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), the adjusted coefficient of determination (R²_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 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 refinem 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 ombrophílicas e sazonais no estado de Roraima, na Amazônia Norte. Diâmetro do tronco e altura total foram medidos de forma direta em 65 árvores tombadas recentemente (vivas e mortas). Regressões lineares e não-lineares 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 (R²_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 ecotônicas estudadas em Roraima, porque ele reflete realista e 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
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” (Feldpausch et al. 2014). 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 kumbiana Hoo.k.f. (Chrysobalanaceae) and Pelogyne 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...
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
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_e = higher goodness of fit), reflecting the accuracy of the fitted regression; (2) adjusted coefficient of determination (higher R²_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_e) could be ordered by higher explanatory power (R²_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 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        |

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); β_1, β_2, and β_3 = coefficients of the equations.

| Equation number | Allometric models 1 | Type               |
|-----------------|---------------------|--------------------|
| 1               | Y = β_1 + β_2 X    | Linear             |
| 2               | Y = β_1 + β_2 lnX   | Natural Logarithm  |
| 3               | Y = β_1 X + β_2     | Power Function     |
| 4               | Y = β_1 X / β_2 + X | Michaelis-Menten   |
| 5               | Y = β_1 X exp(β_2 X)| Exponential        |
| 6               | Y = β_1 X exp(β_2 X)| Modified Exponential |
| 7               | Y = β_1 exp(β_2 X)  | Logistic Exponential |
| 8               | Y = β_1 β_2 X + X   | Modified Hoerl     |
| 9               | Y = β_1 X (1 - exp(β_2 X)) | Weibull Function |
| 10              | Y = β_1 X exp(−exp(β_2 X)) | Gompertz Function |
| 11              | Y = β_1 + β_2 + β_3 X | Polynomial (2nd Order) |
| 12              | Y = β_1 X + β_2 X exp(−β_3 X) | Logistic |

* Models are based on the following sources: Feldpausch et al. (2011), Feldpausch et al. (2012), Hess et al. (2014), Hulshof et al. (2015), Hyam (2016), Venter 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 (Pan-tropical; 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 ±10% error range (Figure 2). However, ~11% of the predicted tree heights calculated by this model were overestimates (> 20% error) for individuals with diameters between 20 and 40 cm.

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 | $\beta_0$ | $\beta_1$ | $\beta_2$ | $S_{yx}$ | $R^2_{adj}$ | 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        | $Y = \beta_0 \times \beta_1^\ast \times X^{\beta_2}$ | 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 ± CI_{0.05} = 24.1 ± 1.5 m; range = 11.7 - 37.7 m) was higher than the heights estimated by the climate-based model (21.8 ± 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 ± 1.6 m; 14.0 - 41.7 m), the South American Continent (26.2 ± 1.4 m; 14.5 - 38.9 m) and the Guyana Shield region (30.3 ± 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](https://example.com/figure3.png)

**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 (ectone 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 \( H = 50.874 \times (1 - \exp(-0.042 \times D^{0.784})) \), South American \( H = 42.574 \times (1 - \exp(-0.0482 \times D^{0.8307})) \), Guyana Shield \( H = 42.845 \times (1 - \exp(-0.0433 \times D^{0.9372})) \), and Climate-Based \( \ln(H) = 0.893 - E + 0.760 \times \ln(D) - 0.0340 \times (\ln(D))^2 \), where \( E = 0.1290219 \).
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 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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REFERENCES

Alves, L.F.; Santos, E.A.M. 2002. Tree allometry and crown shape of four tree species in Atlantic rain forest, south-east Brazil. *Journal of Tropical Ecology*, 18: 245–260.

Barbosa, R.I. 1997. *Distribuição das chuvas em Roraima*. In: Barbosa, R.I.; Ferreira, E.G.; Castellon, E.G. (Eds.). *Homem, Ambiente e Ecologia no Estado de Roraima*. Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas, Brazil, p.325-335.

Barbosa, R.I.; Castilho, C.V.; Perdiz, R.O.; Damasco, G.; Rodrigues, R.; Fearnside, P.M. 2017. Decomposition rates of coarse woody debris in undisturbed Amazonian seasonally flooded and unflooded forests in the Rio Negro-Rio Branco Basin in Roraima, Brazil. *Forest Ecology and Management*, 397: 1-9.

Barni, P.E.; Manzi, A.O.; Conde, T.M.; Barbosa, R.I.; Fearnside, P.M. 2016. Spatial distribution of forest biomass in Brazil’s state of Roraima, northern Amazonia. *Forest Ecology and Management*, 377: 170-181.

