

ORIGINAL ARTICLE

Allometric models to estimate tree height in northern Amazonian ecotone forests

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ABSTRACT

Allometric models defining the relationship between stem diameter and total tree height in the Amazon basin are important because they refine the estimates of tree carbon stocks and flow in the region. This study tests different allometric models to estimate the total tree height from the stem diameter in an ecotone zone between ombrophilous and seasonal forests in the Brazilian state of Roraima, in northern Amazonia. Stem diameter and total height were measured directly in 65 recently fallen trees (live or dead). Linear and nonlinear regressions were tested to represent the D:H relation in this specific ecotone zone. Criteria for model selection were the standard error of the estimate (S_{yx}) and the adjusted coefficient of determination (R^2_{adj}), complemented by the Akaike Information Criterion (AIC). Analysis of residuals of the most parsimonious nonlinear models showed a tendency to overestimate the total tree height for trees in the 20-40 cm diameter range. Application of our best fitted model (Michaelis-Menten) indicated that previously published general equations for the tropics that use diameter as the independent variable can either overestimate tree height in the study area by 10-29% (Weibull models) or underestimate it by 8% (climate-based models). We concluded that our site-specific model can be used in the ecotone forests studied in Roraima because it realistically reflects the local biometric relationships between stem diameter and total tree height. Studies need to be expanded in peripheral areas of northern Amazonia in order to reduce uncertainties in biomass and carbon estimates that use the tree height as a variable in general models.

KEYWORDS: allometry, Amazon forest, hypsometric relationships, dendrometry, seasonal forest

Modelos alométricos para estimar altura de árvores em florestas ecotonais do norte da Amazônia

RESUMO

Modelos alométricos que definem o relacionamento entre diâmetro do tronco e a altura total da árvore na bacia amazônica são importantes porque refinam as estimativas de fluxo e estoques de carbono arbóreo na região. Este estudo testou diferentes modelos alométricos para estimar a altura total de árvores a partir do diâmetro do tronco em uma zona de ecótono entre florestas ombrófilas e sazonais no estado de Roraima, norte da Amazônia. Diâmetro do tronco e altura total foram medidos de forma direta em 65 árvores tombadas recentemente (vivas e mortas). Regressões linear e não-linear foram testadas para representar a relação D:H nesta zona específica de ecótono. Os critérios de seleção dos modelos foram o erro padrão da estimativa (S_{yx}), o coeficiente de determinação ajustado (R^2_{adj}) e o Critério de Informação de Akaike (AIC). A análise dos resíduos dos modelos não-lineares mais parcimoniosos mostrou uma tendência de superestimar a altura total para árvores entre 20-40 cm de diâmetro do tronco. A aplicação do modelo melhor ajustado (Michaelis-Menten) indicou que equações gerais publicadas previamente para os trópicos que usam diâmetro como variável independente podem superestimar em 10-29% (modelos Weibull) ou subestimar em 8% (modelos baseados no clima) a altura das árvores na área de estudo. Nós concluímos que o modelo de melhor ajuste pode ser usado nas florestas ecotonais estudadas em Roraima, porque ele reflete realisticamente o relacionamento biométrico local entre diâmetro do tronco e altura total da árvore. É necessário expandir os estudos para outras áreas periféricas do norte da Amazônia, com o intuito de reduzir as incertezas em estimativas de biomassa e carbono arbóreo que adotem altura da árvore como uma variável em modelos gerais.

PALAVRAS-CHAVE: alometria, floresta amazônica, relações hipsométricas; dendrometria; florestas estacionais

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INTRODUCTION

Allometric models have been studied in the Amazon in order to improve our knowledge about how tree morphometric attributes are influenced by different ecological and environmental characteristics (Nogueira *et al.* 2008a; Chave *et al.* 2014). These advances have the objective of increasing our predictive capacity to estimate temporal and spatial variability of tree biomass in different forest ecosystems (Brienen *et al.* 2015; Nogueira *et al.* 2015). This reflects our need to quantify carbon stocks and flows in the region to better understand the role of the Amazon rainforest in global climate change (Houghton *et al.* 2009; Doughty *et al.* 2015; Fearnside 2018).

Tree morphometric relationships vary with forest type due to specific environmental conditions acting on individuals and species-specific differences in responses to these environmental drivers. The most important allometric attributes of the tree component are stem diameter (Overman *et al.* 1994; Brown 1997), crown area (Goodman *et al.* 2014; Blanchard *et al.* 2016) and total height (Nogueira *et al.* 2008b; Feldpausch *et al.* 2011). In general, stem diameter has been the most frequently employed variable in allometric models for estimating tree biomass because diameter is easily measured in the field. However, when used by itself, this variable can cause a bias that is difficult to detect in Amazonian studies due to the vastness of the region and the large number of forest types with distinct structural forms (e.g. Fearnside and Ferraz 1995). Although the use of additional variables increases the complexity of the models, using diameter in conjunction with total height generates robust results that reduce the error in biomass estimates (Chave *et al.* 2005; Nogueira *et al.* 2008b; Feldpausch *et al.* 2012).

Few studies in the Amazon provide allometric relations between stem diameter and tree height for different forest types (Hess *et al.* 2014) or for specific forest species of ecological interest (Siliprandi *et al.* 2016). As a consequence regional estimates are generated using general models that may not accurately reflect the morphometric reality of the forest type in question (Hunter *et al.* 2013). The state of Roraima, located in the northernmost part of Brazilian Amazonia, bordering on Venezuela and Guyana, has become the site of a rapidly expanding deforestation frontier (INPE 2017), and planned developments are expected to accelerate this trend (Barni *et al.* 2015). Roraima has become known as a northern “arc of deforestation”, alluding to its similarity with Brazil’s “arc of deforestation”, where clearing activity has been concentrated along the eastern and southern edges of the Amazon region. However, the forests in Roraima are the most deprived of allometric information in Brazilian Amazonia and do not have significant geographical representation in larger regional reviews (e.g. Feldpausch *et al.* 2011; Feldpausch *et al.* 2012; Sullivan *et al.* 2018), in contrast to the representation provided by specific studies for central Amazonia (Higuchi *et al.* 1998),

northwestern Amazonia (Lima *et al.* 2012) and the southern “arc of deforestation” (Nogueira *et al.* 2008b).

