Trees, Forests and People 9 (2022) 100317

Contents lists available at ScienceDirect

Trees, Forests and People

journal homepage: www.sciencedirect.com/journal/trees-forests-and-people

Aboveground biomass allometric models for large trees in southwestern Amazonia☆

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A R T I C L E I N F O

Keywords:
Brazil
Acre
Amazon forest
Tropical forest
Forest management
Carbon stock
Global warming
Climate change

A B S T R A C T

Most of the basal area in Amazon forest is in large trees, many of which are species of interest for forest management. In forest management these trees are divided into the commercial bole that is harvested for wood production and the stump and crown that are left in the forest where they decompose and emit CO_2 over a period of years. Part of the commercial bole is converted to wood products that store carbon according to their durability. The quantification of these components is difficult due to their size, especially in the case of the crown, which causes uncertainties in the estimates of biomass and carbon. Our study estimated the aboveground biomass and carbon of 223 trees and subsequently fit allometric equations to these estimates. Aboveground biomass was calculated from stem volume, wood density and a biomass expansion factor, while total carbon stock estimates used carbon content determined in the laboratory. Linear models (log-transformed) were tested to derive the best-fit allometric model for total aboveground biomass and carbon. The best-fit allometric models used squared tree diameter, tree height, and wood density for biomass, whereas the best carbon model also used carbon content. Our models were more efficient in estimating biomass than were frequently used regional and pan-tropical models. Our equations allow reducing the errors in estimates of forest biomass and carbon stocks, in addition to allowing estimation of the amount of carbon emitted after harvest, although the other models also had good fits and can be used according to the criteria of each researcher and the availability of data.

1. Introduction

Brazil's Amazon rainforest provides environmental services or "regulating" ecosystem services such as maintaining carbon stocks; it also provides products such as wood ("provisioning" ecosystem services) (Fearnside, 2003, 2010). Forests are of paramount importance in the context of global climate change because they are large carbon reservoirs and have an important role in the carbon cycle (Chave et al., 2014; Fearnside, 2018).

Timber harvesting, whether legal or not, results in greenhouse-gas emissions, including a major effect in both increasing the likelihood of forest fires and in increasing the intensity and consequent emission

☆ This article is part of a special issue entitled: "Tropical Forestry: Conservation, Management and Utilization" published at the journal Trees, Forests and People.

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https://doi.org/10.1016/j.tfp.2022.100317
Received 3 April 2022; Received in revised form 4 August 2022; Accepted 6 August 2022
Available online 7 August 2022

when they occur (Barni et al., 2021). Quantifying these emissions requires reliable estimates of forest biomass. Pantropical allometric equations have been developed to estimate the biomass of tropical forests (Chave et al., 2014; Paul et al., 2016); however, although large trees have disproportionate roles in both the estimates of total biomass and in the uncertainty surrounding these estimaes, existing equations generally have few measurements of trees with diameter at breast height (DBH) $\geq$ 80 cm (DBH is measured 1.30 m above the ground or just above any buttresses) (Goodman et al., 2014; Romero et al., 2020a). This is especially so for studies in the Amazon region (Goodman et al., 2014).

In the Amazon region most studies disregard trees $<$ 5 cm in diameter (Chave et al., 2014; Romero et al., 2020b). Estimates for these very small trees are uncertain due to the abundance and high mortality rate of trees until they reach the 10 cm diameter class (Fredericksen and Mostacedo, 2000; Goodman et al., 2014; Fredericksen et al., 2000, 2001). It is possible to fit equations for the biomass of small trees using the destructive method (total weight of individuals) (Higuchi et al., 1998), without forgetting that a correction factor for entry and mortality of individuals of each species must be applied. This is due to the rapid growth of these trees, and not correcting for these effects can lead to underestimation or overestimation of the biomass of these trees. This mortality is due to competition and the felling of large trees during the harvest stage.

For large trees that are designated as being for conservation purposes and for standing forests, as in REDD+ projects, equations must be fit for each type of ecosystem because ecosystems differ in characteristics such as the abundance of species. For example, *Cedrela odorata* can be abundant in some ecosystems and rare or absent in others. Developing an equation that does not describe this situation can cause either under or overestimation of stocks. The large trees of commercial species are measured in forest management projects in Brazil, and they are harvested with a minimum cutting diameter at breast height (DBH) is 50 cm (DBH is measured 1.30 m above the ground or just above any buttresses). It is assumed that at this diameter the trees have reached maturity and that the wood is fully developed for milling and transformation into final products.

Brazilian forest management projects are required to derive their own equations for the bole volumes of the commerical trees at the management site after the second year of the harvest cycle (Brazil, CONAMA, 2009; Romero et al., 2020a, 2020b). These are invariably multi-species equations, although theoretically the companies could develop species-specific equations if they wished. However, it would be prohibitively expensive for the companies to obtain an adequate sample size for each species to generate reliable species-specific equations. The same limitation applies to our study, making the best choice a multi-species equation based on a sample of trees that represents the abundances of large individuals of the different species at the site.

In the context of climate change, the ability of trees, especially large ones, to store carbon in the form of biomass contributes to the mitigation of greenhouse-gas emissions. However, disturbances such as logging and fire can decrease the forest biomass stock (Fearnside, 2003a, 2003b, 2018; Barni et al., 2021), causing the forest to become a source of greenhouse-gas emissions (Fearnside, 2018). Quantifying the carbon stock before and after disturbances represents a necessary step in estimating the amount of carbon emitted to the atmosphere (Fearnside, 2018; Romero et al., 2020a, 2020b). In forest management the commercial bole is removed for wood production and the stump and crown remain in the forest decomposing (Romero et al., 2021). Estimates of the amounts and timing of carbon releases from all these components are needed to reduce uncertainty in global emissions estimates.

Forest management is considered a planned disturbance because it involves technical and administrative procedures for obtaining permission to remove raw forest material. As applied in Brazil, commercial trees with DBH $\geq$ 50 cm diameter are measured in order to obtain information on the quantity and quality of forest resources for wood production (Husch et al., 2003; Romero et al., 2020a, 2020b). The measurement unit used for management calculations and for log sales is volume in cubic meters (m^3) (Husch et al., 2003; Goodman et al., 2019; Romero et al., 2020b, 2021).

The stock potential of managed commercial species can be obtained from forest inventories that provide the data for estimating volume, biomass and forest carbon stocks (Husch et al., 2003; Chave et al., 2014; Vidal et al., 2016). Quantifying these resources requires a rigorous estimate of tree and forest stocks (Brown, 1997; Chave et al., 2005; Barni et al., 2021). The accuracy of this estimate depends not only on technical, human and financial capacity, but also on methodologies, tools, information, and data analysis (Brown et al., 1989; Fearnside, 2003a; Barni et al., 2021). Regression models are used for this, requiring the fitting of allometric equations to obtain good estimators for biomass and carbon (Picard et al., 2012; Chave et al., 2014; Vidal et al., 2016; Romero et al., 2020a). Fitting allometric models to forest data is not a simple task, and it becomes more complex when fitting regressions with multiple predictors. This requires refining and standardizing analytical methods (Picard et al., 2012; Taskinen and Warton, 2013; Sileshi, 2014; Packard et al., 2014).

Regression estimators are obtained by least squares, maximum likelihood and non-linear regression methods (Xiao et al., 2011; Gujarati and Porter, 2011; Sileshi et al., 2014), which are used to fit allometric equations for volume and biomass (Chave et al., 2014; Goodman et al., 2014; Vidal et al., 2016; Romero et al., 2020a). Application of different regression methods can produce different values for allometric parameters, and consequently different results for forest stocks (Sileshi, 2014). Attention must be paid to the choice of methods and methodologies in order to avoid errors and inconsistencies in modeling (Seleshi, 2014; Romero et al., 2020a). It is also important to develop local allometric equations because these describe characteristics of the forest for the climate and relief of the specific areas under study (Baker et al., 2004; Gujarati and Porter, 2011; Goodman et al., 2014; Romero et al., 2020a).

Various researchers have described the arboreal physiognomy of tropical forests by fitting allometric equations (Fernandes et al., 1983; Higuchi et al., 1998; Nelson et al., 1999; Baker et al., 2004; Nogueira et al., 2008a; Colpini et al., 2009; Tonini and Borges, 2015; Thaines et al., 2010; Chave et al., 2014; Vidal et al., 2016). Despite these efforts, estimates are still inadequate for dealing with the great number of tropical species, regions and forest types, and this is especially true in the case of the southwestern Amazon (Fernandes et al., 1983; Baker et al., 2004; Goodman et al., 2014). Inconsistencies in some models for tropical forests, the lack of symmetry and the lack of consensus among researchers on established methodologies lead to a range of widely differing results, even among similar studies (Sileshi, 2014). Models often underrepresent or fail to include large trees, despite the fact that trees with DBH $\geq$ 50 cm contribute about half of the forest's biomass and carbon storage (Goodman et al., 2014; Lutz et al., 2018).

