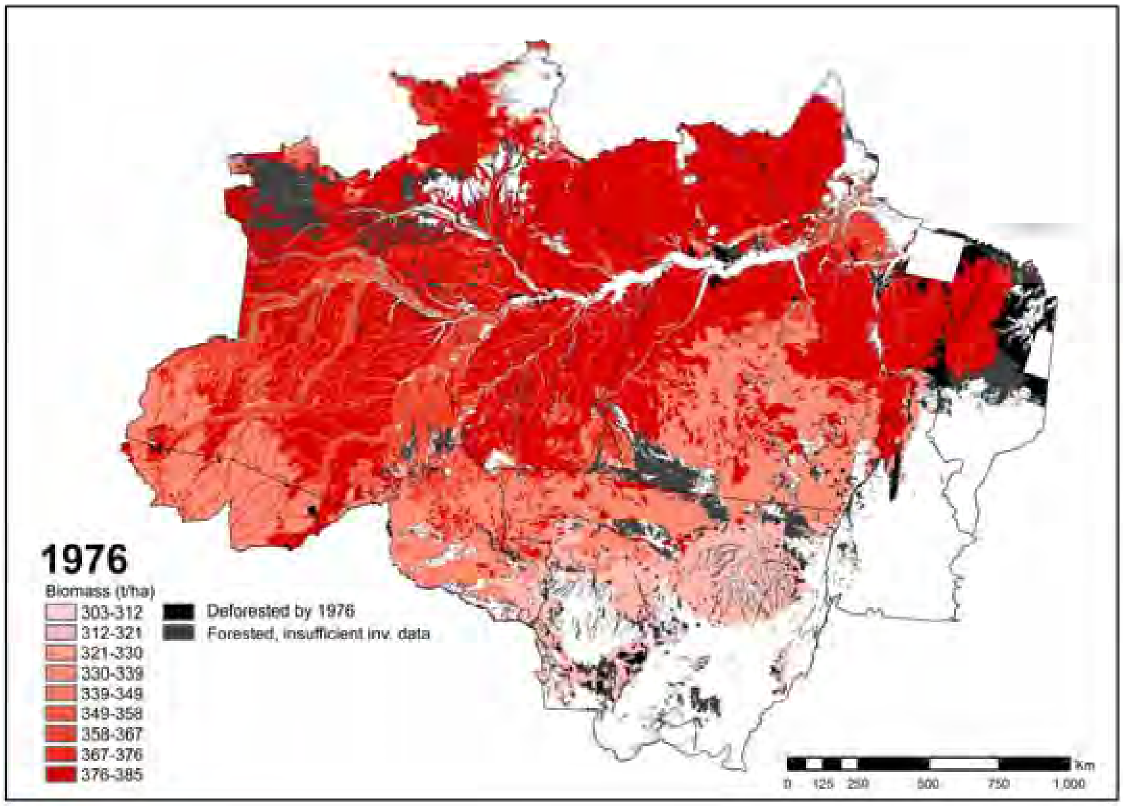

1.2
0.9
0.6
0.3
0.0
Form factor
(A)
0
40
80
120
Diameter (cm)
1.2
0.9
0.6
0.3
0.0
(B)
0
40
80
120

Figure 6


1976
Biomass (t/ha)
303-312
312-321
321-330
330-339
339-349
349-358
358-367
367-376
376-385
Deforested by 1976
Forested, insufficient inv. data
0
125
250
500
750
1,000
Km

Supplementary Material

[FORECO4370: Estimates of forest biomass in the Brazilian Amazon: New allometric equations and adjustments to biomass from wood-volume inventories.

Authors: Euler M Nogueira; Philip Fearnside; Bruce W Nelson; Reinaldo I Barbosa; Edwin W Keizer]

Table 5. Forest biomass below + aboveground and aboveground only [in square brackets] by state for the year 1976. The column "biomass class" has units in tons ha^{-1}. All other columns are in millions of tons for the entire state, but excluding some areas lacking data (see methods and Table 7).

