



ELSEVIER

Forest Ecology and Management 117 (1999) 149–167

---

---

Forest Ecology  
and  
Management

---

---

## Allometric regressions for improved estimate of secondary forest biomass in the central Amazon

Bruce W. Nelson<sup>a,\*</sup>, Rita Mesquita<sup>a</sup>, Jorge L.G. Pereira<sup>b</sup>, Silas Garcia Aquino de Souza<sup>c</sup>, Getulio Teixeira Batista<sup>d</sup>, Luciana Bovino Couto<sup>e</sup>

<sup>a</sup> INPA, National Institute for Amazon Research, Ecology Dept, Caixa Postal 478, 69.011-970 Manaus, AM, Brazil

<sup>b</sup> INPE, National Institute for Space Research, Remote Sensing Division, Av. dos Astronautas, s/n, 12.227-010 São José dos Campos, São Paulo, Brazil

<sup>c</sup> EMBRAPA/CPAA, Caixa Postal 319, 69.048-660 Manaus, AM, Brazil

<sup>d</sup> INPE, National Institute for Space Research, Remote Sensing Division, Av. dos Astronautas, s/n, 12.227-010 São José dos Campos, São Paulo, Brazil

<sup>e</sup> INPA, National Institute for Amazon Research, a/c Agronomy Dept., Caixa Postal 478, 69.011-970 Manaus, AM, Brazil

Received 24 April 1998; accepted 20 August 1998

---

### Abstract

Estimates of the sequestering of carbon by secondary forests – which occupy almost half the deforested area of the Brazilian Amazon – will be improved by the use of accurate allometric relationships for non-destructive measurement of standing biomass and by an evaluation of the suitability of existing equations for application in secondary forest. Species-specific and mixed-species regressions for estimating total above-ground dry weight (DW) were therefore developed using eight abundant secondary forest tree species in the central Amazon. Using only DBH as the input variable, the species-specific equations estimated DW of individual trees with an average error of 10–15%. For the mixed-species equations, developed using 132 trees from seven of the eight species (excluding *Cecropia*), average error in estimating DW of individual trees was 19.8% using only DBH and 15.0% using DBH plus specific density of the wood (SD). Average SD for each species can be substituted without increasing the error of the estimate. Adding total tree height (*H*) as an input variable provided only a slight reduction in error to 14.0%. Previously published mixed-species biomass regression models, based on primary and secondary forest trees of the Amazon, were also cross-validated against the trees of this study. Two of these models, based on primary forest plots and using only DBH as an input, overestimated biomass by 10–60% for central Amazonian secondary forest trees in the size range 5–25 cm. The overestimate was greatest for the larger trees. Including *Cecropia* in the test group will make the overestimate even greater. Those published equations using DBH, *H* and SD as inputs, whether from secondary or primary forest plots, showed better agreement with the sample-derived regressions and lower average errors in estimation of individual tree dry weights. © 1999 Elsevier Science B.V. All rights reserved.

**Keywords:** Amazon; Secondary forest; Biomass; Carbon; Allometry

---

\*Corresponding author. Tel.: +55-92-643-1906; fax: +55-92-236-3088; e-mail: bnelson@internext.com.br

## 1. Introduction

The contribution of the Brazilian Amazon to net carbon release to the atmosphere has been estimated at 0.27 GT/year (Fearnside, 1991) which is 17% of the  $1.6 \pm 1.0$  GT/year derived from worldwide tropical land use change (Schimel et al., 1996). These estimates suffer from many sources of uncertainty. One vector of change which must be quantified is the re-absorption of carbon by secondary forest on fallowed swiddens or abandoned pastures. This is not a trivial sink. As of 1990, ca. 47.6% of the deforested Brazilian Amazon was, in fact, occupied by regrowth >3 years old (Fearnside, 1996) and more than one third of this was at least 20 years old. Several case studies have attempted to quantify the biomass accumulation and consequent carbon sequestration in secondary vegetation plots in the Amazon Basin (e.g., Saldarriaga et al., 1988; Uhl et al., 1988; Fearnside and Guimarães, 1996; Pereira, 1996; Alves et al., 1997). Most of these studies estimated total above-ground biomass by using or developing allometric equations. These were derived by performing regressions between destructively measured dry weights of trees as the dependent variable and field measurements of biometric parameters as the independent variables. Once developed, such regressions allow inventories of standing biomass to be conducted quickly and non-destructively.

The accuracies of standing biomass estimates in secondary forest plots are likely to be diminished by three factors. First, few species-specific allometric equations have been developed for the suite of common secondary forest tree species of the region. Second, published mixed-species equations are generally derived from primary forest trees, which have different growth forms and denser wood than secondary forest species. Third, even when an equation was developed for secondary forests, its application to trees with biometric input parameters outside the range of those trees used to develop the equation can lead to large errors.

To the best of our knowledge, only two taxon-specific studies have been published for Amazonian trees. Uhl et al. (1988) obtained high  $R^2$  values in multiple regressions for three tree and two shrub taxa in the eastern Amazon. But these equations should not be applied to trees larger than the individuals in their study sites, which were eight-year-old abandoned

pastures. Saldarriaga et al. (1988) developed a regression for palms in secondary succession plots up to 80 years of age in the northwest Amazon, but the data did not cluster well along the regression line ( $r^2=0.89$ ). Given this situation, non-destructive biomass inventories have relied heavily on mixed-species equations (Uhl et al., 1988; Saldarriaga et al., 1988; Brown et al., 1989; Overman et al., 1994; Brown et al., 1995; Higuchi et al., 1998).

In order to improve future estimates of carbon stocks and absorption rates by secondary forest in the Amazon, species-specific allometric relationships were therefore developed for estimating total above-ground biomass for eight secondary forest species common in the central Amazon. Relationships were tested for above-ground dry weight in kilograms (DW) against three biometric parameters: diameter at breast height in centimeters (DBH), total height in meters ( $H$ ), and specific density in grams dry weight per cubic centimeter of fresh volume over bark (SD). One-hundred-and-thirty-two trees in five genera (excluding *Cecropia*, which has very light wood and hollow branches) were then combined to develop a set of mixed-species allometric equations for secondary forest in the Amazon. Finally the study examined the question: “How well do previously reported mixed-species equations predict the dry weight of the secondary forest trees of this study?” The evaluated regressions are from Uhl et al. (1988), Saldarriaga et al. (1988), Overman et al. (1994), Brown et al. (1989) modified by Honzák et al. (1996), and Higuchi et al. (1998).

## 2. Methods

The study area is located at an experimental station of the Brazilian Agency for Agricultural and Range Research (EMBRAPA) 52 km north of Manaus on the BR 174 Highway, in the Brazilian state of Amazonas ( $\approx 60^\circ 00'W$ ,  $2^\circ 30'S$ ). Primary forest on latosol clay ‘terra firme’ had been cut for a rubber tree plantation. A 50 m wide buffer zone between the plantation and primary forest had been cut and probably burned once, then abandoned to secondary succession for fifteen years. Smaller specimens of secondary forest species were found in the overgrown rubber plantation, which

had been scraped by a bulldozer before planting, then abandoned for eight years prior to the study.

The eight selected species are: *Bellucia grossularioides* (L.) Triana, *Bellucia* sp., *Cecropia sciadophylla* Mart., *Croton matourensis* Aubl., *Goupia glabra* Aubl., *Laetia procera* (Poepp) Eichl., *Vismia cayennensis* (Jacq.) Pers., and *Vismia japurensis* Reichart. They represent six plant families (Melastomataceae, Cecropiaceae, Euphorbiaceae, Celastraceae, Flacourtiaceae and Clusiaceae). Locally common, these usually constitute >50% of the trees in second-growth forests <20 years old, even with different land use histories prior to abandonment.

For each species, 17–27 individuals were selected to destructively estimate total biomass. Individuals with damaged crowns or broken trunks were not considered. All selected individuals were at least 10 m from the access road. For each species, five individuals were sought from each of five size classes within the range 0–25 cm diameter at breast height (DBH). For *Goupia glabra*, only two individuals over 10 cm DBH were found. For *Cecropia sciadophylla*, individuals up to 38 cm DBH were included and only the independent variable DBH was obtained. The two morphologically similar species of *Bellucia* were combined in the numerical analyses.

Total above-ground dry weight (DW) was estimated by obtaining fresh weight of three components: trunk; branch; and leaf+fine branches (<1 cm diameter). Fresh weights were measured with a suspended cantilever scale of 80 kg capacity set up in the forest. Smaller specimens were weighed on suspended spring scales of 500, 2000 and 5000 g capacities. After obtaining fresh weights, a small sample (<2 kg) of each component was sealed in a 2.2 g plastic bag, weighed the same day on a digital electronic scale of 2000 g capacity with accuracy of  $\pm 1\%$ , then emptied into double paper bags where it was dried to constant weight at a temperature of  $\sim 105^\circ\text{C}$ . The paper bags at Amazonian ambient temperature and humidity held several grams of water, so tare weights were obtained by heating the empty bags overnight and weighing while hot and dry. Fresh weight of each major component previously determined with the field scales was multiplied by the dry-weight/fresh-weight ratio of the corresponding sample, to give an estimate of total dry weight of each tree broken down into three components. A single wood sample taken at 1.3 m above the

base of the tree was used to estimate dry weight of the entire main stem. To detect a possible variation of water content as a function of height in the stem, two additional samples were taken from a subsample of trees, one near the top of the trunk and one exactly halfway between this sample and the 1.3 m high sample. Total height ( $H$ ) was measured on the felled trees from the base to the top of the crown. Wood specific density (SD) was calculated for a pie-slice or cylinder of the trunk (both with bark) at breast height, determining its fresh volume then drying to a constant weight. Fresh volume was measured by water displacement, impaling the sample on a needle and forcibly submerging in a beaker of water tared on the digital scale of 2000 g capacity. The increase in weight in grams is equivalent to the volume in cubic centimeters. Volume estimates based on geometry of trunk slices were not used due to the non-cylindrical shape of many samples.