Most forests in Roraima are characterized as ecotones, defined by the Brazilian vegetation classification system as contact zones (or ecological-tension areas) between different forest and/or non-forest types (Barni *et al.* 2016). Many of the ecoregions in the northern “arc of deforestation” are climatically drier areas with significant hydro-edaphic restrictions, causing distinctions in the structure and floristic composition in relation to other Amazonian forests (Silva *et al.* 2016; Barbosa *et al.* 2017). Despite these distinctions, biomass and carbon stocks have been estimated using general allometric equations, meaning that large uncertainties remain in biomass and carbon estimates for this portion of Brazilian Amazonia (e.g. Nascimento *et al.* 2007; Nascimento *et al.* 2014).

The specific goals of this study were (i) to select allometric models to provide the morphometric relationship between stem diameter and total height of individual trees located in ecotone forests in the northern Brazilian Amazon, and (ii) to examine how well published general models predict the total height of trees in this portion of the Amazon.

MATERIAL AND METHODS

Study area

The study was carried out in a PPBio (Biodiversity Research Program, <https://ppbio.inpa.gov.br>) 25-km² research grid established in the eastern portion of the Maracá Ecological Station (03°22'54"N, 61°27'50"W), a Brazilian conservation area located in the state of Roraima (Figure 1). The study area represents the ecotone zone in the southern portion of the Guyana Shield, which is dominated by mosaics of ombrophilous and seasonal forests that are in contact with the large savanna area of northern Brazilian Amazonia (Milliken and Ratter 1998). The main tree species in the study area are *Pradosia surinamensis* (Eyma) T.D. Penn. (Sapotaceae), *Ecclinusa guianensis* Eyma (Sapotaceae), *Licania kunthiana* Hook.f. (Chrysobalanaceae) and *Peltogyne gracilipes* Ducke (Fabaceae). All of these occur with abundances varying according to the environmental factors that determine the dominant forest types (Nascimento *et al.* 2017). The ecotone zone that encompasses the PPBio/Maracá grid is an environmental mosaic characterized by a range of reliefs (51-99 m a.s.l.) on different drainage types, including areas free of seasonal flooding, wet lowlands and dry rocky slopes (Carvalho *et al.* 2018).

The soils of eastern Maracá are sandy with low nutrient concentrations and acid pH. Soil classes vary with relief and drainage, where hills and slopes (well-drained soils) are dominated by quartzite or granite with a predominance of rocks that are rich in bases, while in the lowlands (poorly

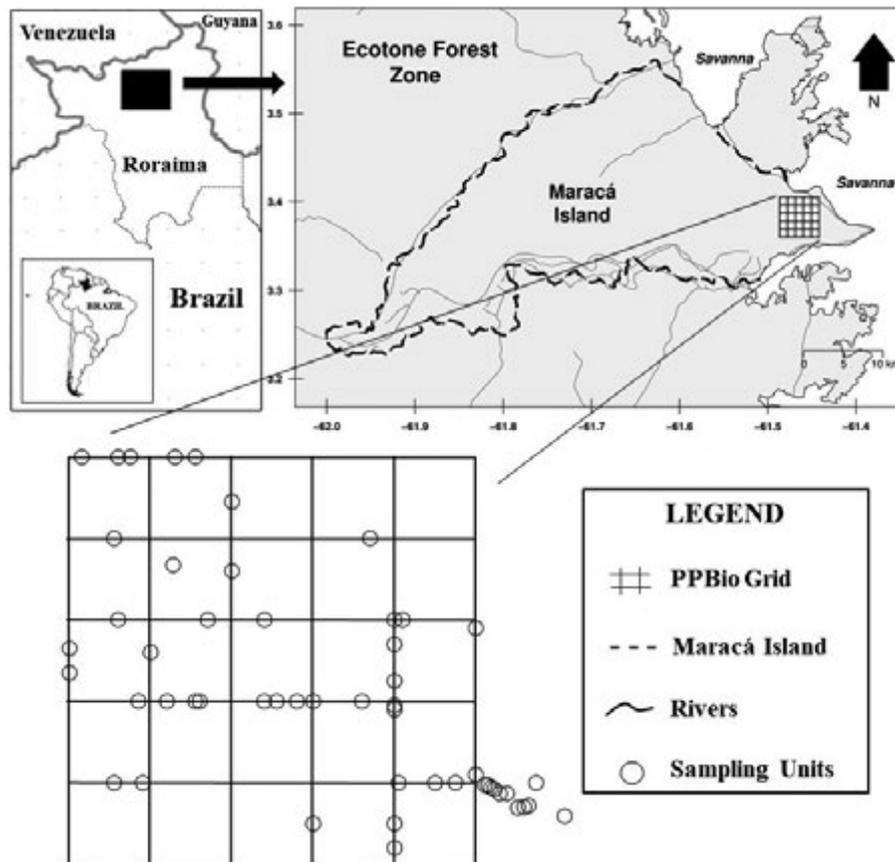


Figure 1. Location of the PPBio trail grid in Maracá Ecological Station, Roraima, northern Brazilian Amazonia, where sampling was carried out. The location of the sampling units (individual trees) is indicated by the circles on the enlarged grid.

drained soils) there is a dominance of hydromorphic soils (Robison and Nortcliff 1991). Maracá has climatic seasonality and is located in a border zone between the “Aw” and “Am” climatic sub-types in the Köppen classification (Barbosa 1997). Data from the Maracá agrometeorological station (1986-2010) indicate a mean annual precipitation of ~1900 mm, with the rainy season between April and September (140-420 mm month⁻¹), and the dry period between October and March (40-130 mm month⁻¹) (Couto-Santos *et al.* 2014).