Few studies have been dedicated to quantifying biomass and carbon in managed forests in the southwestern Amazon (Goodman et al., 2014; Romero et al., 2020a, 2020b). A recent study by Romero et al. (2020a) used allometric equations for estimating commercial volume, biomass and carbon in managed areas in the southwestern Amazon with the purpose of obtaining values of biomass and carbon stored in timber products. However, the commercial stocks are not the only components that must be studied when quantifying CO_2 emissions. The stump and crown are normally not quantified. Crowns in southwestern Amazonia represent 44% $\pm$ 2% of the total aboveground tree biomass (Goodman et al., 2014). These determine the interception of light, carbon and water exchange (Goodman et al., 2014; Lutz et al., 2018; Loubota Panzou et al., 2021). Therefore, this component has a direct impact on the emission estimate. These values must be accounted for to generate information on the balance of biomass and carbon in areas under management, especially for the large trees that contribute 50% of the forest's biomass and carbon stock (Lutz et al., 2018). The stump and crown emit CO_2 over time (Lutz et al., 2018; Loubota Panzou et al., 2021) and therefore must be included in the modeling and in fitting of equations to obtain total estimates of the biomass and carbon in the aboveground biomass (Husch et al., 2003; Gujarati and Porter, 2011; Romero et al., 2020a). In addition, equations to estimate total aboveground biomass (TAGB) and carbon (TAGC), including the stumps and crowns, are lackng for large trees. Allometric models for these trees in tropical forests are essential to guarantee accurate estimates and to guide international emission-reduction measures. The objective of this study is to estimate the biomass and carbon stocks in the stumps, commercial logs and crowns of commercial trees in a forest under management in Brazil's state of Acre, providing allometric equations that generate unbaised estimates of these stocks.

2. Materials and methods

2.1. Data and study area

All tree data in this study were provided by Romero et al. (2020a). We used 223 commercial boles, representing 20 species, 18 genera and 9 families. These were collected at Fazenda Antimary I and II (9°23′43′'S and 67° 58′50′' W) in a 1251 ha area located in the municipality (county) of Porto Acre, Acre, Brazil, in the southwestern Amazon (Fig. 1). The vegetation of the southwestern Amazon is classified as *terra firme* (unflooded upland) humid forest (Salimon et al., 2011), with a predominance of dense forest, open forest with presence of bamboo and open forest with presence palms (Acre, SEMA Secretaria do Meio Ambiente, 2010; Salimon et al., 2011; Ziccardi et al., 2019). The commercial boles used in this study are from dense forest and open forest with presence of bamboo.

Absolute and relative values for phytosociological parameters used to characterize the horizontal structure of the 20 species under study are presented in Table 1 in order of importance. For each of the 223 trees, diameter at breast height (d; cm) was measured before the tree was felled and total height (h) and commercial height (hc; m) and the volume of each commercial bole (m^3) (using the cubing method) was measured after the tree had been felled, while the basic wood density (ρ; g cm^{-3}) of each commercial bole was measured in the laboratory (Table 2) (Romero et al., 2020a). Basic wood density is oven-dried mass divided by saturated volume.

2.2. Biomass and carbon content of the commercial bole

Biomass of the commercial bole (w_b) in megagrams (Mg, or metric tons), was calculated as the product of the volume of the commercial bole and the basic density of its wood (Chave et al., 2005; Romero et al., 2020a, 2020b, 2021). The harvested trunks were cut into sections by the management company to allow them to be transported to a sawmill. We cut disks approximately 2 cm thick from both ends of the first section and from the top end of each subsequent section. From each disk we cut a wedge (similar to a pizza slice) to serve as a sample that represents the radial variation in the trunk, including the bark. For the analysis of carbon content, composite samples were prepared for each wedge. These samples were ground, sieved, and packed in metal capsules. The samples were then completely incinerated at 1200 °C in a universal element analyzer, model Vario Micro Cube. Carbon content was obtained by adding the elements and subtracting the ash content.

2.3. Expansion factors used for determining stump and crown stocks

The equation of a cylinder with a radius $d_0/2$ was used to estimate the volume of the stump, where d_0 was the diameter at the cutting height (0.3 m above the ground or at a height of 0.5 m if the tree had significant buttresses) (Lima, 1991; Karjalainen and Kellomãki, 1996). Stump biomass (w_t; Mg) was calculated as the product of the volume of the stump and the basic density of its wood (Romero et al., 2020a).

To estimate crown biomass (w_c; Mg) an expansion factor was used, which was obtained from the relationship between the biomass of the canopy and the total stem biomass (Goodman et al., 2014; Romero et al., 2021). Following Goodman et al. (2014), we assumed that 44% (Fig. 2) of the tree was comprised of branches, leaves and fruits (crown biomass) and the rest (56%) was composed of the commercial bole and stump, together termed the "total stem biomass" (*FT*) (Eq. (1)).

$$w_c = \frac{0.44}{0.56} \times \; FT \quad (1)$$

where:w_c = Crown biomass (Mg); 0.44 and 0.56 = Expansion factors

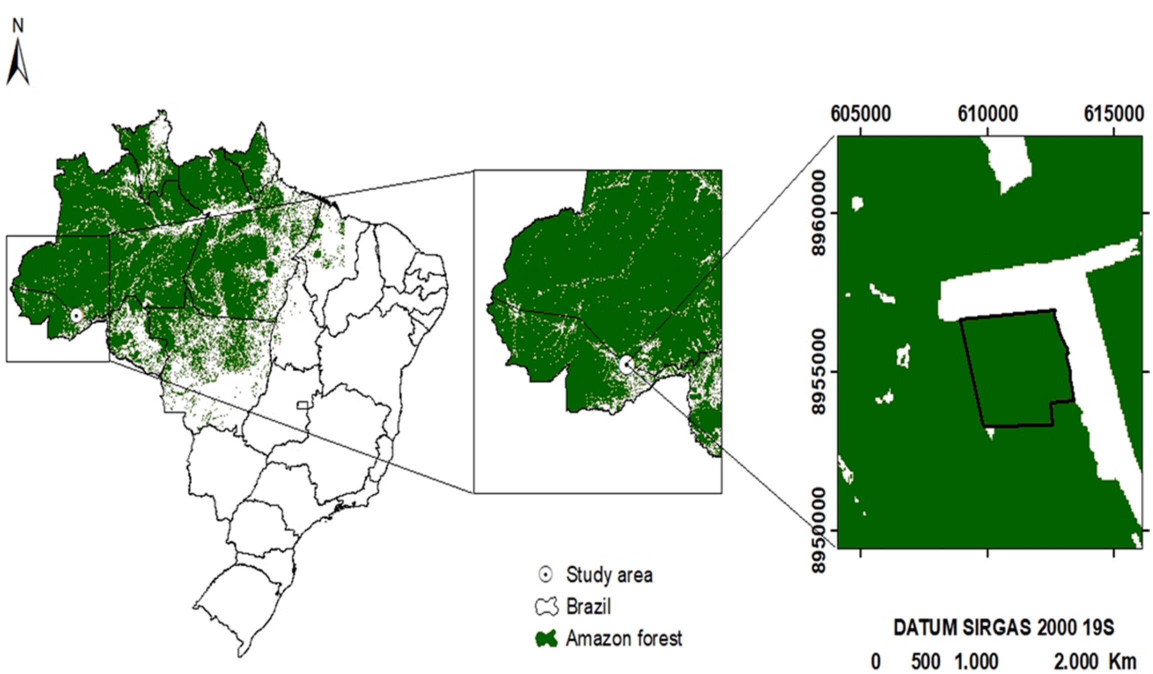


Fig. 1. Location of the study area in the southwestern Amazon (municipality of Porto Acre, Acre, Brazil).

Table 1
Values of absolute and relative phytosociological parameters for the horizontal structure of species in order of importance (highest VC%): n = Number of individuals, DA = Absolute density (ind. ha^{-1}), DR% = Relative density (%), DoR% = Relative dominance (%), DoA = Absolute dominance (m^2 ha^{-1}), VC% = Coverage value (%) for the 20 tree species of inventoried trees in 1251 ha.

