Wood Basic Density in Large Trees: Impacts on Biomass Estimates in the Southwestern Brazilian Amazon

Flora Magdaline Benitez Romero 1,2,3, Thais de Nazaré Oliveira Novais 1, Laércio Antônio Gonçalves Jacovine 2,3, Eronildo Braga Bezerra 4,5, Rosana Barbosa de Castro Lopes 3, Juliana Sousa de Holanda 6, Edi Flores Reyna 7,8, and Philip Martin Fearnside 1,9,*

Abstract: Wood basic density (WD) plays a crucial role in estimating forest biomass; moreover, improving wood-density estimates is needed to reduce uncertainties in the estimates of tropical forest biomass and carbon stocks. Understanding variations in this density along the tree trunk and its impact on biomass estimates is underexplored in the literature. In this study, the vertical variability of WD was assessed along the stems of large trees that had a diameter at breast height (DBH) ≥ 50 cm from a dense ombrophilous forest on terra firme (unflooded uplands) in Acre, Brazil. A total of 224 trees were sampled, including 20 species, classified by wood type. The average WD along the stem was determined by the ratio of oven-dry mass to saturated volume. Five models were tested, including linear and nonlinear ones, to fit equations for WD, selecting the best model. The variation among species was notable, ranging from 0.288 g cm⁻³ (Ceiba pentandra, L., Gaertn) to 0.825 g cm⁻³ (Handroanthus serratifolius, Vahl., S. Grose), with an average of 0.560 g cm⁻³ (±0.216, standard deviation). Significant variation was observed among individuals, such as in Schizolobium parahyba var. amazonicum (H. ex D.), which ranged from 0.305 to 0.655 g cm⁻³. WD was classified as low (≤0.40 g cm⁻³), medium (0.41–0.60 g cm⁻³), and high (≥0.61 g cm⁻³). The variability in WD along the stem differs by wood type. In trees with low-density wood, density shows irregular variation but tends to increase along the WD, whereas it decreases in species with medium- and high-density wood. The variation in WD along the stem can lead to underestimations or overestimations, not only in individual trees and species but also in total stocks when estimating forest biomass. Not considering this systematic bias results in significant errors, especially in extrapolations to vast areas, such as the Amazon.

Keywords: tropical forest; wood density; climate change; commercial species; Acre; Brazil

1. Introduction

Large trees play a crucial role in forest conservation, contributing significantly to the hydrological and carbon cycles, as well as sustaining biodiversity and carbon storage [1]. Storage in large trees (≥50 cm diameter at breast height (DBH)) represents 40 to 60% of
the forest’s dry aboveground biomass. Due to their specific architecture, these trees are particularly important for issues related to climate change, given their disproportionate contribution to the total forest biomass [1–3]. The lack of data on large trees can be attributed to the high cost of sampling and to legal restrictions, because extracting these trees from the forest in Brazil is only permitted with the approval of a forest management plan [4].

In the Brazilian Amazon, forest management plans are developed for the harvest of roundwood for sawn timber production. The true impact of this management on mitigating climate change is still debated, as it faces significant challenges in achieving effective sustainability [5] and has both positive and negative environmental effects [6]. The beneficial effects include the contribution of forest regeneration to carbon-stock recovery and the temporary storage of carbon in timber products. The negative aspects include the reduction of forest carbon stock due to the removal of large commercial trees, emissions from the decay of the crowns, stumps, and roots of harvested trees, and biomass loss due to collateral damage from things such as access roads, skid tracks, and log landings. Forest fires and degradation related to logging and illegal logging can turn the forest into a potential source of greenhouse gas emissions [7,8].

Quantifying greenhouse gas emissions from deforestation and forest degradation requires determining biomass, and for this it is essential to obtain values for wood basic density (WD), which varies according to species and spatial distribution. Wood basic density is a crucial variable in the allometric models used to estimate biomass in tropical forests [9–14]. These estimates are essential for assessing carbon stocks and flows, contributing to the understanding of the influence of these factors on global climate change [15,16].

Determining WD requires caution due to the influence of various factors, such as radial and vertical variations in relation to tree height [3,15,17], differences between species and taxonomic groups [10,18], and spatial variations in forest typologies [10,11,19–21]. Local environmental conditions, such as soil fertility and light conditions, also influence WD [11,22,23].

Vertical variation along the stem must be considered when estimating forest biomass because not considering this source of systematic bias results in significant errors in estimates for vast areas, such as the Amazon [3,17,24–27].

Equations have been developed to correct for vertical variations within trees [3,15,17] or to determine “ideal” sampling points for a single species [28] or a group of species [26]. However, these results, while satisfactory, cannot be generalized to all species, especially tropical ones, which have patterns of variation that differ from other regions [3].

There is a knowledge gap regarding vertical variation in WD in species in the southwest region of the Brazilian Amazon [21], especially in studies that include large trees (with diameter at breast height (DBH) ≥ 50 cm). The present study aims to determine the vertical variation of WD in the stems of large trees, to propose allometric equations and corrections for this variation, and to discuss their influences on forest biomass estimates in the southwestern Brazilian Amazon.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Antimary I and II ranches (9°23'43" S latitude and 67°58'50" W longitude), located in the municipality of Porto Acre, in the state of Acre in the southwestern Brazilian Amazon (Figure 1). The research area corresponds to an annual production unit of 1253.02 ha, designated as UPA 02, integrated into the Sustainable Forest Management Plan (PMFS) and governed by the Annual Operational Plan [28], both implemented by Fox Laminados Ltda (Porto Acre, AC, Brazil). A 100% forest inventory of commercial trees with DBH ≥ 50 cm was conducted in the area in May 2015, and the management project received approval from the Acre Environmental Institute (IMAC) in 2016 [29].

