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

Euler Melo Nogueira a, Philip Martin Fearnside b,*, Bruce Walker Nelson b, Reinaldo Imbrozio Barbosa b, Edwin Willem Hermanus Keizer c

a Graduate Program in Tropical Forest Science, National Institute for Research in the Amazon - INPA, Av. Andre´ Arau´jo, No. 2936, C.P. 478, CEP 69 011-970 Manaus, Amazonas, Brazil

b Department of Ecology, National Institute for Research in the Amazon - INPA, Av. Andre´ Arau´jo, No. 2936, C.P. 478, CEP 69 011-970 Manaus, Amazonas, Brazil

c Network for Environmental Modeling in Amazonia (GEOMA), National Institute for Research in the Amazon - INPA, Av. Andre´ Arau´jo, No. 2936, C.P. 478, CEP 69 011-970 Manaus, Amazonas, Brazil

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 km² of forest lacking sufficient RadamBrasil inventory data. After forest losses of 676,000 km² by 2006 – not counting 175,000 km² 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, in 2006 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.

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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 height estimated ‘by eye’ resulted in more representative size–class distribution in 5-cm dbh intervals. 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 et al., 2006) was used to adjust the felled samples to a more representative size–class distribution in 5-cm dbh intervals. In SA an inventory of 11 ha was used for trees ≥10 cm dbh (Feldpausch et al., 2005) and an inventory of 30 ha was used for trees 5–10 cm dbh (Pereira et al., 2005).

2.2. Data collection

In CA, 302 trees (5–106 cm dbh or above buttresses) were collected at six different locations distributed over an area of 45 km². Approximately 50 trees per site were sampled in plots measuring 30 m × 30 m. In SA, 300 trees were collected (5–124 cm dbh or just above any buttresses) in four counties: 30 trees in Juruenã (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): \[ \text{volume} = \frac{(A_s + A_f)/2}{C_2} \times h; \] where \( A_s \) = area of the cross section at breast height, \( A_f \) = 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 (5–124 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 (\( M_c \)) of the bole of each tree. The mean \( M_c \) (0.416 ± 0.068) was used for trees that had no \( M_c \) mean of the bole (Nogueira et al., 2008a). The \( M_c \) of the crown was not measured, but rather estimated using data from the literature. Hirayama 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 \( M_c \) for roots, boles, branches and leaves obtained from 128 trees, also sampled in CA. From da Silva (2007), crown \( M_c \) = 44.4%. Because bole \( M_c \) 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. \( M_c \) was estimated for the crowns of trees in SA from the \( M_c \) 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 \( M_c \), namely: \( (M_{crown} \text{in CA trees} \times M_{cbole} \text{in SA trees})/(M_{cbole} \text{in CA trees}) \). The crown \( M_c \) 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: \( (EF \times BA) \) (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 \( EF = \frac{(\{[(BA \times (bole height - BA height))/2] + (BA \times cross-sectional area at the top of the bole)/2\} \times (bole height – BA height) \} \). 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 \times Enlargement factor 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 (Magnussen 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 \( \sqrt{\text{residual mean square}} \) (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: \( ff = \left( \frac{A_{si,c}}{A_{sf}} \right) \) where: \( A_{si,c} \) = corrected area of the cross section at breast height, \( A_{sf} \) = corrected area of the cross section at the top of the bole; and \( h_t \) = 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 \( \frac{A_{si,c}}{A_{sf}} \) 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 10–31.7 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 ≥3.18 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 ≥3.18 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 ≥3.18 cm stem diameter (see Section 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(fresh mass) = −1.754 + 2.665 × ln(diameter) and ln(fresh mass) = −0.151 + 2.177 × ln(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 ha 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-wyody) and campos (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 1–10 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.

