

Allometric Models for Tree Volume and Total Aboveground Biomass in a Tropical Humid Forest in Costa Rica¹

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ABSTRACT

Allometric equations for the estimation of tree volume and aboveground biomass in a tropical humid forest were developed based on direct measurements of 19 individuals of seven tree species in Northern Costa Rica. The volume and the biomass of the stems represented about two-thirds of the total volume and total aboveground biomass, respectively. The average stem volume varied between 4 and 11 Mg/tree and the average total aboveground biomass ranged from 4 to 10 mg/tree. The mean specific gravity of the sampled trees was 0.62 ± 0.06 (g/cm³). The average biomass expansion factor was 1.6 ± 0.2 . The best-fit equations for stem and total volume were of logarithmic form, with diameter at breast height ($R^2 = 0.66 - 0.81$) as an independent variable. The best-fit equations for total aboveground biomass that were based on combinations of diameter at breast height, and total and commercial height as independent variables had R^2 values between 0.77 and 0.87. Models recommended for estimating total aboveground biomass are based on diameter at breast height, because the simplicity of these models is advantageous. This variable is easy to measure accurately in the field and is the most common variable recorded in forest inventories. Two widely used models in literature tend to underestimate aboveground biomass in large trees. In contrast, the models developed in this study accurately estimate the total aboveground biomass in these trees.

RESUMEN

Ecuaciones alométricas para la estimación de volumen y biomasa aérea de árboles en un bosque húmedo tropical fueron desarrollados basados en mediciones directas de 19 individuos de siete especies de árboles al norte de Costa Rica. El volumen y la biomasa del tronco representaron cerca de dos terceras partes del volumen total del árbol y de la biomasa aérea total. El volumen promedio del tronco varió entre 4 y 11 Mg/árbol y el promedio de la biomasa aérea total varió entre 4 y 10 mg/árbol. La gravedad específica promedio de los árboles muestreados fué de 0.62 ± 0.06 (g/cm³). El factor de expansión de biomasa promedio fué de 1.6 ± 0.2 . Las ecuaciones de mejor ajuste para el volumen de tallo y total fueron de tipo logarítmico, con el diámetro a la altura de pecho ($R^2 = 0.66$ a 0.81) como variable independiente. Las ecuaciones de mejor ajuste para biomasa aérea total, las cuales fueron basadas en combinaciones de diámetro a la altura de pecho y altura total y comercial como variables independientes, presentaron valores de R^2 entre 0.77 y 0.87. Los modelos recomendados para estimar biomasa aérea total están basados en diámetro a la altura de pecho, porque la simplicidad de estos modelos es ventajosa. Esta variable es de fácil medición en el campo y tiene mayor precisión, además, es la más comúnmente registrada en inventarios forestales. Dos modelos ampliamente usados en la literatura tienden a subestimar la biomasa aérea total en árboles grandes. En contraste, los modelos desarrollados en este estudio, estiman con mayor precisión la biomasa aérea total de estos árboles.

Key words: allometric equations; biomass expansion factor; commercial stem; Costa Rica; specific gravity; total volume; tropical humid forest.

FOREST INVENTORIES HAVE OFTEN BEEN USED AS STARTING POINTS for the estimation of biomass and carbon storage in natural forests in Brazilian Amazon (Brown & Lugo 1992) and Europe (Kauppi *et al.* 1992). Often, biomass equations have been developed on the basis of forest inventory data (stand tables) (*e.g.*, Brown 1997, Brown *et al.* 1989). In some cases, equations are constructed from individual tree measurements (*e.g.*, Brown & Iverson 1992).

In the tropics, the information gathered in forest inventories usually includes only tree diameter at breast height and commercial height. In many cases, commercial tree height is difficult to measure with accuracy. This problem results in biased estimates when tree height is included as an independent variable in volume and biomass models. Considering these sources of error, it is necessary to develop volume and total aboveground biomass estimation models using variables, such as diameter at breast

height, which can be accurately measured in the field. This method is fast, requiring less work, and is therefore cost efficient in forest inventories.