The genus *Bellucia* was examined first, as it had a large number of individuals ( $n=27$ ). Predictive value of the three independent variables was explored beginning with the simplest relationship. Following the example of Overman et al. (1994) – who developed allometric relationships for a set of mixed-species primary forest trees in the western Amazon – successive transformations were then applied to satisfy the assumptions of linear regression and to examine the effect on indicators of accuracy in estimation of DW.

For each linear regression model, the following indicators of goodness of fit are reported:

1.  $r^2$  of the simple regression (or  $R^2$  of the multiple regression): indicates the spread of the data in the y-direction about the regression line, relative to its spread about the average y value, which is a horizontal line.
2. *Standard error*: reported for the intercept and for partial regression coefficients of the independent variables.
3. *Significance of t-value*: reported for each independent variable in different combinations with other independent variables.
4. *Average unsigned deviation*: Also referred to as average error of estimate, this is an indicator of accuracy in the estimation of individual tree biomass values. For each tree used in a regression the difference between predicted dry weight and

observed dry weight was expressed as a percentage of observed dry weight. The absolute values of all cases (deviations) were then averaged.

A mixed-species regression obtained from 132 trees of this study was compared with other mixed-species regression equations for above-ground biomass, published for sites in the eastern and the western Amazon. These include an equation based on DBH and  $H$  for eight-year-old pioneer species in abandoned pastures of the eastern Amazon (Uhl et al., 1988;  $n=30$ ); equations for three different diameter classes of 9–80 years old successional forests in the northwest Amazon, all based on DBH,  $H$  and SD (Saldarriaga et al., 1988;  $n=49$ , 30 and 43); equations based on DBH,  $H$  and wood density for a mixture of tropical forest trees from Amazonia and Southeast Asia (data from Brown et al., 1989 subsetted to 5–35 cm diameter by Honzák et al., 1996;  $n=142$ ); equations based on different combinations of DBH,  $H$  and SD for a set of primary forest trees 10–45 cm diameter near Araracuara, Colombia (Overman et al., 1994;  $n=33$ ) and finally, an equation for estimate of *fresh weight* of primary forest trees  $\geq 5$  cm DBH near Manaus based only on DBH (Higuchi et al., 1998;  $n=341$ ).

Two methods were employed to answer the question, “How well do previously reported mixed-species equations predict the dry weight of the 132 trees from secondary forest of this study?” First, the real biometric input variables (DBH,  $H$ , and/or SD), measured in the field for each of the 132 trees, were used to estimate DW for every tree using a published equation. The signed percent error of prediction for each tree was plotted against DBH, similar to a residuals plot. A 50% locally weighted least squares regression (LOWESS) was performed on each plot to show the tendency of the equation’s percent error as a function of DBH.

Second, each published equation was used to predict DW at seven DBH values ranging from 5 to 25 cm. Predicted dry weights were then plotted on an arithmetic scale against DBH to show how the different equations behave with increasing tree size. The same graph includes the ‘correct’ prediction line, based on a regression developed in this paper using the single independent variable DBH. This line was, of course, based on the true dry weights

of the 132 trees. To plot the results of all equations in two dimensions, values of  $H$  and SD were fixed for each of the seven DBH values. The most reasonable values of  $H$  and SD for each value of DBH were determined by inverting regressions of  $\ln(H)$  vs.  $\ln(\text{DBH})$  and  $\ln(\text{SD})$  vs.  $\ln(\text{DBH})$ , based on field data for the 132 trees. Using these particular sets of DBH,  $H$  and SD has the convenient effect of making the ‘correct’ simple regression (based only on DBH) give precisely the same predictions of DW as each of the multiple regressions developed in this study. By this means, the published equations could be cross-validated against just one (any one) of the models in this study.

### 3. Results

#### 3.1. Species-specific regressions

Scatter plots were devised for *Bellucia* spp. to determine which of the three biometric parameters showed a strong relationship with total dry weight (Fig. 1(A)–(C)). The plots show a clear non-linear relationship for DBH vs. dry weight, a similar curve but with more scatter for  $H$  vs. dry weight, and no clear relationship for SD vs. dry weight. The best predictor of dry weight in a simple regression model will therefore be DBH. Exponential, growth, cubic, quadratic and power curves were fitted to the DBH vs. DW data of *Bellucia*, restraining the intercept to zero. The best fit was obtained from a power curve, yielding an  $r^2$  value of 0.993:

$$\text{DW} = \alpha(\text{DBH})^\beta$$

The solution for  $\beta$  in the case of the studied *Bellucia* trees was 2.37. Plotting DW against the exponentiated term provided a linearized relationship (Fig. 2(A)) which can be more easily regressed and evaluated:

$$\text{DW} = \alpha(\text{DBH})^{2.37} \quad (\text{Model 1}) \quad (1)$$

The regression coefficients and indicators of accuracy and significance are shown in Table 1 for all models applied to *Bellucia*.

It is interesting to note why the exponent is greater than 2.0 in model 1. *Bellucia* trees of 20 cm DBH allocate fully 30% of their weight to large branches (>1 cm diameter) while trees of 10 cm DBH dedicate

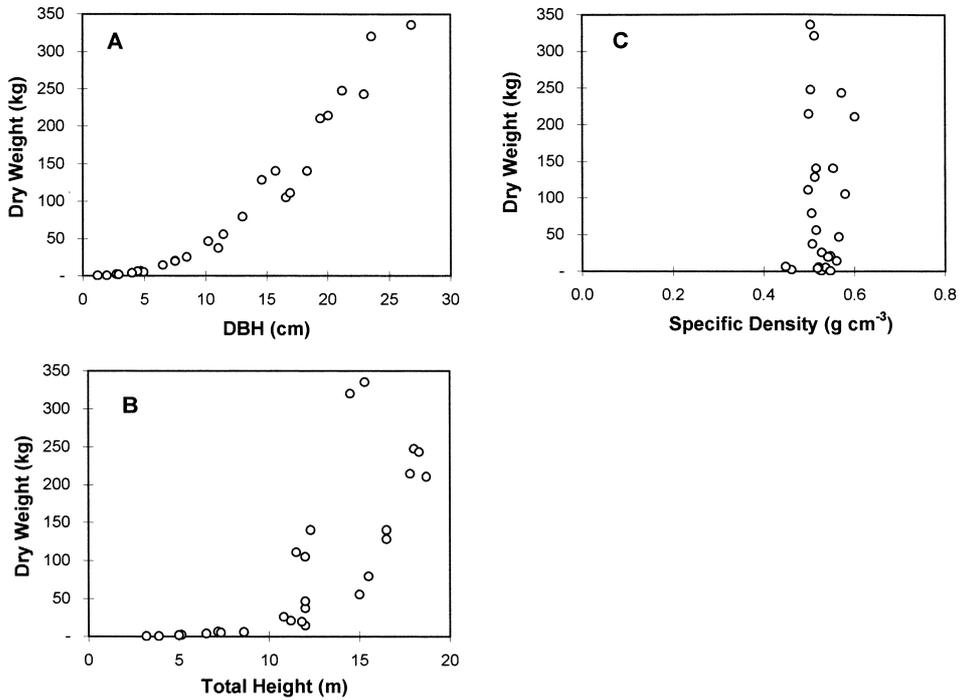


Fig. 1. Scatter plots of biometric parameters vs. total above-ground dry weight (DW) for *Bellucia* spp. ( $n=27$ ); (A) diameter at breast height vs. DW; (B) total height vs. DW; (C) specific density vs. DW.

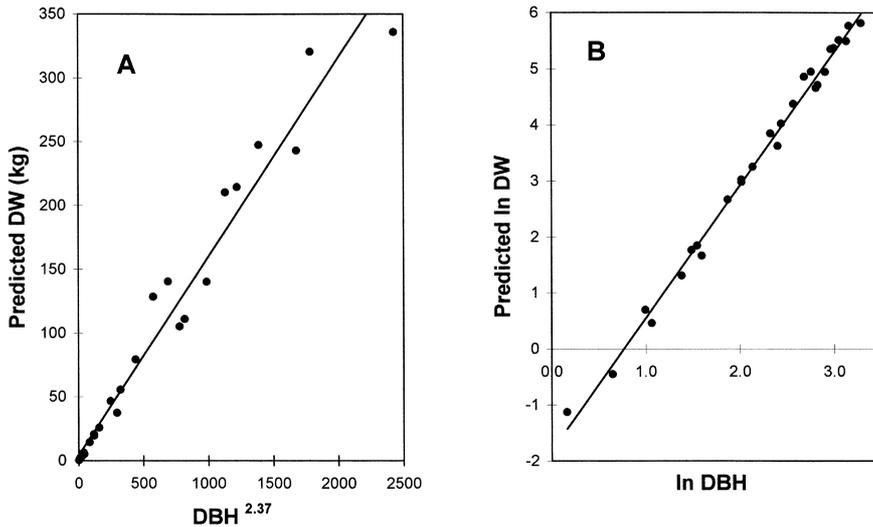


Fig. 2. Linear regressions of transformed data from *Bellucia* spp. ( $n=27$ ); (A) model 1:  $DW=0.1591(DBH^{2.37})$ ; (B) model 2:  $\ln(DW)=2.37 \ln(DBH)-1.8158$ .

just 10% of their weight to large branches. The tree becomes relatively top heavy as it grows, which is similar to changing the shape of a cone to a more

cylindrical form. If the shape did not change, the volume (and weight) would increase as the square of the diameter.