Barni, P.E.; Pereira, V.B.; Manzi, A.O.; Barbosa, R.I. 2015. Deforestation and forest fires in Roraima and their relationship with phytoclimatic regions in the Northern Brazilian Amazon. *Environmental Management*, 55: 1124-1138.

Blanchard, E.; Birnbaum, P.; Ibanez, T.; Boutreux, T.; Antin, C.; Ploton, P.; et al. 2016. Contrasted allometries between stem diameter, crown area, and tree height in five tropical biogeographic areas. *Trees*, 30: 1953-1968.

Brienen, R.J.; Phillips, O.L.; Feldpausch, T.R.; Gloor, E.; Baker, T.R.; Lloyd, J.; et al. 2015. Long-term decline of the Amazon carbon sink. *Nature*, 519: 344-348.

Brokaw, N.; Thompson, J. 2000. The H for DBH. *Forest Ecology and Management*, 129: 89-91.

Brown, S. 1997. *Estimating biomass and biomass change of tropical forests: A Primer*, vol. 134. FAO, Roma. 55p.

Carvalho, L.C.S.; Fearnside, P.M.; Nascimento, M.T.; Barbosa, R.I. 2018. Amazon soil charcoal: Pyrogenic carbon stock depends of ignition source distance and forest type in Roraima, Brazil. *Global Change Biology*, 24: 4122-4130.

Cassol, H.L.G.; Shimabukuro, Y.E.; Carreiras, J.M.B.; Moraes, E.C. 2018. Improved tree height estimation of secondary forests in the Brazilian Amazon. *Acta Amazónica*, 48: 179-190.

Castilho, C.V.; Schiatti, J.; Freitas, M.A.; Araújo, M.C.; Coelho, E.; Magnusson, W.; Costa, F. 2014. Manual para medição e marcação de árvores em grades e módulos RAPELD do PPBio (https://ppbio.inpa.gov.br/sites/default/files/Protocolo_estrutura_vegetacao_2014_0.pdf), Accessed on 18 February 2016.

Chave, J.; Andalo, C.; Brown, S.; Cairns, M.A.; Chambers, J.Q.; Eamus, D.; et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia*, 145: 87-99.

Chave, J.; Réjou-Méchain, M.; Búrquez, A.; Chidumayo, E.; Colgan, M.S.; Delitti, W.B.C.; et al. 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology*, 20: 3177–3190.

Couto-Santos, F.R.; Luizão, F.J.; Carneiro-Filho, A. 2014. The influence of the conservation status and changes in the rainfall regime on forest-savanna mosaic dynamics in Northern Brazilian Amazonia. *Acta Amazônica*, 44: 197-206.

Doughty, C.E.; Metcalfe, D.B.; Girardin, C.A.; Amezquita, F.F.; Cabrera, D.G.; Huasco, W.H.; et al. 2015. Drought impact on forest carbon dynamics and fluxes in Amazonia. *Nature*, 519: 78-82.

Fearnside, P.M. 2018. Brazil’s Amazonian forest carbon: the key to Southern Amazonia’s significance for global climate. *Regional Environmental Change*, 18: 47-61.

Fearnside, P.M.; Ferraz, J. 1995. A conservation gap analysis of Brazil’s Amazonian vegetation. *Conservation Biology*, 9: 1134-1147.

Feldpausch, T.R.; Banin, L.; Phillips, O.L.; Baker, T.R.; Lewis, S.L.; Quesada, C.A.; et al. 2011. Height-diameter allometry of tropical forest trees. *Biogeosciences*, 8: 1081-1106.

Feldpausch, T.R.; Lloyd, J.; Lewis, S.L.; Brienen, R.J.W.; Gloor, E.; Monteagudo Mendoza, A.; et al. 2012. Tree height integrated into pan-tropical forest biomass estimates. *Biogeosciences Discussions*, 9: 2567-2622.

Goodman, R.C.; Phillips, O.L.; Baker, T.R. 2014. The importance of crown dimensions to improve tropical tree biomass estimates. *Ecological Application*, 24: 680-698.

Hess, A.E.; Braz, E.M.; Thaines, E.; Mattos, P.P. 2014. Adjustment of the hypsometric relationship for species of Amazon Forest. *Ambiência*, 10: 21-29.

Higuchi, N.; Santos, J.; Ribeiro, R.J.; Minette, L.; Biot, Y. 1998. Biomassa da parte aérea da vegetação da floresta úmida de terra-firme da Amazônia brasileira. *Acta Amazônica*, 28: 153-166.

Houghton, R.A.; Hall, E.; Goetz, S.J. 2009. Importance of biomass in the global carbon cycle. *Journal of Geophysical Research: Biogeosciences* (2005–2012), 114(G2): G00E03.

