Forest Ecology and Management 570 (2024) 122195

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

To improve estimates of neotropical forest carbon stocks more direct measurements are needed: An example from the Southwestern Amazon

Antonio Willian Flores de Melo [a,b,*,1], Adriano José Nogueira Lima [a], Marcus Vinicio Neves d'Oliveira [c], Joaquim dos Santos [a], I. Foster Brown [b,d], Eufran Ferreira do Amaral [c], Sonaira Souza da Silva [a,b], Igor Oliveira [b], Plínio Barbosa de Camargo [e], Niro Higuchi [a]

[a] *National Institute for Amazonian Research, Av. André Araújo, 2936, C.P. 478, Manaus, Amazonas CEP 69011-970, Brazil*
[b] *Federal University of Acre, Campus Floresta, Estrada da Canela Fina, KM 12 Gleba Formoso, São Francisco, Cruzeiro do Sul, Acre 69980-000, Brazil*
[c] *Embrapa Acre, Rodovia BR-364, km 14, C.P. 321, Rio Branco, Acre CEP 69900-970, Brazil*
[d] *Woodwell Climate Research Center, 149 Woods Hole Road, Falmouth, MA 02540-1644, USA*
[e] *Center for Nuclear Energy in Agriculture, University of São Paulo, Av. Centenário, 303, São Dimas, Piracicaba, São Paulo CEP 13400-970, Brazil*

ARTICLE INFO

Keywords:
Carbon stock uncertainty
Tree biomass
Plant allometry
Southwestern Amazon
Open forests

ABSTRACT

Tropical forests play a critical role in the global carbon cycle, storing 40–55 % of terrestrial plant carbon and significantly contributing to primary productivity. However, uncertainties persist in estimating carbon stocks and fluxes, exhibiting variation across the Neotropics, Africa, and Asia tropical forest regions. Despite hosting some of the most densely sampled forests, significant uncertainties persist in biomass and forest carbon stock estimates in the Neotropics. Although the Southwestern Amazon (SWA) forests span over 20 million hectares, no specific biomass or above- and below-ground carbon model has been calibrated for this region thus far. In our study, we conducted direct forest inventories in the SWA to address the following question: Do the allometric patterns, biomass, and carbon stocks observed in the Southwestern Amazon differ from those found in other regions of the Amazon or Pantropical? Our research reveals substantial differences in water and carbon content, biomass stocks, above- and below-ground oven-dry biomass ratios, and allometric patterns between SWA forests and other Amazonian and Pantropical forests. We have demonstrated that these differences result in overestimations of forest biomass when applying allometric equations developed for other Amazonian and Pantropical regions to the open forests of Southwestern Amazonia. This overestimation can reach up to 37 % when using equations from the eastern Amazon, and between 26 % and 46 % depending on the applied Pantropical equation. The use of an inappropriate factor for the root-to-shoot ratio in the Southwestern Amazon (SWA) can lead to overestimates of belowground oven-dry biomass by up to 20 %. To reduce uncertainties related to estimates of forest carbon stock and flux in Neotropical forests, it is necessary to enhance the density of direct biomass measurements, particularly in southwestern Amazonia.

1. Introduction

Tropical forests play a critical role in the global carbon cycle, storing 40–55 % of terrestrial plant carbon and significantly contributing to primary productivity. (Baccini et al., 2017; Cuni-Sanchez et al., 2021; Houghton and Nassikas, 2017; Hubau et al., 2020; Pan et al., 2011). However, uncertainties persist in estimating carbon stocks and fluxes, exhibiting variation across the Neotropics, Africa, and Asia tropical forest regions. (Erb et al., 2018; Mitchard et al., 2013; Reichstein and Carvalhais, 2019). Notably, African and Asian tropical forests show greater uncertainty in biomass stocks compared to Neotropical regions, particularly the Amazon Biome. (Baccini et al., 2012; Erb et al., 2018).

The Neotropics host some of the most densely sampled forests in terms of field plots for biomass and carbon stock measurements in tropical regions (Araujo et al., 2023; Chave et al., 2014; Malhi et al., 2013). However, despite this extensive sampling effort, uncertainties

* Correspondence to: Rodovia BR-307, 2671, Aeroporto Velho, Cruzeiro do Sul, Acre 69980-000, Brazil.
E-mail addresses: willian.flores@ufac.br, willianflores@gmail.com (A.W.F. Melo).
[1] **Professional address:** *Estrada da Canela Fina, KM 12 Gleba Formoso, São Francisco, 69980–000, Cruzeiro do Sul, Acre, Brazil.*

https://doi.org/10.1016/j.foreco.2024.122195
Received 13 March 2024; Received in revised form 30 July 2024; Accepted 31 July 2024
Available online 23 August 2024

persist in these measurements (Houghton and Nassikas, 2017; Mitchard et al., 2014). Baccini et al. (2017), while quantifying the carbon stock in Neotropical forests, arrived at an estimate of 91.2±84.2 Pg, with uncertainty accounting for 92 % of the total.

In the Amazon, the largest forest biome in the Neotropics, this pattern persists. It underscores the challenge of precisely quantifying biomass across different Amazonian forest types (Ometto et al., 2014; Tejada et al., 2020). In the Brazilian Amazon, deforestation-related emissions range more than three-fold, from 0.06 to 0.21 Pg C yr^{-1} (Lapola et al., 2023), with associated uncertainties of approximately ±0.11 Pg C yr^{-1} (Houghton and Nassikas, 2017).

In addition to other factors, these uncertainties arise from the limited availability of destructive samples required to calibrate allometric equations capable of capturing the diverse range of environments and vegetation types present in the Amazon Biome (Chave et al., 2004; Houghton and Nassikas, 2017; Picard et al., 2015; Wayson et al., 2015). Despite its importance for global climate, the carbon content of the Amazon Forest is based on few *in situ* measurements that are the basis for extrapolations. Most studies that conducted destructive inventories of forest biomass in the Amazon to adjust allometric equations focused on the central and eastern regions (Araújo et al., 1999; Brown et al., 1995a; Chambers et al., 2001; Goodman et al., 2013; Higuchi et al., 1998; Imbert and Rollet, 1989; Lescure et al., 1983; Lima et al., 2012; Mackensen et al., 2000; Nelson et al., 1999; Nogueira et al., 2008a; Overman et al., 1994; Saldarriaga et al., 1988; Silva, 2007; Woortmann et al., 2018) [see Figure S1 in the supplementary material]. Only three of these studies (Lima et al., 2012; Silva, 2007; Woortmann et al., 2018) determined forest below-ground biomass (BGB), and there are no studies of this nature in the Southwestern Amazon [see Figure S1 in the supplementary material]. Measuring BGB is methodologically challenging, yet it is crucial in quantifying total biomass in forest ecosystems (Mokany et al., 2006) since it can be used as an estimator of the amount of below-ground carbon based on the existing above-ground carbon biomass (Schenk and Jackson, 2002). Based on existing references, the BGB:AGB ratio can vary significantly, ranging from 0.10 to 0.37, depending on the selected source (Houghton et al., 2001; IPCC, 2006; Lima et al., 2012; Nogueira et al., 2008a). In Amazonia, the most commonly used values are from Nogueira et al. (2008a) — 0.10 for Open Forests and 0.31 for Dense Forests — and the IPCC (2006) — a generic factor of 0.37 for Tropical Forests.

Other sources of uncertainty stem from the factors used to quantify oven-dry biomass and carbon content in forest biomass (Araujo et al., 2023; Paul et al., 2017). Typically, due to limited studies on this topic, a factor of 0.5 or one determined in another region is conventionally used to evaluate the ratio of oven-dry biomass to fresh biomass and the proportion of carbon relative to oven-dry biomass (Araujo et al., 2023; Araújo et al., 1999; Nogueira et al., 2008a; Thomas and Martin, 2012). However, small regional variations in this factor may result in either overestimation or underestimation of carbon stocks and flux in the Amazon (Paul et al., 2017; Picard et al., 2012). In the international context, the IPCC (IPCC, 2006) recommends using a generic factor of 0.47 for converting oven-dry biomass to carbon in Tropical Forests. Silva (2007), in a study conducted in the Central Amazon, came to a similar value — 0.485. To address this challenge, additional research is needed across the gradient of pantropical forests, involving direct measurements of these parameters in representative forest samples.

The Amazon basin presents a high diversity of environmental features such as climate, geology, topography, soil, vegetation, and biodiversity (Bohlman et al., 2008; Davidson et al., 2012; Laurance et al., 2010; Pitman et al., 1999; Steege et al., 2013). These multiple factors determine the occurrence of unique forest typologies such as the bamboo-dominated open forests in the Southwestern Amazon (Carvalho et al., 2013; Ferreira, 2014; Griscom and Ashton, 2006), which occupy between 15.5 and 16.1 million ha (Carvalho et al., 2013; Dalagnol et al., 2018). Together with the area occupied by the open forest without bamboo dominance (ACRE, 2007), this forest typology extends to more than 20 million hectares in the Southwestern Amazon. Nevertheless, information is still missing on the structure, dynamics, and carbon stock in these types of forests.

The improvement of the accuracy of the forest carbon stock estimate also depends on the knowledge of allometric relationships of the groups of plant species that compose forests in specific regions of the Neotropical Regions (Chave et al., 2014; Lima et al., 2012; Nogueira et al., 2008b). Although previous studies have provided direct biomass estimates for some areas of the Neotropical forests (Araújo et al., 1999; Brown et al., 1995a; Chambers et al., 2001; Chave et al., 2014; Higuchi et al., 1998; Lima et al., 2012; Nelson et al., 1999; Nogueira et al., 2008a; Silva, 2007), research of this nature is practically absent in the Southwestern Amazon.

In the context of mitigating the impacts of global climate change in tropical forest regions, one of the most important mechanisms is Reducing Emissions from Deforestation and Forest Degradation (REDD+) (Voigt and Ferreira, 2016). Several national and subnational governments have implemented policies and projects to payment for environmental services (Duchelle et al., 2018; Lima et al., 2017). Initiatives such as the Global REDD Early Movers (REM) Program, developed by the Governments of Acre and Mato Grosso in Brazil (ACRE, 2024; FUNBIO, 2024; GIZ, 2024), exemplify this effort. Additionally, the private sector, traditional communities, and indigenous peoples have implemented projects under the REDD+ and CDM (Clean Development Mechanisms) frameworks (Barbosa et al., 2021; Benites-Lazaro et al., 2018; BIOFÍLICA, 2022; Simonet et al., 2019).

These initiatives require accurate data tailored to local realities, primarily to adhere to the principles of MRV (Measurable, Reportable, and Verifiable) (Gibbs et al., 2007; Plugge and Koehl, 2012; Vargas et al., 2013; Yanai et al., 2020). They also report the level of uncertainty associated with emission reduction estimates (Yanai et al., 2020), which creates a significant demand for scientific studies at local and regional scales to support these efforts. Minimizing uncertainties in estimates of carbon stock and flux within tropical forests will enable more accurate monitoring of climate change impacts on these ecosystems. Specifically, in the context of developing REDD+ projects within jurisdictional frameworks or voluntary markets, reducing uncertainties becomes essential for precisely assessing the contributions of these mechanisms to climate change mitigation.

In this study, we conducted destructive forest inventories in the Southwestern Amazon to address the following question: Do the allometric patterns, biomass and carbon forest stocks observed in the Southwestern Amazon differ from those found in other regions of the Amazon or Pantropical? For this purpose, we conducted the following analyses: (i) We determined the water and carbon content of forest biomass above and below ground and compared the results with studies carried out in other regions of the Amazon. (ii) Using our determined fractions of forest below-ground biomass (BGB) and above-ground biomass (AGB), we conducted analyses to identify the most effective method for estimating BGB as a function of AGB. (iii) Allometric equations were adjusted to estimate oven-dry biomass and carbon above and below-ground, comparing them to determine the optimal performance. (iv) We examined whether the allometric patterns observed in the Southwestern Amazon significantly differ from those identified in other regions of the Amazon. (v) We assessed the uncertainty related to applying allometric equations calibrated for other Amazon regions or the pantropical level to the Southwestern Amazon.