Family	Scientific name	n	DA	DR%	DoA	DoR%	VC%
Moraceae	*Castilla ulei* Warb.	37	0.030	16.59	0.015	16.23	16.41
Fabaceae	*Parkia paraensis* Ducke	20	0.016	8.97	0.010	11.00	9.99
Malvaceae	*Ceiba samauma* (Mart.) K. Schum.	22	0.018	9.87	0.009	9.29	9.58
Fabaceae	*Apuleia leiocarpa* (Vogel) J.F. Macbr.	13	0.010	5.83	0.008	8.19	7.01
Fabaceae	*Schizolobium parahyba var. amazonicum* (Huber ex Ducke) Barneby	16	0.013	7.17	0.004	4.32	5.75
Lecythidaceae	*Eschweilera bracteosa* (Poepp. ex O. Berg) Miers	15	0.012	6.73	0.004	4.74	5.73
Lecythidaceae	*Eschweilera grandiflora* (Aubl.) Sandwith	13	0.010	5.83	0.005	5.28	5.55
Fabaceae	*Dipteryx odorata* (Aubl.) Willd.	11	0.009	4.93	0.006	6.17	5.55
Fabaceae	*Hymenaea courbaril* L.	8	0.006	3.59	0.005	4.82	4.20
Combretaceae	*Terminalia tetraphylla* (Aubl.) Gere & Boatwr.	9	0.007	4.04	0.003	3.09	3.56
Fabaceae	*Copaifera multijuga* Hayne	6	0.005	2.69	0.004	3.99	3.34
Euphorbiaceae	*Hura crepitans* L.	6	0.005	2.69	0.004	3.82	3.26
Meliaceae	*Cedrela odorata* L.	8	0.006	3.59	0.003	2.86	3.22
Malvaceae	*Ceiba pentandra* (L.) Gaertn.	4	0.003	1.79	0.004	4.64	3.22
Bignoniaceae	*Handroanthus serratifolius* (Vahl) S. Grose	8	0.006	3.59	0.002	2.08	2.83
Fabaceae	*Albizia niopoides* (Spruce ex Benth.) Burkart	7	0.006	3.14	0.002	2.05	2.59
Anacardiaceae	*Astronium lecointei* Ducke	6	0.005	2.69	0.002	1.67	2.18
Fabaceae	*Barnebydendron riedelii* (Tul.) J.H. Kirkbr.	5	0.004	2.24	0.002	1.99	2.12
Malvaceae	*Sterculia apetala* (Jacq.) H. Karst.	5	0.004	2.24	0.002	1.93	2.09
Moraceae	*Ficus insipida* Willd.	4	0.003	1.79	0.002	1.85	1.82
	Total	223	0.178	100	0.09	100	100

Table 2
Descriptive statistics for diameter at breast height (d), commercial height (hc), and basic wood density (ρ) by species used to estimate volume, biomass, and carbon in a forest-management area in Acre state, Brazil (Information provided by Romero et al., 2020a). n=number of trees sampled, sd= standard deviation.

Scientific Name	n	*d* (cm)		*hc (m)*		ρ (g cm^{-3})	
		Range	Mean (±sd)	Range	Mean (±sd)	Range	Mean (±sd)
Handroanthus serratifolius	8	50.9–78	61.8 ± 9.5	23–28.8	25.7 ± 1.62	0.76–0.87	0.82 ± 0.04
Terminalia tetraphylla	9	50.4–89.1	70.7 ± 12.9	21.6–25.9	23.0 ± 1.61	0.64–0.76	0.69 ± 0.04
Hura crepitans	6	74.9–121	96.5 ± 17.1	14.4–23	19.0 ± 3.08	0.27–0.43	0.36 ± 0.05
Albizia niopoides	7	54.7–79.3	65.8 ± 8.1	22.8–24.5	22.8 ± 1.30	0.61–0.68	0.64 ± 0.03
Apuleia leiocarpa	13	64.3–130.5	957 ± 17.6	20.4–27.4	24.8± 1.87	0.71–0.83	0.77 ± 0.03
Barnebydendron riedelii	5	66.8–85.9	77 ± 7.6	24.5–28.8	26.5± 2.18	0.54–0.62	0.57 ± 0.03
Copaifera multijuga	6	78.9–136.9	97.8 ± 21.8	21.6–23	22.3 ± 0.79	0.47–0.60	0.52 ± 0.05
Dipteryx odorata	11	70–123.5	90.4 ± 16.2	24.5–31	29.2 ± 2.50	0.75–0.89	0.80 ± 0.04
Hymenaea courbaril	8	66.2–121	93.5 ± 17.6	28.8–31.2	30.6 ± 1.68	0.71–0.84	0.76 ± 0.04
Parkia paraensis	20	51.2–149.6	86.9 ± 27	18.7–29.9	24.8 ± 2.27	0.38–0.56	0.46 ± 0.06
Schizolobium parahyba var. *amazonicum*	16	50.9–89.1	62.8 ± 10.8	17.3–27.7	24.4 ± 2.55	0.31–0.65	0.48 ± 0.08
Eschweilera grandiflora	13	55.4–111.4	76.4 ± 16.4	25.9–31.7	29.0 ± 1.94	0.69–0.79	0.73 ± 0.03
Ceiba pentandra	4	99.9–149.9	130.2 ± 24.4	28.8–33	31.0 ± 1.86	0.27–0.32	0.29 ± 0.03
Ceiba samauma	22	66.5–111.4	78.9 ± 10.3	14.4–24.6	20.4 ± 3.24	0.42–0.65	0.51 ± 0.06
Sterculia apetala	5	70–82.8	75.9 ± 5.3	25.9–28.8	27.6 ± 1.58	0.31–0.47	0.38 ± 0.06
Cedrela odorata	8	57.3–118.1	70.7 ± 20.2	14.4–25	20.0 ± 2.71	0.34–0.47	0.43 ± 0.04
Castilla ulei	37	56.7–121	79.7 ± 15.1	13–21	19.4 ± 2.48	0.34–0.48	0.41 ± 0.04
Ficus insipida	4	74.8–99.9	82.5 ± 11.8	18.7–25.9	23.4 ± 3.19	0.34–0.39	0.35 ± 0.03
Astronium lecointei	6	52.6–96.4	62.7 ± 16.7	24–31.7	27.4 ± 2.88	0.73–0.85	0.82 ± 0.05
Eschweilera bracteosa	15	54.1–95.5	68.1 ± 10.2	22–28.8	27.0 ± 1.84	0.54–0.72	0.65 ± 0.05
Grand total/ Mean ± standard deviation	223	50.4–149.9	79.6 ± 19.8	13–31	24 ± 4.26	0.27–0.89	0.56 ± 0.16

FT = Total stem biomass (sum of stump biomass and biomass of the commercial bole) (Mg).

The aboveground biomass for each individual tree was obtained as the sum of the stem (stump + commercial bole) and crown biomasses. Aboveground carbon stock was calculated as the product of the tree's biomass and its carbon content (Romero et al., 2020a, 2020b, 2021).

2.4. Models tested

For estimating the aboveground biomass equations, we compared linear and non-linear models (MBA): Husch (1963); Schumacher and Hall (1933); Loetsch et al. (1973); Chave et al. (2005) and Romero et al. (2020a). We also compared combinations of these models. The following independent variables were used: outside-bark diameter at 1.3 m above the ground (d, in cm), total height (h, in m) and basic wood density (ρ, in g cm^{-3}) (Table 3). For carbon estimation, the same variables were selected as those used for biomass, plus carbon content (t, in percent or decigrams kg^{-1}) (Table 4).