Biomass content can be measured through direct or indirect methods. The direct (destructive) method consists of harvesting the tree to determine biomass through the actual weight of each of its components, for example, roots, stem, branches, and foliage (Parresol 1999). The indirect method is usually used when the tree has large dimensions, which is the case in natural tropical forests. In this case, tree dimensions are measured, and the volume of the stem + larger branches is calculated using the formulas of Smalian and Huber (Loetsch *et al.* 1973). Subsequently, this information is used to calculate the biomass using specific gravity. The most common procedure used for estimating individual tree biomass is mathematical models calculated by regression analysis (Parresol 1999).

Quantification of tree biomass in the tropics is a time-consuming activity, especially the measurement of certain biomass components, such as the foliage and branches. In addition, a good database for developing

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regression equations should contain large-diameter trees because they are the main component of the aboveground biomass of mature tropical forests (Brown & Lugo 1992, Pinard & Putz 1996). Generic equations, stratified by ecological zones, for estimating aboveground biomass exist (e.g., Brown *et al.* 1989, Brown & Iverson 1992) but they may not accurately reflect the tree biomass in a specific area or region.

In this study, allometric models for estimating stem volume, total volume (stem plus branches), and total aboveground biomass (stem plus branches and foliage) for individual trees in a tropical humid forest of Costa Rica are developed and compared with two frequently used models.

METHODS

This study was carried out in two natural forests located on private farms (Tirimina and Corinto) in the Sarapiquí and Guápiles regions of Northern Costa Rica. Tirimbina (10°25'N; 84°47'W; 180–220 m. a.s.l.) is in the per-humid premontane transitional forest zone (Holdridge 1996). The annual mean rainfall is 3833 mm and the mean annual temperature is 25.3°C (Quirós & Finegan 1994). Corinto (10°13'N; 83°53'W; 200 m. a.s.l.) is in the per-humid tropical forest zone (Holdridge 1996), with annual mean rainfall of 4000 mm and mean annual temperature of 23.7°C (Quirós 1998).

Data were collected from permanent sample plots dominated by *Pentaclethra macroloba* (Willd.) Kuntze. Experimental areas are located in the Tirimbina Rain Forest Center, and in the Laurels of Corinto where Tropical Agricultural Research and Higher Education Center (CATIE) have monitored the vegetation dynamics since the late 1980s.

Basal area (BA) was calculated from 18 permanent sample plots, nine plots in each forest. In addition, the number of species was registered, showing 249 and 244 species per hectare at Corinto and Tirimbina, respectively. The dominant tree species for each zone were determined based on BA data and these species were selected for direct biomass measurements (Table 1).

In total, 19 individual trees were measured before harvest (diameter at breast height: DBH, commercial height: H_c , and total height: H).

Volume and biomass were calculated immediately after commercial harvest. The harvest criteria for these trees were a DBH \geq 60 cm. Limiting the factors for selection were (a) the number of trees and species felled during the harvest and (b) isolated crowns.

After the felling, each tree was divided into five components:

1. *Commercial stem*: The total commercial volume (V_c) was calculated as the sum of each log volume, using Smalian's formula (Loetsch *et al.* 1973). The length of the logs varied between 10.1 and 22.7 m.
2. *Stump*: The bottom part of the stem, which is left in the field after a harvest. The stump volume (V_{stump}) was obtained using the formula for truncated Neloid (Loetsch *et al.* 1973).
3. *Non-commercial stem*: Stem section that is not merchantable due to defects. The total non-merchantable volume ($V_{\text{non-m}}$) was calculated using Smalian's formula.
4. *Large branches*: Branches with diameter \geq 25 cm, whose volume ($V_{\text{L-branch}}$) was calculated using Smalian's formula for long branches and Huber's formula for short branches (Loetsch *et al.* 1973).
5. *Small branches*: Branches with a diameter \leq 24.9 cm. The biomass of small branches was determined in the field, using a conventional scale. Samples were taken to determine dry weight to estimate biomass. The volume of small branches ($V_{\text{S-branch}}$) was calculated using biomass and specific gravity.