2. Material and methods

2.1. Study area

The present study was developed in the Antimary State Forest (ASF), located in the eastern region of the state of Acre, Brazil, between the municipalities of Rio Branco and Sena Madureira [68∘ 01' 30" to 68° 24' 30" W; 9° 11' 00" to 9° 25' 30" S] (Fig. 1). The climate has been

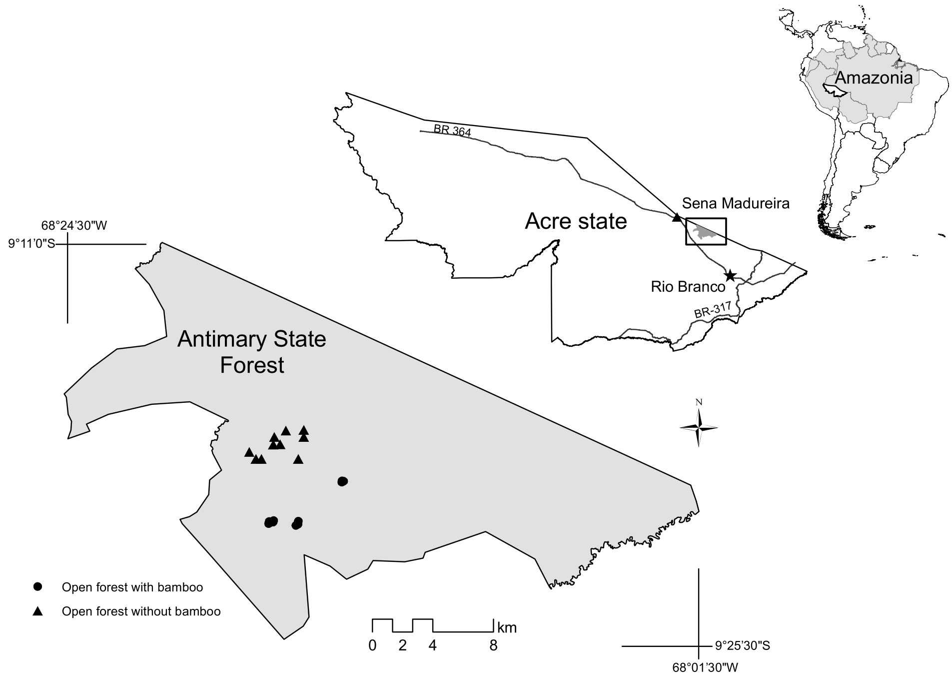

Fig. 1. Localization of the Antimary State Forest (ASF) in the eastern region of the state of Acre, Brazil, 50 km east of the city of Sena Madureira and 110 km northwest of Rio Branco. The circles and triangles on the map indicate the precise locations of our 100 m^2 (10 ×10 m) sample plots.

classified as Am (Köppen) with average annual temperatures between 24 °C and 26 °C, marked dry (June to August) and rainy (October to April) seasons, and total annual precipitation between 2200 and 2.500 mm (Alvares et al., 2013; Duarte, 2006). The regional climate, however, is changing with increasing temperatures and an expanding dry season (Marengo et al., 2018). There are four types of vegetation: Open Forest with Bamboo, Open Forest with Palm Trees, Alluvial Open Forest, and Dense Forest (ACRE, 2007). Deforested area accounts for about 12 % of ASF (INPE, 2024). The landscape presents undulating to slightly undulating relief and elevations varying from 141 to 250 m (Farr et al., 2007). The predominant soils are Oxisols, and Ultisols (Bardales et al., 2015; Santos et al., 2018).

2.2. Data collection and processing

We established 20 random 100 m^2 (10 ×10 m) plots in the ASF, 10 in open rainforest without bamboo and 10 in open rainforest with bamboo (*Guadua weberbaueri* Pilg) (Fig. 1). It's important to note that due to the sampling process being restricted to open forests typical of the Southwestern Amazon, the application of the allometric equations and the factors we developed is limited to this specific forest type. In total, we sampled 190 trees (5–90 cm DBH or above the buttresses) from 93 species or morphospecies (6 individuals were not identified), grouped in 35 families and 61 genera (see Figure S2 and Table S1 of the supplementary material). Sample collection and processing to directly determine forest oven-dry biomass and carbon content was performed in seven steps, according to Silva (2007): i. delimitation of plots; ii. forest inventory; iii. cutting of understory, palm trees, and lianas; iv. felling of trees; v. sectioning and weighing of trees; vi. sample collection to determine the oven-dry biomass and carbon; and vii. laboratory analysis (see Figure S3 in the supplementary material).

During the forest inventory, we measured and recorded the Diameter at Breast Height (DBH, ~1.3 m above ground level or above the buttresses, when present) of individual trees with diameter ≥ 5 cm, after botanic identification. All shrubs with DBH < 5 cm, palm trees, and lianas were cut and weighed for each plot. Before felling the trees (DAP ≥ 5 cm), we measured their crown diameter (m), the volume of bole (m^3), and the commercial and total height (m). Then, each tree was sectioned to determine its fresh biomass within the following compartments: i) *crown* – leaves, small branches (diameter, ∅ < 10 cm), large branches (∅ ≥ 10 cm), flowers, and fruits; ii) *bole* and iii) coarse *roots* – divided into two subgroups: small roots (2 mm ≤ ∅ < 5 cm) and large roots (∅ ≥ 5 cm) (see Figure S4 in the supplementary material). Fine roots < 2 mm were not collected because they are considered part of soil biomass, according to IPCC (IPCC, 2006, p. 4.72). That is the reason why we defined a subclass of small roots between ≥ 2 mm and < 5 cm. To determine oven-dry biomass and carbon content samples were collected, these materials were weighed in the field and subsequently processed in the laboratory (as described in 2.3). For leaves, small branches, small roots, flowers, and fruit samples of ~1 kg was collected. For large roots and boles, discs of constant width of ~3 cm were collected.

2.3. Water and carbon content of forest biomass

To determine the percentage of water and carbon content, the samples from each sectioned compartment (as described in 2.2) of each tree were placed into a forced-air ventilation drier at the constant temperature of 65±2 °C. After ten days, the samples were weighed daily until three consecutive equal measures with constant weight were reached (Silva, 2007). The oven-dry biomass (D_m) was obtained by subtracting the relative weight of water from the fresh biomass (F_m) of each categorized compartment of the tree first. Then we summed the oven-dry biomass measures of all compartments to provide the total oven-dry biomass of each tree.

Carbon content was determined in the dried samples with constant weight. These samples were crushed and sieved down to 0.25 mm, and then a subsample was weighed inside a tin capsule. After this, the subsamples were burned in oxidizing medium and the gases produced from this process were split by gas chromatography, purified, and carried by a continuous flow of helium to the Carlo Erba EA 1110 elemental analyzer coupled to a stable isotope mass spectrometer, Finnigan Delta Plus, where the carbon concentration (%) was determined.

We calculated the weighted mean of water content (bole n=190; large root n=187; small root n=182; coarse branch n=47; fine branch

Table 3
Weighted water contents relative to the total weight of the tree compartments. Numbers between parenthesis indicate uncertainty calculated by error propagation, $\frac{\delta Q}{/Q/} = \sqrt{\left(\frac{\delta a}{a}\right) + \left(\frac{\delta b}{b}\right) + \cdots + \left(\frac{\delta z}{z}\right)}$ for multiplication/division, and $\delta Q = \sqrt{(\delta a)^2 + (\delta b)^2 + \cdots + (\delta z)^2}$ for addition. The weighted mean was calculated using the formula $\overline{X}_b = \frac{\sum X_i p_i}{\sum p_i}$, where X_i is the mean water content in each compartment, and p_i is the average contribution index of the respective compartment to the total weight of the trees.

	Tree compartments	Content – % (± CI)	Biomass contribution index (± CI)	Weighted content – %[a]
Fresh biomass water content				
	Bole	45.2 (±1.0)	0.599 (±0.020)	27.0 (±0.1)
	Large roots	48.2 (±1.1)	0.115 (±0.008)	5.6 (±0.1)
	Small roots	51.0 (±1.1)	0.028 (±0.008)	1.4 (±0.3)
	Coarse branches	45.4 (±1.7)	0.172 (±0.029)	7.8 (±0.2)
	Fine branches	50.2 (±1.2)	0.191 (±0.018)	9.6 (±0.1)
	Leaves	60.3 (±1.2)	0.039 (±0.005)	2.4 (±0.1)
Total fresh biomass	Weighted mean			47.0 (±0.4)
	Bole	45.2 (±1.0)	0.695 (±0.024)	31.4 (±0.1)
	Coarse branches	45.4 (±1.7)	0.195 (±0.033)	8.8 (±0.2)
	Fine branches	50.2 (±1.2)	0.221 (±0.020)	11.1 (±0.1)
	Leaves	60.3 (±1.2)	0.045 (±0.006)	2.7 (±0.1)
Above-ground fresh biomass	Weighted mean			46.8 (±0.3)
	Large roots	48.2 (±1.1)	0.831 (±0.026)	40.1 (±0.1)
	Small roots	51.0 (±1.1)	0.170 (±0.026)	8.7 (±0.2)
Below-ground fresh biomass	Weighted mean			48.7 (±0.2)

n=182; leaves n=161) and carbon (bole n=174; large root n=173; small root n=128; coarse branch n=43; fine branch n=174; leaves n=170) [Table 3] in the above-ground, below-ground and total fresh biomass, taking into account the content and the contribution of each compartment to the total dry weight of the trees.

To determine the oven-dry biomass and carbon content of the 190 trees, first, we calculated the content per compartment, using data from the water and carbon content of each tree, and then, we summed the values. When water and/or carbon content was absent for a given compartment, we used the mean values of these measures of the compartment of the whole samples.

2.4. Relationship of below:above-ground oven-dry biomass

We tested two methods to estimate below-ground forest oven-dry biomass (BGB) as a function of above-ground oven-dry biomass (AGB). i. we calculated the average BGB:AGB ratio using the following expression: $\overline{BGB:AGB} = \sum\left(\frac{\frac{BGB}{AGB_1} + \frac{BGB}{AGB_2} + \ldots + \frac{BGB}{AGB_n}}{n}\right)$, where $\overline{BGB:AGB}$ = the average ratio of below-ground oven-dry biomass to above-ground oven-dry biomass, BGB = below-ground oven-dry biomass for each sampled tree, AGB = above-ground oven-dry biomass for each sampled tree, and ii. we adjusted linear equations using Model 1 $BGB = aAGB^b$ and Model 2 $BGB = a\mathrm{AGB}$, according to Lima et al. (2012). To compare the results of the two methods employed, we conducted an analysis of variance and the Tukey post-hoc test at a 5 % significance level. To compare the results obtained from applying the equation adjusted using Model 1 with the results obtained by Lima et al. (2012), we used analysis of covariance at a 5 % significance level.

2.5. Testing allometric models to estimate oven-dry biomass and carbon in trees

Based on previous allometry studies conducted in the Amazon (dos Santos, 1996; Higuchi et al., 1998; Lima et al., 2012; Nogueira et al., 2008a; Silva, 2007), we tested six known models (Models 1–6; Table 1) to estimate oven-dry biomass of below-ground, above-ground and total tree as functions of diameter at breast height (*D*), total height (*H*), and commercial or bole height (*Hb*). For allometric relationships of above-ground and total carbon density and tree crown oven-dry biomass estimation, Models 1 and 4 (Table 1) were tested.

The criteria adopted to select the models with the best fit were: adjusted coefficient of determination (r^2); Alaike information criterion – AIC (Akaike, 1974), and Bayesian information criterion – BIC (Schwarz, 1978) to models of the same nature (linear or non-linear); analysis of collinearity (VIF – Variance Inflation Factor); relative standard error ($S_{yx\,\%}$), and residual distribution pattern (*studentized residuals*). We also considered the model's applicability in terms of cost, accuracy, and ease of collecting the independent variables in the field.

To adjust the allometric equations, we applied the ordinary least square method for Models 4–6 and the non-linear least square method for Models 1–3 (Table 1). We applied correction factor *CF* to reduce bias by logarithmic transformation for logarithmic models (Models 4–6; Table 1) according to Sprugel (1983): $CF = \exp(SEE^2/2)$, where *SEE* is the standard error of the estimate. All statistical analyses were conducted using the R software (R Core Team, 2023), within the RStudio Integrated Development Environment (RStudio Team, 2022).

Table 1
Allometric models were tested to estimate the oven-dry biomass of trees.