2.5. Goodness-of-fit indicators and model-selection criteria

The following goodness-of-fit measures were used to compare the equations: coefficient of determination (R^2), adjusted coefficient of determination ($\overline{R}^2$), root mean square error ($RMSE$) and mean absolute deviation (MAD) (Gujarati and Porter, 2011). The estimators used were:

$$R^2 = 1 - \sum_{i=1}^{n}\left(y_i - \widehat{y}_i\right)^2 \sum_{i=1}^{n}(y_i - \overline{y})^{-2}$$

$$\overline{R}^2 = 1 - (n-1)\sum_{i=1}^{n}\left(y_i - \widehat{y}_i\right)^2 (n-p-1)^{-1}\sum_{i=1}^{n}(y_i - \overline{y})^{-2}$$

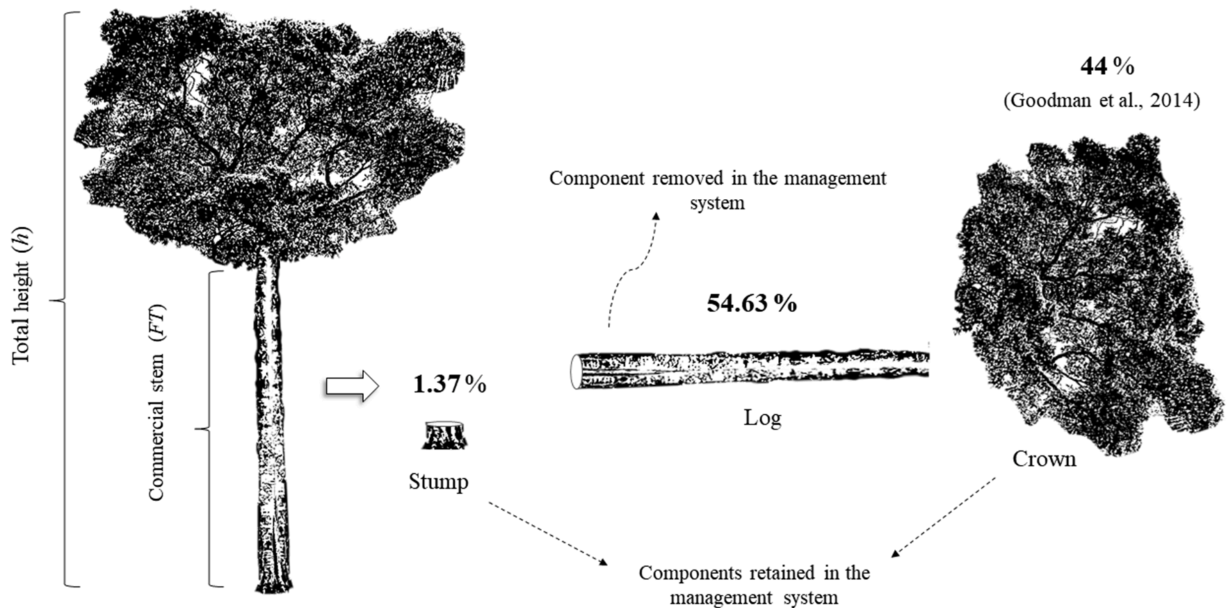


Fig. 2. Representation of a tree after harvest in the management system.

Table 3
Linear regression models tested to estimate aboveground biomass (w) content of commercial trees in southwestern Amazonia, Brazil.

Nº	Model
MBA1	$\ln w = \beta_0 + \beta_1 \ln d + \varepsilon$
MBA2	$\ln w = \beta_0 + \beta_1 \ln d + \beta_2 \ln \rho + \varepsilon$
MBA3	$\ln w = \beta_0 + \beta_1 \ln d^2 h + \beta_2 \ln \rho + \varepsilon$
MBA4	$\boldsymbol{\ln w = \beta_0 + \beta_1 \ln d^2 h + \beta_2 \ln \rho + \varepsilon}$
MBA5	$\ln w = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \beta_3 \ln \rho + \varepsilon$
MBA6	$\ln w = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \varepsilon$

Where: β_0, β_1, β_2 and β_3 are the model parameters and ε is the random error.

Table 4
Linear regression models tested to estimate carbon (c) stock in commercial trees in southwestern Amazonia, Brazil.

Nº	Model
MCA1	$\ln c = \beta_0 + \beta_1 \ln d + \varepsilon$
MCA2	$\ln c = \beta_0 + \beta_1 \ln d + \beta_2 \ln \rho + \varepsilon$
MCA3	$\ln c = \beta_0 + \beta_1 \ln d^2 h + \beta_2 \ln \rho + \varepsilon$
MCA4	$\ln c = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \varepsilon$
MCA5	$\ln c = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \beta_3 \ln \rho + \varepsilon$
MCA6	$\ln c = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \beta_3 \ln \rho + \beta_4 \ln t + \varepsilon$
MCA7	$\ln c = \beta_0 + \beta_1 \ln d^2 h + \beta_2 \ln \rho + \beta_3 \ln t + \varepsilon$
MCA8	$\ln c = \beta_0 + \beta_1 \ln d^2 h + \beta_2 \ln \rho t + \varepsilon$

Where: β_0, β_1, β_2, β_3 and β_4 are the model parameters and ε is the random error.

$$RMSE = \left(n^{-1} \sum_{i=1}^{n} \left(y_i - \widehat{y}_i \right)^2 \right)^{0.5}$$

$$MAD = n^{-1} \sum_{i=1}^{n} \left| y_i - \widehat{y}_i \right|$$

Where:

y_i= *i*th observed value of dependent variable *y* (*w* or *c*).

$\widehat{y}_i$= *i*th predicted value of dependent variable *y* (*w* or *c*).

$\bar{y}$ = arithmetic mean of the dependent variable.

n = number of cases of variable *y*.

p = number of parameters.

To compare models we used the original units of measurement. For this, transformations of the logarithmic (ln) models were carried out by applying a correction factor in order to remove the bias of the predictions made with log-transformed values; the value of the correction factor is always greater than 1 (Chave et al., 2005). The correction factor (CF) is CF $= e^{0.5RMSE^2}$.

The best equations for volume, biomass and carbon were selected using the Akaike information criterion, AIC $= -2\ln L + 2p$, where L is the maximum value of the likelihood function for the adjusted model and p is number of parameters in the model (Akaike, 1974).

3. Results

3.1. Biomass and carbon content

Aboveground biomass represents 100% of the tree components: stump, commercial bole and crown (Fig. 2). On average, the percentage of the aboveground biomass represented by the stump was 1.37%, and the commercial bole represented 54.6% of the aboveground biomass. Of this percentage, 45.4% (stump and crown) remains in the management system and 54.6% is removed in the form of the commercial log for wood production (Fig. 2). The carbon content *(t)* for twenty species in ten families ranged from 45.0 to 52.5%, with mean ± standard deviation of 49.9 ± 1.66% (Supplementary Material, Annex 1).

3.2. Stocks in tree components and equations generated for aboveground biomass of individual trees

Tree biomass varied substantially, with a mean of 6.63 ± 4.97 Mg, ranging from 3.13 to 16.14 Mg (Supplementary Material, Annex 2). The species with the highest percentage of the total biomass was *Dipteryx odorata* (12%) and the lowest was *Ficus insipida* (1.3%) (Supplementary Material, Annex 2). The relations between diameter at breast height and observed biomass for individual trees of the different species are shown in Fig. 3.

Six biomass equations were estimated. The six log-transformed equations all had significant regression coefficients at the 0.001 probability level. The residuals of the logarithmic equations were normally