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
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)

<table>
<thead>
<tr>
<th>Forest</th>
<th>State</th>
<th>Biomass all trees ≥ 10 cm</th>
<th>Palms</th>
<th>% Vines</th>
<th>% Under story; seedlings (wood + leaves)</th>
<th>% Dead wood (fallen + standing)</th>
<th>% Litter/root</th>
<th>% Below ground</th>
<th>Source</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dense</td>
<td>Amazonas</td>
<td>7.3</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Klinge and Rodrigues (1968)</td>
<td>(01)</td>
</tr>
<tr>
<td></td>
<td>Amazonas</td>
<td>357.0</td>
<td>23.0</td>
<td>6.4</td>
<td></td>
<td>25.8</td>
<td>7.2</td>
<td>7.2</td>
<td>Klinge et al. (1975); Klinge and Rodrigues (1973)</td>
<td>(02)</td>
</tr>
<tr>
<td></td>
<td>Amazonas</td>
<td>325.5</td>
<td>3.5</td>
<td>1.1</td>
<td>10.8</td>
<td>2.5</td>
<td>21.1</td>
<td>6.5</td>
<td>Klinge (1977)</td>
<td>(03)</td>
</tr>
<tr>
<td></td>
<td>Rondônia</td>
<td>306.8</td>
<td>16.6</td>
<td>5.4</td>
<td>0.6</td>
<td>0.2</td>
<td>14.0</td>
<td>4.6</td>
<td>30.5</td>
<td>9.0</td>
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<td></td>
<td>Pará</td>
<td>258.0</td>
<td>35.0</td>
<td>13.6</td>
<td>16.0</td>
<td>6.2</td>
<td>55.0</td>
<td>21.3</td>
<td>Gerwing (2002)</td>
<td>(14)</td>
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<td></td>
<td>Pará</td>
<td>398.4</td>
<td>96.1</td>
<td>33.4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Keller et al. (2004)</td>
<td>(15)</td>
</tr>
<tr>
<td></td>
<td>Pará</td>
<td>48.4</td>
<td>58.4</td>
<td>5.9</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Keller et al. (2004)</td>
<td>(16)</td>
</tr>
<tr>
<td></td>
<td>Pará</td>
<td>305.1</td>
<td>6.3</td>
<td>2.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Lucasio et al. (2005)</td>
<td>(17)</td>
</tr>
<tr>
<td></td>
<td>Amazonas</td>
<td>306.1</td>
<td>2.3</td>
<td>1.8</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Monteiro et al. (2006)</td>
<td>(18)</td>
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<td></td>
<td>Amazonas</td>
<td>306.1</td>
<td>2.1</td>
<td>0.7</td>
<td>19.5</td>
<td>6.4</td>
<td></td>
<td></td>
<td>Noguera et al. (2006)</td>
<td>(19)</td>
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<td>Non-dense</td>
<td>Pará</td>
<td>126.1</td>
<td>2.0</td>
<td>2.3</td>
<td>6.0</td>
<td>4.8</td>
<td>7.5</td>
<td>5.0</td>
<td>da Silva (2007)</td>
<td>(20)</td>
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<td></td>
<td>Pará</td>
<td>362.5</td>
<td>10.8</td>
<td>3.0</td>
<td>2.6</td>
<td>0.7</td>
<td>5.5</td>
<td>1.5</td>
<td>Martellini et al. (1988)</td>
<td>(21)</td>
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<tr>
<td></td>
<td>Pará</td>
<td>303.0</td>
<td>30.0</td>
<td>0.0</td>
<td></td>
<td>27.0</td>
<td>8.9</td>
<td>10.0</td>
<td>Scott et al. (1992)</td>
<td>(22)</td>
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<td></td>
<td>Acre</td>
<td>320.0</td>
<td>12.8</td>
<td>4.0</td>
<td></td>
<td>35.0</td>
<td>10.0</td>
<td>38.0</td>
<td>Reville Cardenas (1986)</td>
<td>(23)</td>
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<td></td>
<td>Rondônia</td>
<td>285.0</td>
<td>21.6</td>
<td>9.0</td>
<td>11.0</td>
<td>5.0</td>
<td>34.5</td>
<td>12.1</td>
<td>Reville Cardenas (1986)</td>
<td>(24)</td>
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<tr>
<td></td>
<td>Rondônia</td>
<td>293.4</td>
<td>17.5</td>
<td>7.3</td>
<td>0.5</td>
<td>0.2</td>
<td>14.1</td>
<td>5.0</td>
<td>Cummings et al. (2002)</td>
<td>(25)</td>
</tr>
<tr>
<td></td>
<td>Rondônia</td>
<td>270.1</td>
<td>37.9</td>
<td>14.0</td>
<td>0.6</td>
<td>0.2</td>
<td>11.4</td>
<td>4.2</td>
<td>Peulotto (2006)</td>
<td>(26)</td>
</tr>
<tr>
<td></td>
<td>Mato Grosso</td>
<td>253.8</td>
<td>3.1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Palace et al. (2007)</td>
<td>(27)</td>
</tr>
<tr>
<td>All data</td>
<td></td>
<td>286.8</td>
<td>12.0</td>
<td>4.6</td>
<td>10.0</td>
<td>3.1</td>
<td>11.0</td>
<td>4.2</td>
<td>Cummings et al. (2002)</td>
<td>(28)</td>
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</table>