ID	Models	Application
1	$DM = aDBH^b + \varepsilon_i\ (0 < a,\ 0 < b)$	Oven-dry biomass, carbon, and tree crown
2	$DM = aDBH^bH^c + \varepsilon_i\ (0 < a,\ 0 < b,\ 0 < c)$	Oven-dry biomass
3	$DM = aDBH^bHb^c + \varepsilon_i\ (0 < a,\ 0 < b,\ 0 < c)$	Oven-dry biomass
4	$ln(DM) = ln(a) + b(LnDBH) + \varepsilon_i\ (0 < b)$	Oven-dry biomass, carbon, and tree crown
5	$ln(DM) = ln(a) + b(lnDBH) + c(lnH) + \varepsilon_i\ (0 < b,\ 0 < c)$	Oven-dry biomass
6	$ln(DM) = ln(a) + b(lnDBH) + c(lnHb) + \varepsilon_i\ (0 < b,\ 0 < c)$	Oven-dry biomass

Notes: *ID = id model; DM = oven-dry biomass (kg); ln = natural logarithm; a, b e c = coefficient of models; DBH = diameter at breast height (cm, measured at 1.3* m or above buttresses); H = tree height (m); *Hb = commercial or bole height (m).*

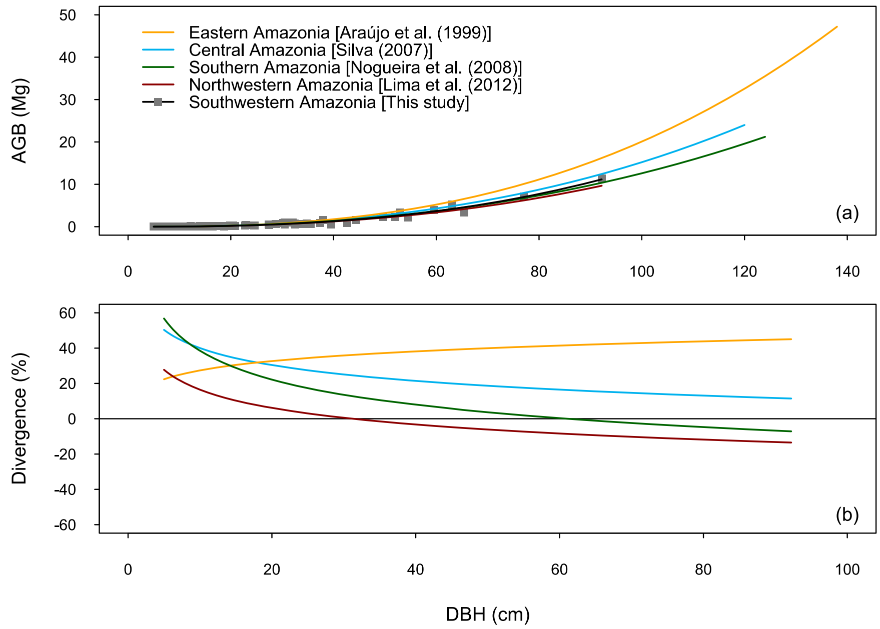

Fig. 4. Comparison of allometric logarithmic equations to estimate oven-dry biomass above ground (AGB) in five localities in the Amazon. Adjusted equations for East, Center, and Northwest Amazon were published by Lima et al. (2012). In Fig. 4a, we plotted curves adjusted using allometric equations from various Amazon regions, including the one tailored by our study. Fig. 4b illustrates the divergence between equations derived from other Amazon regions and those specifically adjusted in our research.

2.6. Patterns of allometric relationship in the Amazon

To compare the allometric patterns of trees across the Amazon, we used equations fitted with the data from Araújo et al. (1999) with DBH 10 – 138 cm [east – EA]; Silva (2007) with DBH 5 – 85 cm [center – CA]; Nogueira et al. (2008a) with DBH 5 – 124 cm [south – SA]; and Lima et al. (2012) with DBH 5 – 61 cm [northwest – NWA] (Fig. 4) to estimate above-ground oven-dry biomass of trees. The equations related to the east, center and northwest Amazon were adjusted by Lima et al. (2012), using the data from respective bibliographic sources previously mentioned, applying the index of water content according to Silva (2007), to obtain the oven-dry biomass. All four equations and their respective parameters are available in Table S4 of the supplementary material. We tested statistical differences between the intercept and the slope of the curves resulting from the application of the equations to the data with an interval of DBH from 5 to 92.2 cm randomly distributed, using a covariance analysis (ANCOVA) and Tukey post-hoc test, both at the level of 95 % of confidence. To verify the practical performance of the equations for the four Amazonian regions and compare with Equation 5 (Table 5), we applied all the equations to the data from 10 one-hectare plots forest inventory in the ASF (data from d'Oliveira et al., 2021).

2.7. Validation of Chave et al.'s (2016) pantropical equations

To assess the uncertainty of a widely used pantropic allometric equations at the local scale, we applied Equation 4 [$AGB_{est} = 0.673 \times (\rho D^2 H)^{0.976}$] and Equation 7 [$AGB_{est} = \exp[-1.803 - 0.976E + 0.976\ln(\rho)] + 2.673\ln(D) - 0.0299[\ln(D)]^2]$] of Chave et al. (2014) to estimate tree oven-dry biomass (AGB) using the diameter (DBH) and height (H) data from our inventory data conducted in this study, as well as wood density (ρ) compiled by Chave et al. (2016) and environmental stress index (E) data from Réjou-Méchain et al. (2017). The resulting AGB estimates were compared with the AGB obtained in the destructive inventory conducted in this study. In Table 2, the parameters used in the validation process of the equation are listed.

All the analyses were performed in the environment of the software R (R Core Team, 2023) and BIOMASS package (Réjou-Méchain et al., 2017).

3. Results

3.1. Water and carbon content of forest biomass

Water content (%)[2] varied in the studied tree compartments (Table 3). The bole had the lowest water content of 45.2 ± 1.0 (mean ± CI[3]; n=190), followed by coarse branch with 45.4 ± 1.6 (n=47), large root 48.2 ± 1.1 (n=187), fine branch 50.2 ± 1.2 (n=182), small root 51.0 ± 1.1 (n=182), leaves 60.3 ± 1.2 (n=161), and flowers/fruits 79.3 ± 9 (n=11) (Table 3).

In general, the mean water content (%) of the fresh biomass of trees increased from the base to the extremity in the boles, large roots, and coarse branches. In the boles, the water content (%) at the base, middle, and top positions differed significantly ($p < 0.05$; Tukey test), with the means of 42.5 ± 1.1, 44.0 ± 1.0 (n=190) and 46.3 ± 1.1 (n=190), respectively. In the coarse branches, there were no differences ($p > 0.05$) in the water content (%) among the three sampled positions, and the means were 43.8 ± 1.5 (n = 47), 44.6 ± 1.7 (n = 47) and 45.8 ± 2.0 (n = 47), at base, middle and top, respectively. In the large roots, there was a significant difference (p < 0.05) between the base (46.1 ± 1.3; n=188) and the top (50.0 ± 1.2; n=179), while the middle position (48.2 ± 1.1; n=179) did not differ from the others (Table 3).

The water content accounted for 47 % ± 2.1 % in the total fresh biomass (Table 3). Thus, oven-dry biomass represents 53 % of fresh biomass. For above-ground fresh biomass, the weighted water content percent was 46.8 % ± 0.9 %, and for below-ground fresh biomass, it was 48.7 % ± 2.1 % (Table 3).

We found low variability of carbon oven-dry biomass content among the tree compartments, although we observed significant differences

[2] Relationship between dry weight – obtained by drying the material in greenhouse at 65 ± 2 °C until the weight become constant – and the fresh weight.

[3] Average confidence interval – 95 %.

Table 5
Coefficients and statistics of the allometric equations (Models 1–6, Table 1) were used to estimate oven-dry biomass and carbon content above ground, below ground, crowd, and total in trees. Values in parentheses indicate 95 % confidence intervals. *a*, *b*, and *c* are model coefficients. CF is the correction factor to reduce the bias of log-transformation (Sprugel, 1983). AIC is the Akaike Information Criterion (Akaike, 1974). BIC is the Bayesian Information Criterion (Schwarz, 1978). r^2 is the adjusted coefficient of determination. $S_{yx\%}$ is the relative standard error.

Equations	*a*	*b*	*c*	*N*	*CF*	AIC	*BIC*	r^2	$S_{yx\%}$
Tree oven-dry biomass									
Below-ground									
1	0.009 (±0.006)	2.685 (±0.165)	-	190	-	2060		0.901	8.11
2	0.005 (±0.005)	2.515 (±0.232)	0.353 (±0.367)	190	-	2058		0.902	8.05
3	0.003 (±0.003)	2.544 (±0.154)	0.603 (±0.217)	190	-	2033		0.914	7.54
4	−4.104 (±0.245)	2.457 (±0.095)		190	1.099	226		0.853	9.87
5	−4.322 (±0.323)	2.319 (±0.164)	0.226 (±0.220)	190	1.097	224		0.846	10.11
6	−4.112 (±0.248)	2.433 (±0.144)	0.036 (±0.160)	190	1.099	228		0.850	9.97
Above-ground									
1	0.064 (±0.022)	2.671 (±0.078)	-	190	-	2508		0.977	3.69
2	0.024 (±0.008)	2.333 (±0.081)	0.695 (±0.130)	190	-	2412		0.986	2.86
3	0.040 (±0.014)	2.584 (±0.073)	0.299 (±0.092)	190	-	2472		0.981	3.35
4	−2.511 (±0.258)	2.593 (±0.100)	-	190	1.109	244		0.976	3.72
5	−3.528 (±0.259)	1.946 (±0.132)	1.059 (±0.177)	190	1.061	140		0.964	4.57
6	−2.613 (±0.238)	2.273 (±0.137)	0.477 (±0.153)	190	1.090	211		0.953	5.22
Crown									
1	0.001 (±0.001)	3.490 (±0.172)	-	184	-	2287		0.952	6.72
2	0.001 (±0.001)	3.277 (±0.208)	0.402 (±0.268)	184	-	2280		0.954	6.59
3	0.001 (±0.001)	3.592 (±0.193)	−0.283 (±0.199)	184	-	2281		0.954	6.59
4	−4.179 (±0.642)	2.664 (±0.250)	-	184	1.896	572		0.919	8.72
5	−5.429 (±0.828)	1.859 (±0.431)	1.306 (±0.583)	184	1.787	555		0.857	11.58
6	−4.098 (±0.644)	2.925 (±0.375)	−0.387 (±0.417)	184	1.881	570		0.920	8.65
Whole individual									
1	0.073 (±0.026)	2.673 (±0.082)	-	190	-	2578		0.974	3.89
2	0.029 (±0.011)	2.354 (±0.091)	0.657 (±0.147)	190	-	2507		0.982	3.22
3	0.043 (±0.016)	2.578 (±0.075)	0.333 (±0.096)	190	-	2538		0.979	3.49
4	−2.310 (±0.230)	2.572 (±0.090)	-	190	1.085	199		0.971	4.09
5	−3.187 (±0.236)	2.015 (±0.118)	0.913 (±0.159)	190	1.050	103		0.957	5.04
6	−2.397 (±0.213)	2.299 (±0.123)	0.408 (±0.137)	190	1.072	169		0.948	5.52
Tree carbon density									
Above-ground									
1	0.025 (±0.009)	2.705 (±0.080)	-	190	-	2210		0.977	3.73
4	−3.349 (±0.233)	2.602 (±0.091)	-	190	1.113	250		0.976	4.80
Crown									
1	0.0003 (±0.0002)	3.552 (±0.179)	-	184	-	1999		0.951	6.92
4	−5.018 (±0.648)	2.668 (±0.252)	-	184	1.917	575		0.913	9.16
Whole individual									
1	0.029 (±0.009)	2.709 (±0.080)	-	190	-	2277		0.975	3.89
4	3.147 (±0.233)	2.582 (±0.091)	-	190	1.089	206		0.971	4.20

Table 2
Parameters used for the validation of the pantropical equations by Chave et al. (2014).

ID	Parameter	Formula
1	Bias	$B_i = \hat{y}_i - y_i$
2	Sum of squared residuals	$SSR = \sum_{i=1}^{n} (\bar{y} - \hat{y})^2$
3	Total sum of squares	$TSS = \sum_{i=1}^{n} (y - \bar{y})^2$
4	Coefficient of determination	$r^2 = 1 - \frac{SSR}{TSS}$
5	Adjusted coefficient of determination	$r^2_{adj} = 1 - \frac{n-1}{n-(k+1)} \times (1 - r^2)$
6	Standard error of the estimate	$SEE = \sqrt{\frac{\sum (y_i - \hat{y}_i)^2}{(n-k)}}$
7	Relative standard error	$S_{yx\%} = \frac{SEE/\sqrt{n}}{\bar{y}} \times 100$

Notes: B_i = Bias; y = observed value; $\hat{y}$ = estimated value; $\bar{y}$ = average of observed values; SSR = sum of squared residuals; TSS = total sum of square; r^2 = coefficient of determination; r^2_{adj} = adjusted coefficient of determination; n = total number of observations; k =number of model coefficients; SEE = standard error of the estimate; $S_{yx\%}$ = relative standard error.

between the most extreme compartments in the context of the tree structure, like fine branches and leaves (see Figure S5 in the supplementary material). Boles, large roots, and small roots differed significantly from fine branch and leaves, while coarse branches did not differ from the other compartments ($p < 0.05$; Tukey test; see Figure S5 in the supplementary material). The average carbon content (%) of boles was 44.6 ± 0.2 (mean ± CI; n=174), large roots 44.5 ± 0.2 (n=173), small roots 44.7 ± 0.4

(n=128), coarse branches 43.9 ± 4.4 (n=43), fine branches 43.6 ± 0.2 (n=174) and leaves 43.7 ± 0.5 (n=170). Unlike water content, there were few variations of carbon content from the base to the top of the bole, large root, and coarse branch (see Figure S6 in the supplementary material). In the bole, the base and middle differed significantly from the top ($p < 0.05$; Tukey test). The weighted mean of the carbon content of total, above, and below-ground oven-dry biomass, were 44.3 % ± 0.3, 44.3 % ± 0.3, and 44.6 % ± 0.2, respectively (Table 4).