Biomass Class*	Acre	Amapá	Amazonas	Maranhão	Mato Grosso	Pará	Rondônia	Roraima	Tocantins
303				0.047	130.240		10.825		
[252]				[0.039]	[108.619]		[9.028]		
309								21.634	
[258]								[18.042]	
311					22.962		7.757		
[259]					[19.150]		[6.469]		
314			39.525		38.925		95.238		
[262]			[32.962]		[32.462]		[79.426]		
316					6457.241	1.125	482.833	149.050	0.909
[264]					[5394.602]	[0.940]	[403.375]	[124.522]	[0.760]
336	3579.075	1.431	4198.171		4588.931	9686.806	4365.737	326.904	337.526
[280]	[2984.941]	[1.193]	[3501.266]		[3827.159]	[8078.776]	[3641.016]	[272.637]	[281.496]
361	817.947	151.836	9912.632	70.589	94.526	1828.517	226.455	732.179	4.130
[300]	[678.377]	[125.928]	[8221.199]	[58.544]	[78.396]	[1516.509]	[187.814]	[607.262]	[3.425]
363	0.151		4677.466	0.0002	342.502	1082.842	749.243	129.000	28.978
[303]	[0.126]		[3900.998]	[0.0002]	[285.646]	[903.089]	[624.868]	[107.585]	[24.168]
385	757.279	3817.620	30426.173	2003.563	1046.825	24545.478	661.645	4041.554	387.448
[320]	[628.082]	[3166.303]	[25237.091]	[1661.738]	[868.228]	[20357.810]	[548.764]	[3353.797]	[321.347]
Total	5154.454	3970.888	49253.969	2074.200	12722.155	37144.770	6599.737	5400.323	758.993
	[4291.528]	[3293.425]	[40893.519]	[1720.321]	[10614.267]	[30857.126]	[5500.762]	[4483.848]	[631.196]

*Biomass classes correspond to 12 forest types, as follows:
303 t ha^{-1} = "Forested portion of contact zone between savanna and seasonal forest";
309 t ha^{-1} = "Seasonal semideciduous forest on non-flooding lowlands";
311 t ha^{-1} = "Ecotone or contact zone between rainforest and seasonal forest";
314 t ha^{-1} = "Forested portion of contact zone between savanna and rainforest";
316 t ha^{-1} = "Seasonal semideciduous forest, submontane";
336 t ha^{-1} = "Open-canopy rainforest, submontane";
361 t ha^{-1} = "Dense-canopy rainforest on river floodplain" + "Dense-canopy rainforest, montane";
363 t ha^{-1} = "Open-canopy rainforest on non-flooding lowlands";
385 t ha^{-1} = "Dense-canopy rainforest on non-flooding lowlands" + "Dense-canopy rainforest, submontane" + "Forested portion of contact zone between rainforest and vegetation on white sand".

Table 6. Forest biomass below + aboveground and aboveground only [in square brackets] by state for the year 2006. The column "biomass class" has units in tons ha^{-1}. All other columns are in millions of tons for the entire state, but excluding some areas lacking data (see methods and Table 7).

Biomass Class	Acre	Amapá	Amazonas	Maranhão	Mato Grosso	Pará	Rondônia	Roraima	Tocantins
303				0.047	50.060		3.373		
[252]				[0.039]	[41.749]		[2.813]		
309								17.501	
[258]								[14.595]	
311					15.848		2.086		
[259]					[13.217]		[1.739]		
314			34.383		38.892		79.511		
[262]			[28.674]		[32.435]		[66.310]		
316					3848.410	0.423	214.875	134.920	0.471
[264]					[3215.095]	[0.353]	[179.514]	[112.716]	0.394
336	3369.259	1.431	4119.170		2971.804	7542.797	2658.219	308.075	40.537
[280]	[2809.955]	[1.193]	[3435.379]		[2478.478]	[6290.677]	[2216.950]	[256.934]	[33.808]
361	700.623	142.078	9699.186	15.614	63.169	1668.715	207.692	727.656	0.517
[300]	[581.073]	[117.835]	[8044.174]	[12.950]	[52.390]	[1383.975]	[172.252]	[603.511]	[0.429]
363	0.151		4616.366		325.547	933.304	573.848	112.736	3.667
[303]	[0.126]		[3850.041]		[271.505]	[778.374]	[478.588]	[94.022]	[3.058]
385	481.722	3769.461	29775.729	749.654	844.344	20325.373	353.792	3821.346	50.256
[320]	[399.537]	[3126.361]	[24697.618]	[621.756]	[700.293]	[16857.693]	[293.433]	[3171.133]	[41.682]
Total	4551.757	3912.972	[48244.836]	765.316	8158.078	30470.614	4093.399	5122.236	95.451
	[3790.692]	[3245.390]	[40055.889]	[634.746]	[6805.166]	[25311.074]	[3411.601]	[4252.914]	[79.373]

Table 7. Details about areas for which biomass was estimated in the Brazilian Legal Amazon, in 1976 and in 2006. Each unit represents 1 km^2 .

