PRIMARY RESEARCH PAPER

Allometric models for aboveground biomass estimation of the mangrove *Avicennia schaueriana*

**Gustavo Calderucio Duque Estrada · Mário Luiz Gomes Soares ·
Daniel Medina Corrêa Santos · Viviane Fernandez · Paula Maria Moura de Almeida ·
Marciel Rocha de Medeiros Estevam · Maria Rita Olyntho Machado**

Abstract As mangroves become recognized as important carbon storages, the need for reducing the uncertainty of carbon inventories becomes increasingly emphasized. Accordingly, the objective of this study was to develop allometric models to estimate the total aboveground biomass (AGB) and the biomass per compartment of *Avicennia schaueriana* and to compare them with other models previously published for the genus *Avicennia*. Fifty three *A. schaueriana* trees, with different diameters at breast height (DBH) and height, were felled in a mangrove from Southeastern Brazil and their dry weight determined. Simple linear regression analysis was used to develop the equations after log-transformation, using the following independent variables: DBH and $DBH^2 *$ height. All the equations were significant and presented high R_a^2 (adjusted coefficient of determination). DBH provided the lowest SEE (standard error of estimation) in the regressions associated to leaves and total AGB, while $DBH^2 *$ height generated the most precise regressions for trunk, branches, and twigs. In comparison with other 11 equations previously developed for the genus *Avicennia*, the equation developed in the present study for total AGB showed the lowest mean deviation in relation to trees with known biomass, underscoring the importance of developing species- and site-specific equations.

G. C. D. Estrada · M. L. G. Soares ·
D. M. C. Santos · V. Fernandez · P. M. M. de Almeida ·
M. R. M. Estevam · M. R. O. Machado
Departamento de Oceanografia Biológica, Núcleo de Estudos em Manguezais, Faculdade de Oceanografia, Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier, 524, 4023-E, Maracanã, Rio de Janeiro, RJ 20550-013, Brazil
e-mail: mariolgs@uerj.br

D. M. C. Santos
e-mail: danielmcs@gmail.com

V. Fernandez
e-mail: vi.oliveira@gmail.com

P. M. M. de Almeida
e-mail: almeida.pmm@gmail.com

M. R. M. Estevam
e-mail: marciel.estevam@gmail.com

M. R. O. Machado
e-mail: mromachado@gmail.com

G. C. D. Estrada (✉)
Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Federal do Rio de Janeiro, Av. Carlos Chagas Filho, 373, A1-008, Cidade Universitária, Caixa Postal: 68020, Rio de Janeiro, RJ 21941-599, Brazil
e-mail: gustavo.estrada@uerj.br

Introduction

The aboveground biomass in mangrove forests has been estimated for various purposes over the past few decades, such as understanding the nutrient cycling in the ecosystem (Clough, 1998; Alongi et al., 2003), characterizing the vegetation structure and dynamics (Fromard et al., 1998, 2004; Ross et al., 2001; Kairo et al., 2009; Kauffman & Cole, 2010), and analyzing the relationship between structural development and the physicochemical conditions of the substrate (Saintilan, 1997; Sherman et al., 2003; Smith & Whelan, 2006; Suwa et al., 2008).

Additionally, increased awareness about the social and economic damage that can be caused by ongoing climate change, and the need to reduce and/or offset greenhouse-gas emissions have directed such studies to quantify the carbon storage and sequestration capacity of mangrove forests (Donato et al., 2011; Ray et al., 2011). The inclusion of forest ecosystems in the market of carbon credits or in REDD (reducing emissions from deforestation and forest degradation) projects requires highly precise carbon inventories (Gibbs et al., 2007). A major source of uncertainty in carbon inventories is the low precision of the available allometric models for estimating aboveground biomass (Chave et al., 2004). To increase the precision of inventories of wetlands, where tree species richness is generally low, Brown (2002) and Soares & Schaeffer-Novelli (2005) suggest the use of species- and site-specific models that address the full range of sizes in the forest under study.