Huang, S.; Titus, S.J.; Wiens, D.P. 1992. Comparison of nonlinear height–diameter functions for major Alberta tree species. *Canadian Journal of Forest Research*, 22: 1297-1304.

Hulshof, C.M.; Swenson, N.G.; Weiser, M.D. 2015. Tree height-diameter allometry across the United States. *Ecology & Evolution*, 5: 1193-1204.

Hunter, M.O.; Keller, M.; Victoria, D.; Morton, D.C. 2013. Tree height and tropical forest biomass estimation. *Biogeosciences*, 10: 8385-8399.

Hyams, D.G. 2016. *CurveExpert Professional Documentation* (Release 2.4.0), Trial Version (https://www.curveexpert.net/products/curveexpert-professional/). Accessed on 23 April 2016.

INPE. 2017. Projeto PRODES: Monitoramento da Floresta Amazônica Brasileira por Satélite. Instituto Nacional de Pesquisas Espaciais (INPE). São José dos Campos, São Paulo, Brazil (http://www.obt.inpe.br/prodes/index.html). Accessed on 25 March 2017.

INPE. 2017. Projeto PRODES: Monitoramento da Floresta Amazônica Brasileira por Satélite. Instituto Nacional de Pesquisas Espaciais (INPE). São José dos Campos, São Paulo, Brazil (http://www.obt.inpe.br/prodes/index.html). Accessed on 25 March 2017.
Johnson, J.B.; Omland, K.S. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution, 19: 101-108.

Lima, A.J.N.; Suwa, R.; de Mello Ribeiro, G.H.P.; Kajimoto, T.; dos Santos, J.; da Silva, R.P.; et al. 2012. Allometric models for estimating above- and below-ground biomass in Amazonian forests at São Gabriel da Cachoeira in the upper Rio Negro, Brazil. Forest Ecology and Management, 277: 163-172.

Malhi, Y.; Phillips, O.L.; Lloyd, J.; Baker, T.; Wright, J.; Almeida, S.; et al. 2002. An international network to monitor the structure, composition and dynamics of Amazonian forests (RAINFOR). Journal of Vegetation Science, 13: 439-450.

Milliken, W.; Ratter, J.A. 1998. The vegetation of the Ilha de Maracá. In: Milliken, W.; Ratter, J.A. (Eds.). Maracá: the biodiversity and environment of an Amazonian rainforest. Wiley, Chichester, UK, p.71-112.

Mitchard, E.T.A.; Feldpausch, T.R.; Brienen, R.J.W.; Lopez-Gonzalez, G.; Monteagudo, A.; Baker, T.R.; et al. 2014. Markedly divergent estimates of Amazon forest carbon density from ground plots and satellites. Global Ecology and Biogeography, 23: 935–946.

Nascimento, M.T.; Barbosa, R.I.; Dexter, K.G.; Castilho, C.V.; Silva Carvalho, L.C.; Villela, D.M. 2017. Is the Peltogyne gracilipes monodominant forest characterised by distinct soils? Acta Oecologica, 85: 104-107.

Nascimento, M.T.; Barbosa, R.I.; Villela, D.M.; Proctor, J. 2007. Above-ground biomass changes over an 11-year period in an Amazon monodominant forest and two other lowland forests. Plant Ecology 192: 181-191.

Nascimento, M.T.; Carvalho, L.C.S.; Barbosa, R.I.; Villela, D.M. 2014. Variation in floristic composition, demography and above-ground biomass over a 20-year period in an Amazonian monodominant forest. Plant Ecology & Diversity, 7: 293-303.

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. Forest Ecology and Management, 256: 1853-1867.

Nogueira, E.M.; Nelson, B.W.; Fearnside, P.M.; França, M.B.; Oliveira, A.C.A. 2008b. Tree height in Brazil’s ‘arc of deforestation’: Shorter trees in south and southwest Amazonia imply lower biomass. Forest Ecology and Management, 255: 2963-2972.

Nogueira, E.M.; Yanai, A.M.; Fonseca, E.O.; Fearnside, P.M. 2015. Carbon stock loss from deforestation through 2013 in Brazilian Amazonia. Global Change Biology, 21: 1271–1292.

Overman, J.P.M.; Witte, H.J.L.; Saldarriaga, J.G. 1994. Evaluation of regression models for above-ground biomass determination in Amazon rainforest. Journal of Tropical Ecology, 10: 207-218.