Sampling design

In this study, we present a simple alternative method to obtain the total height of trees by direct measurement, thus avoiding (i) the high costs of traditional destructive methods, (ii) errors associated with indirect measurements taken with rangefinder cameras or clinometers, and (iii) the use of general models that may induce substantial errors when applied to a site-specific database. The sampling unit in this study was defined as any recently dead fallen tree, either alive or dead (preferentially with persistent leaves and the stem humid and/or with exudates), with stem diameter ≥ 10 cm (Supplementary Material, Figure S1). Sampling was designed to be performed considering regular walks on the access trail to the grid and on

additional 12 5-km trails (six parallel trails in N-S direction and six in E-W direction at perpendicular angles with the N-S trails, forming a grid with 1-km resolution; see <https://ppbio.inpa.gov.br> for details on the PPBio grid structure), totaling ~60 km of trails covered in each of four one-week stages of our fieldwork, which was carried out between July 2015 and October 2016. As all trails are georeferenced (UTM), we also recorded the geographical location of each tree (sampling unit) (Figure 1).

A total of 65 individual trees were sampled and associated with its field taxonomic identification (Table 1; Supplementary Material, Table S1). All sampled trees were selected from an initial set of 176 individuals observed along the trails in the grid. The selected trees were characterized as natural treefalls, that is, live trees toppled by wind or individuals that were physically felled by other trees that fell against them. The selection criteria for including trees in the sample took into consideration a careful inspection in order to choose only recently fallen individuals (live or dead) that were in a good state of preservation, discarding all individuals with hollow trunks, broken stems, broken canopies or with signs of rotting. These criteria were used to ensure a realistic sampling of the variables (total height and stem diameter), which is specially

Table 1. Number of samples and description of the parameters (stem diameter and total height) observed in 65 individual trees, by diameter class, in an ecotone forest studied in the northern Brazilian Amazon. Numbers between parentheses represent structural information (density and stem diameter) of the tree community in the study area (excluding palms).

Diameter class (cm)	Number of samples (n; ind ha ⁻¹)	Parameters (mean ± SD)	
		Stem diameter (cm)	Total height (m)
10-20	8 (254)	16.3 ± 2.3 (13.9 ± 2.8)	14.7 ± 3.3
20-30	14 (86)	25.3 ± 2.5 (24.3 ± 2.8)	20.1 ± 3.5
30-40	11 (46)	35.3 ± 2.5 (34.3 ± 2.9)	23.6 ± 4.5
40-50	18 (24)	43.8 ± 2.8 (44.2 ± 2.9)	26.4 ± 3.2
> 50	14 (26)	70.9 ± 19.6 (62.9 ± 12.6)	30.8 ± 4.1

important because these variables were directly measured. The number of sampling units (65) is compatible with the minimum required for height-diameter allometric estimates (at least 50), and also included more than ten large-diameter trees (≥ 50 cm), as recommended by Sullivan *et al.* (2018).

Direct measurements of stem diameter (D; cm) and total height (H; m) were made for each sampling unit. Total height was considered to be the distance between the base of the stem and the top of the canopy and was measured using a 50-m tape. The stem diameter was measured with a graduated tape at the most suitable point of measure (POM). All of the direct measurements were made as would be done for a standing live individual, at 1.30 m above the base of the tree, or 0.5 m above any buttress roots, according to the manual for measuring and marking live and standing trees in PPBio grids and modules (Castilho *et al.* 2014). As suggested by Brokaw and Thompson (2000), we adopted this POM as the standard for measuring stem diameter because it best represents the relationship between D and H and does not cause distortion in the results.

The POM and the protocol of Castilho *et al.* (2014) for live standing trees were used as the basis for obtaining biometric measurements because most forestry inventories in tropical forests have been performed in this way (e.g. RAINFOR, Malhi *et al.* 2002). This methodological solution was chosen because it would not make any logical sense to carry out another type of biometric measurement different from those used by the most representative global studies involving tropical forest inventories. Otherwise, it would be impossible to apply any allometric model derived from this study. This allows construction of local allometric models that are more realistic than general models, have lower bias and have a parsimonious performance for application in biomass estimates (Chave *et al.* 2014).

The selection process for the sampling units was totally independent. However, the number of individuals in each diameter class cannot be considered strictly representative because they were not proportional to the numbers of individuals in the diameter classes in each forest type.

Data analysis

Linear and nonlinear regression analyses were used to test 12 different models associating the 65 data pairs (H, total height = dependent variable; D, stem diameter = independent variable) obtained in the field (Table 2). The models tested were selected because they are commonly used in the scientific literature for the diameter-height relationship due to their simplicity of application. The objective was to find the best morphometric relationship between D and H for the entire set of individuals representing the ecotone forest zone. The five best-performing models were hierarchically ranked based on three criteria, which were considered in the following order: (1) standard error of the estimate (lower S_{yx} = higher goodness of fit), reflecting the accuracy of the fitted regression; (2) adjusted coefficient of determination (higher R^2_{adj} = higher explanatory power), as the most parsimonious criterion indicating the proportion of the total variation that is explained by the fitted regression; and (3) Akaike Information Criterion with correction (lower AICc = lower complexity and higher generality), the second most parsimonious criterion based on an estimator that indicates the relative quality of the model (Johnson and Omland 2004). The three criteria were hierarchically used to perform model comparisons and allow that the models similarly ranked on criterion 1 (S_{yx}) could be ordered by higher explanatory power (R^2_{adj}) associated to the lower complexity and higher generality (AICc). All graphical and statistical analyses to test the suitability and validity of the selected models were performed with R software (R Core Team 2016).