Since structural development and architecture of trees are often related (Lovelock & Feller, 2003; Sobrado & Ewe, 2006; Pellegrini et al., 2009), taking into account, the spatial scales of the structural variability of mangrove forests are required for studies that aim to produce species- and site-specific allometric models. Globally, mangrove forests, similarly to most forest systems, tend to form latitudinal gradients of structural development determined primarily by solar radiation, temperature, and rainfall (Cintron et al., 1985; Schaeffer-Novelli et al., 1990). In the same latitudinal range (regional scale), factors such as the water balance and tidal amplitude determine whether the maximum potential development of the forest is reached, maintaining the same conditions of solar radiation and temperature (Schaeffer-Novelli et al., 1990, 2000). On a local scale, structural variability is determined by the interaction among the frequency of tidal flooding, freshwater input, and nutrient supply. The interaction often leads to inter-tidal gradients of structural development or physiographic types (Lugo & Snedaker, 1974; Cintron et al., 1985; Schaeffer-Novelli et al., 2000). Additionally, we must also consider the influence of disturbances that hinder the progress of forest succession, and limit the development of trees (Jimenez et al., 1985; Fromard et al., 2004). Therefore, standardization of the environmental conditions and of the successional stage is critical as a tree-sampling criterion to ensure highly precise allometric models. It is also important that these criteria are mentioned by the authors so that the developed model can be used for the same species in other forests with similar environmental conditions.

The various allometric models developed in recent decades for mangrove species generally have a species-specific nature (Day et al., 1987; Imbert & Rollet, 1989; Amarasinghe & Balasubramaniam, 1992; Fromard et al., 1998; Cole et al., 1999; Soares & Schaeffer-Novelli, 2005; Kauffman & Cole, 2010), while only four studies present multi-specific models (Komiyama et al., 2002, 2005; Chave et al., 2005; Ray et al., 2011). For the *Avicennia* species, which are widely distributed throughout the mangrove forests of the world (Tomlinson, 1986), the scenario is not different, and although they are included in the multi-specific models mentioned above, most of the allometric models were developed specifically for *A. germinans* (Day et al., 1987; Fromard et al., 1998; Imbert & Rollet, 1989; Ross et al., 2001; Sherman et al., 2003; Smith & Whelan, 2006) and *A. marina* (Amarasinghe & Balasubramaniam, 1992; Clough et al., 1997; Comley & McGuiness, 2005; Abohassan et al., 2012). Although most of the existing models are "site-specific," several present low sample size ($n < 20$), limited range of sizes or do not satisfactorily describe the environmental conditions in which the trees were collected, limiting the use of the model. This is the case for the only existing model for *Avicennia schaueriana* (Medeiros & Sampaio, 2008), developed in Itamaracá/Northeast Brazil (7°48′S;

34°49′39″W) from trees with a reduced range of sizes (diameter at breast height—DBH: 3.4–10.2 cm; height: 3.1–7.5 m) that were collected in a forest where this species has a development performance well below its maximum potential, considering the latitudinal range of the studied region.

Brazilian mangrove forests are the second largest of the world (13,000 km^2—Spalding et al., 2010) and, therefore, play a primary role in maintaining the global carbon stock in this ecosystem. However, the existing allometric models are insufficient to produce a reliable national inventory. From the six species occurring in Brazil, there are specific allometric models developed for only three of them: *Rhizophora mangle, Laguncularia racemosa,* and *A. schaueriana*. Furthermore, those models concentrate in two distant latitudinal ranges: Northeast (7°S: Medeiros & Sampaio, 2008) and Southeast Brazil (23°S: Soares & Schaeffer-Novelli, 2005). While in the former, models for those three species were developed, in the latter, there are no models for *A. schaueriana*.