The vegetation in the southwestern Brazilian Amazon is classified as moist terra firme (unflooded upland) forest [12,30]. In the managed area, the predominant vegetation
is dense ombrophilous forest, although open ombrophilous forest with bamboo is also present in smaller proportions [29]. The local climate is classified as “Am” (Köppen), characterized as a tropical monsoon climate with distinct dry and rainy seasons [31]. The annual average temperature is 24 to 26 °C, and the annual precipitation ranges from 1750 to 2500 mm [32]. The dry season extends from June to September, while the rainy season extends from October to April or May, with the first quarter of the year having the highest precipitation [33]. The predominant soils in the region are classified as ultisols, dystrophic ultisols, and typic dystrophic oxisols, with soil texture ranging from clayey to very clayey [28,34].

Figure 1. Location of the study area in the Antimary I and II ranches in the Porto Acre municipality, Acre state, within an annual production unit of 1253.02 ha.

2.2. Species and Sampled Trees Selection

Species selection was based on the coverage value index, providing information on tree density (individuals ha$^{-1}$) and basal area (m$^2$ ha$^{-1}$) derived from the 100% forest inventory conducted by the management company, where all commercially relevant trees with DBH ≥ 50 cm were measured [29]. Scientific names were verified in Brazil’s Flora 2020 database [35]. The twenty species with the highest coverage values (basal area per hectare) were selected [36]. The number of individuals sampled (224) was determined according to the sample size (n) for a population considered to be infinite using Equation (1). The variable used to determine sample size was volume (m$^3$).

\[ n = \frac{t^2 \times (CV)^2}{(E\%)^2} \]  

where \( n \) = number of individuals sampled; \( t \) = tabulated value of Student’s t-statistic at 5% significance with “n” degrees of freedom; \( CV \) = coefficient of variation; and \( E\% \) = required accuracy (10%).

2.3. Collection of Wood Disks along the Commercial Bole

The sampled trees were all cut at 30 cm above the ground, including those with buttresses. The commercial stems were sectioned into logs, and wood disks of constant thickness (≈3 cm) were taken from the base of each log. For individuals with DBH ≥ 80 cm, the stem was sectioned every 4.30 m until the total length of the commercial stem was...
reached. In individuals with a DBH from 50 to 80 cm, the log length was 8.30 m. The first disk in all trees was taken at 30 cm above the ground (Figure 2). A total of 479 disks were collected and analyzed. The number of disks removed per tree varied according to the diameter and length of the tree (Figure 2). This methodology for disk sampling along the stem was adapted to the operational procedures of the company for practical activities in the management area, such as log length classification to facilitate the logging stage. The number of sampled wood disks per tree ranged from 2 to 5 and they were classified into sections named A, B, C, and D according to their positions along the stem. For all sampled individuals, Section A corresponded to the position of the base of the stem, i.e., 30 cm above the ground, while Sections B, C, and D varied in height depending on the stem section.

![Sample trees](image1)

**Figure 2.** Sampling of wood disks removed along the commercial bole.

### 2.4. Determination of WD and Classification of Species by Wood Type

The wood discs collected in the field were brought to the laboratory and a wedge-shaped sample was extracted from each disc, including parts of the heartwood, sapwood, and bark, to adequately represent the disc. The wedges were immersed in water until saturation to obtain the saturated volume using the immersion method, which involves measuring the water displacement related to the saturated volume of the piece (cm$^3$).

Subsequently, the samples were dried in a forced-air-circulation oven at a temperature of 100 ± 2 °C until reaching constant mass. WD was determined by using the ratio of dry mass (g—0% moisture) to saturated volume (Equation (2)) [37].

$$\rho = \frac{m_s}{V_{\text{sat}}}$$

where $\rho = \text{WD (g cm}^{-3}\text{)}, m_s = \text{Dry mass of the wood (g), } V_{\text{sat}} = \text{volume of saturated wood (cm}^3\text{)}$.

The WD for each sampled species was obtained as the arithmetic mean of the densities of samples of the same species [12,38]. Additionally, deviations and a 95% confidence interval were calculated.

The 20 species were categorized by wood type based on the mean value of WD (Table 1). The designations used were adapted to “low-density wood”, “medium-density wood”, and “high-density wood” [39].
Table 1. Categories and criteria describing wood types based on basic wood density (WD).

<table>
<thead>
<tr>
<th>Category</th>
<th>Criterion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low density</td>
<td>WD of the stem ≤ 0.40 g cm$^{-3}$</td>
</tr>
<tr>
<td>Medium density</td>
<td>WD of the stem 0.41–0.60 g cm$^{-3}$</td>
</tr>
<tr>
<td>High density</td>
<td>WD of the stem ≥ 0.61 g cm$^{-3}$</td>
</tr>
</tbody>
</table>

2.5. Models Tested to Estimate the WD of the Stem

Five regression models were fitted (Table 2) to estimate the WD throughout the stem ($\rho_{\text{stem}}$) using independent variables such as the WD at the base ($\rho_{\text{base}}$, g cm$^{-3}$), diameter at breast height (DBH, cm), and commercial height (h, m). Regression models were applied to the WD of the 20 species in three phases. First, a general equation was fitted, considering all arboreal individuals of the 20 species evaluated in this study. In the second phase, the “low-density” and “medium-density” species were included in a single data set, as the number of samples for low-density-wood species was insufficient to fit an equation just for this category. In the last phase, only “high-density” species were considered when fitting the equation.