Table 2. Models tested to describe the allometric relationships between total height (Y) and stem diameter (X) in trees in an ecotone zone (ombrophilous forest and seasonal forest) in Roraima, northern Brazilian Amazonia. Where: Y = total height (m); X = stem diameter (cm); $\beta_0, \beta_1, \beta_2$ = coefficients of the equations.

Equation number	Allometric models 1	Type
1	$Y = \beta_0 + \beta_1 \times X$	Linear
2	$Y = \beta_0 + \beta_1 \times \ln X$	Natural Logarithm
3	$Y = \beta_0 \times X^{\beta_1}$	Power Function
4	$Y = \frac{\beta_0 \times X}{\beta_1 + X}$	Michaelis-Menten
5	$Y = \beta_0 \times \exp(\beta_1 X)$	Exponential
6	$Y = \beta_0 \times \exp\left(\frac{\beta_1}{X}\right)$	Modified Exponential
7	$Y = \frac{\beta_0}{1 + \left(\frac{X}{\beta_1}\right)^{\beta_2}}$	Logistic Power
8	$Y = \beta_0 \times \beta_1^X \times X^{\beta_2}$	Modified Hoerl
9	$Y = \beta_0 \times (1 - \exp(-\beta_1 X))$	Weibull Function
10	$Y = \beta_0 \times \exp(-\exp(\beta_1 - \beta_2 X))$	Gompertz Function
11	$Y = \beta_0 + \beta_1 X + \beta_2 X^2$	Polynomial (2nd Order)
12	$Y = \frac{\beta_0}{(1 + \beta_1 \times \exp(-\beta_2 X))}$	Logistic

¹ Models are based on the following sources: Feldpausch *et al.* (2011), Feldpausch *et al.* (2012), Hess *et al.* (2014), Hulshof *et al.* (2015), Hyams (2016), Vibrans *et al.* (2015), and Zhang *et al.* (2014).

All 65 data pairs (H:D) were used as a basis to examine whether models previously published for the tropics accurately predicted tree total height in the study area. We used two model families as reference: (i) one climate-based model relating stem diameter to total height in association with a climate variable (E) representing the local climatic characteristics (Chave *et al.* 2014), and (ii) three Weibull-H general allometric models (Pantropical; South American Continent; Guyana Shield region) used to estimate total height using only stem diameter as the independent variable (Feldpausch *et al.* 2012). These models were chosen because they were derived from studies using large databases that resulted in parsimonious equations with high predictive power. Besides this, they are simple models that are widely used in estimates involving Amazonian forests. The comparison between predicted values of all models was performed by analysis of residuals (%).

RESULTS

The most parsimonious models to predict total tree height as a function of stem diameter were nonlinear (Table 3). All five models ranked in Table 3 are similarly supported considering the AIC -157-159. However, based on our criteria for choosing the best-performing model, the Michaelis-Menten model ($S_{yx} = 3.35$; $R^2 = 0.715$; AIC = 157.1) had the best fit, as well as less complexity and higher generality as compared to the other models. This model shows higher slope in the asymptotic curvature (lower growth in height) for $D > 40$ cm.

The analysis of residuals indicated that 80-85% (frequency) of the estimated values for the most parsimonious model (Michaelis-Menten) were in the $\pm 10\%$ error range (Figure 2). However, $\sim 11\%$ of the predicted tree heights calculated by this model were overestimates ($> 20\%$ error) for individuals with diameters between 20 and 40 cm.

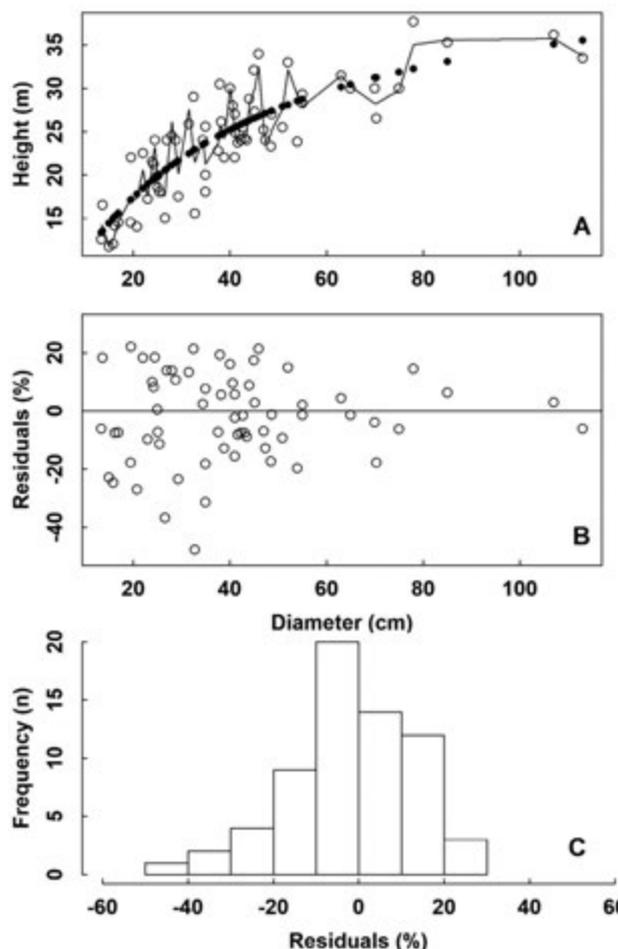


Figure 2. Best-performing allometric model (Michaelis-Menten) fitted to predict total height from stem diameter for trees in an ecotone zone of northern Brazilian Amazonia. Where: A = observed values (empty circles), estimated values (black circles) and black line (smoothed fit, 10%), B = dispersion of residuals (%), C = distribution of frequencies of occurrence of residuals (n).