The aim of this study is to develop allometric models to estimate the total aboveground biomass and biomass per compartment of *A. schaueriana* in fringe forests of Southeastern Brazil (~23°S) and to compare them with other models already published for the *Avicennia* genus, either specific or multi-specific. For this purpose, the existing allometric models of *Avicennia* were reviewed and information on species, site, size range, and sample size were extracted from each article. By providing allometric models for *A. schaueriana*, this study also fills in a gap for biomass estimation in Southeast Brazil, since the models for the other species that occur in this region—*Rhizophora mangle* and *Laguncularia racemosa*—were developed previously by Soares & Schaeffer-Novelli (2005).

Materials and methods

Study area

Sampling was conducted in a mangrove forest located in the Biological Reserve of Guaratiba (23°00′S; 43°34′W), Sepetiba Bay (Rio de Janeiro, Brazil) (Fig. 1). According to the Köppen classification (Peel et al., 2007), the regional climate can be divided into Aw (tropical hot and wet with a dry season during the winter), which is typical of the lowlands, and Af (tropical hot and wet with no dry season), which is characteristic of the adjacent slopes. According to Estrada et al. (2008), the average annual temperature is 23.5 °C, and the average annual precipitation is 1,067 mm, with the highest rainfall occurring during the months of January and March; June and August are the driest months. The tidal amplitude is less than 2 m.

The Guaratiba mangrove forests are characterized by a gradient of decreasing structural development from the fringe forests to the forests located at the transition with adjacent salt flats (Estrada et al., 2013). This variation is determined by a gradual reduction in the tidal flooding frequency in the fringe-salt flat direction. *R. mangle* and *A. schaueriana* alternate as dominant or co-dominant in the fringe, basin, and transitional forests, depending on the prevailing environmental conditions and the forest successional stage. The occurrence of *L. racemosa* is significantly lower and concentrated in areas with greater freshwater input. Table 1 shows the average structural and soil parameters of the fringe forest where sampling took place.

Sampling design, field, and laboratory procedures

Between March 2009 and May 2011, 53 *A. schaueriana* trees were felled. Samples were taken only in mature fringe forests to ensure the site-specific nature of the model. The selection of the trees to be felled took into account the trees' representativeness in terms of size and architecture. Tree architecture should include individuals with a straight trunk and a DBH/height relationship typical of the dominant trees with this physiographic type. In terms of size, care was taken to collect trees from the range of DBH values observed in the Guaratiba fringe forests: up to 40 cm.

Seeking to achieve a balance between sample representativeness per size range, the sampling effort needed to collect each individual, the negative impact caused by the felling of larger trees, and the positive impact of the inclusion of a greater number of individuals in model fitting, the following sampling strategy was defined: (1) DBH < 13 cm: three trees per 1-cm class; (2) 13 cm ≤ DBH < 24 cm: one tree per 1-cm class; and (3) DBH ≥ 24 cm: one tree per 3-cm class. Following this sampling strategy, 55 trees should be felled. However, there were no individuals of the 15.5 cm and 31.5 cm classes suitable for

Fig. 1 Map of the study area (Biological Reserve of Guaratiba, Southeast Brazil), indicating the distribution of mangrove forests, salt flats, and water bodies
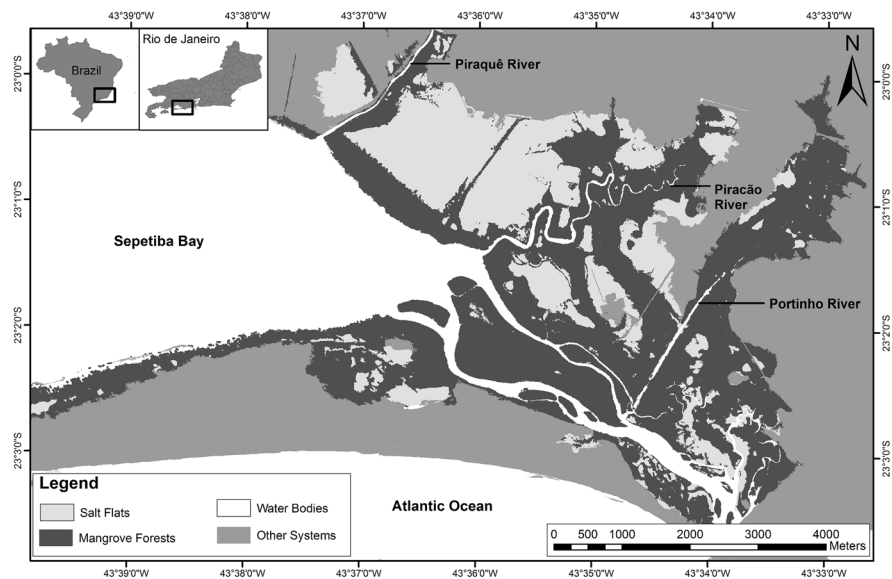

