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Significance of Topographic Gradient in Stem Diameter – Height Allometry for Precise Biomass Estimation of a Tropical Moist Forest in the Central Amazon

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Abstract

We developed a *stem diameter D-height* H allometric model that included variability in the *D-H* relationship along a topographic gradient. The study site was located along a belt transect (2500 × 20 m) established in a primary tropical forest near Manaus, Brazil. The transect included typical topography of the region, characterized by plateaus and valleys called "*baixios*". The *D-H* allometric model ($n = 1307$) indicated that potential tree height increased significantly, from 28 m at the lowest *baixio* plot to 35 m at the highest plateau plot. Consequently, by combining the *D-H* allometric model and an allometric equation with the variable D^2H, biomass was estimated for trees ($D > 10$ cm) in each sub-plot (20 × 20 m). Ignoring variability in the *D-H* relationship introduced wide-ranging error to biomass estimation; error values ranged from -5% at a *baixio* plot to +6% at a plateau plot. Average biomass was 317 ± 28 (SE) Mg ha^{-1}, and tree density and biomass fell significantly with decreasing relative elevation.

Discipline: Forestry and forest products
Additional key words: asymptotic height , Brazilian Amazon , REDD+

Introduction

Accurately estimating the forest biomass in the Amazon basin is crucial for evaluating the global carbon budget, as the Amazonian forest occupies a large portion of carbon stocks among terrestrial ecosystems[10]. The main topographic feature of the basin is a gently undulating landscape, called *terra firme*, composed of layers of alluvial soil. The vegetation structure within the *terra firme* varies depending on soil conditions[3, 9] along a topographic gradient characterized by sequentially-appearing plateaus and valleys called "*baixios*".

The relationship between stem diameter at breast height *D* and tree height *H* often varies within a given forest due to local-scale heterogeneity in climate[14], elevation1, and species[13]. Such local variation in the *D-H* relationship can also result in local variation in the biomass of the *terra firme*. However, almost all previous studies[3, 4, 9] have estimated biomass using allometric equations that only include the variable *D*, without accounting for *H*.

In the present study, biomass was estimated for a *terra firme* forest in the central Amazon by including local variation in the *D-H* relationship along a topographic gradient. A long belt transect (2500 × 20 m) was established near Manaus, Brazil (Fig. 1) and oriented to include major topographical components. First, we developed a *D-H* allometric model to estimate tree height with *D*, emphasizing possible changes in the *D-H* relationship along the topographic gradient. In particular, we focused on rela-

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tive elevation (i.e. the depth of a *baixio* relative to the plateau level) as the main topographic component, because soil conditions depend strongly on relative elevation[5, 7] and affect vegetation structure at the landscape level in this region[3, 9]. Second, to evaluate the significance of the topographic gradient of the *D-H* relationship used to estimate biomass, we compared biomass estimates based on two *D-H* allometric models including and excluding relative elevation. Finally, the significance of topographic gradients in biomass estimation at the landscape level in this region was discussed.

Materials and Methods

1. Study site

This study was conducted in the ZF-2 Experimental Forest of the National Institute for Amazon Research (INPA) near Manaus, Brazil (2°36'S 11°35'W). We used one of the two belt transects established in 1996 as permanent, long-term monitoring plots of the Jacaranda Project. This transect was 20 m wide by 2500 m long and oriented east-west (E-W); including “plateau”, “slope”, and ‘‘*baixio*” (valley bottom) sites (Fig. 1). The study site was dominated by dense *terra firme* forest[8]. The area also exhibited an apparent parallel change in clay content with relative elevation; soil textures at plateau, *baixio*, and slope sites ranged from very clayish and sandy to moderately clayish and sandy, respectively[7].

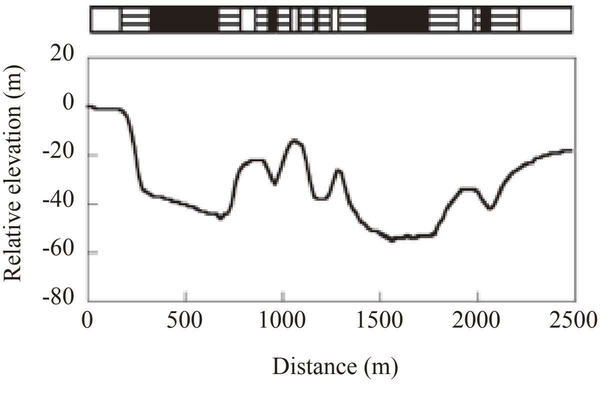

Fig. 1. Vertical profile of the belt transect (2500 m in length). The bar above the figure indicates topographic categories

Open, striped, and closed bars represent plateau, slope, and *baixio* sites, respectively.