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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 | *Couratari cf. tauri*    | 78.0              | 37.7            | 300      |
| 4          | Sapotaceae | *Pradosia surinamensis*       | 23.0              | 17.2            | 130      |
| 5          | Sapotaceae | *Pradosia surinamensis*       | 31.5              | 25.9            | 130      |
| 6          | Sapotaceae | *Ecclinusa sp.*              | 19.5              | 14.5            | 130      |
| 7          | Fabaceae | *Peltogyne gracilipes*       | 35.0              | 20.0            | 130      |
| 8          | Sapotaceae | *Ecclinusa sp.*              | 13.4              | 12.5            | 130      |
| 9          | Sapotaceae | *Pradosia surinamensis*       | 38.2              | 26.1            | 130      |
| 10         | Sapotaceae | *Pouteria 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 | *Peltogyne gracilipes*       | 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 | *Handroanthus serratifolius* | 65.0              | 30.0            | 160      |
| 21         | Indet.   | Indet.                        | 28.0              | 24.5            | 130      |
| 22         | Tiliaceae | Indet.                        | 29.3              | 17.5            | 130      |
| 23         | Indet.   | Indet.                        | 34.4              | 24.0            | 130      |
| 24         | Sapotaceae | Indet.                    | 16.2              | 14.1            | 150      |
| 25         | Sapotaceae | *Pradosia surinamensis*       | 40.6              | 28.0            | 130      |
| 26         | Sapotaceae | *Pradosia surinamensis*       | 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 | *Licania discolor* | 47.0              | 25.2            | 180      |
| 32         | Fabaceae | *Peltogyne gracilipes*       | 54.0              | 23.8            | 190      |
| 33         | Sapotaceae | *Pouteria cf. surinamensis* | 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 | *Pradosia surinamensis*       | 75.0              | 30.0            | 340      |
| 36         | Fabaceae | *Peltogyne gracilipes*       | 85.0              | 35.3            | 190      |
| 37         | Fabaceae | *Hymenea sp.*              | 107.0             | 36.2            | 180      |
| 38         | Burseraceae | *Protonum sp.*             | 41.0              | 27.0            | 130      |
| 39         | Indet.   | Indet.                        | 63.0              | 31.5            | 130      |
| 40         | Sapotaceae | *Ecclinusa guianensis*       | 27.0              | 24.0            | 130      |
| 41         | Fabaceae | *Ormosia sp.*              | 70.0              | 30.0            | 130      |
| 42         | Burseraceae | *Protonum sp.*             | 113.0             | 33.5            | 130      |
| 43         | Fabaceae | *Centrolobium parasiens*     | 22.0              | 22.5            | 180      |
| 44         | Fabaceae | *Peltogyne gracilipes*       | 52.0              | 33.0            | 385      |
| 45         | Sapotaceae | Indet.                    | 25.5              | 18.0            | 140      |
| 46         | Indet.   | Indet.                        | 15.9              | 12.0            | 130      |
| 47         | Sapotaceae | *Pradosia surinamensis*       | 20.8              | 14.0            | 180      |
| 48         | Sapotaceae | *Pradosia surinamensis*       | 70.3              | 26.5            | 230      |
| 49         | Burseraceae | *Protonum sp.*             | 28.8              | 24.0            | 180      |
| 50         | Burseraceae | *Protonum sp.*             | 13.7              | 16.5            | 160      |
| 51         | Malpighiaceae | *Byronima sp.*           | 24.0              | 21.5            | 130      |
| 52         | Fabaceae | Indet.                        | 25.1              | 18.5            | 160      |
| 53         | Burseraceae | *Protonum sp.*             | 42.3              | 24.0            | 180      |
| 54         | Indet.   | Indet.                        | 38.0              | 30.5            | 130      |
| 55         | Indet.   | Indet.                        | 26.6              | 15.0            | 130      |
| 56         | Sapotaceae | *Pouteria cf. surinamensis* | 24.5              | 24.0            | 170      |
| 57         | Indet.   | Indet.                        | 32.5              | 29.0            | 130      |
| 58         | Fabaceae | *Peltogyne gracilipes*       | 46.0              | 34.0            | 200      |
| 59         | Fabaceae | *Peltogyne gracilipes*       | 42.7              | 25.5            | 200      |
| 60         | Indet.   | Indet.                        | 32.8              | 15.5            | 130      |
| 61         | Sapotaceae | *Pradosia surinamensis*       | 35.0              | 18.0            | 260      |
| 62         | Sapotaceae | *Pradosia surinamensis*       | 50.9              | 25.5            | 450      |
| 63         | Sapotaceae | *Pradosia surinamensis*       | 35.0              | 25.6            | 180      |
| 64         | Sapotaceae | *Ecclinusa guianensis*       | 38.8              | 22.0            | 130      |
| 65         | Fabaceae | cf. *Inga 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.