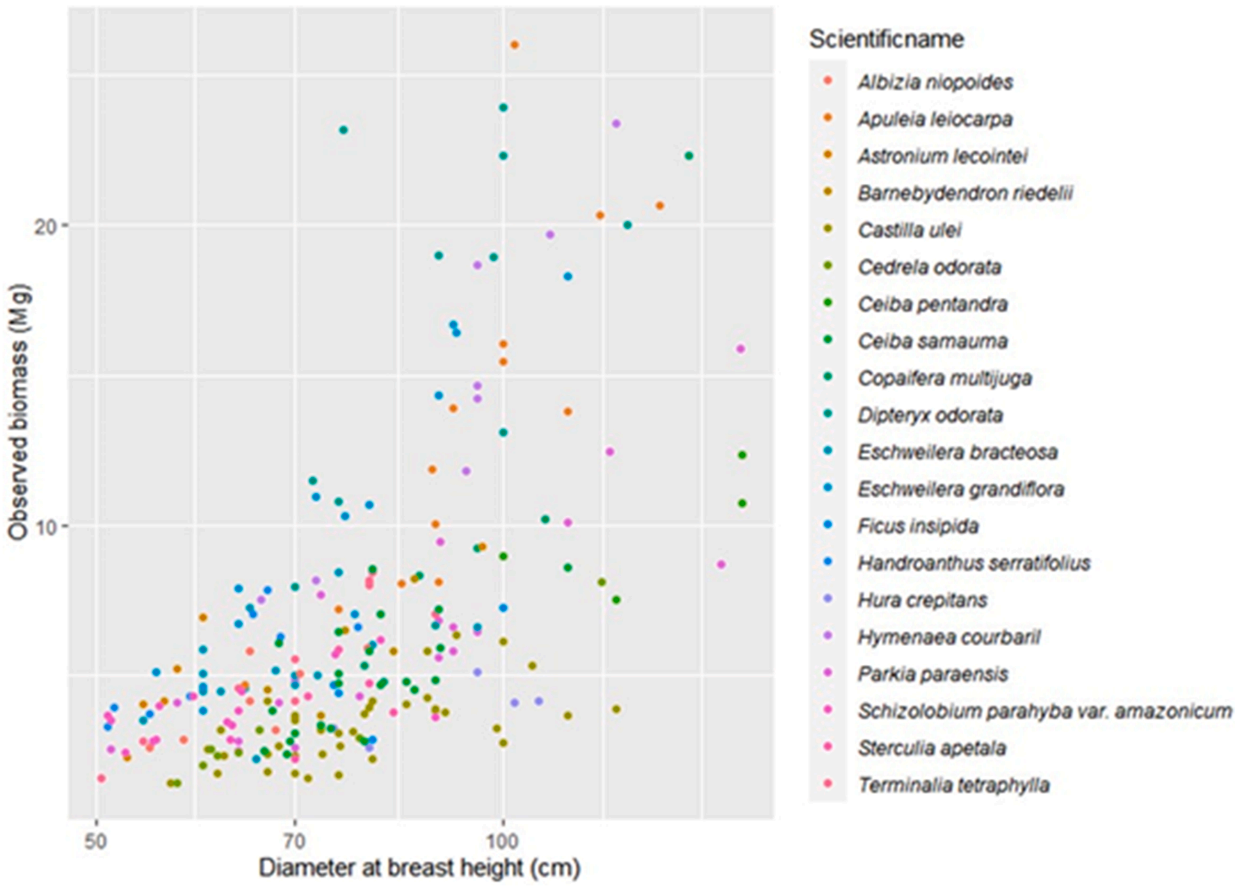


Fig. 3. Scatter plot of diameter at breast height (d) versus observed biomass by species for 223 individual trees in twenty species sampled in a managed forest area in Acre state, Brazil.

distributed (Supplementary Material, Annex 4 and Fig. 4). The MBA3 and MBA5 log-transformed equations (Table 5) had the best coefficients of determination (0.856 and 0.857, respectively) and adjusted coefficients of determination (0.855 and 0.855, respectively). These equations also had the lowest values of RMSE (1.890 and 1.088, respectively), MAD (1.089 and 1.086, respectively) and AIC (921.26 and 922.33, respectively). Because differences between the goodness-of-fit indicators were small between the equations, the AIC was decisive in choosing MBA3 as the best-fit model with the fewest regression coefficients (parsimony): Table 5 and Fig. 4 (graph 3).

When we regressed total aboveground biomass of trees (TAGB = ln*w; Mg*) against the product $d^2h * \rho$, we found the best- model with the best fit to be MBA3 (Eq. (1)):

$$lnw = -7.86305 + 0.85876 * lnd^2h + 0.97441 * ln\rho + \varepsilon$$

$$(Adj.R^2 = 0.855, RMSE = 1.890, MAD = 1.089, AIC = 921.96, CF = 1.023) \quad (1)$$

where *d* is in cm, *h* is in m, and ρ is in g cm^3. This model performed well.

3.3. Stocks in tree components and equations for carbon stock in individual trees

The average carbon stored per species was 3.33 ± 2.55 MgC, with a range from 1.61 to 8.33 MgC. The species that contributed most to carbon storage were *Dipteryx odorata, Apuleia leiocarpa* and *Eschweilera grandiflora*, totaling 33.5% of the carbon present in the 20 species (Supplementary Material, Annex 3). The relations between diameter at breast height and observed carbon for individual trees of the different species are shown in Fig. 5.

Six of the eight estimated equations had all their regression coefficients significant at the 0.001 probability level (Table 6). The residuals of the log-transformed equations were normally distributed (Supplementary Material, Annex 5 and Fig. 6). While MCA6 and MC7 equations showed good fit statistics, equation MCA8 had the best values for coefficient of determination (R^2), adjusted coefficient of determination (Adj. R^2), RMSE, MAD and AIC: Table 6 and Fig. 6 (graph 8). In addition, MCA8 included interactions of variables (*d* and *h, ρ* and *t*) and represented a more parsimonious and consistent equation when compared with the other linear models we tested.

When we regressed total aboveground carbon (TAGC = ln*c;* MgC) in individual trees against the product $d^2h * \rho t$, we found the best-fit model to be MBA8 (Eq. (2)):

$$lnc = -7.87424 + 0.85854 * lnd^2h + 0.97750 * ln\rho t + \varepsilon$$

$$(Adj.R^2 = 0.857, RMSE = 0.961, MAD = 0.548, AIC = 620.34, CF = 1.023) \quad (2)$$

where *d* is in cm, *h* is in m, ρ is in g cm^3 and *t is* in percent or decigrams kg^{-1}. This model performed well.

4. Discussion

4.1. Models for biomass

For biomass the log-linear equations (MBA2 to MBA5) can be used to predict the relationships between biomass and *d, h* (generic variables) and ρ (a specific variable) (Picard et al., 2012; Chave et al., 2014). Wood density is included as an explanatory variable in biomass models (Niklas, 1995; Overman et al., 1994; West et al., 1999; Nelson et al.,

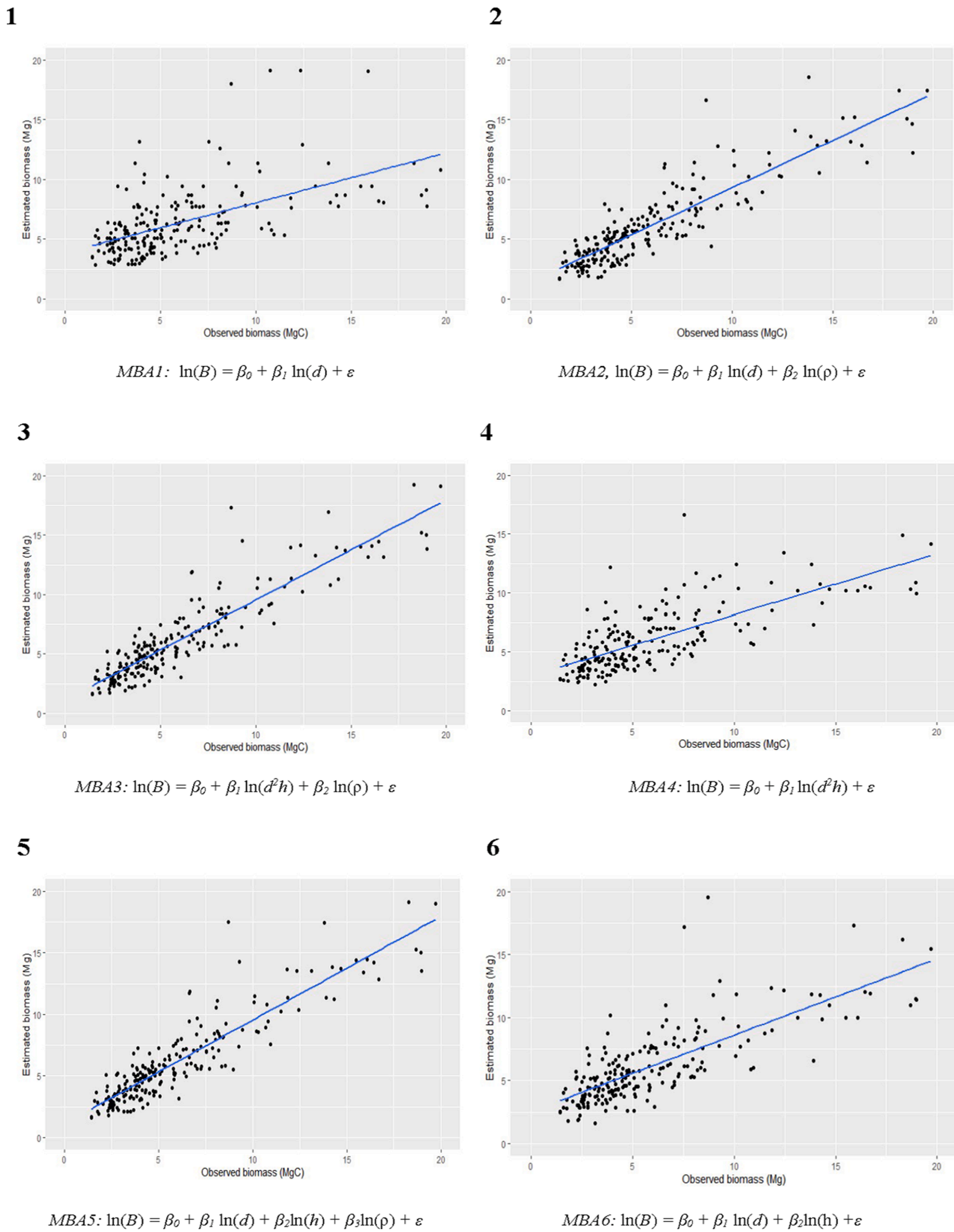


Fig. 4. Linear models (Models 1-6) for estimating aboveground biomass for twenty tree species sampled in a managed forest area in Acre state, Brazil: observed versus estimated values and the parameters that were fit for each equation.