Total stem volume (V_{stem}) was calculated as the sum of the volume of each stem section:

$$V_{\text{stem}} = V_c + V_{\text{non-m}} + V_{\text{stump}}. \quad (1)$$

Total tree volume (V_{tot}) was calculated as the sum of each section volume of the stem and branches:

$$V_{\text{tot}} = V_{\text{stem}} + V_{\text{L-branch}} + V_{\text{S-branch}}. \quad (2)$$

The specific gravity was calculated from 38 samples $5 \times 5 \times 15$ cm (ASTM 1984) that were taken from the top stump section (height between 0.40 and 1.30 m) and from the top commercial stem section of the 19 felled trees (Table 2).

TABLE 1. BA of sampled tree species in 18 permanent sample plots in Tirimbina and Corinto, Costa Rica.

Species	Corinto			Tirimina		
	Mean BA (m ² /ha)	Range (m ² /ha)	Percentage of total	Mean BA (m ² /ha)	Range (m ² /ha)	Percentage of total
<i>Carapa guianensis</i> Aubl.	0.755	(0.015–2.216)	2.913	0.260	(0.014–0.548)	1.223
<i>Inga coruscans</i> Kunth ex Willd.	0.001	(0–0.010)	0.004	0.081	(0–0.405)	0.381
<i>Laetia procera</i> (Poepp.) Eichler.	0.015	(0–0.101)	0.059	0.376	(0.037–0.692)	1.768
<i>Pentaclethra macroloba</i> (Willd.) Kuntze	11.488	(6.905–16.182)	44.272	6.700	(3.606–8.492)	31.474
<i>Stryphnodendron microstachyum</i> Poepp. & Endl.	0.001	(0–0.012)	0.005	0.221	(0.01–0.480)	1.040
<i>Tapirina guianensis</i> Aubl.	0.639	(0–2.021)	2.462	0.389	(0.145–0.841)	1.829
<i>Vochysia ferruginea</i> Mart.				0.696	(0–1.644)	3.267
Total of seven dominant species	12.901	(9.442–18.032)	49.716	8.724	(5.867–10.568)	40.981
Total of other species	13.048	(10.295–17.800)	50.284	12.564	(9.007–15.905)	59.019
Total of all species	25.949	(21.962–31.567)	100	21.287	(14.874–25.856)	100

TABLE 2. Specific gravity of top stump section and top commercial stem of the sampled trees. Values are means of the 19 sampled trees. Standard deviation is in parentheses.

Species	Top stump			Top commercial stem			Average per species
	Average diameter (cm)	N of sampled in total	Specific gravity (g/cm ³)	Average diameter (cm)	N of sampled in total	Specific gravity (g/cm ³)	Specific gravity (g/cm ³)
<i>C. guianensis</i>	136.7 (33.9)	3	0.62 (0.04)	24.6 (8.4)	3	0.65 (0.05)	0.64 (0.04)
<i>I. coruscans</i>	110.3 (20.6)	3	0.70 (0.02)	17.4 (2.2)	3	0.68 (0.04)	0.69 (0.03)
<i>L. procera</i>	106.0 (22.6)	2	0.72 (0.02)	24.5 (3.5)	2	0.69 (0.04)	0.70 (0.03)
<i>P. macroloba</i>	114.0 (23.3)	4	0.63 (0.07)	17.3 (1.6)	4	0.58 (0.03)	0.60 (0.08)
<i>S. microstachyum</i>	65.0	1	0.60	25.0	1	0.58	0.59 (0.01)
<i>T. guianensis</i>	84.7 (15.7)	3	0.62 (0.04)	20.2 (6.2)	3	0.49 (0.07)	0.55 (0.09)
<i>V. ferruginea</i>	101.3 (17.8)	3	0.50 (0.06)	19.8 (4.6)	3	0.62 (0.02)	0.56 (0.08)
Average	106.9 (25.91)	19	0.62 (0.09)	20.26 (5.05)	19	0.62 (0.07)	0.62 (0.06)

Samples were submerged in distilled water in a container placed on a pan balance. The mass of the sample was obtained using water displacement method (ASTM 1983). Descriptive statistics (means and standard deviations) for the tree wood specific gravity values were calculated for each section per species. Means and standard deviations were also calculated for all species. The specific gravity data were examined for normality and homogeneity. Analysis of variance (ANOVA) was carried out to evaluate the variation in specific gravity among sections using SAS Statistical Software.