Table 1 Structure and edaphic parameters of the forests where the samples were taken

Parameter	Mean $\pm$ SD
Mean DBH[a] of the forest (cm)	11.6 $\pm$ 0.8
Mean DBH[a] of *Avicennia schaueriana* (cm)	21.7 $\pm$ 2.4
Mean height of the forest[a] (m)	9.68 $\pm$ 0.72
Mean height of *Avicennia schaueriana*[a] (m)	13.05 $\pm$ 0.85
Density[a] (live trunks ha^{-1})	2,745 $\pm$ 264
Density of live trunks per species[a] (%)	
Rhizophora mangle	75.7 $\pm$ 6.9
Avicennia schaueriana	13.6 $\pm$ 0.6
Laguncularia racemosa	0.9 $\pm$ 0.8
Live basal area[a] (m^2 ha^{-1})	29.06 $\pm$ 2.41
Live basal area per species[a] (%)	
Rhizophora mangle	43.5 $\pm$ 3.7
Avicennia schaueriana	50.1 $\pm$ 2.3
Laguncularia racemosa	1.6 $\pm$ 1.8
Interstitial water salinity[b]	27.8 $\pm$ 4.7
Total N concentration in the sediment[c] (g Kg^{-1})	1.82 $\pm$ 0.13
Total P concentration in the sediment[c] (g Kg^{-1})	0.79 $\pm$ 0.08

[a] Mean of three plots from Estrada et al. (2013); [b] mean of six samples seasonally monitored between 1996 and 2009, partially published by Estrada et al. (2013); [c] mean of three samples (unpublished data)

collection, which reduced the sample size to 53. The collected trees ranged in DBH and height between 0.7 and 37.3 cm and 1.19 and 18.70 m, respectively.

DBH and height of all of the selected trees were measured. Height was firstly measured with an optical rangefinder and then checked after felling with a measuring tape. This procedure revealed a mean deviation of 7.2 $\pm$ 4.5% (max. = 17.7%; min. = 0.2%) between standing height measurements and the actual felled tree heights, confirmed by a *t* test (standing height = 9.7 $\pm$ 3.8 m; actual height = 10.5 $\pm$ 4.1 m; $t = -7.3$; $p < 0.01$). Those trees were felled using saws and chainsaws. After felling, the material was carefully separated into the following compartments, according to the procedure adopted by Soares & Schaeffer-Novelli (2005): leaves; twigs (diameter at large end <2.5 cm); branches (diameter at large end ≥2.5 cm); and trunk. All of the compartments were weighed in the field (wet biomass). When it was not possible to cut the basal portion of the trunk (stump), its height and diameter were measured to enable subsequent estimation of the wet weight from the volume. This estimation was based on the regression between the wet weight and volume of all of the trunk sections ($n = 279$) taken from the sampled trees, the procedure for which is described in the "Statistical analysis" section. The following equations were used to calculate the volume of the stump and trunk sections:

$$\text{Stump volume} = \text{volume of a cylinder} = \pi * r^2 * h \quad (1)$$

where r stump radius; h stump height.