Table 1

Regression models for estimation of above-ground biomass of 27 trees of *Bellucia* spp. from secondary forest of the central Amazon. Trees range in size 1.2–26.8 cm DBH, with the following number of individuals in each 5 cm DBH interval: 0–4.9 cm: 8; 5.0–9.9 cm: 4; 10.0–14.9 cm: 5; 15.0–19.9 cm: 5; 20.0–24.9 cm: 4; 25.0–29.9 cm: 1

Regression model	Coefficient symbol	Coefficient value	Standard error	$r^2$	Average unsigned deviation (%)	Significance level of $t$ -value
Model 1: $DW = \alpha(DBH^{2.37})$	$\alpha$	0.1591	0.0044	0.965	14.5	<0.0001
Model 2: $\ln(DW) = c + \alpha \ln(DBH)$	$c$	-1.8158	0.0944	0.993	14.3	<0.0001
	$\alpha$	2.3700	0.0403			<0.0001
Model 3: $\ln(DW) = c + \alpha \ln(DBH) + \beta \ln(H)$	$c$	-2.4387	0.2290	0.995	10.9	<0.0001
	$\alpha$	2.0751	0.1070			<0.0001
	$\beta$	0.5360	0.1837			<0.01
Model 4: $\ln(DW) = c + \alpha \ln(H)$	$c$	-5.8514	0.5856	0.912	44.9	<0.0001
	$\alpha$	3.8980	0.2422			<0.0001
Model 5: $\ln(DW) = c + \alpha \ln(DBH) + \beta \ln(SD)$	$c$	-1.7437	0.3757	0.993	14.3	<0.0001
	$\alpha$	2.3688	0.0415			<0.0001
	$\beta$	0.1081	0.5443			NS (0.8)

Model 1 does not obey one of the assumptions of a linear regression. Variance of the distribution of the dependent variable should be constant for all values of the independent variable; i.e. there should not be increasing data spread in the  $y$ -direction for larger trees (Fig. 2(A)). A  $\ln$ - $\ln$  transformation of model 1 (Fig. 2(B)) makes the data cluster more evenly along the regression line. A further advantage of using this transformation is the property of logarithms,  $\ln(x^\alpha) = \alpha \ln(x)$ , which allows simplification of the exponent to unit value:

$$\ln(DW) = c + \alpha \ln(DBH) \quad (\text{Model 2})$$

With the simple linear regression of model 2, the single independent variable  $\ln(DBH)$  reduces the sum-of-squares variation of  $\ln(DW)$  by 99.3%. Yet the estimates of  $DW$  for individual trees still diverge from the observed values by an average 14.3%. A modest improvement might be found by adding a second biometric predictor which accounts for differences in weight between trees of similar diameter. Adding  $H$  as a separate independent variable gives:

$$\ln(DW) = c + \alpha \ln(DBH) + \beta \ln(H) \quad (\text{Model 3})$$

$R^2$  is increased slightly for the estimate of  $\ln(DW)$ . When a second independent variable is added to the best single independent variable, the result is always

$R^2 \geq r^2$  (Neter and Wasserman, 1974). Since  $r^2$  was already very high for the single variable model, average percent deviation between observed and expected values of  $DW$  provides a more useful indicator of improvement. Relative to model 2, average deviation dropped by 3.4 percentage points to 10.9% when using model 3. The  $t$ -value for the coefficient of  $H$  is significant only at the  $p < 0.01$  level, however, and the standard error of 0.184 is large relative to the coefficient value of 0.536.

When correlation between two independent variables is high, multicollinearity imposes itself on a multiple linear regression model, causing estimated partial regression coefficients for one or both independent variables to become less precise ( $t$ -values become less significant). This can occur even when both variables are very good predictors of the dependent variable (Neter and Wasserman, 1974). Height by itself is a fair predictor of biomass ( $r^2 = 0.912$ ;  $t$ -value of coefficient significant at the  $p < 0.0001$  level; see model 4 in Table 1, also Fig. 1), so the lower confidence in its estimated coefficient in a multiple regression is a consequence of the high correlation between  $H$  and  $DBH$ . The correlation between these two variables is 0.85 for *Bellucia*. For some other species, the correlation between  $H$  and  $DBH$  exceeded 0.90, forcing the use of a regression model with a

single coefficient, derived from model 3 (see Section 4):

$$\ln(\text{DW}) = c + \alpha \ln(\text{DBH}^{4.6}H) \quad (\text{Model 3A})$$

The simple model based on  $H$  alone has the form:

$$\ln(\text{DW}) = c + \alpha \ln(H) \quad (\text{Model 4})$$

Inspection of Fig. 1 indicates that this model will have low accuracy in estimating DW of individual trees. The average deviation of estimated vs. observed DW values was indeed quite large: 44.9% (Table 1).

Rotting or partially hollowed trees will have lower specific density causing lower dry weight. In some fast growing tropical tree species, specific density has been reported to increase with age (Wiemann and Williamson, 1989). Its value as a predictor of tree dry weight was therefore tested. If DBH and  $H$  are held constant, the relationship between DW and SD is expected to be linear. For a two variable case:  $\text{DW} = c + k(\text{DBH}^{2.37})(\text{SD})$ . The  $\ln$ – $\ln$  transformation is:

$$\ln(\text{DW}) = c + \alpha \ln(\text{DBH}) + \beta \ln(\text{SD}) \quad (\text{Model 5})$$

Applying the data for *Bellucia*, the 95% confidence interval for the partial regression coefficient of the specific density term includes zero and the  $t$ -value is not statistically significant (Table 1). The correlation coefficient between SD and DBH is only 0.12 for *Bellucia*, so this is clearly not due to multicollinearity. Rather, it indicates that specific density has no value for predicting biomass, in the case of the 27 *Bellucia* specimens studied.

Models 2, 3, and 5 were applied to the other taxa. Model 1 was excluded as it does not obey the assumptions of a linear regression. Model 4 was excluded because of the very high average deviation between observed and predicted values of total dry weight for *Bellucia*. Model 3A was added when correlation between  $H$  and DBH did not permit statistically significant estimates of both partial regression coefficients using model 3 (i.e. when  $p \geq 0.01$ ). The results are given in Tables 2–7.

### 3.2. Mixed-species regressions

The species-specific regressions will be very useful in the central Amazon. In other parts of Amazonia, however, different taxa dominate regrowth forests. Thus, a set of mixed-species equations was developed. These are based on all 132 trees from seven species of this study, excluding *Cecropia* due to its peculiar growth form. These equations should be applicable to any species with growth form and joint ranges of DBH,  $H$  and SD similar to those of the trees in this study. Table 8 shows the results for three models developed above (models 2, 3 and 5) plus two new models of the form:

$$\ln(\text{DW}) = c + \alpha \ln(\text{DBH}) + \beta \ln(H) + \chi \ln(\text{SD}) \quad (\text{Model 6})$$

$$\ln(\text{DW}) = c + \alpha \ln(\text{DBH}) + \beta \ln(\text{avgSD}) \quad (\text{Model 7})$$

where ‘avgSD’=the average specific density of trunk wood with bark for a given species.

Table 2

Regression models for estimation of above-ground biomass for 17 trees of *Goupia glabra* from secondary forest of the central Amazon. Trees range in size 1.5–12.2 cm DBH, with the following number of individuals in each 5 cm DBH interval: 0–4.9 cm: 7; 5.0–9.9 cm: 8; 10.0–14.9 cm: 2

Regression model	Coefficient symbol	Coefficient value	Standard error	$r^2$	Average unsigned deviation (%)	Significance level of $t$ -value
Model 2: $\ln(\text{DW}) = c + \alpha \ln(\text{DBH})$	$c$	–1.7972	0.1082	0.991	10.9	<0.0001
	$\alpha$	2.4206	0.0598			<0.0001
Model 3: $\ln(\text{DW}) = c + \alpha \ln(\text{DBH}) + \beta \ln(H)$	$c$	–2.4990	0.1776	0.996	7.7	<0.0001
	$\alpha$	2.1283	0.0786			<0.0001
	$\beta$	0.5508	0.1270			<0.001
Model 5: $\ln(\text{DW}) = c + \alpha \ln(\text{DBH}) + \beta \ln(\text{SD})$	$c$	–1.5602	0.3363	0.991	10.6	<0.001
	$\alpha$	2.3728	0.0883			<0.0001
	$\beta$	0.3976	0.5332			NS (0.5)

Table 3

Regression models for estimation of above-ground biomass for 22 trees of *Laetia procera* from secondary forest of the central Amazon. Trees range in size 1.6–24.8 cm DBH, with the following number of individuals in each 5 cm DBH interval: 0–4.9 cm: 3; 5.0–9.9 cm: 8; 10.0–14.9 cm: 5; 15.0–19.9: 5; 20.0–24.9: 1