Table 2. Linear and nonlinear regression models to estimate the WD of the stem.

<table>
<thead>
<tr>
<th>Model Name</th>
<th>Statistical Model</th>
<th>Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Linear model</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model 1</td>
<td>$\rho_{\text{stem}} = \beta_0 + \beta_1 \rho_{\text{base}} + \epsilon$</td>
<td>Simple linear regression</td>
</tr>
<tr>
<td>Model 2</td>
<td>$\rho_{\text{stem}} = \beta_0 + \beta_1 \rho_{\text{base}} + \beta_2 \rho_{\text{base}} + \epsilon$</td>
<td>Multiple linear regression</td>
</tr>
<tr>
<td>Model 3</td>
<td>$\rho_{\text{stem}} = \beta_0 + \beta_1 \rho_{\text{base}} + \beta_2 h + \beta_3 \rho_{\text{base}} + \epsilon$</td>
<td>Multiple linear regression</td>
</tr>
<tr>
<td>Nonlinear model</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model 1</td>
<td>$\rho_{\text{stem}} = \beta_0 \times \rho_{\text{base}} \times \epsilon$</td>
<td>Simple nonlinear regression</td>
</tr>
<tr>
<td>Model 2</td>
<td>$\rho_{\text{stem}} = \beta_0 \times \rho_{\text{base}} \times h \times \epsilon$</td>
<td>Multiple nonlinear regression</td>
</tr>
</tbody>
</table>

$\beta_0$, $\beta_1$, and $\beta_2$ refer to the coefficients of the equation and $\epsilon$ to the error; $\rho_{\text{stem}}$ = the WD of the entire stem; $\rho_{\text{base}}$ = WD at the stem base; $d$ = the diameter at breast height; and $h$ = the commercial height.

Evaluation of the goodness-of-fit was conducted based on indicators described by Campos and Leite [40]. These include the coefficient of determination ($R^2$), representing the quality of regression line fitting; the square root of the mean squared error (RMSE), which amplifies and penalizes errors of greater magnitude more strongly; the coefficient of regression variation; and a graphical analysis of the distribution of residuals. Additionally, the mean absolute deviation (MAD) and the Akaike information criterion (AIC) were computed. Both MAD and AIC serve as valuable tools in the selection and evaluation of statistical models, providing crucial insights for choosing models that balance precision and simplicity.

3. Results

3.1. Aboveground Stocks in Commercial Trees

The stem WD ($\rho_{\text{stem}}$) of individual trees displayed considerable variation, ranging from 0.288 to 0.825 g cm$^{-3}$ (Figure 3). The mean ± standard deviation (SD) was $0.560 \pm 0.164$ g cm$^{-3}$ for the total of 224 individuals, encompassing 20 commercial species. Significantly divergent densities were noted among species ($p < 0.000$). Beyond interspecies differences, there was a noteworthy, albeit statistically non-significant ($p = 0.368$), variability among individuals of the same species, exemplified by Schizolobium parahyba var. amazonicum (Huber ex Ducke), whose individuals ranged in WD from 0.305 to 0.655 g cm$^{-3}$.
3. Results

3.1. Aboveground Stocks in Commercial Trees

The stem WD of 20 tree species from the southwestern Brazilian Amazon. ‘•’ represents the mean and 0 represents individual observations. The 95% confidence interval for the mean is indicated, which was calculated using individual standard deviations. Species: 1—*Albizia nigroides* (Spruce ex Benth., Burkart); 2—*Apuleia leioarpa* (Vogel, J.F. Macbr.); 3—*Astronium lecointei* (Ducke); 4—*Barnebydendron riedelii* (Tul., J.H. Kirkbr.); 5—*Castilla ulei* (Warb.); 6—*Cedrela odorata* (L.); 7—*Ceiba pentandra* (L., Gaertn.); 8—*Ceiba samauma* (Mart., K. Schum.); 9—*Copiapera multijuga* (Hayne); 10—*Diptyeryx odorata* (Aubl., Willd.); 11—*Eschweileria bracteosa* (Poeppe. Ex O. Berg, Miers); 12—*Eschweileria grandiflora* (Aubl., Sandwith); 13—*Ficus insipida* (Willd.); 14—*Handroanthus serratifolius* (Vahl., S. Grose); 15—*Hura crepitans* (L.); 16—*Hymenaea courbaril* (L.); 17—*Parkia paraensis* (Ducke); 18—*Schizolobium amazonicum* (H. ex D.) B.; 19—*Sterculia apetala* (Jacq., H. Karst.); 20—*Terminalia tetrathyalla* (Aubl., Gere & Boatwt.).