Section volume $=$ volume of a truncated cone
$$= \left[1/3 * \pi * h * (R^2 + r^2 + R * r) \right] \tag{2}$$

where h section length; R radius of section base; r radius of section top.

After weighing in the field, the fresh material was taken to the laboratory for drying in an oven at 70 °C, until constant weight was reached (3–4 weeks for leaves and twigs; 5–8 weeks for branches trunk samples). For smaller trees (DBH < 8.0 cm), all of the material was dried in the laboratory (dry weight). In the case of larger trees (DBH > 8.0 cm), subsamples of 25–50% of the wet weight of each compartment were randomly selected and taken to the laboratory. In the case of trunks and main branches of larger trees, subsamples consisted of 3–10 sections per tree, each with 15 cm of height. The determination of dry weight of trees whose compartments were subsampled was based on the application of regressions between the wet and dry weights, the procedure for which is described in the "Statistical analysis" section.

Statistical analysis

Simple linear regression was used to test the existence of a dependent relationship between the dry weight and the wet weight of the sample and between the dry weight of the trees and their size. The procedure adopted for such analyses followed, in general, the methodological guidelines described by Draper & Smith (1981) and Zar (1996). Multiple regression analyses were discarded after preliminary tests indicated the occurrence of high degrees of collinearity between the independent variables.

The validity of the regressions was checked against three basic premises: (1) a linear relationship between X and Y, (2) homogeneity of variances of Y, (3) a normal distribution of Y values. To test assumption (1), the significance of the regression coefficient was determined using an ANOVA F test ($\alpha = 0.01$). To evaluate the compliance with assumption (2)—homogeneity of variances—graphical analysis of the residuals was used. The residual analysis was also used to verify compliance with assumption (3). Normality was assessed initially using a graphical analysis and subsequently tested using the Chi squared test

($\alpha = 0.01$). In the case of regressions that do not meet assumptions 2 and 3, the values of X and Y must be submitted to logarithmic transformation in order to normalize the data distribution, homogenize variances, and also linearize the relationships between X and Y that are curvilinear in their original units. Preliminary tests showed that the relationship between the dry weight and the tree measurements was curvilinear. Thus, only transformed variables were used for these regressions.

Those regressions considered valid were analyzed regarding both the degree of dependence of Y with respect to X (coefficient of determination, R^2) and the precision of the estimate (standard error of the estimate—SEE). Although widely used, R^2 is not a good metric for the comparison of regressions with a different number of variables or samples (Healy, 1984). Therefore, the adjusted coefficient of determination (R_a^2) was used, which was calculated according to Zar (1996).

The allometric equations were back-transformed from natural logarithm to the original unit to facilitate their use by other authors. The deviation associated to this back-transformation was corrected by multiplying the exponential value of the intercept (a) by the logarithmic correction factor (LCF) (Baskerville, 1972; Sprugel, 1983; Wood, 1986), following the steps described below:

$$y = a_c * x^b \tag{3}$$

where:

$$a_c = e^a * \text{LCF} \tag{4}$$

$$\text{LCF} = e^{(\text{MSQResiduals}/2)} \tag{5}$$

and

MSQ Residuals $=$ mean square of the residuals.

The LCF was also used to calculate the corrected standard error of the estimate (SEE$_c$), by multiplying the exponential value of each estimated Y (Y_e) by the LCF, following the method described by Payandeh (1981). Because the SEE$_c$ is dependent on the magnitude of the values of Y, it is necessary to standardize it in relation to some measure representing the dispersion of Y, such as its mean (Y_{mean}), to accurately identify the precision of a regression. Therefore, the %SEE$_c$ was calculated through the procedure suggested by Rezende et al. (2006):

$$\%\text{SEE}_c = (\text{SEE}_c / Y_{\text{mean}}) * 100 \qquad (6)$$

Considering the biological standpoint that the regressions developed in the present study should always pass through the origin, the significance of the intercept was tested using Student's t test ($\alpha = 0.01$). In the regressions in which the null hypothesis ($a = 0$) was not rejected, a new regression was generated by forcing its passage through the origin. Gordon ([1981]) and Eisenhauer ([2003]) demonstrated that the R_a^2 calculated from equations with $a = 0$ are overestimated and should not be compared to R_a^2 values calculated for regressions with $a \neq 0$. Therefore, this parameter was computed for the regressions with $a = 0$ but was not used in comparisons with the regressions where $a \neq 0$.