Regression model	Coefficient symbol	Coefficient value	Standard error	$r^2$	Average unsigned deviation (%)	Significance level of $t$ -value
Model 2: $\ln(DW)=c+\alpha\ln(DBH)$	$c$	-2.2244	0.1120	0.993	13.3	<0.0001
	$\alpha$	2.5105	0.0483			<0.0001
Model 3: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(H)$	$c$	-2.6385	0.1361	0.996	9.9	<0.0001
	$\alpha$	2.1976	0.0881			<0.0001
	$\beta$	0.4565	0.1167			<0.001
Model 5: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(SD)$	$c$	-2.0619	0.4735	0.993	13.3	<0.001
	$\alpha$	2.4882	0.0802			<0.0001
	$\beta$	0.2086	0.5898			NS (0.7)

Table 4

Regression models for estimation of above-ground biomass for 20 trees of *Vismia cayennensis* from secondary forest of the central Amazon. Trees range in size 1.6–21.8 cm DBH, with the following number of individuals in each 5 cm DBH interval: 0–4.9 cm: 5; 5.0–9.9 cm: 5; 10.0–14.9 cm: 5; 15.0–19.9: 3; 20.0–24.9: 2

Regression model	Coefficient symbol	Coefficient value	Standard error	$r^2$	Average unsigned deviation (%)	Significance level of $t$ -value
Model 2: $\ln(DW)=c+\alpha\ln(DBH)$	$c$	-2.3706	0.1100	0.993	12.2	<0.0001
	$\alpha$	2.5392	0.0486			<0.0001
Model 3: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(H)$	$c$	-2.4240	0.1923	0.994	12.0	<0.0001
	$\alpha$	2.4855	0.1641			<0.0001
	$\beta$	0.0738	0.2152			NS (0.7)
Model 3A: $\ln(DW)=c+\alpha\ln(DBH^{4.6} H)$	$c$	-2.7062	0.1272	0.992	11.6	<0.0001
	$\alpha$	0.4759	0.0100			<0.0001
Model 5: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(SD)$	$c$	-2.5023	0.4382	0.993	12.2	<0.0001
	$\alpha$	2.5523	0.0654			<0.0001
	$\beta$	-0.1300	0.4179			NS (0.8)

### 3.3. Cross validation with published mixed-species regressions

Scatter plots of DBH vs. signed percent error in the estimate of individual tree biomass values are shown in Fig. 3 for nine published equations. A similar plot for the best mixed-species equation of this paper is shown in the upper left of Fig. 3, useful for comparing the degree of scatter. Based on model 6, this scattergram has an average deviation of 14.0% and the points are symmetrically distributed above and below the zero-error line, as expected. All other scatter plots

show percent differences between directly observed total above-ground biomass for 132 secondary forest trees of the central Amazon vs. biomass predicted by an equation from the literature. All plots have 132 points and use dry weights, except the one for Higuchi et al. (1998) which uses fresh weights and is limited to the 99 trees of this study with  $DBH \geq 5$  cm. The percent error axes are all truncated at  $\pm 80\%$  to standardize for visual comparison, but the locally weighted regression lines are based on all the data. For this particular sample of secondary forest trees, the scatter plots with locally weighted regression lines

Table 5

Regression models for estimation of above-ground biomass for 23 trees of *Vismia japurensis* from secondary forest of the central Amazon. Trees range in size from 1.5–28.6 cm DBH, with the following number of individuals in each 5 cm DBH interval: 0–4.9 cm: 8; 5.0–9.9 cm: 6; 10.0–14.9 cm: 4; 15.0–19.9: 3; 20.0–24.9: 0; 25.0–29.9: 2

Regression model	Coefficient symbol	Coefficient value	Standard error	$r^2$	Average unsigned deviation (%)	Significance level of $t$ -value
Model 2: $\ln(DW)=c+\alpha\ln(DBH)$	$c$	-1.7829	0.0992	0.992	14.7	<0.0001
	$\alpha$	2.3651	0.0466			<0.0001
Model 3: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(H)$	$c$	-2.0118	0.3634	0.992	14.6	<0.0001
	$\alpha$	2.2557	0.1735			<0.0001
	$\beta$	0.1877	0.2864			N.S. (0.5)
Model 3A: $\ln(DW)=c+(\ln(DBH)^{4.6} H)$	$c$	-2.3362	0.1106	0.992	14.9	<0.0001
	$\alpha$	0.4560	0.0091			<0.0001
Model 5: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(SD)$	$c$	-1.2148	0.2517	0.994	13.5	<0.0001
	$\alpha$	2.3129	0.0473			<0.0001
	$\beta$	0.7264	0.3008			<0.05

Table 6

Regression models for estimation of above-ground biomass for 23 trees of *Croton matourensis* from secondary forest of the central Amazon. Trees range in size 2.3–25.3 cm DBH, with the following number of individuals in each 5 cm DBH interval: 0–4.9 cm: 5; 5.0–9.9 cm: 5; 10.0–14.9 cm: 5; 15.0–19.9: 5; 20.0–25.3: 3

Regression model	Coefficient symbol	Coefficient value	Standard error	$r^2$	Average unsigned deviation (%)	Significance level of $t$ -value
Model 2: $\ln(DW)=c+\alpha\ln(DBH)$	$c$	-2.7009	0.1304	0.991	12.5	<0.0001
	$\alpha$	2.5996	0.0550			<0.0001
Model 3: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(H)$	$c$	-3.4630	0.2565	0.994	11.6	<0.0001
	$\alpha$	2.2885	0.1053			<0.0001
	$\beta$	0.5906	0.1804			<0.01
Model 5: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(SD)$	$c$	-2.9214	0.5500	0.991	12.3	<0.0001
	$\alpha$	2.6226	0.0791			<0.0001
	$\beta$	-0.1850	0.4477			NS (0.7)

Table 7

Regression model for estimation of above-ground biomass for 27 trees of *Cecropia sciadophylla* from secondary forest of the central Amazon. Trees range in size 5.1–38.2 cm DBH, with the following number of individuals in each 5 cm DBH interval: 5.0–9.9 cm: 4; 10.0–14.9 cm: 7; 15.0–19.9: 4; 20.0–24.9: 5; 25.0–29.9: 3; 30.0–34.9: 3; 35.0–38.2: 1

Regression model	Coefficient symbol	Coefficient value	Standard error	$r^2$	Average unsigned deviation (%)	Significance level of $t$ -value
Model 2: $\ln(DW)=c+\alpha\ln(DBH)$	$c$	-2.5118	0.1986	0.980	14.6	<0.0001
	$\alpha$	2.4257	0.0690			<0.0001

show: (1) how much a particular published equation, derived from a different set of trees, tends to over or underestimate biomass of trees in this study; (2) how

the errors of estimate change in sign and magnitude as a function of DBH; and (3) the degree of scatter induced by the different published equations.

Table 8

Regression models for estimation of above-ground biomass for 132 trees of seven species from secondary forest of the central Amazon (excluding *Cecropia*). Average specific density of the sample is 0.54. DBH range is 1.2–28.6 cm, with the following number of individuals in each 5 cm DBH interval: 0–4.9 cm: 36; 5.0–9.9 cm: 36; 10.0–14.9 cm: 26; 15.0–19.9 cm: 21; 20.0–24.9 cm: 9; 25.0–29.9 cm: 4

Regression model	Coefficient symbol	Coefficient value	Standard error	$r^2$	Average unsigned deviation (%)	Significance level of $t$ -value
Model 2: $\ln(DW)=c+\alpha\ln(DBH)$	$c$	-1.9968	0.0610	0.984	19.8	<0.0001
	$\alpha$	2.4128	0.0273			<0.0001
Model 3: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(H)$	$c$	-2.5202	0.1254	0.986	17.7	<0.0001
	$\alpha$	2.1400	0.0636			<0.0001
	$\beta$	0.4644	0.0993			<0.0001
Model 5: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(SD)$	$c$	-1.4278	0.0819	0.9896	15.0	<0.0001
	$\alpha$	2.3836	0.0221			<0.0001
	$\beta$	0.7655	0.0885			<0.0001
Model 6: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(H)+\chi\ln(SD)$	$c$	-1.8985	0.1219	0.991	14.0	<0.0001
	$\alpha$	2.1569	0.0504			<0.0001
	$\beta$	0.3888	0.0791			<0.0001
	$\chi$	0.7218	0.0820			<0.0001
Model 7: $\ln(DW)=c+\alpha\ln(DBH)+\beta\ln(\text{avgSD})$	$c$	-1.4702	0.0802	0.9894	15.0	<0.0001
	$\alpha$	2.4449	0.0224			<0.0001
	$\beta$	0.9028	0.1083			<0.0001

The overlain arithmetic plots of estimated DW vs. DBH for eight mixed-species equations found in the literature are shown in Fig. 4. This figure provides a better visualization of how different equations' estimates of tree biomass can be expected to diverge from the true regression line (heavy line in the graph) as DBH increases. Derivation of the true regression line in this graph was model-independent, as explained in the Section 2.

## 4. Discussion

### 4.1. Species-specific regressions

Accuracy of models derived from the trees of this study is best measured using average unsigned percent deviation between predicted and observed dry weights (Fig. 5). Average deviation of model 2, for the species-specific regressions, ranges from 10.9% (*Goupia glabra*) to 14.7% (*Vismia japurensis*). Because DBH alone is such a good predictor, only marginal improvement can be expected by adding a second or third

independent variable to species-specific regressions. Adding  $H$  as the second independent variable – or incorporating it into the term  $\alpha\ln(DBH^{4.6}H)$  – decreases the average deviation between observed and expected dry weight by 3.4% for *Bellucia* (model 3), 3.4% for *Laetia procera* (model 3), 3.2% for *Goupia glabra* (model 3), 0.9% for *Croton matourensis* (model 3), 0.6% for *Vismia cayennensis* (model 3A) and increases error by 0.2% for *Vismia japurensis* (model 3A). Specific density is a statistically significant predictor of DW only in the case of *Vismia japurensis*, where it reduces the average deviation by 1.2% compared with model 2. Several individuals of this tree had less compact, partially degraded wood, with lower SD.