2. Tree census

All trees ($D > 10$ cm) were marked, and values of D were recorded for 20 × 20-m sub-plots within the belt transect in 2000. For trees with buttresses, D was measured above the latter.

To assess the *D-H* relationship, 1307 individual trees ($D > 1$ cm) were sampled from part of the transect. The sampling area was selected at a distance of 0 to 760 m (Fig.1), encompassing wide-ranging clay content (3–36%) with varying topography[7]. Tree height was measured using a scale hypsometer.

3. Allometry to estimate tree height

The stem diameter D-height H relationship was preliminarily compared between two contrasting sites (Fig. 2): a plateau (0–200 m, $n = 493$; left-side plateau in Fig. 1) and a *baixio* (300–720 m, $n = 664$; the first *baixio* in Fig. 1) using the following hyperbolic equation[11]:

$$\frac{1}{H}=\frac{1}{aD}+\frac{1}{b} \quad , \tag{1}$$

where a and b are coefficients. The difference in the *D-H* relationship was tested using an F-test based on residuals. A significant difference in the *D-H* relationship was detected between the two sites (F-test, $p < 0.01$). Therefore, the following *D-H* allometric model was developed to express variability in the *D-H* relationships according

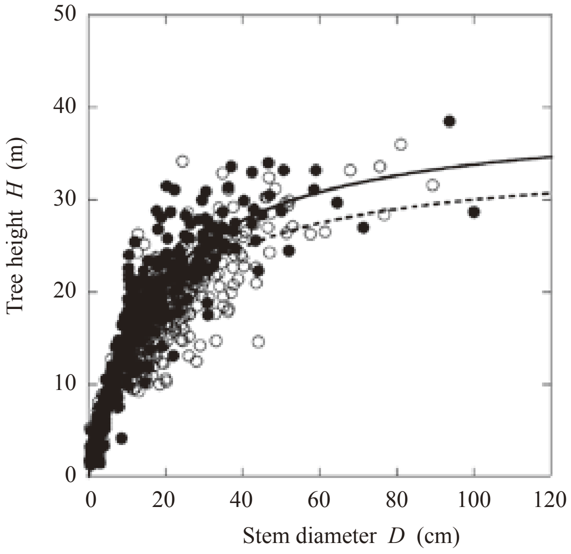

Fig. 2. Relationships between stem diameter at breast height *D* and tree height *H* for individual trees sampled from plateau- and *baixio*-dominated sites

Closed circles and solid lines, plateau-dominated sites; open circles and dashed lines, *baixio*-dominated sites. Each regression curve is derived from Eq. 1.

to topography:

$$\frac{1}{H}=\frac{1}{(c+dx_2)\,D}+\frac{1}{e+fx_2} \quad , \qquad (2)$$

where x_2 is the relative elevation with a standard point at the beginning of the transect (see the left side of Fig.1), and c, d, e, and f are coefficients. Here, $e + fx_2$ denotes the potential tree height specific to a site, since $e + fx_2 = \mathrm{H}|_{D\to\infty}$.

The nonlinear least-squares method based on the Levenberg-Marquardt algorithm (KaleidaGraph v4.1.0; Synergy Software, USA) was applied for Eqs. 1 and 2 and Akaike's information criterion (*AIC*) was used to determine the relative goodness of fit. The *AIC* was calculated based on the residual sum of squares (*RSS*) and the number of coefficients (*K*) as follows[2]: $AIC = n \ln (RSS / n) + 2K$, where n is the number of samples.