Comparing the water content of the fresh biomass in the tree compartments sampled by Silva (2007) in the Central Amazonia (CA), our results indicate higher water content in SWA than the average found in the CA. Among the compartments, the greatest difference between Silva (2007) and our study was found in the boles, ∼ +6.4 %, while to the weighted mean of the total fresh mass (above- and below-ground), the difference was ∼ +5.4 %. Meanwhile, our study found that the carbon

Table 4
Weighted carbon contents relative to the total weight of the tree compartments. Numbers between parenthesis indicate uncertainty calculated by error propagation, $\frac{\delta Q}{/Q/} = \sqrt{\left(\frac{\delta a}{a}\right) + \left(\frac{\delta b}{b}\right) + \cdots + \left(\frac{\delta z}{z}\right)}$ for multiplication/division, and $\delta Q = \sqrt{(\delta a)^2 + (\delta b)^2 + \cdots + (\delta z)^2}$ for addition. The weighted mean was calculated using the formula $\overline{X}_b = \frac{\sum X_i p_i}{\sum p_i}$, where X_i is the mean water content in each compartment, and p_i is the average contribution index of the respective compartment to the total weight of the trees.

	Tree compartments	Content – % (± CI)	Biomass contribution index (± CI)	Weighted content – %[a]
Oven-dry biomass carbon content				
Total oven-dry biomass	Bole	44.6 (±0.2)	0.620 (±0.020)	27.7 (±0.1)
	Large roots	44.6 (±0.2)	0.120 (±0.009)	5.3 (±0.1)
	Small roots	44.7 (±0.4)	0.019 (±0.003)	0.9 (±0.2)
	Coarse branches	43.9 (±0.4)	0.166 (±0.029)	7.3 (±0.2)
	Fine branches	43.6 (±0.2)	0.185 (±0.018)	8.1 (±0.1)
	Leaves	43.7 (±0.5)	0.029 (±0.004)	1.3 (±0.1)
	Weighted mean			44.3 (±0.3)
Above-ground oven-dry biomass	Bole	44.6 (±0.2)	0.722 (±0.024)	32.2 (±0.1)
	Coarse branches	43.9 (±0.4)	0.187 (±0.033)	8.2 (±0.2)
	Fine branches	43.6 (±0.2)	0.212 (±0.021)	9.3 (±0.1)
	Leaves	43.7 (±0.5)	0.033 (±0.005)	1.5 (±0.1)
	Weighted mean			44.3 (±0.3)
Below-ground oven-dry biomass	Large roots	44.6 (±0.2)	0.863 (±0.018)	38.5 (±0.1)
	Small roots	44.7 (±0.4)	0.150 (±0.022)	6.7 (±0.1)
	Weighted mean			44.6 (±0.2)

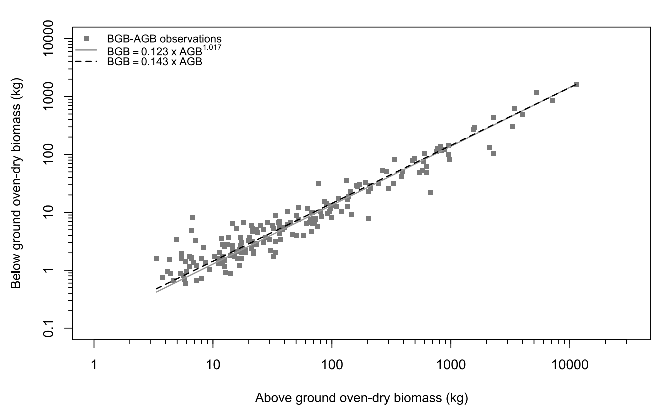

Fig. 2. Relationship of below- and above-ground forest oven-dry biomass.

content of oven-dried biomass differed negatively from Silva (2007) by approximately 4.0 % in the bole, 2.5 % in large roots, and 1.0 % in small roots. On average, this difference amounted to −4.2 % for total oven-dry biomass.

3.2. Relationship of below:above-ground oven-dry biomass

The mean root-to-shoot (BGB/AGB) ratio in our dataset was 0.167 ±0.017 (mean ± CI; n=190). To estimate BGB as a function of AGB and better understand such relation, we fitted two equations: $BGB = 0.123(\pm 0.046)AGB^{1.017(\pm 0.050)}(r^2_{adj} = 0.933)$ [Eq. 1] and $BGB = 0.143(\pm 0.005)AGB(r^2_{adj} = 0.933)$ [Eq. 2] (Fig. 2). The statistics of the resulting equations are in Table S3 of the supplementary material.

Comparing the three approaches of below-ground oven-dry biomass estimates (BGB-AGB relationship, application of Eq. 1, and Eq. 2 with our data directly determined, we found the following mean divergences, −29±9 %, −2±8 % and −11±8 % (mean ± CI95 %), respectively. The application of the BGB-AGB relationship differed significantly from the applications of the equations 1 and 2 ($p < 0.01$; Tukey test) (see Figure S9 of the supplementary material).

Comparing the results of applications to our dataset of Eq. 1 and the equation adjusted by Lima et al. (2012) ($BGB = 0.125AGB^{1.020}$, $r^2 = 0.928$) for the Central and Northern Amazon, we observed significant differences in the intercept coefficients (ANCOVA, $p = 8.1e\text{-}06$) and slope of the curves (ANCOVA, $p = 2.2e\text{-}16$).

Our determination of the BGB:AGB ratio in trees, as well as the statistical analyses conducted, showed that the best method for determining this ratio was the adjustment of Equations 1 and 2 (Fig. 2 and Table S3 of the supplementary material), where the results of the application differed significantly from the application of the method of the mean ratio between BGB and AGB. Additionally, we found that the patterns of the BGB:AGB ratio in the region sampled by this study differ from those found in the Central and Northern Amazon by Lima et al. (2012) and Silva (2007). Through an analysis of covariance (ANCOVA), we detected a significant difference in the slope coefficients of the curves of the equations adjusted for the Southwestern Amazon (this study) compared to the Central and Northern Amazon (Lima et al., 2012; Silva, 2007), suggesting that the BGB:AGB ratio is distinct in the forests of these two regions.

3.3. Allometric equations to estimate forest oven-dry biomass and carbon

We fitted allometric equations to estimate the oven-dry biomass and carbon of trees (both in kg) in the above-ground, below-ground, crown, and whole tree, based on the models presented in Table 1. The coefficients and statistics of the fitted allometric equations are presented in Table 5. The oven-dry biomass and carbon content of all trees are available in Table S2 of the supplementary material.

To estimate oven-dry biomass, except for below ground, Equation 2 [$DM^4 = aD^bH^c$] showed higher r^2 (below-ground, 0.902; above-ground, 0.986; crowd, 0.954; total, 0.982 %) and the lowest value of $S_{yx\%}$ [relative standard error] (below-ground, 8.05 %; above-ground, 2.86 %; crown, 6.59; total, 3.22 %) (Table 5). However, the diameter at breast height (*DBH*) presented a significant correlation with total height – H (r=0.85; p=0.02e-14; Pearson) and commercial or bole height – Hb (r=0.74; p=0.02e-14; Pearson), suggesting collinearity of these variables when used in the same equation. High collinearity levels lead to imprecise parametrization and a decrease in the statistical power of the equation (Graham, 2003). Another issue to be considered is the accuracy of the tree height measurements in tropical forests. According to Hunter et al. (2013), the accuracy of individual tree height measurements varies between 3 % and 20 % of the total height. In our study, the bias of the tree total height measurements is widely superior to the performance gain of prediction with the addition of this variable in an allometric equation.

In this context, the best options for practical use are the equations

[4] DM = Oven-dry Biomass.

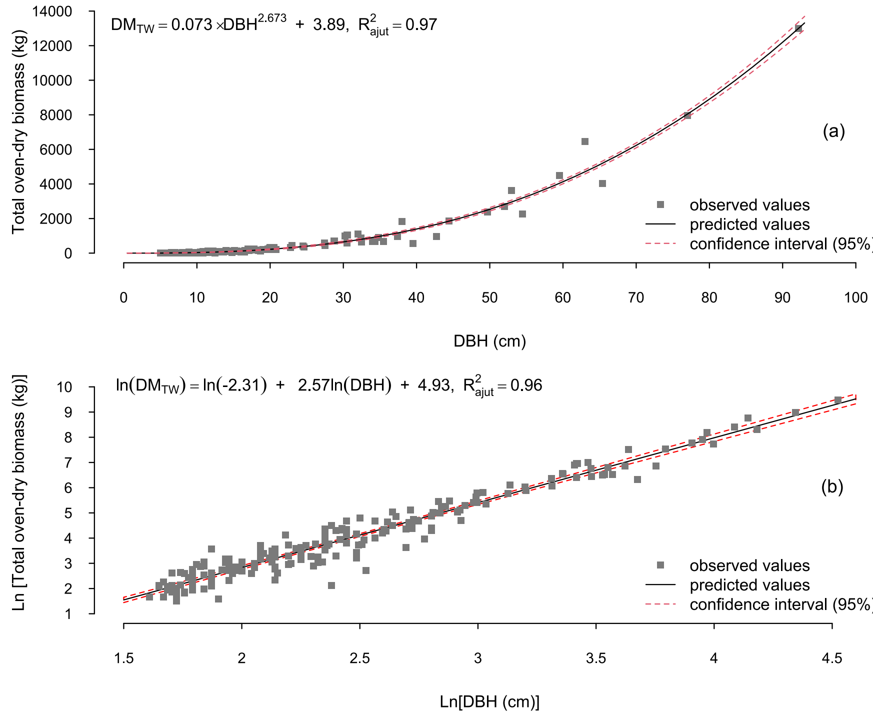

Fig. 3. Equations of simple entry to estimate total oven-dry biomass with observed values, predicted values, and confidence interval of 95 %. (a) Simple power equation – $DM_{TW} = aDBH^b + \varepsilon_i$. (b) Simple linear logarithmic equation – $ln(DM_{TW}) = ln(a) + b\ln(DBH) + \varepsilon_i$.

fitted applying the Models 1 [$DM = aDBH^b$] and 4 [$ln(DM) = ln(a) + b\text{Ln}(DBH)$] (Fig. 3). Although with lower performance indicators than the other equations, their values of r^2 and $S_{yx\%}$ are sufficiently high to not compromise the prediction capabilities of the equations and provide the advantage of easy utilization, given the practicality of DBH measurements in the field.

We used Models 1 and 4 (Table 1) to fit allometric equations to estimate carbon density in the compartments above ground, crown, and total for sampled trees (Table 5). Except for the crown compartment, which had relative standard errors higher than 5 %, the other equations had excellent estimation performance (Table 5).

Considering our comparisons in terms of AIC (Akaike, 1974), BIC (Schwarz, 1978), adjusted coefficient of determination (r^2), and relative standard error ($S_{yx\%}$) for diagnosing the performance of the estimates from the adjusted equations, as well as the accuracy and practicality of gathering predictors in the field, we recommend Eq. 1 and 4 (Table 5) to estimate the oven-dry biomass of trees from the Southwestern Amazon (Fig. 2). Nevertheless, it is known that transforming arithmetic data into logarithmic data results in biased estimates when inverting the transformation of estimated data (Finney, 1941; Smith, 1993). Furthermore, log-transformed models predict the geometric mean for the dependent variable, instead of the arithmetic mean, producing biased results (Packard, 2013). Robust statistical models can be directly fitted to the original data by non-linear regression, thus avoiding problems related to logarithmic transformation (Packard, 2013). Within this context, it is preferable to use Eq. (1) (Table 5), with simple entry and without logarithmic transformation, to estimate the dry mass and carbon below-ground, above-ground, total, and in the canopy of trees.

3.4. Patterns of allometric relationships in the Amazon

Comparing patterns of allometric relationships evidenced in adjusted equations to estimate above-ground oven-dry biomass of trees in four different regions of the Amazon, East – EA [Araújo et al. (1999); DBH 10 – 138 cm], Center – CA [Silva (2007); DBHP 5 – 85 cm], South – SA [Nogueira et al. (2008a); DBH 5 – 124 cm] and Northwest Amazon – NWA [Lima et al. (2012); DBH 5 – 61 cm] (Fig. 4a), with the equation 5 (Table 5), revealed significant differences in the regression slope ($p < 0.001$; ANCOVA). Only the equation fitted in the NWA did not differ from the fitted equation in this study, while the others differed both from our equation and each other ($p < 0.001$ Tukey; see Figure S7 of the supplementary material). In general, in the EA, CA, and SA, trees with similar diameters present higher oven-dry biomass than trees in SWA. Applying these equations to the inventory data of 10 one-hectare plots in the ASF (d'Oliveira et al., 2021), we verified that EA, CA and SA overestimated the mean AGB, on 37.1±1.5 %, 13.3±2.1 % and 1.3±3.1 % respectively and NWA underestimated AGB means in 1.3±3.1 % (see Figure S8 in the supplementary material). For trees with DBH > 30 cm, the AGB decreased in the following order: EA > CA > SA > SWA > NWA (Fig. 4b).

3.5. Validation of Chave et al.'s (2016) pantropical equations

We estimated above-ground biomass (AGB) using Equations 4 and 7 from Chave et al. (2014). Our inputs included diameter (DBH) and height (H) data obtained from our direct inventory. Additionally, we incorporated wood density data (σ) compiled by Chave et al. (2016) and environmental stress index (E) data from Réjou-Méchain et al. (2017).