Class*	Acre	Amapá	Amazonas	Maranhão	Mato Grosso	Pará	Rondônia	Roraima	Tocantins
1	18554	2450	32223	94078	198082	212383	80356	8024	29806
2	3050	7890	149484	80418	134508	99719	18231	16607	19007
3	1143	6962	144281	20440	76662	69338	11445	16015	7601
4	2401	930	3124	41801	13976	24981	3898		3695

*Classes:
1 = Deforestation up to 2006;
2 = Portion of primitive forest extent lacking RadamBrasil data;
3 = Portion of forest extent in 2006 lacking RadamBrasil data;
4 = Deforested prior to 1976; no biomass estimated.

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

Appendix A (continued)

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

Appendix A (continued)

Scientific name	Diameter	Bole	Crown	Scientific name	Diameter	Bole	Crown
Inga flagelliformis (Vell.) Mart.	12.414	40.466	44.278	*Sclerolobium sp.*	15.279	60.103	52.505
Hirtella cf. *racemosa* Lam.	12.414	95.553	37.309	*Couratari sp.*	15.438	67.562	15.353
Naucleopsis glabra Spruce ex Pittier	12.541	51.467	25.414	*Cheiloclinium cognatum* (Miers) A.C. Smith	15.438	69.035	42.968
Hymenolobium modestum Ducke	12.573	51.999	12.838	*Clarisia racemosa* Ruiz & Pav.	15.438	88.251	38.200
Pouteria anomala (Pires) T.D. Penn.	12.637	71.110	22.008	*Theobroma microcarpum* Mart.	15.756	75.427	44.121
Paypayrola grandiflora Tul.	12.796	28.728	33.117	*Fusaea longifolia* (Aubl.) Saff.	15.756	103.081	57.064
Brosimum lactescens (S. Moore) C.C.Berg.	13.178	62.120	32.488	*Vantanea guianensis* Aubl.	15.915	226.887	65.186
Batocarpus amazonicus (Ducke) Fosberg	13.210	74.652	18.235	*Aspidosperma* cf. *spruceanum* Mull. Arg.	15.979	72.794	33.588
Siparuna sp.	13.210	40.584	9.222	*Aspidosperma* cf. *spruceanum* Mull. Arg.	16.234	99.764	35.422
Toulicia guianensis Aubl.	13.242	98.592	20.122	*Leonia glycycarpa* Ruiz & Pav.	16.297	70.984	77.028
Tetragastris altissima (Aubl.) Swart	13.369	51.973	33.274	*Andira inermis* (W. Wright) Kunth ex. DC.	16.393	96.919	37.466
Brosimum lactescens (S. Moore) C.C.Berg.	13.369	77.545	48.732	*Protium decandrum* (Aubl.) March.	16.457	102.970	47.684
Hymenolobium cf. *pulcherrimum* Ducke	13.369	80.773	28.558	*Ocotea sp.*	16.488	94.238	90.862
Isertia hypoleuca Benth.	13.369	53.783	21.117	*Tetragastris altissima* (Aubl.) Swart	16.520	91.451	92.434
Pseudolmedia laevis (Ruiz & Pav.) Macbr.	13.433	82.510	19.388	*Tetragastris altissima* (Aubl.) Swart	16.616	63.586	70.111
Brosimum guianense (Aubl.) Huber	13.433	97.291	39.824	*Pouteria* cf. *glomerata* (Miq.) Radlk.	16.648	93.245	66.653
Sterculia pruriens (Aubl.) K. Schum.	13.433	37.535	2.096	*Heisteria* aff. *spruceana* Engl.	16.648	132.944	43.387
Apeiba echinata Gaertner	13.496	27.077	8.489	*Metrodorea flavida* K. Krause	16.679	117.125	75.142
Lueheopsis duckeana Burret	13.496	110.742	17.292	*Theobroma microcarpum* Mart.	17.316	80.148	67.229
Astronium le-cointei Ducke	13.592	115.360	9.746	*Ecclinusa guianensis* Eyma	17.603	148.523	78.390
Ecclinusa guianensis Eyma	13.687	61.279	35.108	*Brosimum guianense* (Aubl.) Huber	17.825	253.099	30.025
Toulicia guianensis Aubl.	13.687	110.562	40.348	*Ecclinusa guianensis* Eyma	18.239	154.452	26.934
Metrodorea flavida K. Krause	13.878	55.304	69.063	*Pourouma* cf. *tomentosa* Miq. *ssp. apiculata* (Benoist) C.C. Berg. & van Heusden	18.335	96.571	55.544
Pseudolmedia laevis (Ruiz & Pav.) Macbr.	13.942	87.073	41.448	*Sclerolobium sp.*	18.621	98.250	67.910
Pouteria cf. *anomala* (Pires) T.D. Penn.	14.006	106.683	35.842	*Bixa arborea* Huber	18.876	80.080	39.824
Inga stipularis DC.	14.069	100.868	37.204	*Tetragastris altissima* (Aubl.) Swart	18.939	179.786	94.530
Trichilia micrantha Benth.	14.165	59.181	65.081	*Sclerolobium sp.*	19.099	145.187	47.789
Ocotea nitida (Meissn.) Rohwer	14.324	83.112	38.147	*Paypayrola grandiflora* Tul.	19.099	88.087	52.295
Gustavia augusta L.	14.706	63.104	69.325	*Guapira noxia* (Netto) Lundell	19.226	166.992	26.200
Cheiloclinium cognatum (Miers) A.C. Smith	14.833	50.764	52.767	*Hymenaea courbaril* L.	19.290	280.987	67.491
Maquira calophylla (Planch. & Endl.) C.C. Berg	14.897	151.936	64.871	*Guazuma sp.*	19.735	157.565	77.552
Protium sp.	14.961	51.163	52.505	*Rinoreocarpus ulei* (Melch.) Ducke	19.894	137.729	97.097
Pseudolmedia macrophylla Trécul	15.183	98.427	47.422	*Inga thibaudiana* DC. *ssp. thibaudiana*	19.990	162.424	207.399