When DBH is the only input variable, the species-specific regressions are always more accurate, by 5–9%, than the mixed-species regression (Fig. 5). The improvement in accuracy would be even greater had *Cecropia* been included in the mixed-species sample. Fig. 5 shows that it was worth the trouble of developing species-specific allometric relationships. Nonetheless, some of the species-specific regressions are

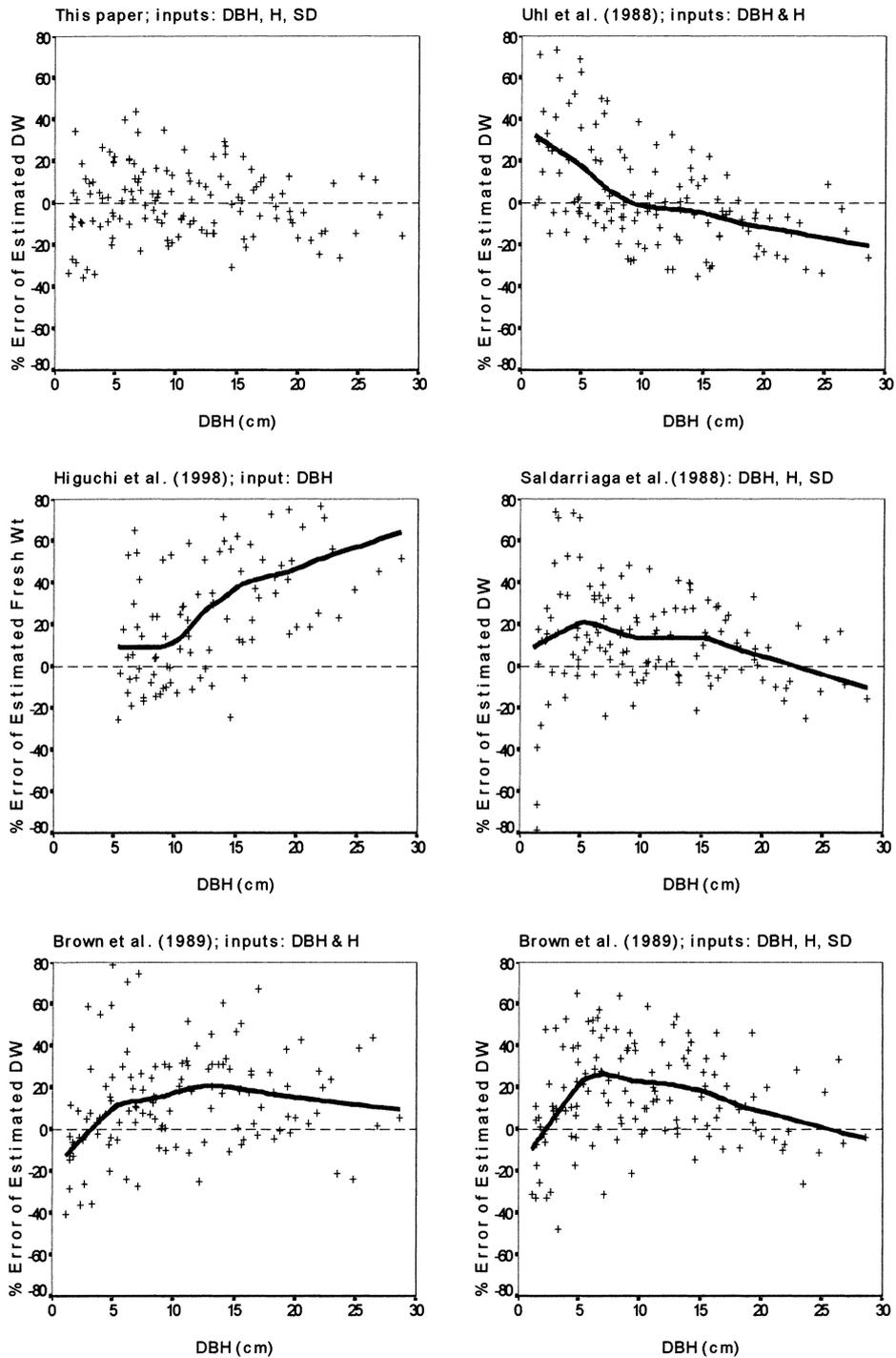


Fig. 3. Errors of nine published mixed-species regression equations when used to predict total above-ground dry weight (fresh weight in one case) of each non-Cecropioid tree of this study. Tendency of a given model to over or underestimate biomass is indicated by distance of LOWESS regression above or below 0% line. See Fig. 4 for details of models, except Higuchi et al. (1998) who predict fresh weight. Their model is: for trees 5–19.9 cm DBH:  $\ln(\text{DW})=2.665 \ln(\text{DBH})-1.754$ ; for trees  $\geq 20$  cm DBH:  $\ln(\text{DW})=2.17 \ln(\text{DBH})-0.151$ .

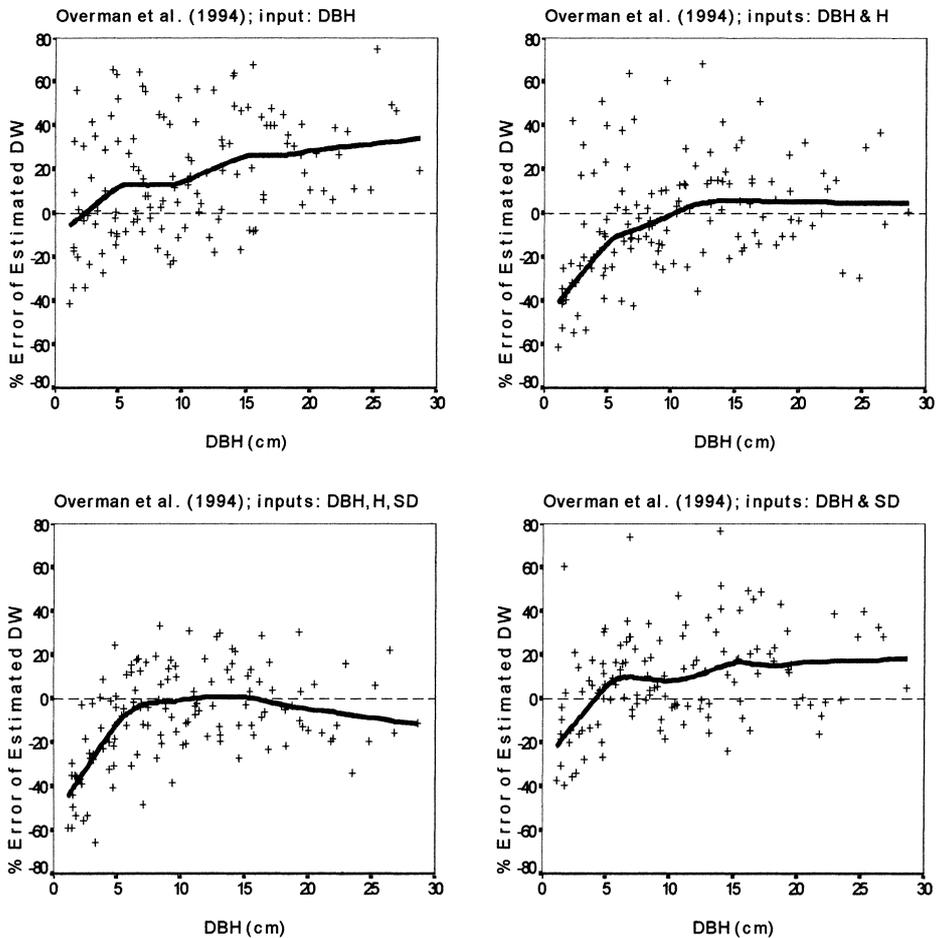


Fig. 3. (Continued)

very similar, as is evident from Table 9 and Fig. 6. Predicted weights for trees of 5, 10, 15, 20, 25 and 30 cm DBH are given for each species in Table 9, using model 2, which is based only on DBH. The logarithmic regression functions from model 2 are plotted on a single graph in Fig. 6. The functions for *Bellucia* and for *Vismia japurensis* are nearly identical. Separate from all other functions is the line for *Cecropia sciadophylla*, which has hollow branches and wood of low density. The line for *Croton matourensis*, which also has light wood, lies between *Cecropia* and all the other trees. *Goupia glabra* follows the *Bellucia/V. japurensis* line very closely for small trees, but diverges slightly for trees above 10 cm DBH (only two trees over 10 cm DBH were found for *G. glabra*). *Laetia procera* and *V. cayennensis* converge on the

*Bellucia/V. japurensis* line when they reach 10 cm DBH, but are very different in the small stages.