Variables selection

The selection of the dependent and independent variables followed, in general, the guidelines of Chave et al. ([2005]), Soares & Schaeffer-Novelli ([2005]), and Komiyama et al. ([2008]). Total dry mass in the aboveground biomass (AGB) and dry mass of each compartment (trunk, branches, twigs and leaves) were selected as dependent variables and DBH and $\text{DBH}^2 *$ height as independent variables. The variables height, DBH^2, basal area, and the different types of trunk volume (truncated cone, cylindrical and parabolic) are used in several studies (Moreira-Burger & Delitti, [1999]; Sherman et al., [2003]; Komiyama et al., [2005]) and were initially considered in the present study. However, preliminary analysis revealed that the regressions with DBH^2 and basal area resulted in SEE and R_a^2 values identical to those observed for the regressions using the DBH. This same equality was also observed between volumetric variables and $\text{DBH}^2 *$ height. These equivalences are easily explained by the fact that DBH^2, basal area, and volumetric parameters change only the raw value of the independent variable in the regression (changing the intercept and regression coefficient) but remain proportional to the simplest forms (DBH and $\text{DBH}^2 *$ height). The regressions with height as the independent variable presented low fits for both AGB and the compartments and were discarded.

All of the models considered as acceptable were compared for precision by analysis of SEE_c or $\%\text{SEE}_c$ and for goodness-of-fit by analyzing the R_a^2. Because

the goal was to determine the model that promotes the most precise estimate possible, SEE was considered as the first criterion for determining the best model.

Comparison with other studies

The most precise equation for estimating the total biomass produced in the present study was compared with other equations already developed for the genus *Avicennia*. This comparison was performed based on the average percentage of deviation in relation to the true weight (observed) of trees with a DBH closest to the following classes: 1, 5, 10, 15, 20, 25, 30, 35, and 40 cm. The calculation of the percentage of deviation for each of these nine classes was performed using the following formula:

$$\text{Deviation} = [(B_{\text{estimated}} - B_{\text{observed}}) / B_{\text{observed}}] * 100 \qquad (7)$$

where B_{observed} observed biomass of the tree with a DBH closest to one of the classes listed above; and $B_{\text{estimated}}$ estimated biomass using the same DBH.

Because the compiled multispecies equations used wood density as an independent variable, wood density was calculated for *A. schaueriana*. Following the methodological recommendations of Chave et al. ([2005]), wood density was obtained from the oven dry weight of the wood samples ($n = 106$) and their green (fresh) volume. Green volume was estimated using the formula of a truncated cone (Eq. [2]), following a similar procedure employed by Komiyama et al. ([2005]) and Soares & Schaeffer-Novelli ([2005]). Wood density was finally considered as the regression coefficient (b) between the dry weight and green volume. The obtained density (0.6751 g/cm^3; $\text{SE}_b = 0.0064$; $R^2 = 0.99$) was then used in the multispecies equations.

Results

Determination of the moisture levels of compartments

The regressions between wet weight and dry weight of the subsamples are shown in Table [2]. With the exception of leaves, the null hypothesis of the intercept ($a = 0$) was accepted for all of the

Table 2 Equations and parameters of the regressions applied to test the dependence of dry mass (DM) on wet mass (WM) of the sub-samples of each compartment