3.2. Vertical Variability of WD along the Stem

There were variations in WD along the stem, and these values were significantly influenced by the wood type (*p* < 0.001, Kruskal–Wallis). The average WD for low-density-wood species was 0.346 ± 0.056 g cm⁻³, for medium-density-wood species it was 0.458 ± 0.068 g cm⁻³, and for high-density-wood species it was 0.738 ± 0.075 g cm⁻³ (Table 3).

Table 3. Mean WD (g cm⁻³) by sample position along the stem and wood type: T = overall mean ¹ of all sections; I = mean ¹ at the base of the stem ²; F = mean ¹ of the final vertical section ³.

<table>
<thead>
<tr>
<th>Basic Density</th>
<th>Species Group</th>
<th>Low Density</th>
<th>Medium Density</th>
<th>High Density</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>χ ± SD</td>
<td>CI 95%</td>
<td>n</td>
<td>χ ± SD</td>
</tr>
<tr>
<td>T</td>
<td>20</td>
<td>0.346 ± 0.056</td>
<td>0.320–0.372</td>
<td>144</td>
<td>0.458 ± 0.068</td>
</tr>
<tr>
<td>I</td>
<td>20</td>
<td>0.338 ± 0.059</td>
<td>0.310–0.366</td>
<td>114</td>
<td>0.477 ± 0.092</td>
</tr>
<tr>
<td>F</td>
<td>20</td>
<td>0.354 ± 0.067</td>
<td>0.323–0.386</td>
<td>114</td>
<td>0.441 ± 0.086</td>
</tr>
</tbody>
</table>

¹ is the arithmetic mean; ² represents Section A; ³ refers to the last section sampled along the stem, which could be Section B, C, or D depending on the species; n refers to the number of tree samples; χ is the arithmetic mean; SD is the standard deviation; and CI is the 95% confidence interval.

Species with low-density wood tend to exhibit an increase in WD from the base to the top of the stem, with the exception of *Ceiba pentandra* (Figure 4).
In percentage terms, there were increases ranging from 14.18% to 35.08% in the mean WD of the last stem section for each species compared to the density at the base (Section A), with Sterculia apetala exhibiting the highest relative variation of 35.08% (Table 4). C. pentandra had the highest mean DBH (130.2 cm) among the species and, due to this, allowed a greater segmentation of the stem (Figure 4). This species did not show significant vertical variation in WD compared to other species in the same category. However, following a subtle trend of both decreasing and increasing WD along the stem, it ended up with a decrease of 16.24% from the base (Section A) to the uppermost section (Section D).

In the medium-density-wood species, there was no consistent pattern observed in terms of the vertical variation in WD (Figure 5).

Ceiba samanuma and Cedrela odorata increased their basic densities by 3.13% and 6.18%, respectively, in the last stem section, represented by Section B for both species. In contrast, other species experienced a decrease ranging from −2.60% to −36.31% in WD from the base to the top of the stem (Table 5). Parkia paraensis and Schizolobium parahyba var. amazonicum had the highest vertical variations, with decreases of 36.31% and 34.79%, respectively.

The high-density-wood species exhibited decreases (Figure 6) in WD from the stem base to the top ranging from −2.71% to −7.96% (Table 6), with the exception of Eschweilera bracteosa and Terminalia tetraphylla, which experienced increases of 9.23% and 2.64%, respectively. It is noteworthy that although E. grandiflora and E. bracteosa belong to the same genus, they exhibit opposite behaviors in terms of the variation in WD along the stem. The vertical variations for each species are listed in Table 6 and range from −7.96% for Albizia niopoides to 9.23% for Eschweilera bracteosa.

Table 3. Mean WD (g cm$^{-3}$) by sample position along the stem and wood type: T = overall mean 1 of the top of the stem, 2 = mean 1 at the base of the stem 2; F = mean 1 of the last section sampled along the stem, which could be Section B, C, or D depending on the species; n refers to the number of tree samples; 1 is the arithmetic mean; 2 represents Section A; 3 refers to the last section sampled along the stem, which can be Section B, C, or D depending on the species.

Table 4. Relative difference (for low-density-wood species) between the WD at the stem base and in the last 1 sampled stem section.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Vertical Variation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceiba pentandra</td>
<td>5</td>
<td>−16.24 2</td>
</tr>
<tr>
<td>Ficus insipida</td>
<td>4</td>
<td>14.18</td>
</tr>
<tr>
<td>Hura crepitaens</td>
<td>6</td>
<td>23.50</td>
</tr>
<tr>
<td>Sterculia apetala</td>
<td>5</td>
<td>35.08</td>
</tr>
</tbody>
</table>

1 This refers to the last section sampled along the stem, which can be Section B, C, or D depending on the species.
2 The negative value indicates a decrease in density along the stem (Figure 4).

Figure 4. Vertical variation in the WD for species with “low-density” wood.
The high-density-wood species exhibited decreases (Figure 6) in WD from the stem base to the top of the stem (Table 5).

The medium-density-wood species had the highest vertical variations, with decreases of 36.31% and 34.79%, respectively, in the last stem section, represented by Section B for both species. In contrast, other species experienced a decrease ranging from 2.71% to 7.96% (Table 6), with the exception of Eschweilera grandiflora and Ceiba samauma, which experienced increases of 9.23% and 2.64%, respectively, in the last stem section.

The low-density-wood species had the lowest vertical variations, with decreases of 0.045% and 0.6% for the last stem section, represented by Section B, C, or D depending on the species; negative values indicate a decrease in density along the stem (Figure 5).