Table 5
Parameter estimates for 10 tested models of biomass (*** = p-value < 0.001), coefficient of determination (R^2), adjusted R^2 (Adj. R^2), root mean square error (RMSE), mean absolute deviation (MAD), Akaike information criterion (AIC), and correction factor (CF).

No	Model	R^2	Adj. R^2	RMSE	MAD	AIC	CF	Parameter estimates $\widehat{\beta}_0$	$\widehat{\beta}_1$	$\widehat{\beta}_2$	$\widehat{\beta}_3$
MBA1	$\ln w = \beta_0 + \beta_1 \ln d + \varepsilon$	0.364	0.361	3.971	2.733	1251.98	1.126482	**-5.9158***	**1.7458***	-	-
MBA2	$\ln w = \beta_0 + \beta_1 \ln d + \beta_2 \ln \rho + \varepsilon$	0.785	0.783	2.315	1.530	1012.32	1.012.315	**-5.92426***	**1.93367*****	**1.30821***	-
MBA3	$\ln w = \beta_0 + \beta_1 \ln d^2 h + \beta_2 \ln \rho + \varepsilon$	0.856	0.855	1.890	1.089	921.96	1.023461	**-7.86305*****	**0.85876***	**0.97441***	-
MBA4	$\ln w = \beta_0 + \beta_1 \ln d^2 h + \varepsilon$	0.584	0.582	3.212	2.000	1154.35	1.06676	**-9.04418*****	**0.90779***	-	-
MBA5	$\ln w = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \beta_3 \ln \rho + \varepsilon$	0.857	0.855	1.888	1.086	922.33	1.023555	**-7.86037*****	**1.73180*****	**0.83960*****	**0.98270*****
MBA6	$\ln w = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \varepsilon$	0.617	0.614	3.087	1.863	1136.67	1.059681	**-8.89407*****	**1.50743*****	**1.29014*****	-

Where: $\widehat{\beta}_0$, $\widehat{\beta}_1$, $\widehat{\beta}_2$, *and* $\widehat{\beta}_3$ are the intercept and the estimated regression parameters (coefficients of the variables in the order they appear in each equation).

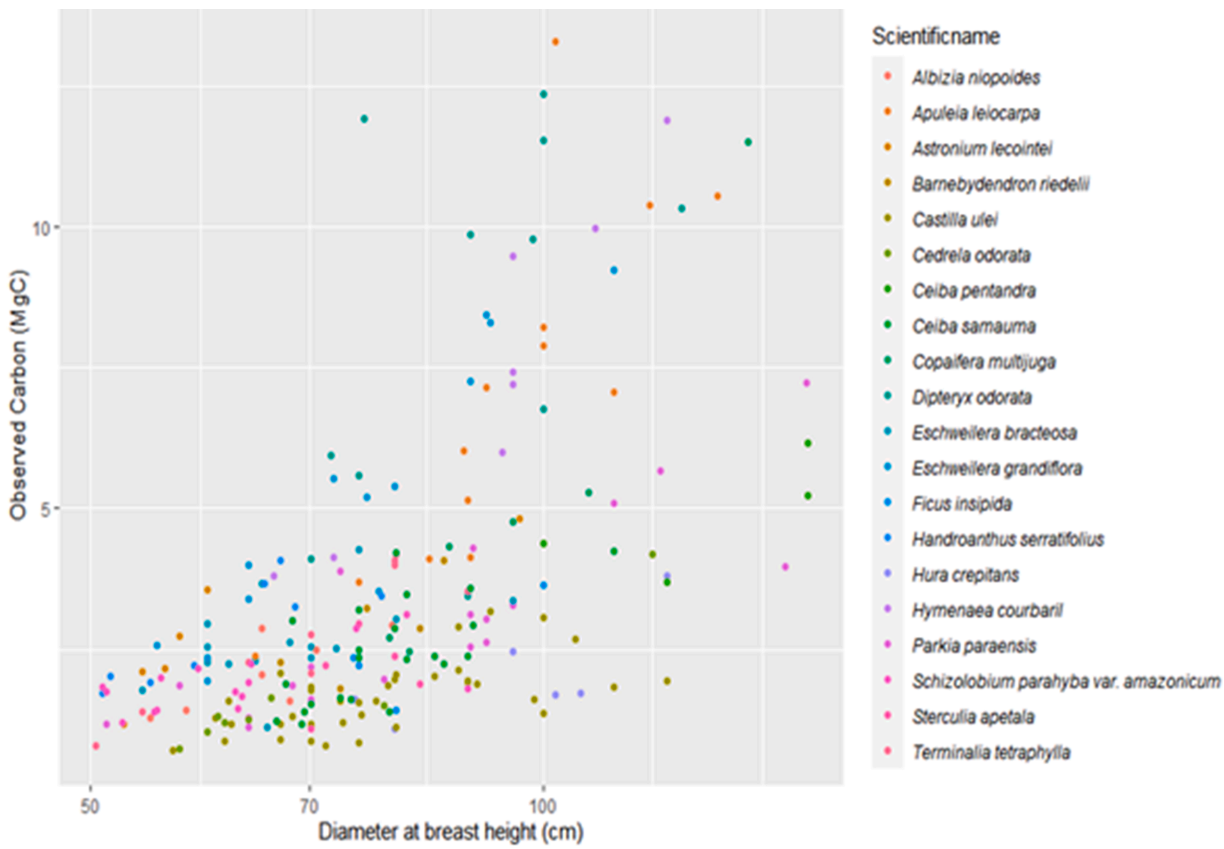


Fig. 5. Scatter plot of diameter at breast height (d) versus observed carbon by species for 223 individual trees in twenty species sampled in a managed forest area in Acre state, Brazil.

1999; Feldpausch et al., 2011, 2012; Chave et al., 2014, Vidal et al., 2016) due to its variation among taxonomic groups and because variations depend on vertical and radial shape and on biogeography (Baker et al., 2004; Chave et al., 2009; Nogueira et al., 2008a; Vidal et al., 2016). Omission of density can lead to errors in biomass estimates and, consequently, in the calculation of emissions from deforestation and forest degradation (Nogueira et al., 2007; Chave et al., 2009; Lima et al., 2012). These errors have serious consequences for emissions due to the scale of carbon releases implied by climate and land-use change (Fearnside, 2018). Among the log-linear equations, the best equation describing the behavior of aboveground biomass was MBA3 (Table 5), which had better consistency and was not biased. The goodness-of-fit tests and selection criteria applied (RMSE, R^2, Adj. R^2, MAD and AIC) demonstrate the better consistency of MBA3 (Table 5).

Our best-fit equation for biomass (MBA3: Table 5) underestimated the biomass of our 223 trees in the southwestern Amazon by 4.69%, a small value when compared with other equations that have been generated to estimate aboveground biomass in the Amazon and in tropical-forests in general. Application of these equations to our 223 trees underestimated or overestimated according to the equation generated for each region. For example, equations developed for the central Amazon by Higuchi et al. (1998) underestimated biomass by 27.51%, Nelson et al. (1999) underestimated by 31.36%, da Silva (2007) overestimated by 35.02% and Lima et al. (2012) overestimated by 29.80% (see Supplementary Material, Table S2). The equation for the southern Amazon developed by Nogueira et al. (2008a) overestimated by 16%. In the case of pantropical equations, Chave et al. (2014) underestimated by 28.68%, Brown (1997) overestimated by 11.17% and Brown et al. (1989) overestimated 42.38%. The differences among these values reflect the methodologies used in obtaining biomass as well as site- and tree-specific effects. The different studies considered trees in different diameter ranges, some including trees with *d* as small as 5 cm. The number of independent variables in the equations range from one to three; some studies only included *d* (Brown, 1997; Nogueira et al., 2005,

Table 6
Parameter estimates for eight tested models for carbon stock (**= p-value < 0.01, *** = p-value < 0.001), coefficient of determination (R^2), adjusted R^2 (Adj. R^2), root mean square error (RMSE), coefficient of determination (R^2), Akaike information criterion (AIC), mean absolute deviation (MAD) and correction factor (CF).