Table 3. Allometric models with the best fit for estimating total height based on the stem diameter of trees in forests in a northern Brazilian Amazonian ecotone. Where: Y = total height (m); X = stem diameter (cm); $\beta_0, \beta_1, \beta_2$ = coefficients of the equations; S_{yx} = standard error of the estimate (m); R^2_{adj} = adjusted coefficient of determination; AICc = Akaike Information Criterion with correction.

Type	Allometric models	β_0	β_1	β_2	S_{yx}	R^2_{adj}	AICc
Michaelis-Menten	$Y = \frac{\beta_0 \times X}{\beta_1 + X}$	45.8528	32.8330	-	3.347	0.7149	157.09
Natural Logarithm	$Y = \beta_0 + \beta_1 \times \ln X$	-15.3629	10.9623	-	3.350	0.7144	157.21
Modified Hoerl	$Y = \beta_0 \times \beta_1^x \times X^{\beta_2}$	17.2660	0.000035	0.1725	3.369	0.7158	159.01
Logistic Power	$Y = \frac{\beta_0}{1 + \left(\frac{X}{\beta_1}\right)^{\beta_2}}$	43.6264	29.7079	-1.0709	3.372	0.7152	159.16
Modified Exponential	$Y = \beta_0 \times \exp\left(\frac{\beta_1}{X}\right)$	38.7760	-16.4933	-	3.393	0.7071	158.85

General models in the literature generated overestimated (Weibull) and underestimated (climate-based) values for total height as compared to our best nonlinear model (Michaelis-Menten), specially for trees > 30 cm in diameter (Figure 3). The mean tree height for all individuals sampled in the eastern portion of Maracá (mean \pm CI_{0.05} = 24.1 \pm 1.5 m; range = 11.7 - 37.7 m) was higher than the heights estimated by the climate-based model (21.8 \pm 1.3 m; 12.3 - 36.5 m). On the other hand, it was lower than the heights estimated by the

Weibull models for the Pantropical region (26.0 \pm 1.6 m; 14.0 - 41.7 m), the South American Continent (26.2 \pm 1.4 m; 14.5 - 38.9 m) and the Guyana Shield region (30.3 \pm 1.5 m; 16.6 - 41.7 m), this last mean representing the ecoregion that contains the study area. The analysis of residuals indicated that the climate-based model we tested underestimated the predicted values by 8.0%, while the three general Weibull models overestimated the predicted values by 10.0%, 11.3% and 29.0%, respectively (Figure 4).

