

## 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  $317 \pm 28$  (SE) Mg ha<sup>-1</sup>, 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<sup>10</sup>. 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<sup>3,9</sup> 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<sup>14</sup>, elevation<sup>1</sup>, and species<sup>13</sup>. 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<sup>3,4,9</sup> 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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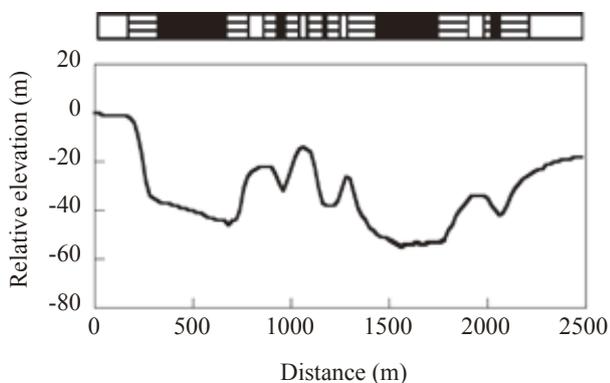
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tive elevation (i.e. the depth of a *baixio* relative to the plateau level) as the main topographic component, because soil conditions depend strongly on relative elevation<sup>5,7</sup> and affect vegetation structure at the landscape level in this region<sup>3,9</sup>. 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<sup>8</sup>. 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<sup>7</sup>.



**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  $20 \times 20$ -m sub-plots within the belt transect in 2000. For trees with buttresses,  $D$  was measured above the latter.

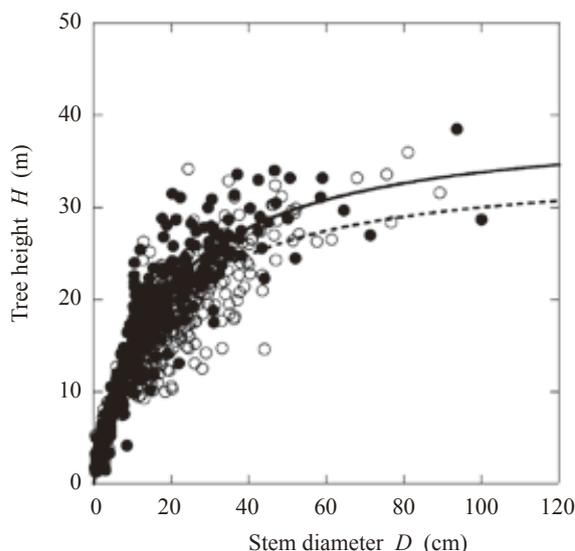
To assess the *D-H* relationship, 1307 individual trees ( $D > 1$  cm) were sampled from part of the transect. The sampling area was selected at a distance of 0 to 760 m (Fig.1), encompassing wide-ranging clay content (3–36%) with varying topography<sup>7</sup>. Tree height was measured using a scale 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<sup>11</sup>:

$$\frac{1}{H} = \frac{1}{aD} + \frac{1}{b} \quad (1)$$

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:

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

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  $e + fx_2 = H|_{D \rightarrow \infty}$ .

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<sup>2</sup>:  $AIC = n \ln(RSS/n) + 2K$ , 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<sup>12</sup>:

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

where the unit of  $D^2H$  is  $\text{cm}^2 \text{m}$ . 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<sup>12</sup>. To calculate the whole-plant dry weight  $W_w$ , an average dry / fresh ratio of 0.584 was

used<sup>12</sup>, and the following allometric model was obtained:

$$\ln W_w = 0.99 \ln(D^2H) - 3.19 \quad (4)$$

## Results

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

Maximum and average  $D$  were 114.2 cm and  $13.7 \pm 0.4$  (SE) cm, respectively, and maximum and average  $H$  were 42.8 m and  $13.3 \pm 0.2$  (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:

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

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

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

$$W_w = 0.0413 \left( \frac{1}{2.18D^3} + \frac{1}{37.49D^2} \right)^{-0.99} \quad (6)$$

$$W_w = 0.0355 \left[ \frac{1}{2.21D^3} + \frac{1}{(39.80+0.0996x_2)D^2} \right]^{-0.99} \quad (7)$$

## 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  $\pm$  SE:  $571 \pm 13$  ha<sup>-1</sup>; Fig.4a) were positively correlated with relative elevation ( $r = 0.32$ ,  $p < 0.001$ ). The average value of  $D$  was  $21.7 \pm 0.3$  (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  $316.6 \pm 28.3$  (SE) Mg ha<sup>-1</sup> (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  $319.6 \pm 28.6$  (SE) Mg ha<sup>-1</sup>, which was similar to that ( $316.6$  Mg ha<sup>-1</sup>) estimated using Eq. 7. This similarity can be explained by the fact that overestimations at plateau and underestimations at *baixio* were balanced.

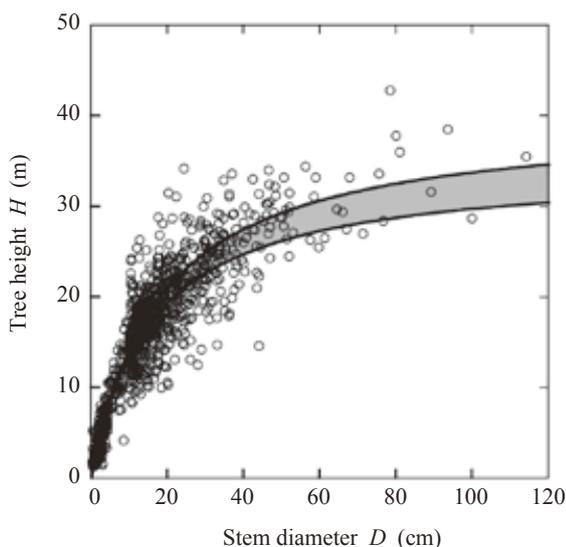
## Discussion

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<sup>7</sup>, and *baixio* areas are seasonally waterlogged. Aiba and Kitayama<sup>1</sup> suggested that a high allocation of biomass to height growth was related to the productive environments in a tropical Malaysian rainforest. Duivenvoorden<sup>6</sup> 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.<sup>3</sup> 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.