No	Model	R^2	Adj. R^2	RMSE	MAD	AIC	CF	Parameter estimates $\widehat{\beta}_0$	$\widehat{\beta}_1$	$\widehat{\beta}_2$	$\widehat{\beta}_3$	$\widehat{\beta}_4$
MCA1	$\ln c = \beta_0 + \beta_1 \ln d + \varepsilon$	0.344	0.342	2.064	1.421	960.23	1.134139	**-6.5236*** **	**1.7256*** **	-	-	-
MCA2	$\ln c = \beta_0 + \beta_1 \ln d + \beta_2 \ln \rho + \varepsilon$	0.785	0.782	1.186	0.769	714.14	1.046092	**-6.53249*** **	**1.92132*** **	**1.36287*** **	-	-
MCA3	$\ln c = \beta_0 + \beta_1 \ln d^2 h + \beta_2 \ln \rho + \varepsilon$	0.797	0.795	1.150	0.213	700.27	1.039786	**-8.71863*** **	**0.87468*** **	**1.09015*** **	-	-
MCA4	$\ln c = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \varepsilon$	0.487	0.482	1.830	1.153	907.53	1.086075	**-10.8029*** **	**1.5572*** **	**1.5852*** **	-	-
MCA5	$\ln c = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \beta_3 \ln \rho + \varepsilon$	0.801	0.798	1.142	0.704	698.17	1.039496	**-8.41771*** **	**1.81619*** **	**0.69886 *** **	**1.14782***	-
MCA6	$\ln c = \beta_0 + \beta_1 \ln d + \beta_2 \ln h + \beta_3 \ln \rho + \beta_4 \ln t + \varepsilon$	0.807	0.804	1.126	0.700	692.98	1.039139	**-7.85340*** **	**1.82712*** **	**0.70428*** **	**1.09413*** **	**0.95185***
MCA7	$\ln c = \beta_0 + \beta_1 \ln d^2 h + \beta_2 \ln \rho + \beta_3 \ln t + \varepsilon$	0.803	0.801	1.135	0.703	690.31	1.039432	**-8.15448*** **	**0.88014*** **	**1.03645*** **	**0.95167***	
MCA8	$\ln c = \beta_0 + \beta_1 \ln d^2 h + \beta_2 \ln \rho t + \varepsilon$	0.804	0.802	1.131	0.703	693.00	1.039253	**-8.10849*** **	**0.88063*** **	**1.03101*** **		

Where: $\widehat{\beta}_0, \widehat{\beta}_1, \widehat{\beta}_2, \widehat{\beta}_3$ *and* $\widehat{\beta}_4$ are the intercept and the estimated regression parameters (coefficients of the variables in the order in which they appear in each equation).

2008a; Chave et al., 2014) while others had combinations of d and h (Fernandes et al., 1983; Higuchi et al., 1998; West et al., 1999) and some equations included d, h and ρ, as in the cases of Chave et al. (2014) and our study. Ecological aspects influence the calculation of biomass, such as the structural characteristics of the species. Geographical characteristics (climate and relief) (Niklas, 1995; Baker et al., 2004; Chave et al., 2014; Chazdon et al., 2016) vary and affect the development of species, affecting horizontal and vertical growth (for example, height may be low or high and the crown may be large or small) (Nogueira et al., 2006; Feldpausch et al., 2011, 2012; Goodman et al., 2014; Loubota et al., 2021).

4.2. Models for carbon

Our carbon equations, including the best-fit equation (MCA8), have two very large trees that fall below the regression line (Fig. 6). We considered applying a piecewise regression analysis (Supplementary Material, Annex 6), but concluded that the single equation (MCA8) is better.

In the context of global climate change, estimates of storage of biomass and carbon are essential inputs for calculating the emissions balance of a forest that is being managed or that has undergone a human intervention that results in negative impacts. Inclusion of carbon content (t) as a predictor variable is important because it provides necessary information for carbon-stock calculations and for estimates of emissions caused by the forest management. Our study provides a database and equations that include carbon content as a predictor for trees that are over 80 years old, which is a life stage when carbon content is different from that in the juvenile stage of the same trees (Supplementary Material, Annex 1 and Table 6) (Ma et al., 2018). We emphasize that our equations are best suited for large trees ($d \geq 50$ cm), and that using these equations for smaller trees could result in either under- or overestimation. Accurate estimates for large trees are critical both for carbon stocks and for forest management. Because most allometric equations for tropical forests are based on large numbers of small trees and very few large ones, they can produce less-reliable results for the large-diameter size classes (Supplementary Material, Table S2).

Our best-fit equation for carbon (MCA8: Table 6) included the interaction of the predictor variables d and h, and ρ and t, and the equation is an allometric model with geometric similarity (Fearnside, 1997; Nogueira et al., 2007, 2008a; Zanne et al., 2009). This equation allows calculation of the substantial part of the forest carbon stock represented by trees with $d \geq 50$ cm. The importance of MCA8 in estimating carbon stocks is the possibility of using it to estimate emissions caused by deforestation, forest fires and forest degradation in general, taking account differences in carbon stock between and within species and taxonomic groups (IPCC, 2006; ter Steege et al., 2013).

The Intergovernmental Panel on Climate Change (IPCC) provides a default value of 47% to describe the carbon content of dry aboveground biomass in general (IPCC, 2006). We present species-specific values for "t" that range from 46.3 ± 1.83% to 51.8 ± 0.46% for large commercial trees in the southwestern Amazon (Supplementary Material, Annex 1), which is important information for calculating CO_2 emissions in areas under forest management. The inclusion of carbon content (t) in our allometric models, together with ongoing research by the scientific community to create new databases of values for this variable (Ma et al., 2018; Romero et al., 2020a), will provide more information on the contribution of this factor in the context of climate change.

4.3. Uncertainties in input parameters

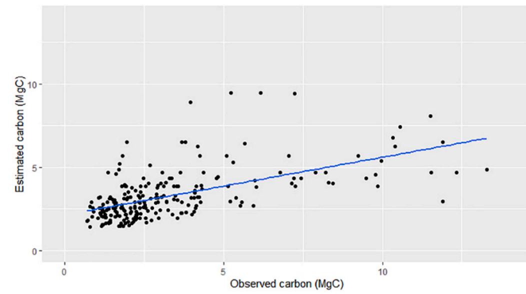
Many allometric equations generated to estimate biomass and carbon have inadequate representation of large trees. In addition, the crown component is usually disregarded.

4.3.1. Tree crowns

The present study lacks direct measurements of crowns. However, we estimated each crown from the tree's commercial stem based on the findings of Goodman et al. (2014), who weighed the crowns and trunks of 51 trees with $d = 11$–169 cm, 33 of which had $d \geq 50$ cm, and found that the crown represented 44 ± 2% (mean ± sd) of the aboveground biomass. Their study was also performed in southwestern Amazonia, which is important because trees are shorter for any given diameter in this part of Amazonia as compared to eastern and central Amazonia, where most allometric equations have been derived (Nogueira et al., 2008a) and crowns represent a larger proportion of aboveground biomass (Goodman et al., 2014). In central Amazonia crowns have been found to represent 34.4% (Higuchi et al., 1998) and 30.8% (da Silva, 2007) of aboveground biomass. In southern Amazonia crowns have been found to represent 39.4% (Nogueira et al., 2008b).

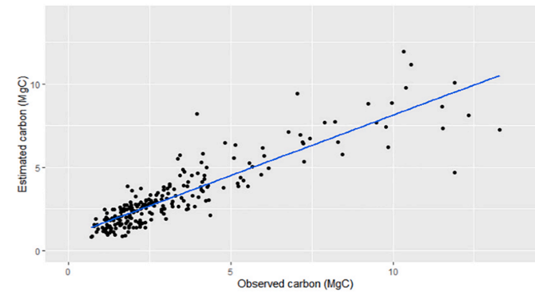
Goodman et al.'s (2014) estimate of 44 ± 2% as the canopy percentage can be considered to have low variability, with a coefficient of variation of 4.5%. However, crown depth (the difference between total height and the length of the stem from the ground to the first branch;

1



MCA1: $\ln(C) = \beta_0 + \beta_1 \ln(d) + \varepsilon$

2



MCA2: $\ln(C) = \beta_0 + \beta_1 \ln(d) + \beta_2 \ln(\rho) + \varepsilon$

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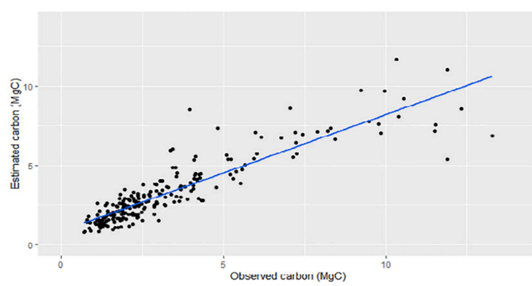
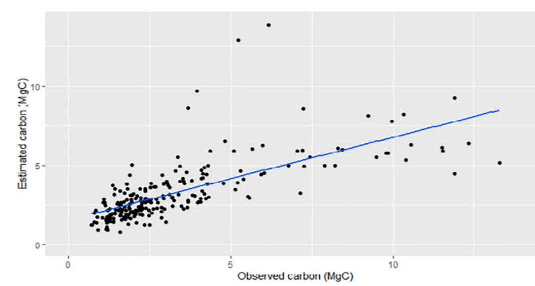