Appendix A (continued)

Scientific name	Diameter	Bole	Crown	Scientific name	Diameter	Bole	Crown
Tetragastris altissima (Aubl.) Swart	20.690	161.175	145.672	*Laetia procera* (Poepp.) Eichler	34.600	647.936	256.026
Pouteria cf. *glomerata* (Miq.) Radlk.	20.849	221.429	115.804	*Guarea grandifolia* DC.	36.478	671.551	376.337
Sapium glandulosum (L.) Morong	21.072	168.438	30.654	*Sarcaulus sp.*	37.561	958.266	481.084
Pouteria cf. *glomerata* (Miq.) Radlk.	21.231	167.727	73.412	*Trattinnickia* cf. *peruviana* Loes.	37.847	701.722	103.752
Pouteria cf. *glomerata* (Miq.) Radlk.	21.804	253.713	205.722	*Celtis schippii* Standl.	38.834	578.894	826.610
Ecclinusa guianensis Eyma	21.868	179.692	137.183	*Pourouma minor* Benoist	42.654	624.374	429.360
Batocarpus amazonicus (Ducke) Fosberg	22.377	145.583	151.960	*Tabebuia sp.*	42.813	1001.629	360.040
Pourouma cf. *tomentosa* Miq. *ssp. apiculata* (Benoist) C.C. Berg. & van Heusden	22.695	103.069	125.655	*Copaifera multijuga* Hayne	43.386	1112.924	594.897
Guatteria citriodora Ducke	22.855	160.868	36.942	*Parkia sp.*	44.245	772.062	803.816
Celtis schippii Standl.	23.619	255.082	113.446	*Castilloa ulei* Warb	44.977	870.831	280.445
Theobroma microcarpum Mart.	23.810	204.364	72.312	*Pouteria* cf. *glomerata* (Miq.) Radlk.	45.200	1123.773	741.612
Cochlospermum orinocense (Kunth) Steud.	24.414	159.851	47.160	*Tetragastris altissima* (Aubl.) Swart	45.200	959.248	918.504
Dialium guianense Steud.	24.605	388.684	270.541	*Inga alba* (Swartz.) Willd.	45.391	971.430	970.710
Chrysophyllum prieurii A.DC.	25.656	346.993	179.627	*Hymenolobium nitidum* Benth.	46.473	2116.318	455.508
Sterculia excelsa Mart.	26.101	230.296	256.021	*Eriotheca globosa* (Aubl.) Robyns	49.020	1537.381	690.417
Brosimum lactescens (S. Moore) C.C.Berg.	26.261	430.842	403.637	*Sclerolobium* cf. *setiferum* Ducke	49.179	797.432	682.248
Protium tenuifolium (Engl.) Engl.	26.674	414.925	154.842	*Pouteria engleri* Eyma	49.179	929.378	1861.405
Chrysophyllum lucentifolium Cronquist *ssp. pachicardium* Pires T. D. Pen	27.566	493.789	304.654	*Hymenolobium* cf. *pulcherrimum* Ducke	50.611	1783.359	586.560
Cecropia sciadophylla Mart.	27.852	162.585	63.771	*Anacardium giganteum* W. Hancock ex Engl.	55.068	1304.826	1588.244
Tetragastris altissima (Aubl.) Swart	28.170	347.705	318.435	*Bowdichia nitida* Spruce ex Benth.	57.296	2908.971	1748.850