#### 4.2. Mixed-species regressions

For the mixed group of 132 trees from seven species (Table 8), a model based only on DBH (model 2) provides an average deviation between observed and expected DW of 19.8%. Including *H* as the second independent variable (model 3) reduces the deviation to 17.7%, not as good as the 15.0% of model 5, which uses SD as the second independent variable. Using all three independent variables – DBH, SD and *H* (model 6) – provides a very small additional improvement to 14.0% deviation. SD was not a good additional predictor of DW in the species-specific equations, but is a

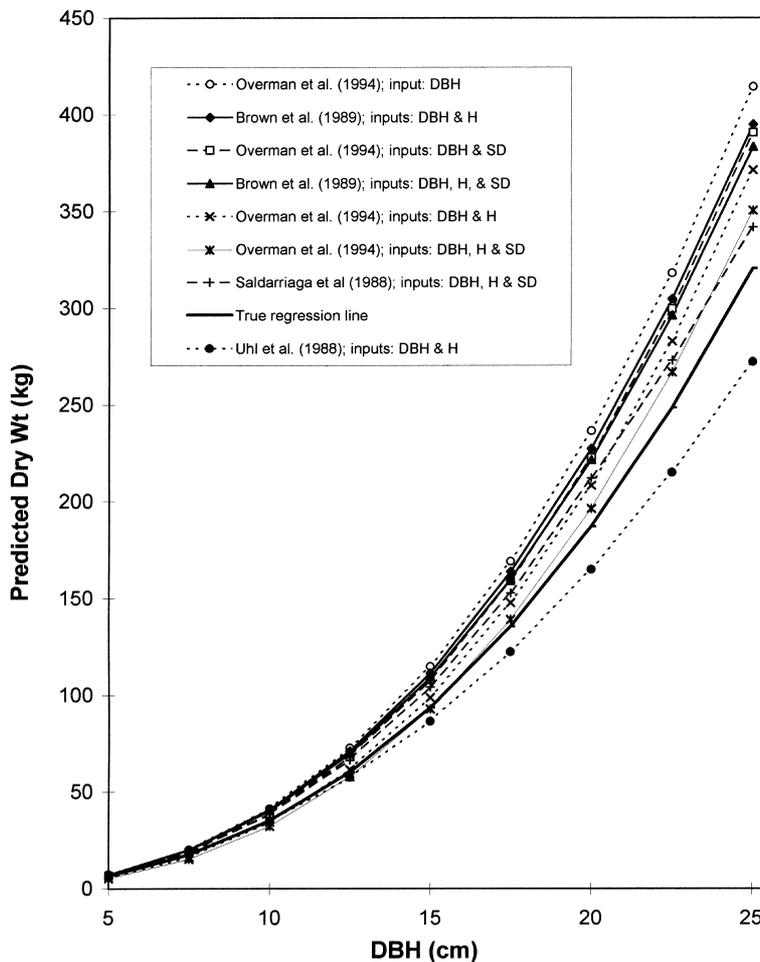


Fig. 4. Predictions of total above-ground dry weight for 132 non-Cecropioid trees using previously published mixed-species regressions, compared with the true regression line for the same trees. Models are listed in the legend top to bottom from highest to lowest total dry weight estimate at the 25 cm DBH position. DW=total above-ground dry weight (kg), DBH=diameter at breast height (cm),  $H$ =total height (m), SD=specific density ( $\text{gm cm}^{-3}$ ). Models are: Overman et al. (1994); input: DBH: for trees <45 cm DBH:  $\ln(\text{DW})=1.256 \ln(\text{DBH}^2)-2.059$ ; Brown et al. (1989), modified by Honzák et al. (1996); inputs: DBH and  $H$ : for trees <35 cm DBH:  $\ln(\text{DW})=0.957 \ln(D^2H)-3.068$ ; Overman et al. (1994); inputs: DBH and SD: for trees <45 cm DBH:  $\ln(\text{DW})=1.239 \ln(\text{DBH}^2)+1.106 \ln(\text{SD})-1.322$ ; Brown et al. (1989), modified by Honzák et al. (1996); inputs: DBH,  $H$  and SD: for trees <35 cm DBH:  $\ln(\text{DW})=0.937 \ln(D^2H \text{ SD})-2.327$ ; Overman et al. (1994); inputs: DBH and  $H$ : for trees <45 cm DBH:  $\ln(\text{DW})=1.002 \ln(\text{DBH}^2H)-3.555$ ; Overman et al. (1994); inputs: DBH,  $H$  and SD: for trees <45 cm DBH:  $\ln(\text{DW})=0.990 \ln(\text{DBH}^2H \text{ SD})-2.885$ ; Saldarriaga et al. (1988); inputs: DBH,  $H$  and SD: for trees 1–4.9 cm DBH:  $\text{DW}=0.369 \text{ DBH}^2-0.087 H-0.292$ , for trees 5–19.9 cm DBH:  $\ln(\text{DW})=1.047 \ln(\text{DBH}^2)+0.572 \ln(H)+0.931 \ln(\text{SD})-1.98$ ; for trees ( $\geq 20$  cm DBH:  $\ln(\text{DW})=0.876 \ln(\text{DBH}^2)+0.604 \ln(H) +0.871 \ln(\text{SD})-1.086$ ; True regression line: derived from observed values (see Section 2):  $\ln(\text{DW})=2.4128 \ln(\text{DBH})-1.9968$ ; Uhl et al. (1988); inputs: DBH and  $H$ : for trees <8 years old:  $\ln(\text{DW-wood})=1.02 \ln(\text{DBH}^2)+0.39 \ln(H)-2.17$ ,  $\ln(\text{DW-leaves})=1.43 \ln(\text{DBH}^2)-2.10 \ln(H)-0.66$ .

good additional predictor in the mixed-species equations. This means that the differences between species-specific regression lines in Fig. 6 are largely due to differences in wood specific density.

The same general pattern for mixed species was found by Overman et al. (1994) in their study of 54 primary forest trees. For model 2, they found  $r^2=0.97$  and a fairly large average deviation of 25.6% between

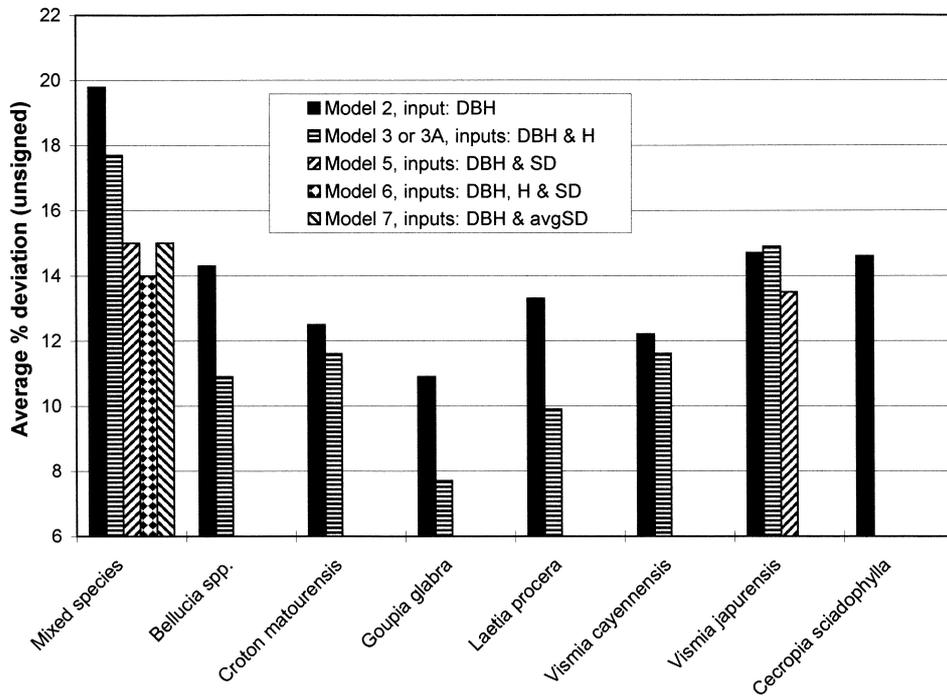


Fig. 5. Average errors of estimates of dry weight (DW), compared by model and by species. Biometric inputs are DBH only (model 2); DBH+ $H$  (model 3 or 3A); DBH+SD (model 5); DBH+ $H$ +SD (model 6); and DBH+average-SD-by-species (model 7).

Table 9  
Predicted dry weights (kg) for each species from model based only on DBH

Taxon →	<i>Goupia glabra</i>	<i>Vismia japurensis</i>	<i>Bellucia spp.</i>	<i>Laetia procera</i>	<i>Vismia cayennensis</i>	<i>Croton matourensis</i>	<i>Cecropia sciadophylla</i>
DBH (cm) ↓							
5	8.15	7.57	7.38	6.15	5.56	4.41	4.02
10	43.7	39.0	38.1	35.0	32.3	26.7	21.6
15	117	102	99.7	96.9	90.5	76.6	57.8
20	—	201	197	200	188	162	116
25	—	340	335	—	—	289	200
30	—	—	—	—	—	—	311

observed and expected DW. Using  $H$  with DBH had little effect, maintaining a high average deviation of 24.3%. Using SD with DBH increased  $R^2$  to 0.99 while the average deviation dropped to 14.7%, very similar to the corresponding general equation of this paper (model 5). A three variable model using  $H$ , SD and DBH, applied by Overman et al. (1994), gave an average deviation of just 11.2%.