4. Allometry to estimate biomass

The following power equations were applied to estimate the whole-plant fresh weight F_w (kg); including above- and below-ground parts[12]:

$$\ln F_W = 0.99\ln(D^2H) - 2.65 \ , \ (R^2 = 0.98), \qquad (3)$$

where the unit of D^2H is cm^2 m. Equation 3 was derived from a dataset of harvested trees (n = 131) in a *terra firme* forest near the present study site. We confirmed that Eq. 3 allows biomass to be estimated more accurately than does the D-based power equation[12]. To calculate the whole-plant dry weight W_w, an average dry / fresh ratio of 0.584 was used[12], and the following allometric model was obtained:

$$\ln W_W = 0.99\ln(D^2H) - 3.19 \qquad (4)$$

Results

1. Development of allometric models to estimate tree height and tree weight

Maximum and average D were 114.2 cm and 13.7 ± 0.4 (SE) cm, respectively, and maximum and average H were 42.8 m and 13.3 ± 0.2 (SE) m, respectively. The regression analysis conducted using Eqs. 1 and 2 (Table 1) indicated that Eq. 2 was a better fit than Eq. 1 (*AIC* Eq. 2: 2591; *AIC* Eq. 1: 2616). In Eq. 2, the range of standard error for coefficient d included 0, indicating that the effect of relative elevation on the initial slope of Eq. 1 was not apparent. Consequently, a simpler equation was derived as follows:

$$\frac{1}{H}=\frac{1}{gD}+\frac{1}{h+ix_2} \quad , \qquad (5)$$

where g, h, and i are coefficients. The D-H relationship was fitted well by Eq. 5 (*AIC*: 2587, which was slightly lower than the *AIC* for Eq. 2; Fig. 3), hence Eq. 5 was selected as the best D-H allometric model for the subsequent analysis described below. The potential tree height, $h + ix_2$ in Eq. 5, increased from 35 m at *baixio* (-46 m in relative elevation) to 40 m at plateau (0 m in relative elevation) sites within the sampled area.

Equations 1 and 5 were incorporated into the D^2H-W_w

Table 1. Results of the regression of stem diameter and tree height relationship according to Eqs. 1, 2 and 5. Mean value, standard error SE, and upper and lower limits of 95 % confidence interval for each coefficient are shown

Coefficients	Mean	SE	Lower limit	Upper limit
Equation 1				
a	2.18	4.31×10^{-2}	2.11	2.25
b	37.49	6.01×10^{-1}	36.50	38.48
Equation 2				
c	2.21	8.19×10^{-2}	2.08	2.34
d	1.94×10^{-5}	3.37×10^{-3}	-5.53×10^{-3}	5.57×10^{-3}
e	39.8	9.75	38.19	41.4
f	9.94×10^{-2}	3.63×10^{-2}	3.96×10^{-2}	1.59×10^{-1}
Equation 5				
g	2.21	4.36×10^{-2}	2.14	2.28
h	39.8	7.67×10^{-1}	38.54	41.06
i	9.96×10^{-2}	1.81×10^{-2}	6.98×10^{-2}	1.29×10^{-1}

model in Eq. 4, and the following equations were derived, respectively:

$$W_{\mathrm{w}} = 0.0413\left(\frac{1}{2.18D^{3}}+\frac{1}{37.49D^{2}}\right)^{-0.99} \qquad (6)$$

$$W_{\mathrm{w}} = 0.0355\left[\frac{1}{2.21D^{3}}+\frac{1}{(39.80+0.0996x_{2})D^{2}}\right]^{-0.99} \qquad (7)$$

2. Biomass estimation along a topographic gradient

Values of D were obtained for all trees ($D > 10$ cm, $n = 2854$) within the belt transect. The tree densities of the 125 sub-plots (average ± SE: 571 ± 13 ha^{-1}; Fig.4a) were positively correlated with relative elevation ($r = 0.32$, $p < 0.001$). The average value of D was 21.7 ± 0.3 (SE) cm (Fig.4b), which was not significantly correlated with relative elevation ($r = -0.09$, $p > 0.05$). The average biomass estimate based on Eq. 7 was 316.6 ± 28.3 (SE) Mg ha^{-1} (Fig.4c), which was correlated with relative elevation ($r = 0.28$, $p < 0.001$).