Biomass values for the five tree components mentioned above (commercial stem, stump, non-commercial stem, large branches, and small branches) were obtained for each individual sample tree. Volumes were converted to biomass using the specific gravity values of each species and component. The biomass expansion factor (BEF) was defined in this study as a ratio of B_{tot} to B_{stem} (Brown 1997; Brown & Lugo 1984, 1992). BEFs are significantly related to the corresponding biomass of the inventoried volume (Brown 1997) or B_{stem} .

The Pearson correlation coefficient (r) was computed for dependent and independent variables. Linear and non-linear regression analyses were used to predict volume based on DBH and H . In addition, models were developed for estimating total biomass (B_{tot}) using DBH, H_c , and H .

The best-fit models were selected based on the criteria of the model's biological logic, the Furnival index (FI) for comparing models with different dependent variables (Furnival 1961) and the PRESS statistic that requires fitting of the P parameter model to each of N different data sets (Clutter *et al.* 1983). Other statistics tested were the coefficient of adjusted determination (R^2), the coefficient of variation (CV%), and the root mean square error (RMSE) of the fitted equation. All models were computed using SAS program. The best-fit model should have the highest R^2 and the lowest FI, PRESS statistic, CV%, and RMSE.

The data and models obtained in this study were also compared with two models for estimating B_{tot} , developed by Brown *et al.* (1989) (Eq. (3)) and Brown & Iverson (1992) (Eq. (4)) for tropical humid forests.

$$B_{\text{tot}} = 13.2579 - 4.8945(\text{DBH}) + 0.6713(\text{DBH})^2 \quad (R^2 = 0.90), \quad (3)$$

$$B_{\text{tot}} = 21.297022 - 6.952649(\text{DBH}) + 0.7403(\text{DBH})^2 \quad (R^2 = 0.92). \quad (4)$$

where B_{tot} is total aboveground biomass (kg/tree) and DBH is diameter at breast height (cm).

RESULTS

Seven species had a DBH ≥ 60 cm, representing, respectively, 41 and 50 percent of the BA (Table 1) in Tirimbina and Corinto. The specific gravity of the top stump was not statistically different ($P > 0.05$) from that of top commercial stem. The mean specific gravity of the sampled species was 0.62 ± 0.06 (g/cm³), varying between 0.55 and 0.70 g/cm³ (Table 2). The species with highest specific gravity was *Laetia procera* (0.70 g/cm³). This value was 27 percent greater than *Tapirira guianensis*, the species with lowest specific gravity (0.55 g/cm³).

Stem volume varied between 2 and 13 m³/tree (Fig. 1a), while total tree volume varied from 5 to 19 Mg/tree (Fig. 1b). Similarly, the total aboveground biomass ranges from 3 to 13 mg/tree (Fig. 2a). In general, stem volume and stem biomass represented about 66 percent of the total tree volume and total aboveground biomass (Table 3). In *Carapa guianensis* and *Vochysia ferruginea*, this percentage was the highest for stem volume (69% and 71%, respectively) and for stem biomass (68% and 65%, respectively). *Stryphnodendron microstachyum* and *T. guianensis* represented the lowest values for the stem volume (55% and 57%, respectively) and for the stem biomass (56% and 60%, respectively).

The BEF averaged 1.6 ± 0.2 , varying from 1.4 to 1.9 (Table 3). The species with highest average BEF was *T. guianensis* (1.8), approximately 33 percent greater than the species with lowest BEF *L. procera* (1.4). The correlation coefficient (r) between BEF and B_{stem} was 0.73 ($P < 0.05$). The BEF decreases as tree size increases (Brown *et al.* 1989). Here, the sampled trees have low BEFs because they are from large trees (Fig. 2b).