Sclerolobium cf. *micropetalum* Ducke	28.234	279.991	278.034	*Hymenolobium sericeum* Ducke	58.887	1934.341	3133.447
Hymenolobium modestum Ducke	28.648	525.526	75.980	*Schefflera morototoni* (Aubl.) Frodin	59.206	1606.274	2154.636
Croton palanostigma Klotzsch	28.903	272.170	184.553	*Diplotropis purpurea var. leptophylla* (Kleinhoonte) Amshoff	59.683	2921.665	2696.195
Neea cf. *oppositifolia* Ruiz & Pav.	28.966	229.555	170.090	*Anacardium giganteum* W. Hancock ex Engl.	60.001	1568.175	1521.329
Guarea trunciflora C. DC.	28.966	425.689	95.473	*Abarema jupunba* (Willd.) Britton & Killip	69.073	2244.257	1560.210
Theobroma microcarpum Mart.	29.921	376.574	297.265	*Sterculia excelsa* Mart.	70.506	2899.104	1506.469
Inga thibaudiana DC. *ssp. thibaudiana*	31.417	236.848	657.096	*Brosimum gaudichaudii* Trécul	74.262	3383.978	3001.760
Schefflera morototoni (Aubl.) Frodin	31.513	218.053	39.981	*Goupia glabra* Aubl.	74.803	5151.810	2158.932
Protium cf. *decandrum* (Aubl.) March.	33.295	316.394	308.112	*Astronium le-cointei* Ducke	82.442	5879.339	3999.676
Sclerolobium cf. *micropetalum* Ducke	33.423	406.630	189.478	*Torresia acreana* Ducke	85.944	5309.510	2877.274
Anacardium giganteum W. Hancock ex Engl.	33.486	453.887	128.223	*Hymenolobium pulcherrimum* Ducke	90.082	6629.034	3026.289
Astronium le-cointei Ducke	33.900	954.535	112.765	*Spondias lutea* L.	95.016	2825.135	1741.252
Tovomita sp.	34.473	738.246	446.553	*Bagassa guianensis* Aubl.	124.777	12118.577	8297.383

Appendix B. Parameters of the biomass equations developed excluding the single tree > 100 cm diameter above buttresses (see Figure 1). All trees were sampled in open forest in the southern Amazonia (SA) (diameter range 5-95 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[a] [ln(Dry weight) = α + β ln(Diameter)]								
		95% CI[b]			*95% CI*[b]				
	α *(±SE)*	*Lower bound*	*Upper bound*	***β*** *(±SE)*	*Lower bound*	*Upper bound*	n	Adjusted r^2	SEE[c]
Whole tree	- 1.717 (0.081)	- 1.875	- 1.558	2.413 (0.029)	2.355	2.471	261	0.963	0.307
Bole	- 1.926 (0.094)	- 2.112	- 1.740	2.334 (0.035)	2.266	2.402	261	0.946	0.359
Crown	- 3.358 (0.148)	- 3.651	- 3.066	2.579 (0.054)	2.473	2.686	260	0.897	0.565

[a]All parameter values are significant ($p \leq 0.0001$).
[b]Confidence Interval
[c]Standard Error of the Estimate (SEE) = √Residual Mean-Square