Table 1 (Continued)

<table>
<thead>
<tr>
<th>Forest State</th>
<th>Biomass all trees &gt;10 cm</th>
<th>Palms</th>
<th>Vines</th>
<th>Understory seedlings (wood + leaves)</th>
<th>Litter/root mat*</th>
<th>Belowground biomass</th>
<th>Source</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dense</td>
<td>299.0</td>
<td>6.5</td>
<td>1.9</td>
<td>11.8</td>
<td>9.4</td>
<td>3.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Non-dense</td>
<td>266.6</td>
<td>22.5</td>
<td>8.6</td>
<td>5.3</td>
<td>9.4</td>
<td>1.9</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Notes: (1) Averages of the years 1963 and 1964. (2) Dry weight for lamas was obtained assuming 50% of the fresh weight (see Klinge et al., 1975). 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 Faria et al. (2007). (3) Vegetation described by the author as submontane broadleaved dense. The biomass of trees >10 cm dbh was calculated starting from Table 3.1, year 1982. In the same way, the mean biomass was estimated for trees <10 cm (3.5) which were added to broadleaved herbs (0.26) mentioned in Table 1:4. (4), (5), (7), (21), (24): the litter and root mat were added together. (8) from Faundez et al. (1993); (10): average of the sites studied by the authors; (9): these estimates only refer to coarse woody litter; (51): 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); (13), (18), (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 Gorenf and Fauai (2000) was used; (15): Rice et al. 2004 report 48 Mg C ha−1 and not the biomass ha−1. It was converted to biomass considering the wood density and 50% content for biomass (see Table 3). The equation of Chambers et al. (1986) was used for the biomass of the 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); (19), (30), (31), (29), (20): 155 was added for standing dead trees, based on Plass et al., 2007; (12–15), Nascimento and Laurance, 2002; (13–14); Other authors consider a larger percentage, such as 16–20% by Summers et al. (1998). (21), 16–25% according to Koller et al. (2004), and Rice et al. (2004); and, 42–70% according to Delaney et al. (1998) (19): the biomass of trees (excluding palms) > 10 cm = 306.11 Mg ha−1. See Appendix A; (22)–(25): the liana biomass was estimated based on equation of Brown et al. (1989). Palms only measured for individuals >10 cm dbh; 45% of the biomass in tree > 10 cm dbh (Table 1). Belowground biomass obtained from Nepstad (1989), who suggests 10% of tree biomass > 50 cm. Data for standing dead trees were obtained from U chuckled (1988) in Paragominas, Para state; (20): 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 Grac a 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; (12): 91 trees with 5–10 cm dbh were completely weighted and replicated for an expected frequency per hectare from Peres et al. (2005): 162.5 ± 24.5 Some of the results were obtained from the annual production of litter, which can differ from the stock per unit area. (13), (28), (31): the liana biomass was estimated based on equation of Brown et al. (1989). Palms only measured for individuals 10 cm dbh: 45% of the biomass in tree >10 cm dbh (Table 1). Belowground biomass obtained from Nepstad (1989), who suggests 10% of tree biomass > 50 cm. Data for standing dead trees were obtained from U chuckled (1988) in Paragominas, Para state; (20): 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 Grac a 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; (12): 91 trees with 5–10 cm dbh were completely weighted and replicated for an expected frequency per hectare from Peres et al. (2005): 162.5 ± 24.5 Some of the results were obtained from the annual production of litter, which can differ from the stock per unit area.

3. Results and discussion

In the light of these figures, several points arise. First, equations developed in the Amazonian forests (Overman et al., 1994; dos Santos et al., 2000) were re-examined, to assess to what extent they can be applied to the area under evaluation. The results of this study show that biomass estimates obtained

3.1. Allometric biomass equation

[Details of the analysis, including references to Overman et al., 1994; dos Santos et al., 2000, are presented in Supplementary Material.]