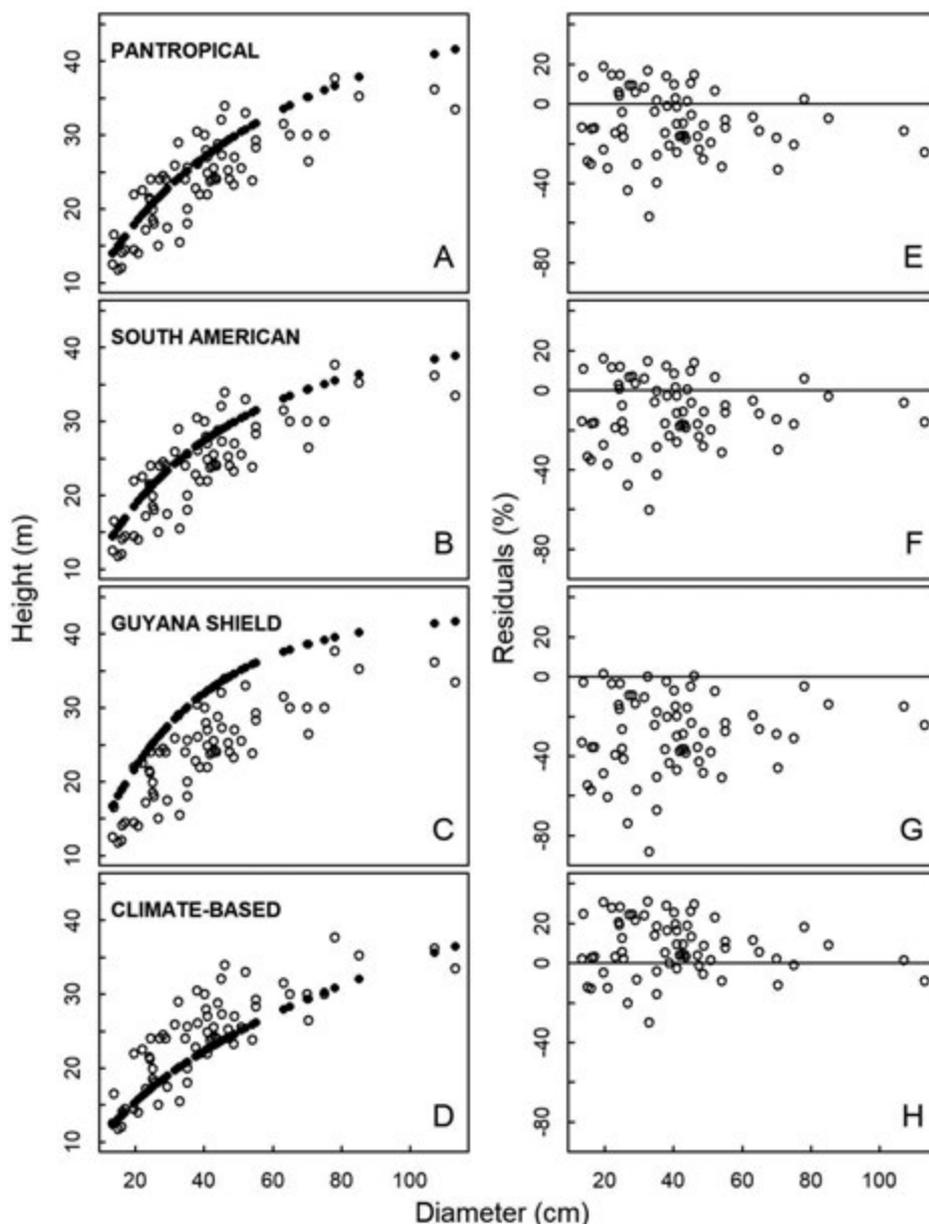


Figure 3. Analysis of residuals for Weibull (Feldpausch *et al.* 2012) and climate-based (Chave *et al.* 2014) height models when compared to observations in our study area (ecotone forest, Maracá Island, northern Brazilian Amazon). (i) A, B, C, D = fitted regression lines where hollow circles represent 65 pairs of H-D values (H = height, m / D = stem diameter, cm) observed in the field, and black circles represent results of the equation used for analysis of residuals, and (ii) E, F, G, H = plots of the residuals. Models tested: Pantropical ($H = 50.874 \times (1 - \exp(-0.042 \times D^{0.76}))$), South American ($H = 42.574 \times (1 - \exp(-0.0482 \times D^{0.8307}))$), Guyana Shield region ($H = 42.845 \times (1 - \exp(-0.0433 \times D^{0.9372}))$), and Climate-Based ($\ln(H) = 0.893 - E + 0.760 \times \ln(D) - 0.0340 \times (\ln(D))^2$, where $E = 0.1290219$).

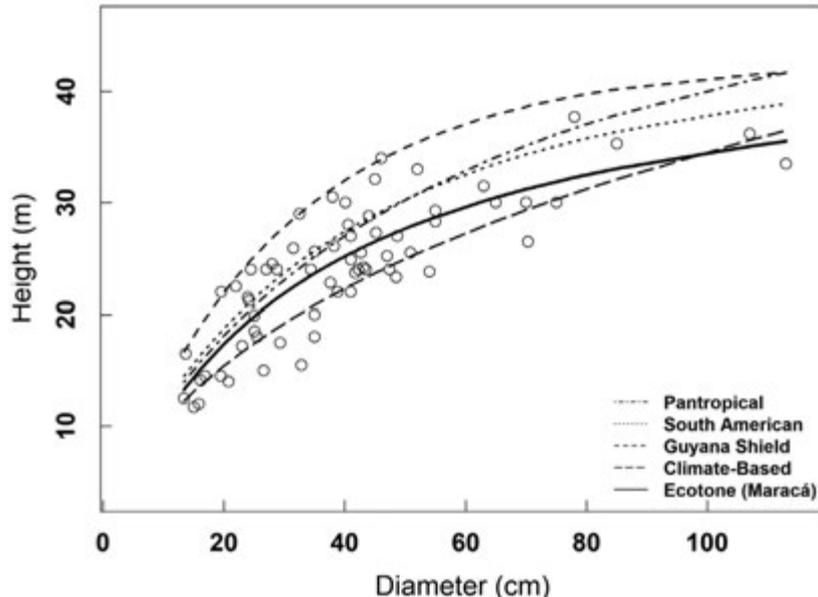


Figure 4. Comparison between general tropical models and the model with the best fit (Michaelis-Menten) for estimating tree height in an ecotone forest region in northern Brazilian Amazonia.

DISCUSSION

The most parsimonious nonlinear allometric models for calculating height from diameter in this study are the first specifically estimated for the ecotone forests on the southern edge of the Guyana Shield in the northern Brazilian Amazon. Nonlinear models relating H to D have also been put forward as general models in studies conducted in other specific regions of the Amazon basin (Nogueira *et al.* 2008b; Hess *et al.* 2014) or in different tropical macro-regions (Feldpausch *et al.* 2011; Feldpausch *et al.* 2012). This implies a regular H:D relationship, but this generality does not exclude site-specific height-diameter models to provide better estimates of stand-level biomass as compared to estimates using observed height, as stipulated by Sullivan *et al.* (2018). In addition, obtaining models from a methodological solution constructed with variables derived from direct measurements in natural treefalls (live or recently dead) representing individuals that are physically intact (no hollow or broken trunks and free of rotting signs) is an advantageous alternative because (i) it can facilitate obtaining a minimum set of sample units (50) that are totally independent and spatially representative of the structure and species composition of the forest formation at a mesoscale (e.g., a 25-km² PPBio grid), (ii) it can reduce the cost of obtaining allometric equations by destructive methods (e.g., displacement of large teams and higher costs for purchase and maintenance of equipment), and (iii) it can reduce errors when indirect measurements of total height of standing trees are obtained from technologies such as rangefinder cameras or clinometers (e.g., problems with observing the tree tops due to a closed canopy). Thus, a careful sampling of recent treefalls (live or recently dead)

can support fully randomized and independent sample units, ensuring, for example, an unbiased spatial distribution of species with different growth patterns, trunk-diameter categories and wood densities, or when access to equipment and resources for extra field effort is limited.