Based on the above two paragraphs, combining the wood specific density variable with DBH (model 5)

should decrease average error of DW estimates by 5–10% for species not included in this paper. It is unlikely that inventories of forest biomass will obtain SD for each tree, but it could be feasible to obtain average SD for those important species of a site not covered by the species-specific equations. Substituting average SD by species in model 5 gives new coefficients (model 7) with nearly the same  $R^2$  value and the same accuracy of 15.0% deviation between observed and expected DW. The elliptical form of the joint

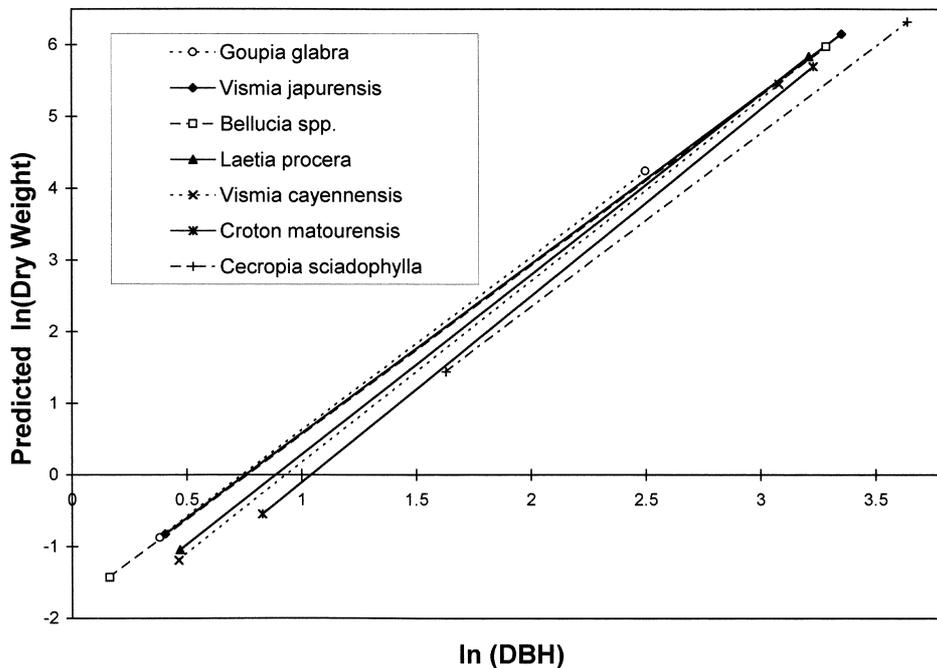


Fig. 6. Species-specific logarithmic regression functions using model 2 (DBH only).

range of the two independent variables DBH and SD is shown graphically in Fig. 7. A regression model should not be applied to trees which fall outside the joint range of observed independent variables (Neter and Wasserman, 1974).

#### 4.3. Cross-validation with previously published mixed-species regressions

From Fig. 3 one can draw several conclusions regarding the value of previously published mixed-species equations for estimating biomass of secondary forest in the central Amazon:

1. The equation of Uhl et al. (1988) is good only in the range 7–20 cm DBH. Below this range their equation overestimates while above it their equation underestimates biomass. This is probably attributable to applying their equation outside the range of their observed input variables. The secondary forest they studied was eight years old, so was unlikely to include non-Cecropioid trees larger than 15 cm DBH. While their equation

was meant only for use in their particular study site, it has been applied to other sites and to trees outside the 7–20 cm interval.

2. The equations of Overman et al. (1994) generally underestimate biomass of trees smaller than 5 cm DBH. This is again likely to be attributable to applying their equations outside the range of their input data. Only a single tree in their study was smaller than 10 cm DBH.
3. Two equations based only on DBH (Overman et al., 1994; Higuchi et al., 1998) overestimate the biomass of central Amazon secondary forest. The overestimate is ca. 10% for trees of 5 cm DBH, progressively increasing to 30% (in the case of Overman et al., 1994) and 60% (in the case of Higuchi et al., 1998) for trees of 25 cm DBH. Specific density of the primary forest trees used in those two studies was probably higher, on average, than the specific density of the pioneer species in this study.
4. Even when SD is included as a driving variable, equations based on primary forest trees tend to overestimate slightly. But when  $H$  or  $H+SD$  are

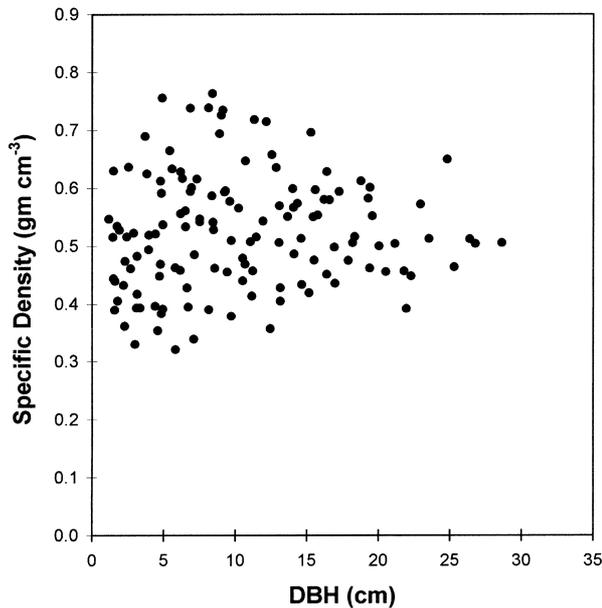


Fig. 7. Joint range of input variables DBH and SD for the mixed-species models.

added to DBH, the equations of Saldarriaga et al. (1988) and Overman et al. (1994) give good predictions for trees over 5 cm DBH.

5. For the three variable mixed-species regression developed in this study for 132 trees (model 6), the errors of estimate, expressed as a percentage of observed dry weight, decrease with increasing tree size.

#### 4.4. Multicollinearity

In the general data set and in some species-specific data sets, multicollinearity between DBH and  $H$  was sufficiently weak to allow use of a multiple regression (model 3). All the authors compared in the previous section proposed models which avoid multicollinearity altogether by devising a compound variable with a single coefficient, as in:

$$\ln(\text{DW}) = c + \beta \ln(\text{DBH}^2 H).$$

These studies have always fixed the exponent of DBH at 2. Allowing the exponent to vary in the above model gives:  $\ln(\text{DW}) = c + \beta \ln(\text{DBH}^\chi H)$ . This is mathemati-

cally equivalent to model 3:

$$\ln(\text{DW}) = c + \beta_\chi \ln(\text{DBH}) + \beta \ln(H),$$

where  $\beta_\chi = \alpha$  of model 3.

Observing the solutions to  $\alpha$  in model 3 for the different data sets of this paper it is clearly not the exponent  $\chi$  which should be fixed at ca. 2, but rather  $\beta_\chi$ . Furthermore, for predicting  $\ln(\text{DW})$ , the variable  $\ln(\text{DBH})$  is a stronger driver than  $\ln(H)$ . By arbitrarily fixing  $\chi=2$ , the partial regression coefficient of  $\ln(H)$  could be forced well away from its ideal value. With the coefficients determined for the 132 trees with model 3 (Table 8), one obtains  $\chi=4.6081$ , about double the arbitrary value chosen by previous workers. This is the derivation of model 3A, presented earlier. Using the exponent value of 4.6 in model 3A and then performing the linear regression, one obtains the same expected values for DW, the same  $r^2$  and the same residuals as model 3. It is important to note, however, that a fixed exponent value of 2 will effect only a very small increase in average percent error of estimated DW, precisely because  $\ln(H)$  is a weaker predictor than  $\ln(\text{DW})$ .

#### 4.5. Sources of bias

Several sources of bias must be kept in mind when applying these or other regression equations to estimate biomass of forests.

##### 4.5.1. Representative size classes

The regressions developed here are based on samples with a more even distribution of trees in each diameter class than would be found in primary or older secondary forest plots, where smaller size classes dominate. Larger trees are therefore over-represented in the equations of this paper. This is not a drawback if one's objective is to estimate total forest biomass, since large trees contain a disproportionate share of the biomass in most forests.

##### 4.5.2. Bias of the logarithmic transform

Two forms of bias exist. The first is visible in a comparison of Fig. 2(A) and (B). Small variations in the weight or the biometric input variables of the very smallest trees can leverage the linear regression much more than the very largest trees. If one's objective is to

estimate total biomass of a forest plot, the smallest trees should be given a lesser importance in the regression or should be eliminated altogether. Second, the regressions employed all minimize the y-distance of observed values in units of  $\ln(\text{kg})$  rather than kg. This results in a consistent bias in the estimate of DW. The bias is evidenced by a non-zero value for the average of the signed deviations between predicted and observed values of DW. The effect was examined for model 2 and found to be very small for all species: 1.0–1.6% overestimate of DW.

#### 4.5.3. Range of observations

Regressions should not be applied beyond the joint range of the input variables used to devise the model. For a simple regression based on DBH, only the limits of this variable need be observed. For the multiple regressions the joint range can be visualized as an ellipse or ellipsoid.

#### 4.5.4. Specific density

This biometric input was measured using volume over bark. Other workers may have developed their equations using volume of fresh wood without bark, or volume of dry wood samples soaked in water, or may have used samples of denser heartwood. In all these cases our measurement of specific density would presumably be lower and the other equations would consequently underestimate biomass of the 132 trees of this study using our SD inputs. The errors of the previously published equations employing density as an input parameter were, however, generally in the opposite direction for trees 5–20 cm DBH.