Equation 7 can be assumed to provide a more precise biomass estimation than that by Eq. 6, as Eq. 7 involves a more precise H estimation model (Eq. 5) than that (namely Eq. 1) incorporated into Eq. 6 (Table 1). As shown in Fig. 5, Eq. 6 resulted in +6% overestimation at a low elevation plot (*baixio* at -53 m in relative elevation; 1700–1800 m in distance) and -5% underestimation at a high elevation plot (plateau at -1 m in relative elevation; 0–100 m in distance) compared with Eq. 7. The average biomass estimated using Eq. 6 was 319.6 ± 28.6 (SE) Mg ha^{-1}, which was similar to that (316.6 Mg ha^{-1}) estimated using Eq. 7. This similarity can be explained by the fact that overestimations at plateau and underestimations at *baixio* were balanced.

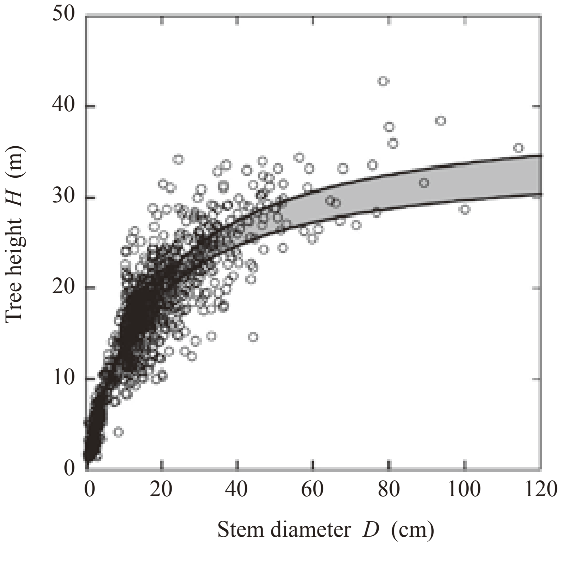

Fig. 3. Relationship between stem diameter at breast height D and tree height H relationships

The grey area represents the range covered by Eq. 7 under the condition that the relative elevation x_2 in Eq. 5 ranges from -46 to 0 m.

Discussion

Our preliminary analysis confirmed that the *D-H* relationship differed significantly between the plateau and *baixio* (valley bottom) topographies (Fig. 2). The *D-H* allometric model was developed considering the dependence of the *D-H* relationships on relative elevation, as expressed in Eq. 5 (Fig. 3). The developed model indicated that potential tree height fell from 40 to 34 m with decreasing relative elevation from 0 m (plateau) to -55 m (*baixio*) within the transect. The plateau and *baixio* sites in the present study are characterized by clayish and sandy soils, respectively[7], and *baixio* areas are seasonally waterlogged. Aiba and Kitayama[1] suggested that a high allocation of biomass to height growth was related to the productive environments in a tropical Malaysian rainforest. Duivenvoorden[6] reported that the canopy height was higher at well-drained sites than those that were poorly drained in an upper Amazonian region. Accordingly, stressful conditions such as sandy and nutrient-poor soils with seasonal waterlogging would explain the decrease in potential height at *baixios*.

Tree density and potential tree height fell significantly with decreasing relative elevation, and the resultant estimate in biomass significantly decreased at *baixios*. Similarly, Castilho et al.[3] reported that structural features, such as tree density and size, depended on absolute elevation in a central Amazonian forest. Omitting the topographic gradient of the *D-H* relationship introduced error ranging from -5 to +6% in biomass models that were dependent on relative elevation (Fig. 5). Our findings emphasize that the topographic gradient in tree height is important for precise biomass estimation in *terra firme* forests in the central Amazon.