The coefficients of determination (0.71 - 0.72) of our best model (Michaelis-Menten) could be considered low and related to an insufficient number of samples (cf. Hunter *et al.* 2013), or to the disproportionality in the number of sampled individuals in the largest and smallest diameter classes as compared to the structural distribution normally found in the ecotone zone (cf. Segura and Kanninen 2005). However, our sampling effort (n = 65) and the distribution of samples in the larger diameter classes (n = 14; > 50 cm) increase the probability that our site-specific models have better explanatory power than do those produced by regional biogeographical models, as pointed out by Sullivan *et al.* (2018). Thus, the low values of the coefficients of determination in our study area do not indicate less predictive capacity, as exemplified by Huang *et al.* (1992) in a study with thousands of felled trees in Alberta (Canada). In any case, allometric models will always be adopted with some degree of uncertainty, but the uncertainties must be sufficiently understood as part of a realistic model that most accurately represents the specific environmental attributes of the studied site.

Our best site-specific model (Michaelis-Menten) aggregates structural variability and species composition across the mosaic of distinct forest types (seasonal and ombrophilous) that characterize this ecotone zone in northern Amazonia. Because the climatic conditions in the eastern portion of Maracá act equally on the forest types forming the ecotone

zone, heterogenic growth among tree species and individuals can be considered to be a phylogenetic sign associated with the micro-environmental conditions. These conditions induce natural biometric variations between H and D, as pointed out by Hulshof *et al.* (2015) and Alves and Santos (2002). For example, in Maracá the forests located in environments with higher hydro-edaphic restrictions are likely to have the morphometric variability of individuals influenced by seasonal anoxia (seasonal flooding) and soil with high Fe⁺² content (Villacorta 2017). These restrictive conditions in Maracá have been highlighted as a probable environmental limitation acting on the increase in height as a function of stem diameter when compared to less-restrictive environments (Ramírez-Narváez 2017). Differences in tree height between forest types along a topographic gradient were also found in central Amazonia (Suwa *et al.* 2016). However, although mathematical distinctions in the H:D relation may exist at the microscale for specific species in the different forest types in the ecotone zone, there is no doubt that, at the level of the major forest formation, the growth trajectories are governed by common environmental fluctuations. Our accuracy measures for the best model support this assertion (standard error of the estimate = ~3.3 m), because the spread of points around the predicted values from the true regression line could be considered to represent a substantial bias due to different forest types and environmental filters acting in the ecotone zone. However, this bias is very close to values obtained by other regional studies based on larger datasets, as in Cassol *et al.* (2018), which indicated an accuracy between 2.3 and 3.0 m for different models formulated to estimate the height of trees in two secondary-forest sites in Brazilian Amazonia. This implies that our best allometric relationship expresses the shared environmental dependence within a standard of accuracy similar to other studies using larger databases.

Our results imply that site-specific models in the study region are preferable for estimating total tree height as a function of stem diameter at the forest-formation level. Our site-specific model can be a useful option for evaluations at landscape scale (ecotone region), when there are uncertainties regarding the specific forest type (e.g. ombrophilous or seasonal), or when comparisons are made with other studies. The inter-model comparison we performed indicated that none of the previously published allometric models relating H to D for tropical ecosystems (see Feldpausch *et al.* 2012; Chave *et al.* 2014) produced accurate values for the study area. All of the general models we tested caused tree-height overestimations (10 - 29%; Weibull models) or underestimations (8%; climate-based model) for predicted values when compared with the site-specific models from the present study. Similar observations have been made by other authors, indicating that even small inaccuracies derived from the use of general allometric equations can result in over or underestimations of biomass or carbon when applied to trees in a specific forest type in the Amazon (Nogueira *et al.* 2008a; Nogueira *et al.* 2008b; Hunter *et al.*

2013). Similarly, our models can be expected to perform poorly if applied to other forest types in different tropical regions, and should be used with caution in these cases.

Because general models fail to accurately predict tree height when applied to specific locations, the biomass estimates they provide will also be inaccurate. This means that locally derived allometric equations are needed that either use measured values of both height and diameter or that relate biomass directly to diameter for trees in the location in question (Sullivan *et al.* 2018). Our study confirms the importance of tree height shown by Feldpausch *et al.* (2012) and demonstrates the need to represent its effect, either explicitly or implicitly, through locally derived allometric equations. This concern is recurrent in Amazonian studies carried out at the macroscale (e.g. Mitchard *et al.* 2014). Therefore, site-specific models should receive more attention, especially in peripheral areas of northern Amazonia, while general models (H:D) should be used with caution because they may favor a multiplication of errors throughout the process of calculating tree biomass and the stocks and flows of carbon for a specific region.

CONCLUSIONS

Nonlinear models had the best performance in describing the relation between total height and tree stem diameter in forests located in an ecotone zone in the northern Brazilian Amazon. All of the models were constructed using data obtained with an alternative methodology based on direct measurements in natural treefalls (live or recently dead trees). Adoption of models developed for specific sites improved our ability to estimate the total height of trees, especially in the forest types that constitute the ecotone zone, thereby increasing accuracy in tree biomass calculations in this portion of the Amazon. The best site-specific model derived in this study is a useful option for evaluations at the landscape level, but it should be adopted with caution for use elsewhere. Our results reduce the uncertainties generated by the application of general models to estimate tree height in this area, contributing to evidence that models need to be developed for specific forest types throughout Amazonia and in tropical forests generally. In our study area, general Weibull models overestimated and a climate-based model underestimated the predicted values of tree height by 10 - 29% and 8%, respectively. These commonly used models can generate multiplicative errors along the entire chain of calculations to estimate carbon stocks and flow in tree biomass.