The results of this study show that biomass estimates obtained from these equations were underestimated, particularly for trees > 10 cm dbh. This is because the equations were developed in the Amazonian forests (Overman et al., 1994; dos Santos et al., 2000) and were not specifically calibrated for the area under evaluation. In addition, the equations are based on data from tropical forests in Central America, which may not be representative of the species present in the area under evaluation. Furthermore, the equations were developed for trees > 10 cm dbh, which may not be representative of the species present in the area under evaluation. Therefore, the equations developed in the Amazonian forests (Overman et al., 1994; dos Santos et al., 2000) may not be appropriate for the area under evaluation, and the equations developed in the Amazonian forests (Overman et al., 1994; dos Santos et al., 2000) may not be appropriate for the area under evaluation.
Table 2
Parameters of the biomass equations [ln(Dry weight) = \( \alpha + \beta \ln(Diameter) \)] in trees sampled in open forest in southern Amazonia (SA) (diameter range 5–124 cm)

<table>
<thead>
<tr>
<th>Model</th>
<th>Parametersa</th>
<th>95% CIb</th>
<th>( \beta (\pm\text{S.E.}) )</th>
<th>95% CIb</th>
<th>( n )</th>
<th>Adjusted ( \bar{f} )</th>
<th>SEEc</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whole tree</td>
<td>(-1.716 (0.079))</td>
<td>(-1.872)</td>
<td>(-1.580)</td>
<td>(2.413 (0.029))</td>
<td>(2.357)</td>
<td>(2.470)</td>
<td>(262)</td>
</tr>
<tr>
<td>Bole</td>
<td>(-1.929 (0.093))</td>
<td>(-2.111)</td>
<td>(-1.746)</td>
<td>(2.335 (0.034))</td>
<td>(2.269)</td>
<td>(2.402)</td>
<td>(262)</td>
</tr>
<tr>
<td>Crown</td>
<td>(-3.355 (0.146))</td>
<td>(-3.642)</td>
<td>(-3.069)</td>
<td>(2.578 (0.053))</td>
<td>(2.474)</td>
<td>(2.682)</td>
<td>(261)</td>
</tr>
</tbody>
</table>

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.

a All parameter values are significant (\( p < 0.0001 \)).
b Confidence interval.
c Standard error of the estimate (SEE) = \( \sqrt{\text{residual mean-square}} \).

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 (Fig. 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 over-estimates of smaller trees (Fig. 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).

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 over-estimated 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 as 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 biomass of 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 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 (Fig. 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.

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 Fig. 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.

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 ± S.D.; dbh ≥ 10 cm) occur with very irregularly shaped boles (Aspidosperma nitidum, Minquartia guianensis, 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 macro-

![Fig. 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.](image-url)
petola 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 (Fig. 5A and B). Because of this, the form...
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; Fig. 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 31.8–49 cm dbh. The form factor found in open forest using non-corrected measurements was 0.760 ± 0.075 (mean ± S.D., \( n = 38 \); 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 ± S.D.; \( n = 33 \); dbh ≥ 45 cm) was found for trees sampled in this study, while using the “corrected” measurement methodology the mean was 0.680 ± 0.170. The results, together with values reported in Table 4, suggest that for large trees in central Amazonia, the effect of irregularities of the bole and hollow trunks will have a strong influence on the estimate of the mean form factor. In spite of large trees storing a substantial portion of the biomass, they have little influence on the mean form factor, which is strongly influenced by the large number of small trees. Eliminating the large trees (dbh ≥ 50 cm; southern Amazonia) or just above any buttresses. Measurements of diameter are in cm and those of bole volume in m³. See Table 3 for details of equations.

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**Table 4.** Relationship between Diameter and 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 dense forest (central Amazonia) or 1.30 m in open forest.
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 31.8–49 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 10–30 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 30–31.7 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 m³ ha⁻¹. In this study the bole volume of the trees 10–31.7 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 30–31.7 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 10–31.7 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 10–30 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 Smit, 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 10–31.7 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 stemwood 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 ± S.D.; 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 ± S.D.; 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 (Fig. 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

![Fig. 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.](image-url)
types and the BEF value for dense forest (1.635) was applied to forest types with bole biomass $\geq$190 Mg ha$^{-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 $\geq$ 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$^{-1}$ $\pm$ 5% (148.2–163.8 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 inventory 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 Fig 6. The total biomass (above- and belowground) 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 Tables 5 and 6. Considering only the 0.501 $\times$ 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 C (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.

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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Appendix A. Supplementary data