Equation	n	SE_a	t_a	$p(t_a)$	SE_b	F	$p(F)$	R_a^2	SEE	%SEE
DM (leaves) = $-84.9604 + 0.3383 *$ WM (leaves)	48	24.5668	−3.46	<0.01	0.0058	3363.15	<0.01	0.9862	114.3410	11.78
DM (leaves) = 0.3234 * WM (leaves)	48	–	–	–	0.0044	5520.85	<0.01	0.9914	126.9749	13.09
DM (twigs) = 0.4833 * WM (twigs)	48	–	–	–	0.0040	14310.41	<0.01	0.9967	129.7222	7.57
DM (branches) = 0.5590 * WM (branches)	29	–	–	–	0.0043	16739.16	<0.01	0.9983	121.4268	5.15
DM (trunk) = 0.5799 * WM (trunk)	52	–	–	–	0.0022	67253.75	<0.01	0.9992	158.5163	4.67

n Number of samples, a intercept, SE_a standard error of the intercept estimation, t_a intercept t test, $p(t_a)$ p of intercept t test, b regression coefficient, SE_b standard error of the regression coefficient estimation, F ANOVA test for the regression coefficient, $p(F)$ p value of the ANOVA test for the regression coefficient, R_a^2 adjusted coefficient of determination, SEE standard error of estimation, %SEE percentage of SEE in relation to mean dry weight of the compartment

compartments, and the regressions were recalculated forcing the line through the origin. Although the null hypothesis of the intercept was rejected for the leaves, there was a high standard error of the intercept (SE_a), and the estimated intercept had a negative sign ($a = -84.9604$), which reduces the reliability of the equation and causes distortions in estimates of dry weight. Because of these problems, a new regression was generated for the relationship between the wet weight and dry weight of leaves forcing the intercept through the origin. All of the regressions showed significant regression coefficients, good fit, and high precision, indicated by the high values of R_a^2 (>0.99) and low values of SEE, respectively.

The regression between volume and wet weight of the trunk sections, required to estimate the weight of the "stump," also corroborated the null hypothesis of the intercept and showed high precision and fit: wet weight = 1.1557 * volume ($SE_b = 0.0043$, $t_b = 266.0757$, $p(t_b) < 0.01$, $F_{(1,278)} = 70796.2948$, $p(F) < 0.01$, $R_a^2 = 0.9961$, SEE = 1526.2342, %SEE = 7.73%).

The analysis of the residuals from the regressions between the wet weight and dry weight of the subsamples confirmed that the residuals fit the normal distribution (Online Resource 1) but had distortions in the variance, which tended to increase as the independent variable increased (Online Resource 2). Such distortion would indicate the need for logarithmic transformation of the variables involved. However, considering that only one of the assumptions (homogeneity of variances) was not fully met and that such a procedure would result in a double transformation of the data, because the variables for the regressions

between the structural measurements and dry weight had already been transformed, it was decided to maintain the variables of the regressions for wet weight × dry weight in their original units. The same decision was made for the regression between the volume and wet weight of the trunk sections, the residuals of which, in addition to having the same type of distortion of variance described for the wet weight x dry weight regressions (Online Resource 2), did not fit a normal distribution ($X^2 = 101.7863$, DF = 10, $p < 0.01$).

Allometric equations

For all of the regressions, the null hypothesis ($b = 0$) of the regression coefficient was rejected (Table 3). The null hypothesis of the intercept ($a = 0$) was accepted only for branches (DBH: $t_a = 0.54/p = 0.60$; DBH^2 * height: $t_a = -1.71/p = 0.10$), so new regressions with the intercept forced through the origin were generated for both independent variables (Table 3). All the regressions were checked regarding the assumptions of normality and homogeneity of variances. The residuals of all of the regressions were normally distributed (Online Resource 1), meeting the assumption of normality. There was no evidence of disturbances in the dispersion of the residuals in relation to the independent variables (Online Resource 2). In general, the residuals tended to disperse homogeneously along the X axis, confirming the assumption of homogeneity of variances.