**Table 5.** Relative difference (for medium-density-wood species) between the average WD at the stem base and in the last 1 sampled stem section.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Vertical Variation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Barnebydendron riedelii</em></td>
<td>5</td>
<td>−2.60 ²</td>
</tr>
<tr>
<td><em>Castilla ulei</em></td>
<td>37</td>
<td>−2.79 ²</td>
</tr>
<tr>
<td><em>Cedrela odorata</em></td>
<td>8</td>
<td>3.13</td>
</tr>
<tr>
<td><em>Ceiba samauma</em></td>
<td>22</td>
<td>6.18</td>
</tr>
<tr>
<td><em>Copaifera multijuga</em></td>
<td>6</td>
<td>−2.64 ²</td>
</tr>
<tr>
<td><em>Parkia paraenses</em></td>
<td>20</td>
<td>−36.31 ²</td>
</tr>
<tr>
<td><em>Schizolobium parahyba var. amazonicum</em></td>
<td>16</td>
<td>−34.79 ²</td>
</tr>
</tbody>
</table>

1 Refers to the last section sampled along the stem, which can be Section B, C, or D depending on the species; 2 Negative values indicate a decrease in density along the stem (Figure 5).

**Figure 5.** Vertical variation in the WD for species with “medium-density” wood.

**Figure 6.** Vertical variation in the WD for high-density-wood species.
Table 6. Relative difference for species in the high-density-wood category between the average WD at the stem base and in the last 1 sampled stem section.

<table>
<thead>
<tr>
<th>Species</th>
<th>n</th>
<th>Vertical Variation (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Albizia niopoides</td>
<td>7</td>
<td>−7.96 2</td>
</tr>
<tr>
<td>Apuleia leiocarpa</td>
<td>13</td>
<td>−7.50 2</td>
</tr>
<tr>
<td>Astronium leciointei</td>
<td>6</td>
<td>−7.85 2</td>
</tr>
<tr>
<td>Dipteryx odorata</td>
<td>11</td>
<td>−7.64 2</td>
</tr>
<tr>
<td>Eschweilera bracteosa</td>
<td>15</td>
<td>9.23</td>
</tr>
<tr>
<td>Eschweilera grandiflora</td>
<td>13</td>
<td>−7.08 2</td>
</tr>
<tr>
<td>Hymenaea courbari</td>
<td>8</td>
<td>−2.71 2</td>
</tr>
<tr>
<td>Terminalia tetraphylla</td>
<td>9</td>
<td>2.64 2</td>
</tr>
</tbody>
</table>

1 Refers to the last section sampled along the stem, which can be Section B, C, or D depending on the species; 2 Negative values indicate a decrease in density along the stem (Figure 6).

3.3. Fitting the Equation for Stem WD for the Large Individuals of 20 Commercial Species

The three fitted models, as noted in Table 7, show that the independent variables explained more than 92% of the variation in the stem WD ($p_{stem}$). RMSE was consistent at 0.045 and the CV was approximately 5%, indicating relatively low variability and narrow dispersion around the mean. However, at a significance level of 10%, some of the coefficients estimated by Models 2 and 3 were not statistically significant, mainly those related to the diameter (d) and height (h) variables. Therefore, Model 1 is the most appropriate according to the AIC and MAD statistics (Table 7); this model uses only the WD at the base as a predictor variable.

Table 7. Linear regression model general equation (including all species in the different wood density categories (low, medium, and high)): coefficients and evaluation criteria of the linear equations for estimating the WD of the stems of large individuals of commercial species.

<table>
<thead>
<tr>
<th>Model</th>
<th>n</th>
<th>Coefficient</th>
<th>p-Value</th>
<th>$R^2$ %</th>
<th>RMSE</th>
<th>AIC</th>
<th>MAD</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>224</td>
<td>$b_0$</td>
<td>0.045930</td>
<td>0.000</td>
<td>92.47</td>
<td>0.04499</td>
<td>−747.69</td>
<td>0.03029937</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_1$</td>
<td>0.892211</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>224</td>
<td>$b_0$</td>
<td>0.036362</td>
<td>0.030</td>
<td>92.49</td>
<td>0.04493</td>
<td>−746.22</td>
<td>0.03042542</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_1$</td>
<td>0.000106</td>
<td>0.467</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_2$</td>
<td>0.894152</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>224</td>
<td>$b_0$</td>
<td>0.033016</td>
<td>0.056</td>
<td>92.51</td>
<td>0.04487</td>
<td>−208.80</td>
<td>0.03043674</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_1$</td>
<td>0.000070</td>
<td>0.643</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>$b_2$</td>
<td>0.000693</td>
<td>0.419</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_3$</td>
<td>0.886929</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

It is noteworthy that the estimates with Model 1 had an average error of 0.69% ± 9.31% but with individual discrepancies in residuals; errors at the tree level ranged from −31.78% to 40.31% (Figure 7). These discrepant errors were mainly associated with trees with a wood density of 0.30 to 0.50 g cm$^{-3}$, i.e., low- and medium-wood-density species.

Of the two nonlinear equations tested with the variables “d” and “h” to estimate the WD of the stems for the 20 commercial species (including species in all wood density categories (low, medium, and high), Model 2 had the better fit, as it had lower RMSE and AIC values (Table 8).