The results were then compared with observed AGB data from our study. Verifying the performance of Chave et al.'s (2014) pantropical Equation 4, we found a relative standard error ($S_{yx\%}$) of 6.88 % and an adjusted coefficient of determination (r^2_{adj}) of 0.92, both excellent indicators of model precision. However, Equation 7 exhibited much lower performance, with $S_{yx\%}$ at 0.89 and r^2_{adj} at 22.73 %. Analyzing the residue distribution (Fig. 5), we observed that both equations tend to linearly overestimate, especially for trees with DBH ≥ 25 cm.

When applied to our observed data set, Equation 4 resulted in an average overestimation of approximately 31±8 % for individual trees and 26±16 % for total oven-dry biomass in the sampled plots. Equation 7 presented even more imprecise measurements, with an average overestimation of 61±16 % for individual trees and 46±17 % for total oven-dry biomass in the sampled plots, approximately twice as high.

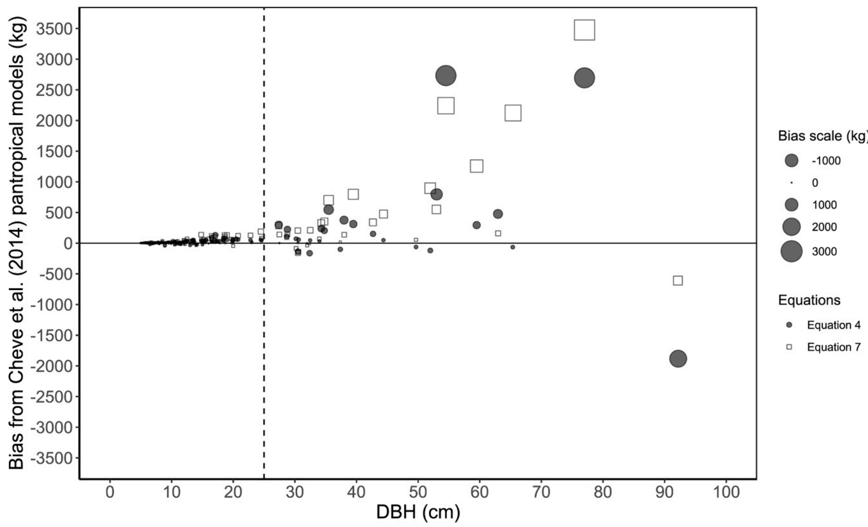

Fig. 5. Validation of Pantropical Equations 4 [$AGB_{est} = 0.673 \times (\rho D^2 H)^{0.976}$] and 7 $AGB_{est} = \exp[-1.803 - 0.976E + 0.976\ln(\rho)] + 2.673\ln(D) - 0.0299[\ln(D)]^2$] by Chave et al. (2014), using observed data from this study (n = 188).

4. Discussion

We found significant differences in water content, carbon content, BGB:AGB ratio, and allometric relationships in trees between the region we sampled and other Amazonian regions sampled by other authors (Araújo et al., 1999; Chave et al., 2014; Lima et al., 2012; Nogueira et al., 2008a; Silva, 2007). Our results suggest that trees with the same physical characteristics such as diameter, height, crown, and root architecture, possess less amount of oven-dry biomass and carbon content in the Southwestern Amazon than in the Central and East Amazon. These differences clearly indicate that applying allometric equations developed for other Amazonian regions to the area sampled by this study may in a significant overestimation of biomass.

By developing the initial set of allometric equations for the SWA, we address a critical gap in biomass (AGB and BGB) estimation for this region. This advancement enhances the accuracy of forest biomass and carbon estimates, which are essential for regional climate change mitigation policies. Furthermore, our work improves the precision of the emissions estimates avoided by REDD+ projects in the region. In addition, the development of more accurate equations to assess forest biomass and carbon stocks, utilizing various techniques and scales (Adinugroho et al., 2023; Daba and Soromessa, 2019; Swinfield et al., 2019), is crucial for ongoing climate change mitigation efforts (Koh et al., 2021).

In several studies on forest carbon stock and flux, sources of uncertainty are either omitted or inadequately combined in the overall calculation of uncertainty associated with the results obtained (Yanai et al., 2020). An important source of uncertainty that is often poorly reported relates to the allometric equations used to estimate individual tree biomass (Henry et al., 2015; Yanai et al., 2020). The selection of inappropriate equations can significantly contribute to increasing uncertainty in estimates. In our case, applying equations developed for forest profiles considerably different from those of our study area resulted in an overestimation of approximately 37 % on average (Araújo et al., 1999). Such difference decreased to an underestimation of approximately −1 % when we applied equations developed for regions with similar forest patterns (Nogueira et al., 2008a). These differences may be related to markedly divergent biomass patterns across the Amazon basin in terms of wood density (Baker et al., 2004; Nogueira et al., 2007) and tree height (Feldpausch et al., 2011; Nogueira et al., 2008a).

The total forest biomass can be summarized into three major components: above-ground Biomass (AGB) (including living trees, shrubs, herbs, and large roots lying on the soil surface), Belowground Biomass (BGB) (roots ≥ 2 mm, both living and dead, excluding soil organic matter), and Dead Above-ground Biomass (DAB) (litter and standing and fallen trunks) (Brown et al., 1995a). In our study, when determining AGB and BGB, on average, AGB contributes 86 %, and BGB contributes 14 % to the total weight of sampled trees. Most studies on forest biomass (65 %) in the Brazilian Amazon focus on estimating AGB, with only 16 % estimating BGB (Araujo et al., 2023). The non-inclusion of belowground biomass carbon means that global carbon models using only above-ground biomass significantly bias estimates of both carbon stocks and flux related to Amazon forests.

These components exhibit varying characteristics, including the water content of fresh biomass, the carbon content of oven-dry biomass, and the BGB:AGB ratio. These factors have conversion coefficients that differ across the ecoregions within the tropical forest-covered area. In our study, we determined these coefficients to be 0.470, 0.443, and 0.167, respectively. Currently, tree allometry studies typically present their results in terms of oven-dry biomass (Chave et al., 2014; Lima et al., 2012; Nogueira et al., 2008b). However, this practice might inadvertently convey the impression that conversion factors from fresh biomass to oven-dry biomass are no longer significant. Interestingly, despite the IPCC (2006) not explicitly listing this factor in its recommendations, our research revealed a divergence of approximately +5 % between work carried out in the Amazon. Another crucial factor is the carbon content of oven-dry biomass. Our findings revealed a divergence of approximately −4 % compared to other references. In the case of the BGB:AGB ratio, we encountered the most significant divergence. For instance, if we were to apply the factor recommended by the IPCC (2006) [0.37] to estimate AGB in the open forests of southwestern Amazonia, it could lead to an overestimation of 20 %. Our research revealed a conversion factor of 0.167 for this specific context. Failure to consider the suitability of these factors for the specific location can introduce significant uncertainty into biomass and forest carbon stock estimates. This concern is particularly pronounced at finer scales, such as in the implementation of REDD+ projects and sub-national emissions reporting.

Environmental factors exhibit high variability in tropical forest zones, and the density of field inventory plots is notably low. It is estimated that these zones have fewer than one sample per 1000 km^2, 15 times less than temperate forests. (Hetzer et al., 2020; Schimel et al., 2015). Considering only direct inventory samples and using the data from Chave et al. (2014) as a reference, the sample density decreases to one per 300,000 km^2 (Chave et al., 2014; FAO, 2020). This could explain why, during our validation of Pantropical Equations 4 and 6 from Chave et al. (2014), based on the data observed in our study, we found a substantial overestimation of forest biomass, 26±16 %, and 46±17 % for our sample plots, respectively. This finding holds important implications for the effectiveness of REDD+ project development, as these equations are among the most employed in this climate change mitigation mechanism. To generate carbon credits within the scope of REDD+ projects, accurate estimates of forest carbon stocks are essential (Yanai et al., 2020).

Even in the Amazon, which is one of the most extensively studied tropical forests globally, the direct inventory density of forest biomass remains remarkably low. A review of the literature revealed 16 studies of this nature in the Amazon, representing approximately 1 sample per 400,000 km^2, with a notable concentration in the central and eastern Amazon [see Figure S1 in the supplementary material]. However, in the Southwestern Amazon, no direct measurements of forest biomass exist, as indicated by Figure S1 in the supplementary material, which highlights an area of approximately 100 million hectares (red hatching) where such information is lacking.

The estimates of forest carbon stocks in neotropical regions still exhibit a high level of uncertainty (Dubayah et al., 2022; Quegan et al., 2019; Rosen et al., 2015). Technological advancements have enabled the development of global satellite missions such as GEDI (NASA's Global Ecosystem Dynamics Investigation Mission), NISAR (NASA-ISRO SAR Mission), and BIOMASS (European Space Agency BIOMASS Mission) (Dubayah et al., 2022; Quegan et al., 2019; Rosen et al., 2015), which hold great potential for reducing uncertainties related to forest carbon stock estimates (Reichstein and Carvalhais, 2019). To achieve this reduction in uncertainty, increasing the density of both destructive and non-destructive forest inventory plots in neotropical regions are necessary (Tejada et al., 2020; Vorster et al., 2020). Currently, space-borne lidar measurements are being used to estimate above-ground forest biomass in the Amazon via GEDI mission data (Duncanson et al., 2022). They apparently underestimate uncertainty by depending on limited field biomass measurements for calibration. As orbital lidar measurements increase to the billions, the precision of the measurements will improve, but the accuracy will depend on field site calibrations that ultimately derive from allometric equations such as this current effort (Brown et al., 1995b; IPCC, 2006).

To reduce uncertainties related to estimates of forest carbon stock and flux in neotropical forests, it is necessary to enhance the density of direct biomass measurements, particularly in Southwestern Amazonia. This adjustment will reduce uncertainty, and facilitate the refinement of allometric equations, enhancing their performance considering the diverse forest structure patterns encountered. Furthermore, it will enable more accurate estimates of belowground biomass, water content, carbon concentration, and wood density in trees.

5. Conclusion

Our findings indicate that over 20 million hectares of open forests in the Southwestern Amazon exhibit significant differences compared to forests in other Amazon and Pantropical regions in terms of water and carbon contents in the biomass, ratio of oven-dry biomass above- and below-ground, and allometric patterns in trees. We have demonstrated that these differences result in overestimations of forest biomass when applying allometric equations developed for other Amazonian and Pantropical regions to the open forests of Southwestern Amazonia. This overestimation can reach up to 37 % when using equations from the eastern Amazon, and between 26 % and 46 % depending on the applied Pantropical equation. The use of an inappropriate factor for the root-to-shoot ratio in the Southwestern Amazon (SWA) can lead to overestimates of belowground oven-dry biomass by up to 20 %. These findings carry significant implications for the precision of carbon stock and flux estimates, particularly at finer scales, such as REDD+ projects and national or sub-national emissions reporting. To reduce uncertainties related to estimates of forest carbon stock and flux in Neotropical forests, it is necessary to enhance the density of direct biomass measurements, particularly in the Southwestern Amazon. These data are needed to calibrate forest carbon stock estimates produced from high-precision remote sensing data, such as those derived from drone-based and orbital LiDAR.

CRediT authorship contribution statement

Plínio Barbosa de Camargo: Validation, Formal analysis. **Niro Higuchi:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Sonaira Souza da Silva:** Writing – review & editing. **Igor Oliveira:** Writing – review & editing. **I. Foster Brown:** Writing – review & editing, Validation, Formal analysis. **Eufran Ferreira do Amaral:** Writing – review & editing, Visualization, Funding acquisition, Formal analysis. **Marcus Vinício Neves d'Oliveira:** Writing – review & editing, Visualization, Methodology, Funding acquisition, Formal analysis, Conceptualization. **Joaquim dos Santos:** Writing – review & editing, Methodology, Conceptualization. **Antonio Willian Flores de Melo:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Conceptualization. **Adriano José Nogueira Lima:** Writing – review & editing, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

This study was funded by the Institute of Climate Change and Environmental Services Regulation (IMC) of the Government of the State of Acre, by Coordination for the Improvement of Higher Education Personnel (CAPES) [Projects N°. 459/2013, and Nº 3172/2013], and The National Council for Scientific and Technological Development (CNPq) (Project N°. 462191/2014–1). We had support from Embrapa Acre, which provided technical support, facilitated transportation, made infrastructure available, and provided a field team. We are grateful for the analytical support of the Isotopic Ecology Laboratory of the Center for Nuclear Energy in Agriculture (CENA) linked to the University of São Paulo (USP), where the analyses were carried out to determine the carbon concentration of the vegetation samples. We thank the institutional support of the National Institute for Amazonian Research (INPA), where the first author developed his Ph.D. thesis. We extend our heartfelt gratitude to Antônio José Barretos dos Santos (Tunico) for his invaluable contributions to the botanical identification of the sampled forest species (in memoriam).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122195.

References

ACRE, 2007. Base de dados do zoneamento ecológico e econômico do Estado do Acre. SEMA, Rio Branco.

ACRE, 2024. Programa REM Acre [WWW Document]. Gov. do Estado do Acre. URL https://programarem.ac.gov.br/ (accessed 7.24.24.