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SUPPLEMENTARY MATERIAL (only available in the electronic version)

BARBOSA *et al.* Allometric models to estimate tree height in northern Amazonian ecotone forests

Table S1. Values of parameters (total height and stem diameter) measured in 65 individual trees observed in an ecotone zone (ombrophilous forest and seasonal forest) in northern Brazilian Amazonia. Indet. = indeterminate family or species and POM = point of measure.

Individual	Family	Species	Stem diameter (cm)	Total height (m)	POM (cm)
1	Fabaceae	Indet.	41.7	23.7	130
2	Fabaceae	Indet.	41.0	24.9	130
3	Lecythidaceae	<i>Couratari cf. tauari</i>	78.0	37.7	300
4	Sapotaceae	<i>Pradosia surinamensis</i>	23.0	17.2	130
5	Sapotaceae	<i>Pradosia surinamensis</i>	31.5	25.9	130
6	Sapotaceae	<i>Ecclinusa</i> sp.	19.5	14.5	130
7	Fabaceae	<i>Peltogyne gracilipes</i>	35.0	20.0	130
8	Sapotaceae	<i>Ecclinusa</i> sp.	13.4	12.5	130
9	Sapotaceae	<i>Pradosia surinamensis</i>	38.2	26.1	170
10	Sapotaceae	<i>Pouteria</i> sp.	43.1	24.2	190
11	Anacardiaceae	Indet.	55.0	28.3	130
12	Indet.	Indet.	24.2	21.2	130
13	Indet.	Indet.	44.0	28.8	130
14	Indet.	Indet.	25.0	19.9	160
15	Fabaceae	<i>Peltogyne gracilipes</i>	19.6	22.0	145
16	Indet.	Indet.	48.7	27.0	130
17	Indet.	Indet.	43.5	24.0	190
18	Indet.	Indet.	37.6	22.8	130
19	Indet.	Indet.	41.0	22.0	130
20	Bignoniaceae	<i>Handroanthus serratifolius</i>	65.0	30.0	160
21	Indet.	Indet.	28.0	24.5	130
22	Tiliaceae	<i>Apeiba</i> sp.	29.3	17.5	130
23	Indet.	Indet.	34.4	24.0	130
24	Sapotaceae	Indet.	16.2	14.1	150
25	Sapotaceae	<i>Pradosia surinamensis</i>	40.6	28.0	130
26	Sapotaceae	<i>Pradosia surinamensis</i>	40.1	30.0	180
27	Anacardiaceae	Indet.	47.4	24.0	200
28	Indet.	Indet.	45.0	32.1	130
29	Melastomataceae	Indet.	55.0	29.3	290
30	Fabaceae	Indet.	15.0	11.7	130
31	Chrysobalanaceae	<i>Licania discolor</i>	47.0	25.2	180
32	Fabaceae	<i>Peltogyne gracilipes</i>	54.0	23.8	190
33	Sapotaceae	<i>Pouteria</i> cf. <i>surumuensis</i>	45.2	27.3	130

Table S1. Continued

Individual	Family	Species	Stem diameter (cm)	Total height (m)	POM (cm)
34	Sapotaceae	Indet.	48.5	23.3	220
35	Sapotaceae	<i>Pradosia surinamensis</i>	75.0	30.0	340
36	Fabaceae	<i>Peltogyne gracilipes</i>	85.0	35.3	190
37	Fabaceae	<i>Hymenea</i> sp.	107.0	36.2	180
38	Burseraceae	<i>Protium</i> sp.	41.0	27.0	130
39	Indet.	Indet.	63.0	31.5	130
40	Sapotaceae	<i>Ecclinusa guianensis</i>	27.0	24.0	130
41	Fabaceae	<i>Ormosia</i> sp.	70.0	30.0	130
42	Burseraceae	<i>Protium</i> sp.	113.0	33.5	130
43	Fabaceae	<i>Centrolobium paraense</i>	22.0	22.5	180
44	Fabaceae	<i>Peltogyne gracilipes</i>	52.0	33.0	385
45	Sapotaceae	Indet.	25.5	18.0	140
46	Indet.	Indet.	15.9	12.0	130
47	Sapotaceae	<i>Pradosia surinamensis</i>	20.8	14.0	180
48	Sapotaceae	<i>Pradosia surinamensis</i>	70.3	26.5	230
49	Burseraceae	<i>Protium</i> sp.	28.8	24.0	180
50	Burseraceae	<i>Protium</i> sp.	13.7	16.5	160
51	Malpighiaceae	<i>Byrsonima</i> sp.	24.0	21.5	130
52	Fabaceae	Indet.	25.1	18.5	160
53	Burseraceae	<i>Protium</i> sp.	42.3	24.0	180
54	Indet.	Indet.	38.0	30.5	130
55	Indet.	Indet.	26.6	15.0	130
56	Sapotaceae	<i>Pouteria</i> cf. <i>surumuensis</i>	24.5	24.0	170
57	Indet.	Indet.	32.5	29.0	130
58	Fabaceae	<i>Peltogyne gracilipes</i>	46.0	34.0	200
59	Fabaceae	<i>Peltogyne gracilipes</i>	42.7	25.5	200
60	Indet.	Indet.	32.8	15.5	130
61	Sapotaceae	<i>Pradosia surinamensis</i>	35.0	18.0	260
62	Sapotaceae	<i>Pradosia surinamensis</i>	50.9	25.5	450
63	Sapotaceae	<i>Pradosia surinamensis</i>	35.0	25.6	180
64	Sapotaceae	<i>Ecclinusa guianensis</i>	38.8	22.0	130
65	Fabaceae	cf. <i>Inga</i> sp.	16.9	14.5	130



Figure S1. Examples of the sampled units (fallen trees) indicating the presence of persistent leaves and/or fresh stem.