The residuals in Model 2 had a more uniform distribution than in Model 1. However, the presence of “residual” points was noted, in addition to under and overestimates of the mean WD of the stem (Figure 8).
accordingly, the AIC and MAD statistics (Table 7); this model uses only the WD at the base as a predictor variable.

Table 7. Linear regression model general equation (including all species in the different wood density categories (low, medium, and high)): coefficients and evaluation criteria of the linear equations for estimating the WD of the stems of large individuals of commercial species.

<table>
<thead>
<tr>
<th>Model</th>
<th>n</th>
<th>Coefficient</th>
<th>p-Value</th>
<th>RSME</th>
<th>AIC</th>
<th>MAD</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>224</td>
<td>b₀</td>
<td>1.07977</td>
<td>0.00613</td>
<td>−171.83</td>
<td>0.1439071</td>
</tr>
<tr>
<td></td>
<td></td>
<td>b₁</td>
<td>−0.15089</td>
<td>0.07117</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>224</td>
<td>b₀</td>
<td>0.43092</td>
<td>0.00348</td>
<td>−220.97</td>
<td>0.1208498</td>
</tr>
<tr>
<td></td>
<td></td>
<td>b₁</td>
<td>−0.24770</td>
<td>0.00101</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>b₂</td>
<td>0.49938</td>
<td>0.0000</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

It is noteworthy that the estimates with Model 1 had an average error of 0.69% ± 9.31% but with individual discrepancies in residuals; errors at the tree level ranged from −31.78% to 40.31% (Figure 7). These discrepant errors were mainly associated with trees with a wood density of 0.30 to 0.50 g cm⁻³, i.e., low- and medium-wood-density species.

Figure 7. Linear models: graphical analysis of the equations fitted for the WD of the stems of large individuals of 20 commercial species. The models include species in all wood density categories (low, medium, and high).

Table 8. Nonlinear regression model general equation (including species in all wood density categories (low, medium, and high)): coefficients and evaluation criteria of the linear equations for estimating the WD of the stems of large individuals of 20 commercial species.

3.3.1. Equation Fitting for Low-Density- and Medium-Density-Wood Species

The models for low- and medium-density-wood species proved less accurate than the models for high-density-wood species. However, Table 9 reports models that showed relatively acceptable results for estimating the WD of the stem in the low- and medium-density-wood categories. In all three models, independent variables explain more than 70% of the variation in stem WD ($p_{stem}$). The preferred estimates came from Model 1, because it has the lowest AIC and because the estimated coefficients were both statistically significant at the 1% level (Table 9).
categories (low, medium, and high), Model 2 had the better fit, as it had lower RMSE and AIC values (Table 8).

Table 8. Nonlinear regression model general equation (including species in all wood density categories (low, medium, and high)): coefficients and evaluation criteria of the linear equations for estimating the WD of the stems of large individuals of 20 commercial species.

<table>
<thead>
<tr>
<th>Model</th>
<th>n</th>
<th>Coefficient</th>
<th>p-Value</th>
<th>$R^2$ %</th>
<th>RQEM</th>
<th>AIC</th>
<th>MAD</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>134</td>
<td>$b_0$ 0.14621</td>
<td>0.000</td>
<td>70.81</td>
<td>0.041616</td>
<td>-465.76</td>
<td>0.03285666</td>
<td>7.45</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_1$ 0.64671</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>134</td>
<td>$b_0$ 0.15300</td>
<td>0.000</td>
<td>70.84</td>
<td>0.041593</td>
<td>-208.81</td>
<td>0.03275438</td>
<td>7.42</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_1$ -0.00006</td>
<td>0.703</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_2$ 0.64320</td>
<td>0.000</td>
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<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>134</td>
<td>$b_0$ 0.15270</td>
<td>0.000</td>
<td>70.84</td>
<td>0.041592</td>
<td>-208.80</td>
<td>0.03276133</td>
<td>7.42</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_1$ -0.00007</td>
<td>0.706</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_2$ 0.00004</td>
<td>0.970</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$b_3$ 0.64300</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Through graphical analysis, it is possible to confirm that Model 1 exhibited a more uniform distribution of residuals (Figure 9). However, the presence of points with residuals, as well as underestimations and overestimations of the mean WD of the stem, are still evident.
because it has the lowest AIC and because the estimated coefficients were both statistically significant at the 1% level (Table 9).

Table 9. Low- and medium-density-wood equation: coefficients and criteria for evaluating linear equations for estimating the WD of the stems of large individuals of commercial species.

<table>
<thead>
<tr>
<th>Model</th>
<th>Coefficient</th>
<th>p-Value</th>
<th>R² %</th>
<th>RSME</th>
<th>AIC</th>
<th>MAD</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>b₀ 0.14621</td>
<td>0.000</td>
<td>70.81</td>
<td>0.041616</td>
<td>-465.76</td>
<td>0.03285666</td>
<td>7.45</td>
</tr>
<tr>
<td></td>
<td>b₁ 0.64671</td>
<td>0.000</td>
<td>70.84</td>
<td>0.041593</td>
<td>208.81</td>
<td>0.03275438</td>
<td>7.42</td>
</tr>
<tr>
<td>2</td>
<td>b₀ 0.15300</td>
<td>0.000</td>
<td>70.84</td>
<td>0.041592</td>
<td>208.80</td>
<td>0.03276133</td>
<td>7.42</td>
</tr>
<tr>
<td></td>
<td>b₁ -0.00006</td>
<td>0.703</td>
<td>70.84</td>
<td>0.041592</td>
<td>208.80</td>
<td>0.03276133</td>
<td>7.42</td>
</tr>
<tr>
<td></td>
<td>b₂ 0.64320</td>
<td>0.000</td>
<td>70.84</td>
<td>0.041592</td>
<td>208.80</td>
<td>0.03276133</td>
<td>7.42</td>
</tr>
</tbody>
</table>

Through graphical analysis, it is possible to confirm that Model 1 exhibited a more uniform distribution of residuals (Figure 9). However, the presence of points with residuals, as well as underestimations and overestimations of the mean WD of the stem, are still evident.