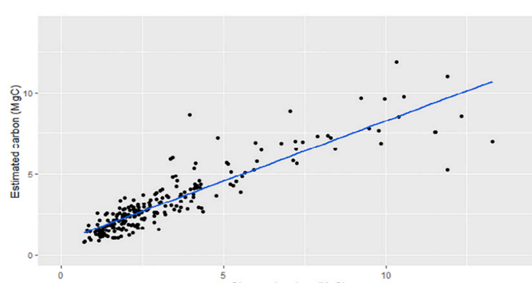
MCA3: $\ln(C) = \beta_0 + \beta_1 \ln(d^2h) + \beta_2 \ln(\rho) + \varepsilon$

4



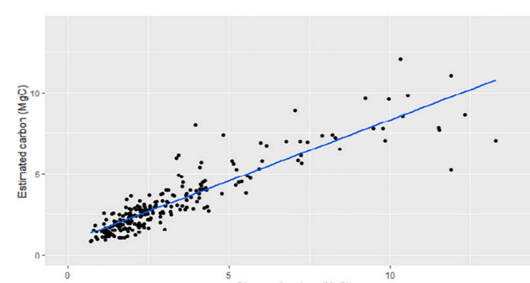
MCA4: $\ln(C) = \beta_0 + \beta_1 \ln(d) + \beta_2 \ln(h) + \varepsilon$

5



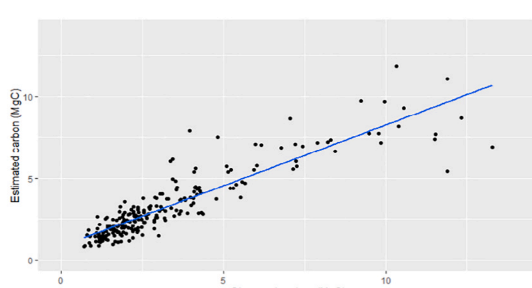
MCA5: $\ln(C) = \beta_0 + \beta_1 \ln(d) + \beta_2 \ln(h) + \beta_3 \ln(\rho) + \varepsilon$

6



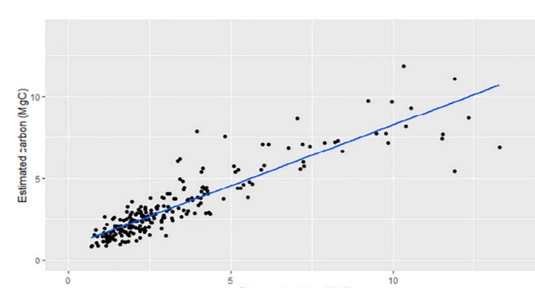
MCA6: $\ln(C) = \beta_0 + \beta_1 \ln(d) + \beta_2 \ln(h) + \beta_3 \ln(\rho) + \beta_4 \ln(t) + \varepsilon$

7



MCA7: $\ln(C) = \beta_0 + \beta_1 \ln(d^2h) + \beta_2 \ln(\rho') + \beta_3 \ln(t) + \varepsilon$

8



MCA8: $\ln(C) = \beta_0 + \beta_1 \ln(d^2h) + \beta_2 \ln(\rho t) + \varepsilon$

Fig. 6. Observed versus estimated values for linear models (Models 1-8) for estimating aboveground carbon for 223 inidvidual trees in twenty species sampled in a managed forest area in Acre state, Brazil. The equation parameters are shown under each graph.

Supplementary Material, Table S1) in our dataset had a mean of 10.56 ± 1.86 m (i.e., a coefficient of variation of 17.6%), which may indicate greater variability at our site.

The size of the crown as indicated by the crown projection area (the area under the perimeter of the crown) is closely correlated with the volume of the commercial bole, as shown by a study in the Antimary State Forest very near our study site, where crown dimensions of 146 commercial trees were measured using airborne LiDAR and were related to commercial-bole volumes measured by the rigorous-cubing method after felling (Figueiredo et al., 2014). This suggests that our study's calculating in the reverse direction (estimating crown biomass based on bole biomass) is a reasonable approach.

The fact that the 44% value for canopy percentage was derived at a different location (Puerto Maldonado, Peru), even though also within southwestern Amazonia, represents an obvious source of uncertainty. Unfortunately, the magnitude of this uncertainty is unknown. However, one may consider a maximum difference to be represented by the difference between the 44% canopy percentage of aboveground biomass in southwest Amazonia (Goodman et al., 2014) and the 39.4% value from southern Amazonia (Nogueira et al., 2008b), that is, a difference of 10.5% in the biomass of the crown or a 4.6% difference in the total aboveground biomass of a tree.

4.3.2. Stumps

The stump has been assumed to be a cylinder with diameter equal to that at the stump cut (30 cm above the ground or at a height of 50 cm if the tree had significant buttresses). This has a downward bias from the fact that the stump is often wider at ground level than at 30 cm height and has an upward bias from the fact that the circumference of the trunk is often fluted or otherwise irregular at this height above the ground, thus making diameter (derived from circumference) overestimate the true cross-sectional area (Nogueira et al., 2006). Significant buttresses, however, would not affect the diameter measure, as they are cut off with a chainsaw before felling in the management area under study.

Despite the possible downward bias from assuming that the stump is a cylinder, our estimated percentage of biomass in stumps is approximately double that found in a more complete study of stumps in four management areas in southern Amazonia (Nogueira et al., 2008b), where stumps represented 1% of the biomass of the commercial boles in 264 harvested trees. Our finding that 1.37% of the total aboveground biomass was in stumps is equivalent to stumps representing 2.51% of the biomass of the commercial boles. Since the 30 cm cutting height in the management area we studied is lower than normal, the difference may be even greater in practice. This may be explained by the effect of irregularities in the shape of the stumps. The study in southern Amazonia by Nogueira et al. (2008b) included corrections for irregularities in the cross-sectional areas both at the top and the bottom of the stump, and also included correction for hollows. (Note: in our study no logs were hollow because such trees were either detected and not felled or were discarded if found to be hollow). The difference is further increased by the Nogueira et al. (2008b) study including an adjustment for wood density, which, on average, was 1.36% higher at the top of the stump as compared to the density at the DBH (d) measurement height of 1.3 m above the ground.

5. Conclusions

Allometric equations specific to the southwestern Amazon that represent the physical and biological characteristics of forests can provide unbiased estimates of forest volume, biomass and carbon. These equations include the stump and crown components that are left in areas under forest management after harvest.

Stump and crown stocks are important in estimating CO_2 emissions in areas under forest management. Information on emissions is important in decision-making and in the formulation of regulations and designing of programs to mitigate forest-sector activities. Carbon stocks in the stump and crown represent a significant percentage of the total aboveground biomass and cannot be ignored in the estimates.

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.

Acknowledgments

This research was supported logistically by Fox Laminados Ltda. We thank the company's owner, Antônio Aparecido Barlati, and his team for their help in the planning, harvesting, and sawmill stages of the study. FMBR thanks Jose de Araújo for technical contributions during the field survey. She also thanks her scientific initiation scholarship students at the Federal University of Acre (PIBIC-UFAC) Ingrid Lana Lima de Moraes and Joatan Araújo da Silva. We thank the Laboratory of Wood Anatomy of the Federal University of Acre (headed by Moisés Silveira Lobão) and the Laboratory of Wood Panels and Energy of the Federal University of Viçosa (headed by Angelica de Cássia Oliveira Carneiro). FMBR thanks the Conselho Nacional de Tecnologia e Desenvolvimento Científico (CNPq) for a scholarship, the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for an internship scholarship at the University of Alabama, Tuscaloosa, Alabama, USA, and INPA's Programa de Capacitação Institucional (PCI) for a post-doctoral fellowship. LAGJ thanks CNPq (408108/2016-9). EV thanks CNPq (309319/2018-8). PMF thanks CNPq (429795/2016-5, 311103/2015-4, 312450/2021-4), the Foundation for the Support of Research of the State of Amazonas (FAPEAM) (708565), the Brazilian Research Network on Global Climate Change FINEP/ Rede CLIMA (01.13.0353-00) and INPA (PRJ15.125). We thank two reviewers for helpful comments.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.tfp.2022.100317.

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