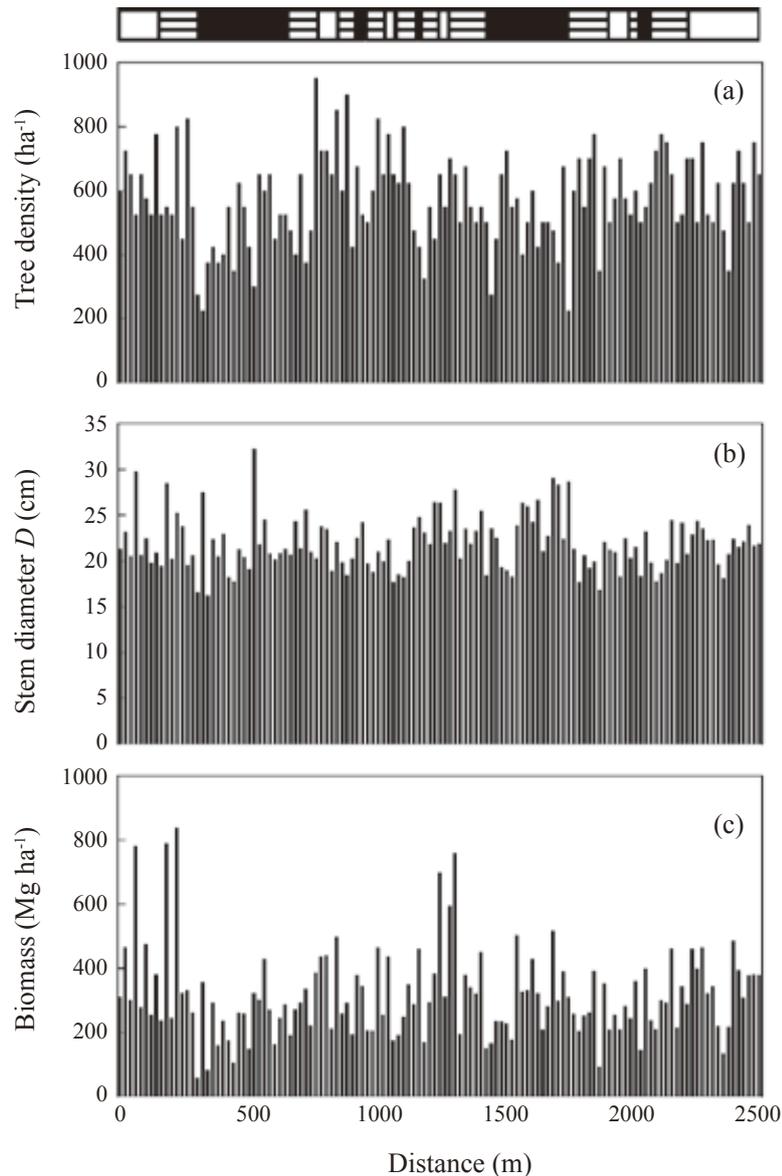
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**Fig. 3. Relationship between stem diameter at breast height  $D$  and tree height  $H$  relationships**

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.



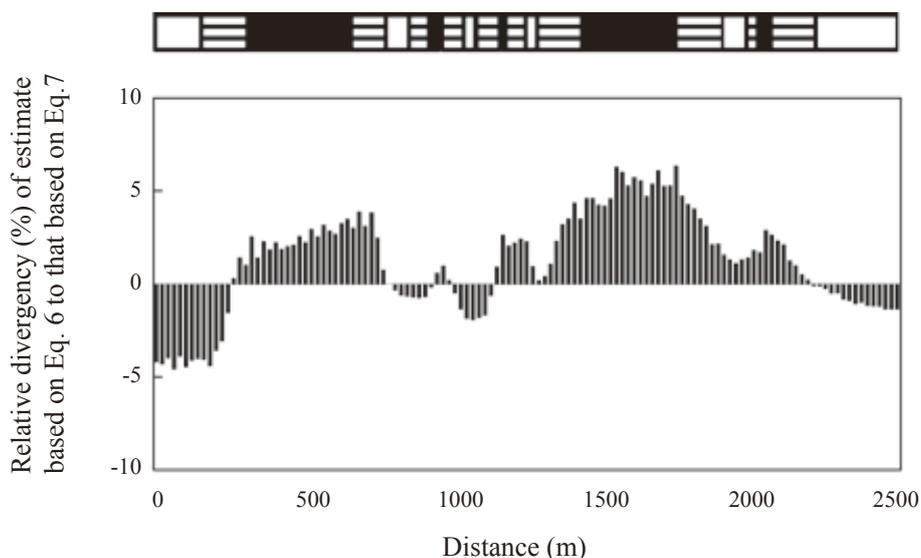
**Fig. 4.** Variation in (a) tree density, (b) stem diameter at breast height  $D$ , and (3) biomass determined for each  $20 \times 20$ -m subplot along the belt transect

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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