3.3.2. Equation Fitting for High-Density-Wood Species

Equations fitted to estimate the stem WD for high-density-wood species explained more than 85% of the variation in the dependent variable (Table 10). Among the three equations, Model 1 yielded the best fit and was the most parsimonious. Although both fitted equations showed very close statistics, the AIC and the significance levels of the coefficients indicated Model 1 as the best model (Table 10). As seen in the previous estimation, both diameter and height do not explain the variation in the dependent variable.

Table 10. Equations for high-density-wood species: coefficients and criteria for evaluating linear equations for estimating the WD of the stems of large individuals of commercial species.

<table>
<thead>
<tr>
<th>Model</th>
<th>n</th>
<th>Coefficient</th>
<th>p-Value</th>
<th>R² %</th>
<th>RSME</th>
<th>AIC</th>
<th>MAD</th>
<th>CV</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>90</td>
<td>b₀ 0.19212</td>
<td>0.000</td>
<td>85.61</td>
<td>0.028115</td>
<td>-381.45</td>
<td>0.020296</td>
<td>2.751</td>
</tr>
<tr>
<td></td>
<td></td>
<td>b₁ 0.72177</td>
<td>0.000</td>
<td>85.85</td>
<td>0.027883</td>
<td>-208.81</td>
<td>0.020326</td>
<td>2.751</td>
</tr>
<tr>
<td>2</td>
<td>90</td>
<td>b₀ 0.1799379</td>
<td>0.000</td>
<td>85.85</td>
<td>0.027883</td>
<td>-208.81</td>
<td>0.020326</td>
<td>2.751</td>
</tr>
<tr>
<td></td>
<td></td>
<td>b₁ 0.0001953</td>
<td>0.231</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>b₂ 0.7178809</td>
<td>0.000</td>
<td>85.85</td>
<td>0.027883</td>
<td>-208.81</td>
<td>0.020326</td>
<td>2.751</td>
</tr>
</tbody>
</table>

Figure 9. Graphical analysis of equations for low- and medium-density-wood species fitted for the stem WD of large individuals of commercial species.
Table 10. Cont.

<table>
<thead>
<tr>
<th>Model</th>
<th>n</th>
<th>Coefficient</th>
<th>p-Value</th>
<th>$R^2$ %</th>
<th>RSME</th>
<th>AIC</th>
<th>MAD</th>
<th>CV</th>
</tr>
</thead>
<tbody>
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<td>90</td>
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<td>0.179281</td>
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<td></td>
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<td>0.0001800</td>
<td>0.291</td>
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<td></td>
<td></td>
<td>$b_2$</td>
<td>0.0002703</td>
<td>0.746</td>
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<td></td>
<td></td>
<td>$b_3$</td>
<td>0.7143200</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The graphical analysis shows that the models for high-density-wood species have good fits, although some discrepant residual data points are present (Figure 10).

Figure 10. Graphical analysis of equations for high-density-wood species fitted for the stem WD of large individuals of commercial species.

4. Discussion

It is well documented that there is a real influence of vertical variability on the average WD along the stem, which can differ significantly from the WD of samples taken solely at breast height (1.30 m above the ground) or the stem base [15,17,25,26,41]. Due to this influence, some studies have suggested percentage values to correct the WD of samples only from the stem base or at breast height, such as the value of 4.3% for the central Amazon [15] and the value of 3.2% for the southwestern Amazon [21].

Based on the data from the current study, which was collected from 224 individuals in 20 species, there is a suggested reduction of 2.89% in the average WD value if samples are collected only at the stem base level. However, it is suggested that this correction be applied depending on the wood-type category, as the vertical variability behavior of density along the stem differs among low-, medium-, and high-density-wood categories. The use of samples from the stem bases of low-density-wood species was found to produce an
underestimation of 2.89% for the WD of the stem as a whole, while the use of stem base samples from medium- and high-density-wood species caused overestimations of 4.12% and 2.46%, respectively.

This classification of wood type based on WD can contribute to better forest management by defining methodologies and management practices applicable to each group [42]. Grouping these species and attempting to explain the different patterns of vertical density variability along the stem aids in understanding how this variable is interconnected with the life history strategies of trees and their ecological functions in the forest [19,43–46]. Because WD is a determinant of biomass, it also affects the forest’s role in carbon storage and the global climate. Species with a high wood density have value for carbon sequestration. These species are also important for carbon in reforestation initiatives [47,48].