A high correlation was found between total and stem volume with DBH. The correlation coefficient (r) between the natural logarithm of DBH (ln DBH) and the natural logarithm of total volume (ln V_{tot}) was 0.91 ($P < 0.05$), and between ln DBH and natural logarithm of stem volume (ln V_{stem}) was 0.82 ($P < 0.05$). The parameters of the best-fit models developed for estimating V_{stem} (Eq. (5); Fig. 1a; $R^2 = 0.66$) and

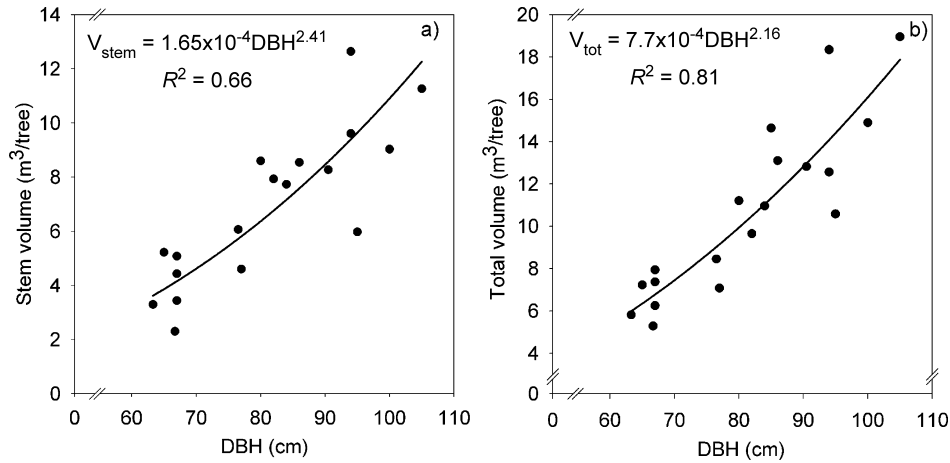


FIGURE 1. Relationship between (a) stem volume (V_{stem}) and DBH and (b) total tree volume (V_{tot}) and DBH. Models are transformations of equations (5) and (8), respectively.

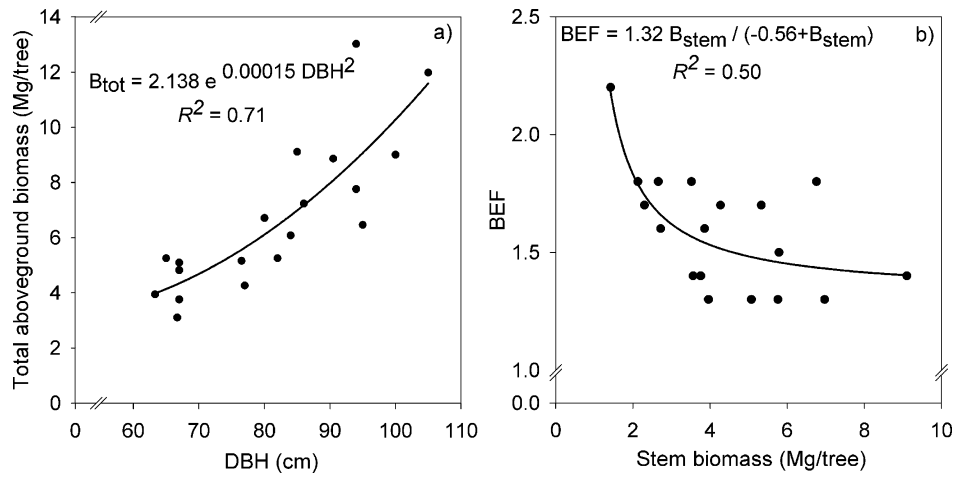


FIGURE 2. Relationship between (a) total aboveground biomass (B_{tot}) and DBH (Eq. (11)) and (b) BEF and stem biomass (B_{stem}) for sampled trees.

TABLE 3. DBH, commercial and total height, stem and total volume, stem and total aboveground biomass and BEF of the sample trees. Values are means of the sampled trees. Standard deviation is in parentheses.