Adinugroho, W.C., Krisnawati, H., Imanuddin, R., Siregar, C.A., Weston, C.J., Volkova, L., 2023. Developing biomass allometric equations for small trees in mixed-

species forests of tropical rainforest ecozone. Trees, For. People 13, 100425. https://doi.org/10.1016/j.tfp.2023.100425.
Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans. Autom. Control 19, 716–723. https://doi.org/10.1109/TAC.1974.1100705.
Alvares, C.A., Stape, J.L., Sentelhas, P.C., de Moraes Gonçalves, J.L., Sparovek, G., 2013. Köppen's climate classification map for Brazil. Meteorol. Z. 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507.
Araujo, E.C.G., Sanquetta, C.R., Dalla Corte, A.P., Pelissari, A.L., Orso, G.A., Silva, T.C., 2023. Global review and state-of-the-art of biomass and carbon stock in the Amazon. J. Environ. Manag. 331, 117251 https://doi.org/10.1016/j.jenvman.2023.117251.
Araújo, T.M., Higuchi, N., Andrade de Carvalho Júnior, J., 1999. Comparison of formulae for biomass content determination in a tropical rain forest site in the state of Pará, Brazil. For. Ecol. Manag. 117, 43–52. https://doi.org/10.1016/S0378-1127(98)00470-8.
Baccini, A., Goetz, S.J., Walker, W.S., Laporte, N.T., Sun, M., Sulla-Menashe, D., Hackler, J., Beck, P.S.A., Dubayah, R., Friedl, M.A., Samanta, S., Houghton, R.A., 2012. Estimated carbon dioxide emissions from tropical deforestation improved by carbon-density maps. Nat. Clim. Change 2, 182–185. https://doi.org/10.1038/nclimate1354.
Baccini, A., Walker, W., Carvalho, L., Farina, M., Sulla-Menashe, D., Houghton, R.A., 2017. Tropical forests are a net carbon source based on aboveground measurements of gain and loss. Science 358, 230–234. https://doi.org/10.1126/science.aam5962.
Baker, T.R., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Lloyd, J., Monteagudo, A., Neill, D.A., Patiño, S., Pitman, N.C.A., M. Silva, J.N., Vásquez Martínez, R., 2004. Variation in wood density determines spatial patterns inAmazonian forest biomass: Wood specific gravity and Amazonian biomass estimates. Glob. Change Biol. 10, 545–562. https://doi.org/10.1111/j.1365-2486.2004.00751.x.
Barbosa, X. de C., Chediak, S., Cardozo, I.B., 2021. The value of the forest: historical trajectory of the Paiter Suruí in the use of forest resources in the Sete de Setembro Indigenous Land. Redes 26, 17. https://doi.org/10.17058/redes.v26i0.16758.
Bardales, N.G., Oliveira, T.K. de, Amaral, E.F. do, 2015. Solos e aptidão agroflorestal do Município do Bujari, Acre, Documentos / Embrapa Acre. Embrapa Acre, Rio Branco.
Benites-Lazaro, L.L., Gremaud, P.A., Benites, L.A., 2018. Business responsibility regarding climate change in Latin America: an empirical analysis from Clean Development Mechanism (CDM) project developers. Extr. Ind. Soc. 5, 297–306. https://doi.org/10.1016/j.exis.2018.02.011.
BIOFÍLICA, 2022. Projeto REDD+ RESEX Jacundá [WWW Document]. Biofílica. URL https://www.biofilica.com.br/projeto-redd-resex-jacunda/ (accessed 8.12.22).
Bohlman, S.A., Laurance, W.F., Laurance, S.G., Nascimento, H.E.M., Fearnside, P.M., Andrade, A., 2008. Importance of soils, topography and geographic distance in structuring central Amazonian tree communities. J. Veg. Sci. 19, 863–874. https://doi.org/10.3170/2008-8-18463.
Brown, I.F., Turcq, B., Alechandre, A., 1995b. Teaching concepts of accuracy, precision, and opportunity cost in environmental sciences: arms, legs, and significant figures. Ciência e Cult. 47, 41–44.
Brown, I.F., Martinelli, L.A., Thomas, W.W., Moreira, M.Z., Cid Ferreira, C.A., Victoria, R. A., 1995a. Uncertainty in the biomass of Amazonian forests: an example from Rondônia, Brazil. For. Ecol. Manag. 75, 175–189. https://doi.org/10.1016/0378-1127(94)03512-U.
Carvalho, A.L. de, Nelson, B.W., Bianchini, M.C., Plagnol, D., Kuplich, T.M., Daly, D.C., 2013. Bamboo-dominated forests of the Southwest Amazon: detection, spatial extent, life cycle length and flowering waves. PLoS ONE 8, e54852. https://doi.org/10.1371/journal.pone.0054852.
Chambers, J.Q., Santos, J. dos, Ribeiro, R.J., Higuchi, N., 2001. Tree damage, allometric relationships, and above-ground net primary production in central Amazon forest. For. Ecol. Manag. 152, 73–84. https://doi.org/10.1016/S0378-1127(00)00591-0.
Chave, J., Condit, R., Aguilar, S., Hernandez, A., Lao, S., Perez, R., 2004. Error propagation and scaling for tropical forest biomass estimates. Philos. Trans. R. Soc. Lond. B 359, 409–420. https://doi.org/10.1098/rstb.2003.1425.
Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Change Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629.
Chave, J., Muller-Landau, H.C., Baker, T.R., Easdale, T.A., Steege, H., ter, Webb, C.O., 2016. Suppl. 1. Database wood Density Species Nat. Occur. Cent. South Am. https://doi.org/10.6084/m9.figshare.3512714.v1.
Cuni-Sanchez, A., Sullivan, M.J.P., Platts, P.J., Lewis, S.L., Marchant, R., Imani, G., Hubau, W., Abiem, I., Adhikari, H., Albrecht, T., Altman, J., Amani, C., Aneseyee, A. B., Avitabile, V., Banin, L., Batumike, R., Bauters, M., Beeckman, H., Begne, S.K., Bennett, A.C., Bitariho, R., Boeckx, P., Bogaert, J., Bräuning, A., Bulonvu, F., Burgess, N.D., Calders, K., Chapman, C., Chapman, H., Comiskey, J., de Haulleville, T., Decuyper, M., DeVries, B., Dolezal, J., Droissart, V., Ewango, C., Feyera, S., Gebrekirstos, A., Gereau, R., Gilpin, M., Hakizimana, D., Hall, J., Hamilton, A., Hardy, O., Hart, T., Heiskanen, J., Hemp, A., Herold, M., Hiltner, U., Horak, D., Kamdem, M.-N., Kayijamahe, C., Kenfack, D., Kinyanjui, M.J., Klein, J., Lisingo, J., Lovett, J., Lung, M., Makana, J.-R., Malhi, Y., Marshall, A., Martin, E.H., Mitchard, E.T.A., Morel, A., Mukendi, J.T., Muller, T., Nchu, F., Nyirambangutse, B., Okello, J., Peh, K.S.-H., Pellikka, P., Phillips, O.L., Plumptre, A., Qie, L., Rovero, F., Sainge, M.N., Schmitt, C.B., Sedlacek, O., Ngute, A.S.K., Sheil, D., Sheleme, D., Simegn, T.Y., Simo-Droissart, M., Sonké, B., Soromessa, T., Sunderland, T., Svoboda, M., Taedoumg, H., Taplin, J., Taylor, D., Thomas, S.C., Timberlake, J., Tuagben, D., Umunay, P., Uzabaho, E., Verbeeck, H., Vleminckx, J., Wallin, G., Wheeler, C., Willcock, S., Woods, J.T., Zibera, E., 2021. High aboveground carbon stock of African tropical montane forests. Nature 596, 536–542. https://doi.org/10.1038/s41586-021-03728-4.
d'Oliveira, M.V.N., Figueiredo, E.O., De Almeida, D.R.A., Oliveira, L.C., Silva, C.A., Nelson, B.W., Da Cunha, R.M., De Almeida Papa, D., Stark, S.C., Valbuena, R., 2021. Impacts of selective logging on Amazon forest canopy structure and biomass with a LiDAR and photogrammetric survey sequence. For. Ecol. Manag. 500, 119648 https://doi.org/10.1016/j.foreco.2021.119648.
Daba, D.E., Soromessa, T., 2019. The accuracy of species-specific allometric equations for estimating aboveground biomass in tropical moist montane forests: case study of Albizia grandibracteata and Trichilia dregeana. Carbon Balance Manag. 14, 18. https://doi.org/10.1186/s13021-019-0134-8.
Dalagnol, R., Wagner, F.H., Galvão, L.S., Nelson, B.W., Aragão, L.E.O. e C. de, 2018. Life cycle of bamboo in the southwestern Amazon and its relation to fire events. Biogeosciences 15, 6087–6104. https://doi.org/10.5194/bg-15-6087-2018.
Davidson, E.A., de Araújo, A.C., Artaxo, P., Balch, J.K., Brown, I.F., C. Bustamante, M.M., Coe, M.T., DeFries, R.S., Keller, M., Longo, M., Munger, J.W., Schroeder, W., Soares-Filho, B.S., Souza, C.M., Wofsy, S.C., 2012. The Amazon basin in transition. Nature 481, 321–328. https://doi.org/10.1038/nature10717.
Duarte, A.F., 2006. Aspectos da climatologia do Acre, Brasil, com base no intervalo 1971 - 2000. Rev. Bras. De. Meteorol. 21, 308–317.
Dubayah, R., Armston, J., Healey, S.P., Bruening, J.M., Patterson, P.L., Kellner, J.R., Duncanson, L., Saarela, S., Ståhl, G., Yang, Z., Tang, H., Blair, J.B., Fatoyinbo, L., Goetz, S., Hancock, S., Hansen, M., Hofton, M., Hurtt, G., Luthcke, S., 2022. GEDI launches a new era of biomass inference from space. Environ. Res. Lett. 17, 095001 https://doi.org/10.1088/1748-9326/ac8694.
Duchelle, A.E., Seymour, F., Brockhaus, M., Angelsen, A., Larson, A.M., Wong, G.Y., Pham, T.T., Martius, C., 2018. REDD+: lessons from national and subnational implementation, Ending Tropical Deforestation: A Stock-Take of Progress and Challenges. World Resour. Inst., Wash., DC.
Duncanson, L., Kellner, J.R., Armston, J., Dubayah, R., Minor, D.M., Hancock, S., Healey, S.P., Patterson, P.L., Saarela, S., Marselis, S., Silva, C.E., Bruening, J., Goetz, S.J., Tang, H., Hofton, M., Blair, B., Luthcke, S., Fatoyinbo, L., Abernethy, K., Alonso, A., Andersen, H.-E., Aplin, P., Baker, T.R., Barbier, N., Bastin, J.F., Biber, P., Boeckx, P., Bogaert, J., Boschetti, L., Boucher, P.B., Boyd, D.S., Burslem, D.F.R.P., Calvo-Rodriguez, S., Chave, J., Chazdon, R.L., Clark, D.B., Clark, D.A., Cohen, W.B., Coomes, D.A., Corona, P., Cushman, K.C., Cutler, M.E.J., Dalling, J.W., Dalponte, M., Dash, J., de-Miguel, S., Deng, S., Ellis, P.W., Erasmus, B., Fekety, P.A., Fernandez-Landa, A., Ferraz, A., Fischer, R., Fisher, A.G., García-Abril, A., Gobakken, T., Hacker, J.M., Heurich, M., Hill, R.A., Hopkinson, C., Huang, H., Hubbell, S.P., Hudak, A.T., Huth, A., Imbach, B., Jeffery, K.J., Katoh, M., Kearsley, E., Kenfack, D., Kljun, N., Knapp, N., Král, K., Krůček, M., Labrière, N., Lewis, S.L., Longo, M., Lucas, R.M., Main, R., Manzanera, J.A., Martínez, R.V., Mathieu, R., Memiaghe, H., Meyer, V., Mendoza, A.M., Monerris, A., Montesano, P., Morsdorf, F., Næsset, E., Naidoo, L., Nilus, R., O'Brien, M., Orwig, D.A., Papathanassiou, K., Parker, G., Philipson, C., Phillips, O.L., Pisek, J., Poulsen, J.R., Pretzsch, H., Rüdiger, C., Saatchi, S., Sanchez-Azofeifa, A., Sanchez-Lopez, N., Scholes, R., Silva, C.A., Simard, M., Skidmore, A., Stereńczak, K., Tanase, M., Torresan, C., Valbuena, R., Verbeeck, H., Vrska, T., Wessels, K., White, J.C., White, L.J.T., Zahabu, E., Zgraggen, C., 2022. Aboveground biomass density models for NASA's Global Ecosystem Dynamics Investigation (GEDI) lidar mission. Remote Sens. Environ. 270, 112845 https://doi.org/10.1016/j.rse.2021.112845.
Erb, K.-H., Kastner, T., Plutzar, C., Bais, A.L.S., Carvalhais, N., Fetzel, T., Gingrich, S., Haberl, H., Lauk, C., Niedertscheider, M., Pongratz, J., Thurner, M., Luyssaert, S., 2018. Unexpectedly large impact of forest management and grazing on global vegetation biomass. Nature 553, 73–76. https://doi.org/10.1038/nature25138.
FAO, 2020. Global Forest Resources Assessment 2020, 1st ed. FAO, Rome.
Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., Alsdorf, D., 2007. The Shuttle Radar Topography Mission. Rev. Geophys 45. https://doi.org/10.1029/2005RG000183.
Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djagbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., França, M. B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B. S., Marimon-Junior, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Patiño, S., Peh, K.S.-H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrodt, F., Sonké, B., Taedoumg, H.E., Tan, S., White, L., Wöll, H., Lloyd, J., 2011. Height-diameter allometry of tropical forest trees. Biogeosciences 8, 1081–1106. https://doi.org/10.5194/bg-8-1081-2011.
Ferreira, E.J.L., 2014. O bambu é um desafio para a conservação e o manejo de florestas no sudoeste da Amazônia. Cienc. Cult. 66, 46–51. https://doi.org/10.21800/S0009-67252014000300015.
Finney, D.J., 1941. On the distribution of a variate whose logarithm is normally distributed. Supplement to. J. R. Stat. Soc. 7, 155–161. https://doi.org/10.2307/2983663.
FUNBIO, 2024. REM Mato Grosso [WWW Document]. FUNBIO. URL ⟨https://www.funbio.org.br/en/programas_e_projetos/rem-mato-grosso/⟩ (accessed 7.24.24).
Gibbs, H.K., Brown, S., Niles, J.O., Foley, J.A., 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. Environ. Res. Lett. 2, 045023 https://doi.org/10.1088/1748-9326/2/4/045023.
GIZ, 2024. REDD+ for Early Movers (REM) [WWW Document]. GIZ. URL https://www.giz.de/en/worldwide/73732.html (accessed 7.24.24).