The patterns of vertical variability in the WD of the species evaluated in this study (Figures 4–6) align with previous findings [3,41,44,45]. When grouped by wood type, low-density-wood species (typically pioneers or early secondary species) tend to increase their WD towards the tree canopy [3] These species have a short lifespan [49,50] and require high growth rates in their early growth stages [19,43,51], initially producing low-density wood but later producing denser wood as growth rates decrease to maintain structural stability [45,52]. In contrast, species in the high-density-wood category, represented by late-secondary and climax species, generally exhibit decreasing vertical variation profiles [6], where they initially produce a greater quantity of wood per unit volume and later this quantity decreases, contributing to a lower density at the top of the stem [45].

The two main sets of characteristics described above represent the extremes of a continuum of possibilities where the observed variations are complex and highly dependent on the functional and strategic characteristics of each species [41]. For example, species with intermediate characteristics, such as the medium-density-wood species in this study, exhibited vertical variations in WD that had increasing (Ceiba samauma), highly decreasing trends (Parkia paraensis), or even practically constant trends (Barnebydendron riedelii), making it challenging to obtain a typical pattern without considering an average.

Vertical variability may be related to radial variation in the stem, and when analyzed together, these types of variation can better explain the trends of many species [15,17,26,44]. It was not possible to analyze radial variations in the present study, but this does not bias the results on vertical variation because the samples were taken in the form of complete disks (heartwood, sapwood, and bark). Radial variations are also related to different life strategies [53] and can be explained by cambial age, growth-ring size, and the proportions of juvenile and mature wood, where these factors may change their proportions, increasing or decreasing with tree height [17,41,54,55] and thus also impacting vertical variation.

Vertical variation has been less studied than radial variation [17], especially for tropical forests. The current study of vertical variability in WD along the stem is therefore important both at the taxonomic level (species) and at the functional level (ecological groups) as it contributes to a better refinement of stem biomass estimates and of carbon accounting for tropical trees [3,17].

In this study, equations were developed to estimate the stem WD of trees with DBH ≥ 50 cm for 20 commercial species (Section 3.3). Regressions were run for each wood-type category, aiming to include the most significant variable (\(\rho_{\text{base}}\)) and the most practical variables for field measurement (d and h). For the three wood density categories evaluated (low, medium, and high), models with only the base WD (\(\rho_{\text{base}}\)) as a predictor variable provided the best fit for linear models to estimate the mean WD of the entire stem.

The findings show that \(\rho_{\text{base}}\) explains more than 70% of the variations in all regressions (Tables 7, 9 and 10, and Figures 7, 9 and 10). Diameter and height, although more convenient for field measurement, were not statistically significant to improve the model fit. Excluding this exception, the possible explanation for diameter and, especially, height not being significant variables is due to the lack of a consistent relationship between WD and tree size [56]. Some studies have found positive and negative correlations, but these correlations were weak [45,48,57,58], while others have found that these variables are largely
independent [15,59,60]. Phillips et al. [56] stated that tree size is not a good indicator of WD, and therefore, tree dimensions (d and h) cannot be used to infer wood density. Therefore, for the equations developed in this study for the “all species” scenario, it is recommended to use those that had only ρ_{base} as the predictor variable. These equations are valuable alternatives for normalizing basic stem wood density [3,50] since sampling entire trees to quantify WD along the stem, as performed in this study, is expensive and rarely conducted for practical applications [61], especially for large trees. Relying on approximate values for WD is often the only pragmatic way to obtain a more accurate estimate [62].

Nonlinear regressions were fitted with the variables d and h (Table 8 and Figure 8) to be used in the estimation of biomass and, consequently, carbon. These equations can be applied to extensive areas that have forest censuses. Equations that are based solely on WD at the base of the tree (ρ_{base}) as a predictor variable have greater utility for these censuses. The choice of equations provided in this study should be guided by the specific objectives of the researcher. Developing equations for different categories of the 20 species with similar characteristics and behaviors represents a significant advance in reducing uncertainties in forest biomass estimates.

5. Conclusions

The behavior of the vertical variation in basic wood density along the stem differs by wood type, where low-density-wood species increase in density with height, while medium- and high-density-wood species decrease. Considering only the WD at the stem base will therefore result in an underestimation of the basic stem density for low-density-wood species and overestimations for medium- and high-density-wood species. This vertical variation can be corrected by using the mentioned percentages or the equations developed in this study. The equations that best estimated the density of the stem were, for the most part, those that had only the base density as the predictor variable. Tree dimensions such as diameter and height are not good indicators for estimating wood density.

Correcting the vertical variability of wood density along the stem is necessary because even a small systematic bias, represented as a percentage, results in substantial errors in biomass and carbon stock estimates when applied on broad scales of forest resources at regional, national, or international levels, as is the case with the Amazon rainforest. Having wood density values closer to the actual (correct) values is crucial for more accurate estimates of carbon stocks, both in forests and in timber products.

Author Contributions: Conceptualization, F.M.B.R. and T.d.N.O.N.; formal analysis, F.M.B.R.; investigation, F.M.B.R., L.A.G.J., T.d.N.O.N. and P.M.F.; supervision, P.M.F.; writing—original draft, F.M.B.R.; writing—review and editing, L.A.G.J., E.B.B., R.B.d.C.L., J.S.d.H., E.F.R. and P.M.F. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available upon request to the corresponding author.

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Conflicts of Interest: The authors declare no conflicts of interest.
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Forests 2024, 34.


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