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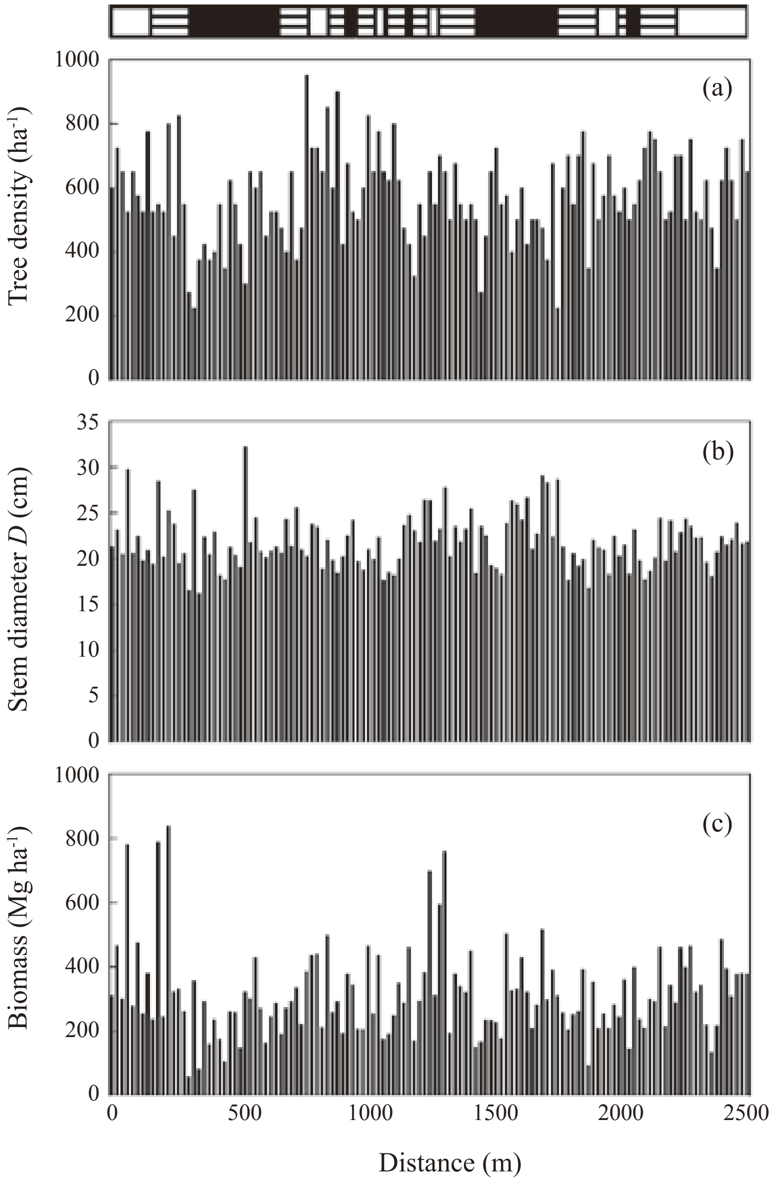

Fig. 4. Variation in (a) tree density, (b) stem diameter at breast height *D*, and (3) biomass determined for each 20 × 20-m subplot along the belt transect

Biomass was estimated using Eq. 7. The bar above the figures indicates topographic categories; open, striped, and closed bars represent plateau, slope, and *baixio* sites, respectively.

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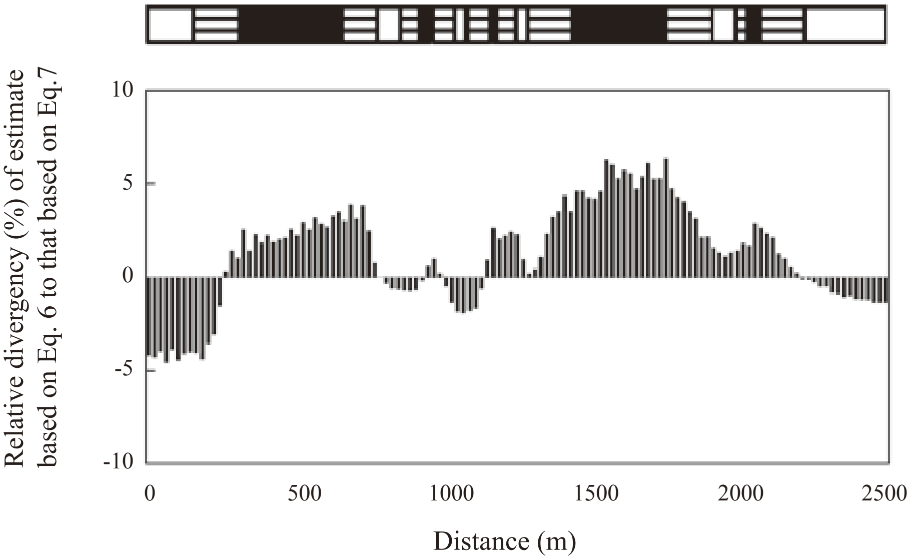

Fig. 5. Relative difference (%) of biomass estimated using Eq. 6 from that estimated using Eq. 7

The bar above the figure indicates topographic categories; open, striped, and closed bars represent plateau, slope, and *baixio* sites, respectively.

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