Goodman, R.C., Phillips, O.L., Del Castillo Torres, D., Freitas, L., Cortese, S.T., Monteagudo, A., Baker, T.R., 2013. Amazon palm biomass and allometry. For. Ecol. Manag. 310, 994–1004. https://doi.org/10.1016/j.foreco.2013.09.045.
Graham, M.H., 2003. Confronting multicollinearity in ecological multiple regression. Ecology 84, 2809–2815. https://doi.org/10.1890/02-3114.
Griscom, B.W., Ashton, P.M.S., 2006. A self-perpetuating bamboo disturbance cycle in a neotropical forest. J. Trop. Ecol. 22, 587–597. https://doi.org/10.1017/S0266467406003361.
Henry, M., Cifuentes Jara, M., Réjou-Méchain, M., Piotto, D., Michel Fuentes, J.M., Wayson, C., Alice Guier, F., Castañeda Lombis, H., Castellanos López, E., Cuenca Lara, R., Cueva Rojas, K., Del Águila Pasquel, J., Duque Montoya, Á., Fernández Vega, J., Jiménez Galo, A., López, O.R., Marklund, L.G., Milla, F., de Jesús Návar Cahidez, J., Malavassi, E.O., Pérez, J., Ramírez Zea, C., Rangel García, L., Rubilar Pons, R., Sanquetta, C., Scott, C., Westfall, J., Zapata-Cuartas, M., Saint-André, L., 2015. Recommendations for the use of tree models to estimate national forest biomass and assess their uncertainty. Ann. For. Sci. 72, 769–777. https://doi.org/10.1007/s13595-015-0465-x.
Hetzer, J., Huth, A., Wiegand, T., Dobner, H.J., Fischer, R., 2020. An analysis of forest biomass sampling strategies across scales. Biogeosciences 17, 1673–1683. https://doi.org/10.5194/bg-17-1673-2020.
Higuchi, N., Santos, J., dos, Ribeiro, R.J., Minette, L., Biot, Y., 1998. Biomassa da parte aérea da vegetação da floresta tropical úmida de terra-firme da Amazônia brasileira. Acta Amaz. 28, 153–166.
Houghton, R.A., Nassikas, A.A., 2017. Global and regional fluxes of carbon from land use and land cover change 1850–2015. Glob. Biogeochem. Cycles 31, 456–472. https://doi.org/10.1002/2016GB005546.
Houghton, R.A., Lawrence, K.T., Hackler, J.L., Brown, S., 2001. The spatial distribution of forest biomass in the Brazilian Amazon: a comparison of estimates. Glob. Change Biol. 7, 731–746. https://doi.org/10.1111/j.1365-2486.2001.00426.x.
Hubau, W., Lewis, S.L., Phillips, O.L., Affum-Baffoe, K., Beeckman, H., Cuní-Sanchez, A., Daniels, A.K., Ewango, C.E.N., Fauset, S., Mukinzi, J.M., Sheil, D., Sonké, B., Sullivan, M.J.P., Sunderland, T.C.H., Taedoumg, H., Thomas, S.C., White, L.J.T., Abernethy, K.A., Adu-Bredu, S., Amani, C.A., Baker, T.R., Banin, L.F., Baya, F., Begne, S.K., Bennett, A.C., Benedet, F., Bitariho, R., Bocko, Y.E., Boeckx, P., Boundja, P., Brienen, R.J.W., Brncic, T., Chezeaux, E., Chuyong, G.B., Clark, C.J., Collins, M., Comiskey, J.A., Coomes, D.A., Dargie, G.C., de Haulleville, T., Kamdem, M.N.D., Doucet, J.-L., Esquivel-Muelbert, A., Feldpausch, T.R., Fofanah, A., Foli, E.G., Gilpin, M., Gloor, E., Gonmadje, C., Gourlet-Fleury, S., Hall, J.S., Hamilton, A.C., Harris, D.J., Hart, T.B., Hockemba, M.B.N., Hladik, A., Ifo, S.A., Jeffery, K.J., Jucker, T., Yakusu, E.K., Kearsley, E., Kenfack, D., Koch, A., Leal, M.E., Levesley, A., Lindsell, J.A., Lisingo, J., Lopez-Gonzalez, G., Lovett, J.C., Makana, J.-R., Malhi, Y., Marshall, A.R., Martin, J., Martin, E.H., Mbayu, F.M., Medjibe, V.P., Mihindou, V., Mitchard, E.T.A., Moore, S., Munishi, P.K.T., Bengone, N.N., Ojo, L., Ondo, F.E., Peh, K.S.-H., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Qie, L., Reitsma, J., Rovero, F., Swaine, M.D., Talbot, J., Taplin, J., Taylor, D.M., Thomas, D.W., Toirambe, B., Mukendi, J.T., Tuagben, D., Umunay, P. M., van der Heijden, G.M.F., Verbeeck, H., Vleminckx, J., Willcock, S., Wöll, H., Woods, J.T., Zemagho, L., 2020. Asynchronous carbon sink saturation in African and Amazonian tropical forests. Nature 579, 80–87. https://doi.org/10.1038/s41586-020-2035-0.
Hunter, M.O., Keller, M., Victoria, D., Morton, D.C., 2013. Tree height and tropical forest biomass estimation. Biogeosciences 10, 8385–8399. https://doi.org/10.5194/bg-10-8385-2013.
Imbert, D., Rollet, B., 1989. Phytomasse aerienne et production primaire dans la mangrove du grand cul-de-sac Marin (Guadeloupe, Antilles françaises). Bull. D. 'Ecol. 20, 27–39.
INPE, 2024. Programa de monitoramento da Amazônia e demais biomas [WWW Document]. TerraBrasilis. URL http://terrabrasilis.dpi.inpe.br/downloads/ (accessed 5.13.24).
IPCC, 2006. 2006 IPCC guidelines for national greenhouse gas inventories. IGES, Hayama.
Koh, L.P., Zeng, Y., Sarira, T.V., Siman, K., 2021. Carbon prospecting in tropical forests for climate change mitigation. Nat. Commun. 12, 1271. https://doi.org/10.1038/s41467-021-21560-2.
Lapola, D.M., Pinho, P., Barlow, J., Aragão, L.E.O.C., Berenguer, E., Carmenta, R., Liddy, H.M., Seixas, H., Silva, C.V.J., Silva-Junior, C.H.L., Alencar, A.A.C., Anderson, L.O., Armenteras, D., Brovkin, V., Calders, K., Chambers, J., Chini, L., Costa, M.H., Faria, B.L., Fearnside, P.M., Ferreira, J., Gatti, L., Gutierrez-Velez, V.H., Han, Z., Hibbard, K., Koven, C., Lawrence, P., Pongratz, J., Portela, B.T.T., Rounsevell, M., Ruane, A.C., Schaldach, R., da Silva, S.S., von Randow, C., Walker, W.S., 2023. The drivers and impacts of Amazon forest degradation. Science 379, eabp8622. https://doi.org/10.1126/science.abp8622.
Laurance, S.G.W., Laurance, W.F., Andrade, A., Fearnside, P.M., Harms, K.E., Vicentini, A., Luizão, R.C.C., 2010. Influence of soils and topography on Amazonian tree diversity: a landscape-scale study. J. Veg. Sci. 21, 96–106. https://doi.org/10.1111/j.1654-1103.2009.01122.x.
Lescure, J.P., Puig, H., Riera, B., Leclerc, D., Beekman, A., Beneteau, A., 1983. La phytomasse épigée d'une forêt dense en Guyane Française. Acta OEcologica 4, 237–251.
Lima, A.J.N., Suwa, R., Ribeiro, G.H.P., de, M., Kajimoto, T., dos Santos, J., da Silva, R.P., de Souza, C.A.S., de Barros, P.C., Noguchi, H., Ishizuka, M., Higuchi, N., 2012. Allometric models for estimating above- and below-ground biomass in Amazonian forests at São Gabriel da Cachoeira in the upper Rio Negro, Brazil. For. Ecol. Manag. 277, 163–172. https://doi.org/10.1016/j.foreco.2012.04.028.
Lima, M.G.B., Visseren-Hamakers, I.J., Braña-Varela, J., Gupta, A., 2017. A reality check on the landscape approach to REDD+:lessons from Latin America. For. Policy Econ. 78, 10–20. https://doi.org/10.1016/j.forpol.2016.12.013.
Mackensen, J., Tillery-Stevens, M., Klinge, R., Fölster, H., 2000. Site parameters, species composition, phytomass structure and element stores of a terra-firme forest in east-amazonia, brazil. Plant Ecol. 151, 101–119. https://doi.org/10.1023/A:1026515116944.
Malhi, Y., Adu-Bredu, S., Asare, R.A., Lewis, S.L., Mayaux, P., 2013. The past, present and future of Africa's rainforests. Philos. Trans. R. Soc. B: Biol. Sci. 368, 20120293. https://doi.org/10.1098/rstb.2012.0293.
Marengo, J.A., Souza, C.M., Thonicke, K., Burton, C., Halladay, K., Betts, R.A., Alves, L. M., Soares, W.R., 2018. Changes in climate and land use over the Amazon Region: current and future variability and trends. Front. Earth Sci. 6, 228. https://doi.org/10.3389/feart.2018.00228.
Mitchard, E.T., Saatchi, S.S., Baccini, A., Asner, G.P., Goetz, S.J., Harris, N.L., Brown, S., 2013. Uncertainty in the spatial distribution of tropical forest biomass: a comparison of pan-tropical maps. Carbon Balance Manag. 8, 10. https://doi.org/10.1186/1750-0680-8-10.
Mitchard, E.T.A., Feldpausch, T.R., Brienen, R.J.W., Lopez-Gonzalez, G., Monteagudo, A., Baker, T.R., Lewis, S.L., Lloyd, J., Quesada, C.A., Gloor, M., Steege, H., Meir, P., Alvarez, E., Araujo-Murakami, A., Aragão, L.E.O.C., Arroyo, L., Aymard, G., Banki, O., Bonal, D., Brown, S., Brown, F.I., Cerón, C.E., Chama Moscoso, V., Chave, J., Comiskey, J.A., Cornejo, F., Corrales Medina, M., Da Costa, L., Costa, F.R.C., Di Fiore, A., Domingues, T.F., Erwin, T.L., Frederickson, T., Higuchi, N., Honorio Coronado, E.N., Killeen, T.J., Laurance, W.F., Levis, C., Magnusson, W.E., Marimon, B.S., Marimon Junior, B.H., Mendoza Polo, I., Mishra, P., Nascimento, M.T., Neill, D., Núñez Vargas, M.P., Palacios, W.A., Parada, A., Pardo Molina, G., Peña-Claros, M., Pitman, N., Peres, C.A., Poorter, L., Prieto, A., Ramirez-Angulo, H., Restrepo Correa, Z., Roopsind, A., Roucoux, K.H., Rudas, A., Salomão, R.P., Schietti, J., Silveira, M., Souza, P.F., Steininger, M.K., Stropp, J., Terborgh, J., Thomas, R., Toledo, M., Torres-Lezama, A., Andel, T.R., Heijden, G.M.F., Vieira, I.C.G., Vieira, S., Vilanova-Torre, E., Vos, V.A., Wang, O., Zartman, C.E., Malhi, Y., Phillips, O.L., 2014. Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites. Glob. Ecol. Biogeogr. 23, 935–946. https://doi.org/10.1111/geb.12168.
Mokany, K., Raison, R.J., Prokushkin, A.S., 2006. Critical analysis of root: shoot ratios in terrestrial biomes. Glob. Change Biol. 12, 84–96. https://doi.org/10.1111/j.1365-2486.2005.001043.x.
Nelson, B.W., Mesquita, R., Pereira, J.L.G., Garcia Aquino de Souza, S., Teixeira Batista, G., Bovino Couto, L., 1999. Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. For. Ecol. Manag. 117, 149–167. https://doi.org/10.1016/S0378-1127(98)00475-7.
Nogueira, E.M., Fearnside, P.M., Nelson, B.W., França, M.B., 2007. Wood density in forests of Brazil's 'arc of deforestation': Implications for biomass and flux of carbon from land-use change in Amazonia. For. Ecol. Manag. 248, 119–135. https://doi.org/10.1016/j.foreco.2007.04.047.
Nogueira, E.M., Fearnside, P.M., Nelson, B.W., Barbosa, R.I., Keizer, E.W.H., 2008a. Estimates of forest biomass in the Brazilian Amazon: new allometric equations and adjustments to biomass from wood-volume inventories. For. Ecol. Manag. 256, 1853–1867. https://doi.org/10.1016/j.foreco.2008.07.022.
Nogueira, E.M., Nelson, B.W., Fearnside, P.M., França, M.B., Oliveira, Á.C.A. de, 2008b. Tree height in Brazil's 'arc of deforestation': shorter trees in south and southwest Amazonia imply lower biomass. For. Ecol. Manag. 255, 2963–2972. https://doi.org/10.1016/j.foreco.2008.02.002.
Ometto, J.P., Aguiar, A.P., Assis, T., Soler, L., Valle, P., Tejada, G., Lapola, D.M., Meir, P., 2014. Amazon forest biomass density maps: tackling the uncertainty in carbon emission estimates. Clim. Change 124, 545–560. https://doi.org/10.1007/s10584-014-1058-7.
Overman, J.P.M., Witte, H.J.L., Saldarriaga, J.G., 1994. Evaluation of regression models for above-ground biomass determination in Amazon rainforest. J. Trop. Ecol. 10, 207–218. https://doi.org/10.1017/S0266467400007859.
Packard, G.C., 2013. Is logarithmic transformation necessary in allometry? Biol. J. Linn. Soc. Lond. 109, 476–486. https://doi.org/10.1111/bij.12038.
Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science 333, 988–993. https://doi.org/10.1126/science.1201609.
Paul, K.I., Roxburgh, S.H., Larmour, J.S., 2017. Moisture content correction: Implications of measurement errors on tree- and site-based estimates of biomass. For. Ecol. Manag. 392, 164–175. https://doi.org/10.1016/j.foreco.2017.02.007.
Picard, N., Saint-André, L., Henry, M., 2012. Manual for building tree volume and biomass allometric equations: from field measurement to prediction. FAO, Rome.
Picard, N., Boyemba Bosela, F., Rossi, V., 2015. Reducing the error in biomass estimates strongly depends on model selection. Ann. For. Sci. 72, 811–823. https://doi.org/10.1007/s13595-014-0434-9.
Pitman, N.C.A., Terborgh, J., Silman, M.R., Nuñez, V., P., 1999. Tree species distributions in an upper amazonian forest. Ecology 80, 2651–2661 https://doi.org/10.1890/0012-9658(1999)080[2651:TSDIAU]2.0.CO;2.
Plugge, D., Koehl, M., 2012. Estimating carbon emissions from forest degradation: implications of uncertainties and area sizes for a REDD+ MRV system. Can. J. . Res. -Rev. Can. Rech. 42, 1996–2010. https://doi.org/10.1139/X2012-129.
Quegan, S., Le Toan, T., Chave, J., Dall, J., Exbrayat, J.-F., Minh, D.H.T., Lomas, M., D'Alessandro, M.M., Paillou, P., Papathanassiou, K., Rocca, F., Saatchi, S., Scipal, K., Shugart, H., Smallman, T.L., Soja, M.J., Tebaldini, S., Ulander, L., Villard, L., Williams, M., 2019. The European Space Agency BIOMASS mission: measuring forest