#### 4.5.5. Estimates of dry weight

Dry weights of the trees were not measured directly. For the trunk component, dry weight was estimated

based on water content of a single slice of wood taken at breast height. If the water content of the trunk changes with height, dry weight will have been improperly estimated. This possibility was assessed in 111 of the trees of this study for which three slices of wood were extracted at evenly spaced intervals along the trunk, then dried to determine water content. Dry weight of the entire trunk was then calculated by two methods: (1) using the single breast-high slice; and (2) arithmetically weighting the specific density of the three slices based on the volume of the bottom, middle and top thirds of the tapered trunk. Total tree dry weights were then compared from the two methods. Here one is concerned with two possible changes using the three slice technique: (1) a consistent change in estimate of total DW; and (2) a reduction in the average unsigned deviation using the best mixed-species model (model 6). Neither of these changes were detected for the mixed species set. Changes in total tree dry weight range from 4% lower to 4% higher than that calculated with a single slice, with no consistent trend as a function of tree size. The single slice method is therefore fine for the mixed species models. The three-slice method does, however, consistently change the estimates of total tree dry weight when examined on a species-by-species basis, albeit by very small amounts. Compared with the three slice technique, the single slice method used in this paper will have under or overestimated total tree dry weights by the following amounts: *Croton matourensis*, 1% underestimate across all DBH sizes; *Laetia procera*, 1.5–2.0% overestimate across all sizes; *Vismia cayennensis*, 1% overestimate across all sizes; *Goupia glabra*, 1.5–2.0% overestimate across all sizes; *Bellucia* spp., 2.0% overestimate for trees <5 cm DBH and 1–3% underestimate for trees 5–25 cm DBH;

Table 10  
Variability of the dry-weight/fresh-weight ratio of trunk wood at 1.30 m

Taxon	n	Mean $\pm$ s	Coefficient of variation
<i>Bellucia</i> spp.	27	0.461 $\pm$ 0.022	4.8%
<i>Croton matourensis</i>	23	0.535 $\pm$ 0.051	9.5%
<i>Goupia glabra</i>	17	0.578 $\pm$ 0.037	6.4%
<i>Laetia procera</i>	22	0.519 $\pm$ 0.045	8.7%
<i>Vismia cayennensis</i>	20	0.502 $\pm$ 0.049	9.8%
<i>Vismia japurensis</i>	23	0.564 $\pm$ 0.054	9.6%
Mixed spp secondary forest (this paper)	132	0.523 $\pm$ 0.059	11.3%
Mixed spp primary forest (Santos, 1996)	38	0.607 $\pm$ 0.079	13.0%

*Vismia japurensis*, no effect. Finally, the dry-weight/fresh-weight ratio for trunk wood taken at breast height was also found to vary within and between species (Table 10). The coefficients of variation range from 4.8 to 9.8% within a species, illustrating the wisdom of determining water content for each component of every tree when devising biomass regressions.

## 5. Conclusions

Species-specific regressions provided good estimates of total above-ground dry weight of central Amazonian secondary forest tree taxa using only diameter as the driving variable (model 2). Dry weight of an individual tree estimated using this model will have an average error of estimate in the range 11–15%, depending on the species. When height is added as a second driving variable (model 3) the average error of estimate will be in the range 7.7–14.6%, depending on the species. Specific density is not an important driving variable when the species-specific equations are used. For the estimation of dry weight of tree taxa not included in this paper, the best approach is to apply a mixed-species equation which uses both diameter and specific density as independent variables (model 7). Dry weight estimates for individual trees will be off by ca. 15% from true values. The joint range limits of diameter and specific density inputs (Fig. 7) should be kept in mind when applying this model. Specific density can be derived from a sample of trees for each species if it does not vary much with age. Adding total height as an additional input variable does not provide much improvement in the mixed-species models. Experience with telescoping poles in closed forest has shown that total tree height is consistently underestimated when compared with the measurement of the same tree after felling. Height should only be included as a driving variable if it is accurately measured and then probably only when using the species-specific models. For secondary forest species with unusual growth forms (e.g., bamboos, palms, lianas, Musaceae), hollow trunks (other *Cecropia* species) or specific density outside the range of this study (*Cochlospermum*, *Jacaratia*), additional taxon-specific equations should be developed.

Two previously published mixed-species regressions for the estimate of tropical forest biomass – based only on DBH and derived from primary forest trees – overestimated the biomass of the central Amazon secondary forest trees by 10–60%, with the greatest divergence found in the largest trees. When height and wood specific density were added as driving variables, regressions based on other forests did provide an unbiased biomass estimate with improved accuracy. The best equations employed three input variables and were published by Overman et al. (1994) and Saldarriaga et al. (1988), but for trees under 5 cm DBH neither of these provided accurate estimates of the trees used in this study.

## Acknowledgements

Field work was supported by grants from the Research Support Foundation of the State of São Paulo (FAPESP) and the G-7 Tropical Forests Pilot Project, both through the National Institute for Space Research (INPE); and by institutional support from the National Institute for Amazon Research (INPA), the Brazilian Agency for Agricultural and Range Research (EMBRAPA) and the Biological Dynamics of Forest Fragments Project (INPA – Smithsonian Institution). We are grateful to Mr. Francisco Bezerra for highly competent assistance in the field and to Dr. Isolde Ferraz for loan of a cantilever scale.

## References

- Alves, D.S., Soares, J.V., Amaral, S., Mello, E.M.K., Almeida, S.A.S., Silva, O.F., Silveira, A.M., 1997. Biomass of primary and secondary vegetation in Rondônia. *Western Brazilian Amazon. Global Change Biology* 3, 451–461.
- Brown, S., Gillespie, A.J.R., Lugo, A.E., 1989. Biomass estimation methods for tropical forests with applications to forestry inventory data. *For. Sci.* 35, 881–902.
- Brown, I.F., Martinelli, L.A., Thomas, W.W., Moreira, M.Z., Ferreira, C.A.C., Victoria, R.A., 1995. Uncertainty in the biomass of Amazonian forests: an example from Rondônia. *Brazil. Forest Ecology and Management* 75, 175–189.
- Fearnside, P.M., 1991. Greenhouse gas contributions from deforestation in Brazilian Amazonia. In: Levine, J.S. (Ed.), *Global Biomass Burning: Atmospheric, Climatic and Biospheric Implications*. MIT Press, Cambridge, MA, USA, pp. 92–105.

- Fearnside, P.M., 1996. Amazonian deforestation and global warming: carbon stocks in vegetation replacing Brazil's Amazon forest. *Forest Ecology and Management* 80, 21–34.
- Fearnside, P.M., Guimarães, W.M., 1996. Carbon uptake by secondary forests in Brazilian Amazonia. *Forest Ecology and Management* 80, 35–46.
- Higuchi, N., Santos, J., Ribeiro, R.J., Minette, L., Biot, Y., 1998. Biomassa da parte aérea da vegetação da floresta tropical úmida de terra firme da Amazônia brasileira, Biomass of the above-ground vegetation of humid tropical forest on terra firme in the Brazilian Amazon. *Acta Amazonica* 28(2), 153–166.
- Honzák, M., Lucas, R.M., Amaral, I., Curran, P.J., Foody, G.M., Amaral, S., 1996. Estimation of the leaf area index and total biomass of tropical regenerating forests: comparison of methodologies. In: Gash, J.H., Nobre, C.A., Roberts, J.M., Victoria, R.L. (Eds.). *Amazonian Deforestation and Climate*. Institute of Hydrology, UK, pp. 365–381.
- Neter, J., Wasserman, W., 1974. *Applied Linear Statistical Models*. Richard D. Irwin Inc., Homewood, Illinois, USA.
- Overman, J.P.M., Witte, H.J.L., Saldarriaga, J.G., 1994. Evaluation of regression models for above-ground biomass determination in Amazon rainforest. *Journal of Tropical Ecology* 10, 207–218.
- Pereira, J.L.G., 1996. Estudos de Áreas de Florestas em Regeneração Através de Imagens Landsat TM, Studies of Regrowth Forest Areas Using Landsat TM Images. Masters Thesis. Publication Number INPE-5987-TDI/578. Instituto Nacional de Pesquisas Espaciais, São José dos Campos, São Paulo.
- Saldarriaga, J.G., West, D.C., Tharp, M.L., Uhl, C., 1988. Long-term chronosequence of forest succession in the upper Rio Negro of Colombia and Venezuela. *Journal of Ecology* 76, 938–958.
- Santos, J. dos, 1996. Análise de Modelos de Regressão para Estimar a Fitomassa da Floresta Tropical Úmida de Terra Firme da Amazônia Brasileira, Analysis of Regression Models for Estimating Plant Biomass of Humid Tropical Forest on Terra Firme in the Brazilian Amazon. Doctoral Thesis. Federal University of Minas Gerais, Viçosa, Brazil.
- Schimel, D., Alves, D., Enting, I., Heimann, M., Joos, F., Raynaud, D., Wigley T., 1996. Radiative forcing of climatic change: CO<sub>2</sub> and the carbon cycle. In: Houghton, J.T., Meira Filho, L.G., Callander, B.A., Harris, N., Kattenberg, A., Maskell, K. (Eds.). *Climate Change 1995: The Science of Climate Change* (IPCC-1995 Vol. 1). Cambridge University Press, pp. 76–86.
- Uhl, C., Buschbacher, R., Serrão, E.A.S., 1988. Abandoned pastures in eastern Amazonia. I. Patterns of plant succession. *Journal of Ecology* 76, 663–681.
- Wiemann, M.C., Williamson, G.B., 1989. Radial gradients in the specific gravity of wood in some tropical and temperate trees. *Forest Science* 35(1), 197–210.