Species	DBH (cm)	N of sampled trees	Height (m)		Volume (m ³)		Biomass (Mg)		BEF
			Commercial	Total	Stem	Total	Stem	Total	
<i>C. guianensis</i>	94.7 (10.0)	3	17.9 (5.1)	32.7 (9.9)	10.8 (1.1)	15.6 (3.3)	6.5 (0.6)	9.6 (2.2)	1.5 (0.3)
<i>I. coruscans</i>	73.6 (14.8)	3	14.6 (2.9)	26.3 (5.5)	5.5 (2.5)	8.7 (3.8)	3.9 (1.8)	6.0 (2.6)	1.5 (0.2)
<i>L. procera</i>	79.5 (20.5)	2	18.9 (3.0)	39.0 (5.7)	8.9 (5.2)	13.0 (7.8)	6.4 (3.8)	9.1 (5.5)	1.4 (0.0)
<i>P. macroloba</i>	88.0 (11.2)	4	13.5 (2.8)	19.5 (4.2)	7.1 (2.1)	11.1 (3.2)	4.2 (1.2)	6.6 (1.9)	1.6 (0.2)
<i>S. microstachyum</i>	67.0	1	20.0	31.0	4.4	8.0	2.7	4.8	1.8
<i>T. guianensis</i>	70.1 (5.6)	3	12.7 (0.2)	26.7 (8.3)	3.9 (1.9)	6.9 (1.6)	2.4 (1.2)	4.0 (1.1)	1.8 (0.4)
<i>V. ferruginea</i>	84.0 (2.0)	3	18.2 (2.8)	29.0 (2.6)	8.1 (0.4)	11.5 (1.7)	4.0 (0.2)	6.2 (1.0)	1.5 (0.2)
General average	81.3 (12.9)	19	15.9 (3.6)	27.9 (7.9)	7.14 (3.0)	10.9 (4.1)	4.4 (1.9)	6.7 (2.7)	1.6 (0.2)

TABLE 4. Models for stem volume V_{stem} (Mg/tree) and total volume V_{tot} (m^3/tree) as a function of DBH (cm). Coefficient of adjusted determination (R^2), CV%, RMSE, and FI.

Equation	Model	Estimated coefficients			R^2	CV (%)	RMSE	FI	PRESS
		c	a						
5	$\ln V_{\text{stem}} = c + a \ln \text{DBH}$	-8.70 ± 1.77	2.41 ± 0.40		0.66	14.6	0.274	1.780	1.604
6	$V_{\text{stem}} = c + a \ln \text{DBH}$	-59.62 ± 11.38	15.21 ± 2.59		0.65	24.6	1.760	1.760	64.642
7	$V_{\text{stem}} = c + a \text{DBH}$	-8.00 ± 2.70	0.18 ± 0.03		0.63	25.2	1.800	1.800	67.526
8	$\ln V_{\text{tot}} = c + a \ln \text{DBH}$	-7.15 ± 1.07	2.15 ± 0.24		0.81	7.2	0.166	0.166	0.559
9	$V_{\text{tot}} = c + a \text{DBH}$	-11.96 ± 2.89	0.28 ± 0.04		0.78	18.0	1.925	1.925	79.240
10	$V_{\text{tot}} = c + a \ln \text{DBH}$	-87.45 ± 12.73	22.37 ± 2.90		0.76	18.4	1.969	1.969	83.085

V_{tot} (Eq. (8); Fig. 1b; $R^2 = 0.81$) as a function of DBH were statistically significant (Table 4). The estimated coefficients were significant ($P < 0.05$) and the statistics of CV%, RMSE, FI, and PRESS were the lowest and R^2 was the highest.

A strong correlation was found between the natural logarithm of total aboveground biomass ($\ln B_{\text{tot}}$) and DBH ($r = 0.85$; $P < 0.05$). No strong correlations were found between B_{tot} and H or H_c (0.47 and 0.11, respectively). Strong correlations were found between $\ln \text{DBH}$ and $\ln H$ ($r = 0.94$) and $\ln \text{DBH}$ and $\ln H_c$ ($R = 0.89$).

The best-fit equations for B_{tot} based on combinations of DBH, H , and H_c as independent variables (Eqs. (15) and (16); Table 5) presented the highest R^2 values (0.87 and 0.77, respectively) and the lowest CV%, RMSE, FI, and PRESS statistics. However, for practical purposes, the recommended equations for B_{tot} were Eq. (11) and (12), which are based on DBH as the independent variable (Table 5; with R^2 of 0.71).