above-ground biomass from space. Remote Sens. Environ. 227, 44–60. https://doi.org/10.1016/j.rse.2019.03.032.
R Core Team, 2023. R: a language and environment for statistical computing.
Reichstein, M., Carvalhais, N., 2019. Aspects of forest biomass in the earth system: its role and major unknowns. Surv. Geophys 40, 693–707. https://doi.org/10.1007/s10712-019-09551-x.
Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. BIOMASS: an R package for estimating above-ground biomass and its uncertainty in tropical forests. Methods Ecol. Evol. 8, 1163–1167. https://doi.org/10.1111/2041-210X.12753.
Rosen, P.A., Hensley, S., Shaffer, S., Veilleux, L., Chakraborty, M., Misra, T., Bhan, R., Raju Sagi, V., Satish, R., 2015. The NASA-ISRO SAR mission: an international space partnership for science and societal benefit, in: 2015 IEEE Radar Conference (RadarCon). Presented at the 2015 IEEE International Radar Conference (RadarCon), IEEE, Arlington, VA, USA, pp. 1610–1613. https://doi.org/10.1109/RADAR.2015.7131255.
RStudio Team, 2022. RStudio: integrated development environment for R.
Saldarriaga, J.G., West, D.C., Tharp, M.L., Uhl, C., 1988. Long-Term Chronosequence of Forest Succession in the Upper Rio Negro of Colombia and Venezuela. J. Ecol. 76, 938–958. https://doi.org/10.2307/2260625.
Santos, H.G. dos, Jacomine, P.K.T., Anjos, L.H.C. dos, Oliveira, V.Á. de, Lumbreras, J.F., Maurício Rizzato, Coelho, Almeida, J.A. de, José Coelho de Araújo Filho, Oliveira, J. B. de, Cunha, T.J.F., 2018. Sistema brasileiro de classificação de solos. Embrapa, 5th ed. Brasília, DF.
dos Santos, J., 1996. Análise de modelos de regressão para estimar a fitomassa da floresta tropical úmida de terra-firme da amazônia brasileira (Tese de Doutorado em Ciências Florestais). Universidade Federal de Viçosa. Viçosa.
Schenk, H.J., Jackson, R.B., 2002. The global biogeography of roots. Ecol. Monogr. 72, 311–328.
Schimel, D., Pavlick, R., Fisher, J.B., Asner, G.P., Saatchi, S., Townsend, P., Miller, C., Frankenberg, C., Hibbard, K., Cox, P., 2015. Observing terrestrial ecosystems and the carbon cycle from space. Glob. Change Biol. 21, 1762–1776. https://doi.org/10.1111/gcb.12822.
Schwarz, G., 1978. Estimating the dimension of a model. Ann. Stat. 6 https://doi.org/10.1214/aos/1176344136.
Silva, R.P. da, 2007. Alometria, estoque e dinâmica da biomassa de florestas primárias e secundárias na região de Manaus (AM) (Tese de Doutorado). Universidade Federal do Amazonas / Instituto Nacional de Pesquisas da Amazônia, Manaus.
Simonet, G., Subervie, J., Ezzine-de-Blas, D., Cromberg, M., Duchelle, A.E., 2019. Effectiveness of a REDD+ Project in reducing deforestation in the Brazilian Amazon. Am. J. Agric. Econ. 101, 211–229. https://doi.org/10.1093/ajae/aay028.
Smith, R.J., 1993. Logarithmic transformation bias in allometry. Am. J. Phys. Anthropol. 90, 215–228. https://doi.org/10.1002/ajpa.1330900208.
Sprugel, D.G., 1983. Correcting for bias in log-transformed allometric equations. Ecology 64, 209–210. https://doi.org/10.2307/1937343.
Steege, H. ter, Pitman, Sabatier, N.C.A., Baraloto, D., Salomão, C., Guevara, R.P., Phillips, J.E., Castilho, O.L., Magnusson, C.V., Molino, W.E., Monteagudo, J.-F., Vargas, A., Montero, P.N., Feldpausch, J.C., Coronado, T.R., Killeen, E.N.H., Mostacedo, T.J., Vasquez, B., Assis, R., Terborgh, R.L., Wittmann, J., Andrade, F., Laurance, A., Laurance, W.F., Marimon, S.G.W., Marimon, B.S., Vieira, B.-H., Amaral, I.C.G., Brienen, I.L., Castellanos, R., López, H., Duivenvoorden, D.C., Mogollón, J.F., Matos, H.F., de, F.D., Dávila, A., García-Villacorta, N., Diaz, R., Costa, P.R.S., Emilio, F., Levis, T., Schietti, C., Souza, J., Alonso, P., Dallmeier, A., Montoya, F., Piedade, A.J.D., Araujo-Murakami, M.T.F., Arroyo, A., Gribel, L., Fine, R., Peres, P.V.A., Toledo, C.A., C, M., Baker, G.A.A., Cerón, T.R., Engel, C., Henkel, J., Maas, T.W., Petronelli, P., Stropp, P., Zartman, J., Daly, C.E., Neill, D., Silveira, D., Paredes, M., Chave, M.R., Filho, J., de, D., Jørgensen, A.L., Fuentes, P. M., Schöngart, A., Valverde, J., Fiore, F.C., Jimenez, A.D., Mora, E.M., Phillips, M.C. P., Rivas, J.F., Andel, G., van, T.R., Hildebrand, P., von, Hoffman, Zent, B., Malhi, E. L., Prieto, Y., Rudas, A., Ruschell, A., Silva, A.R., Vos, N., Zent, V., Oliveira, S., Schutz, A.A., Gonzales, A.C., Nascimento, T., Ramirez-Angulo, M.T., Sierra, H., Tirado, R., Medina, M., Heijden, M.N.U., van der, G., Vela, C.I.A., Torre, E.V., Vriesendorp, C., Wang, O., Young, K.R., Baider, C., Balslev, H., Ferreira, C., Mesones, I., Torres-Lezama, A., Giraldo, L.E.U., Zagt, R., Alexiades, M.N., Hernandez, L., Huamantupa-Chuquimaco, I., Milliken, W., Cuenca, W.P., Pauletto, D., Sandoval, E.V., Gamarra, L.V., Dexter, K.G., Feeley, K., López-González, G., Silman, M.R., 2013. Hyperdominance in the Amazonian tree flora. Science 342, 1243092. https://doi.org/10.1126/science.1243092.
Swinfield, T., Lindsell, J.A., Williams, J.V., Harrison, R.D., Agustiono, Habibi, Gemita, E., Schönlieb, C.B., Coomes, D.A., 2019. Accurate Measurement of Tropical Forest Canopy Heights and Aboveground Carbon Using Structure From Motion. Remote Sens. 11, 928. https://doi.org/10.3390/rs11080928.
Tejada, G., Görgens, E.B., Ovando, A., Ometto, J.P., 2020. Mapping data gaps to estimate biomass across Brazilian Amazon forests. For. Ecosyst. 7, 25. https://doi.org/10.1186/s40663-020-00228-1.
Thomas, S.C., Martin, A.R., 2012. Carbon content of tree tissues: a synthesis. Forests 3, 332–352. https://doi.org/10.3390/f3020332.
Vargas, R., Paz, F., de Jong, B., 2013. Quantification of forest degradation and belowground carbon dynamics: ongoing challenges for monitoring, reporting and verification activities for REDD+. Carbon Manag. 4, 579–582. https://doi.org/10.4155/cmt.13.63.
Voigt, C., Ferreira, F., 2016. The Warsaw Framework for REDD+: implications for national implementation and results-based finance. In: Voigt, C. (Ed.), Research Handbook on REDD-plus and International Law. Edward Elgar Publishing, Cheltenham, pp. 30–60.
Vorster, A.G., Evangelista, P.H., Stovall, A.E.L., Ex, S., 2020. Variability and uncertainty in forest biomass estimates from the tree to landscape scale: the role of allometric equations. Carbon Balance Manag. 15, 8. https://doi.org/10.1186/s13021-020-00143-6.
Wayson, C.A., Johnson, K.D., Cole, J.A., Olguín, M.I., Carrillo, O.I., Birdsey, R.A., 2015. Estimating uncertainty of allometric biomass equations with incomplete fit error information using a pseudo-data approach: methods. Ann. For. Sci. 72, 825–834. https://doi.org/10.1007/s13595-014-0436-7.
Woortmann, C.P.I.B., Higuchi, N., Santos, J. dos, Silva, R.P. da, 2018. Allometric equations for total, above- and below-ground biomass and carbon of the Amazonian forest type known as campinarana. Acta Amaz 48, 85–92. https://doi.org/10.1590/1809-4392201700673.
Yanai, R.D., Wayson, C., Lee, D., Espejo, A.B., Campbell, J.L., Green, M.B., Zukswert, J. M., Yoffe, S.B., Aukema, J.E., Lister, A.J., Kirchner, J.W., Gamarra, J.G.P., 2020. Improving uncertainty in forest carbon accounting for REDD+ mitigation efforts. Environ. Res. Lett. 15, 124002 https://doi.org/10.1088/1748-9326/abb96f.