The two models from the literature (Eqs. (3) and (4); Figs. 3a and 3b) underestimated biomass in large trees. In contrast, using the models from our study (Eqs. (11) and (12)) the B_{tot} was well estimated in all size classes (Figs. 3c and 3d).

DISCUSSION

In general, the average values of wood specific gravity found in this study are within the range reported elsewhere (e.g., Carpio 1992, Oxford Forestry Institute 1997, Muller-Landau 2004). Nevertheless, Fearnside

(1997) reports specific gravity values for some species in the Brazilian Amazon, such as *L. procera*, *T. guianensis*, and *C. guianensis*, which are 3–14 percent lower than those reported in this study. Opposite results were found by Muller-Landau (2004), who reported a higher wood mean specific gravity in Manaus (Brazil) than in La Selva, Costa Rica. The mean specific gravity by species between this study and Muller-Landau (2004) in La Selva was not different; however, the variability of the data in La Selva was considerably higher. The values of specific gravity are necessary to calculate biomass and carbon sequestration in forests (Brown & Lugo 1984, 1992; Brown *et al.* 1989; Fearnside 1997).

The biomass expansion factor indicates that the sampled trees have a big stem, which represents the largest proportion of volume and biomass (Fig. 2b). These results are among the ranges reported by Brown & Lugo (1984) and Brown *et al.* (1989). Biomass expansion factors from inventories in tropical Asia, America, and Africa were reported to be 1.1 and 2.5 (Brown & Lugo 1992, Brown 1997).

The R^2 values for volume and total aboveground biomass equations were lower than those reported by Araújo *et al.* (1999), Overman *et al.* (1994), Brown *et al.* (1989), and Segura & Venegas (1999). The differences may be due to overall small sample size in our study, and because our study only consisted of large trees whereas the other studies also included smaller trees ($\text{DBH} \geq 10$ cm). Most of the equations to estimate tree volume only predict the commercial stem volume (e.g., Loetsch *et al.* 1973, Clutter *et al.* 1983, Segura & Venegas 1999), while the total volume in this study includes the volume of large branches, small branches, and stump.

TABLE 5. Models for total aboveground biomass B_{tot} (mg/tree) as a function of DBH (cm), total height H (m), and commercial height H_c (m). Coefficient of adjusted determination (R^2), CV%, RMSE, and FI.

Equation	Model	Estimated coefficients			R^2	CV (%)	RMSE	FI	PRESS
		c	a	b					
11	$\ln B_{\text{tot}} = c + a \text{DBH}^2$	0.76 ± 0.16	0.00015 ± 0.000023		0.71	11.5	0.210	1.303	0.925
12	$\ln B_{\text{tot}} = c + a \ln \text{DBH}$	-7.27 ± 1.37	2.07 ± 0.31		0.71	11.6	0.212	1.316	0.955
13	$B_{\text{tot}} = c + a \text{DBH}$	-7.45 ± 2.37	0.17 ± 0.02		0.66	23.6	1.580	1.580	53.155
14	$B_{\text{tot}} = c + a \ln \text{DBH}$	-54.13 ± 10.48	13.86 ± 2.38		0.64	24.2	1.622	1.622	56.112
15	$\ln B_{\text{tot}} = c + a \ln \text{DBH} + b (\ln \text{DBH}) H$	-6.93 ± 0.91	1.86 ± 0.21	0.0045 ± 0.00095	0.87	7.7	0.140	0.873	0.448
16	$\ln B_{\text{tot}} = c + a \ln \text{DBH} + b \ln H_c$	-8.80 ± 1.36	2.13 ± 0.27	0.46 ± 0.19	0.77	10.2	0.187	1.162	0.788

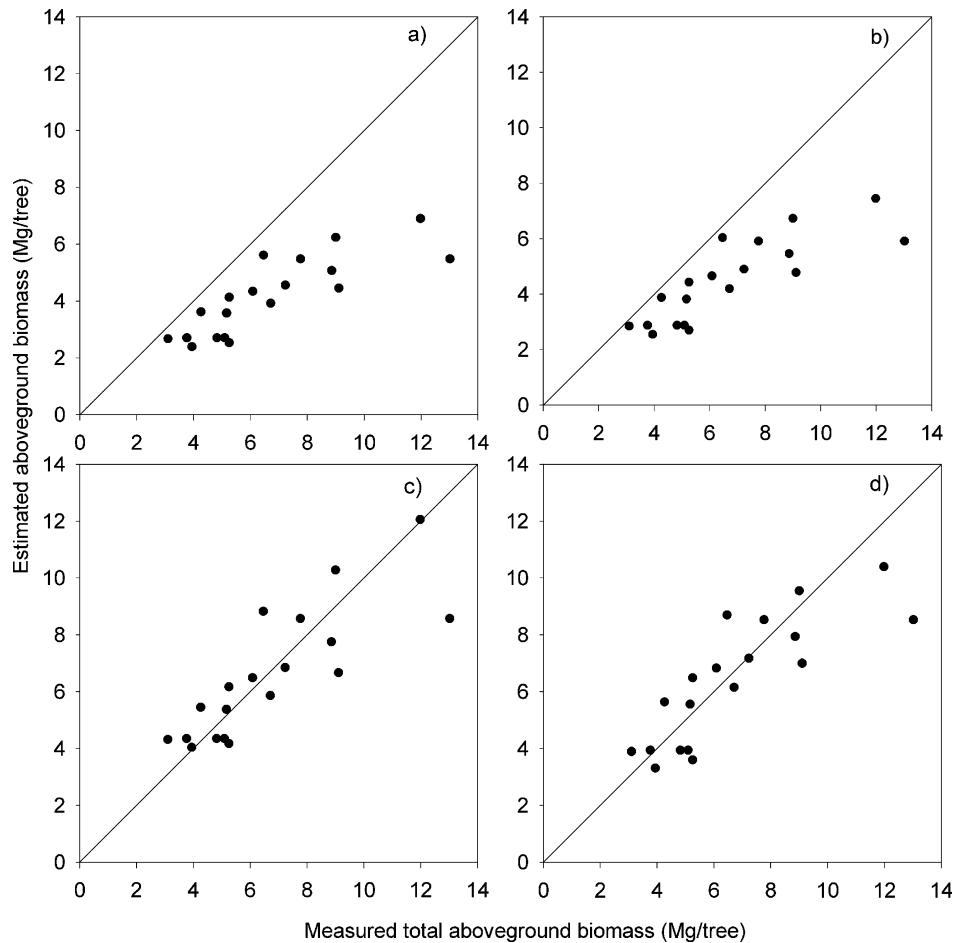


FIGURE 3. Relationship between estimated and measured total aboveground biomass for sampled trees. Equations used were (a) Eq. (3) (Brown *et al.* 1989); (b) Eq. (4) (Brown & Iverson 1992); (c) Eq. (11) (this study); and (d) Eq. (12) (this study).

We recommend the use of models where tree biomass is determined from DBH only, which has a practical advantage because most of the inventories include DBH measurements. Moreover, the DBH is easy to measure accurately in the field. Models that incorporate H and H_c usually give good-fits (Brown *et al.* 1989, Brown 1997, Overman *et al.* 1994, Araújo *et al.* 1999, Schroeder *et al.* 1997). However, in many cases these models are not practical because the measurements of these variables are difficult to carry out with high accuracy, particularly in closed forests.

The best-fit models to estimate total volume and total biomass from DBH adjusted well in the interval of diameters sampled (60–105 cm). These models should be carefully used outside the specified diameter range, due to these equations tend to overestimate the tree biomass and volume.

Results obtained in this study and elsewhere (Brown *et al.* 1989, Brown & Iverson 1992) show the necessity of developing specific biomass models for each region and forest type in the tropics. The general models of total aboveground biomass should be carefully used in specific areas or carbon projects (Noble *et al.* 2000).

CONCLUSIONS

The average wood specific gravity found in this study (0.62 ± 0.08 g/cm³) is in the range reported elsewhere. The biomass expansion factors calculated in this research (1.6 ± 0.2) are within the range reported to other studies. The models developed in this study are recommended only when DBH is between 60 and 105 cm. The two models reported in the literature and tested here underestimated the aboveground biomass, particularly of the large trees. The models developed in this study also included branches in the estimation of total volume in contrast to equations found in literature, which usually include only stems.

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