Having met all of the assumptions, the accepted regressions were analyzed regarding the goodness-of-fit and especially the precision of the estimate. High R_a^2

Table 3 Allometric equations and regression parameters applied to test the dependence of aboveground biomass (g) on size

Equation	n	SE_a	t_a	$p(t_a)$	SE_b	F	$p(F)$	R_a^2	SEE	SEE_c	$\%SEE_c$	LCF
AGB = 123.87716 * DBH$^{2.5282}$	53	0.0596	80.50	<0.01	0.0269	8816.65	<0.01	0.9941	0.1874	26652.0654	23.75	1.0177
AGB = 68.8881 * (DBH^2 * Ht)$^{0.9397}$	53	0.0606	69.55	<0.01	0.0093	10233.42	<0.01	0.9949	0.1740	31663.9354	46.31	1.0153
Trunk = 83.1806 * DBH$^{2.5361}$	53	0.0793	55.36	<0.01	0.0358	5019.75	<0.01	0.9897	0.2491	36190.0815	49.08	1.0315
Trunk = 45.1753 * (DBH^2 * Ht)$^{0.9444}$	53	0.0647	58.61	<0.01	0.0099	9071.44	<0.01	0.9943	0.1857	15493.8897	21.01	1.0174
Branches = DBH$^{3.4546}$	35	–	–	–	0.0353	9572.71	<0.01	0.9964	0.5412	22433.8633	86.93	1.1577
Branches = (DBH^2 * Ht)$^{1.1819}$	35	–	–	–	0.0135	7661.40	<0.01	0.9955	0.6047	11294.4186	43.76	1.2006
Twigs = 22.9198 * DBH$^{2.3344}$	53	0.1376	22.09	<0.01	0.0621	1412.80	<0.01	0.9645	0.4322	5263.4443	51.58	1.0979
Twigs = 13.3515 * (DBH^2 * Ht)$^{0.8676}$	53	0.1495	16.72	<0.01	0.0229	1434.89	<0.01	0.9650	0.4290	4016.8983	39.37	1.0964
Leaves = 19.0708 * DBH$^{2.1418}$	53	0.1508	18.80	<0.01	0.0681	989.7707	<0.01	0.9500	0.4738	2507.6268	42.91	1.1188
Leaves = 12.1262 * (DBH^2 * Ht)$^{0.7922}$	53	0.1787	13.23	<0.01	0.0274	837.2942	<0.01	0.9415	0.5128	3415.7632	58.45	1.1405

n Number of samples, SE_a standard error of the intercept estimation, t_a intercept t test, $p(t_a)$ p value of intercept t test, SE_b standard error of the regression coefficient, F ANOVA test for the regression coefficient, $p(F)$ p value of the ANOVA test for the regression coefficient, R_a^2 adjusted coefficient of determination, SEE standard error of estimation, SEE_c corrected standard error of estimation, $\%SEE_c$ percentage of SEE_c in relation to mean dry weight of the compartment, LCF Logarithmic correction factor, DBH diameter at breast height (cm), Ht height (m), AGB aboveground biomass

values were observed, varying between 0.9415 and 0.9949 (Table 3; not considering branches, whose equations were forced through the origin), as well as highly variable $\%SEE_c$ values, ranging from 21.01 to 86.93% of the average dry aboveground biomass. DBH was the variable that provided the lowest $\%SEE_c$ in the regressions related to total AGB and leaves, while DBH^2 * height provided the most precise regressions for woody compartments (trunk, branches, and twigs).

Considering only the independent variable that provided the greatest precision among the regressions tested for each compartment, total AGB and trunk biomass had the lowest $\%SEE_c$ values (23.75 and 21.01%, respectively), while the remaining compartments produced regressions with higher $\%SEE_c$ values (39.37–86.93%). The same trend was observed for the R_a^2 values, which were higher for total AGB (0.9949) and trunks (0.9943) and lower for the other compartments (from 0.9415 to 0.9650; not considering branches).

Discussion

Determination of the moisture levels of compartments

The regression coefficients (b) for wet weight × dry weight can be understood as the percentage of dry weight of the compartments. Thus, the moisture content would be equivalent to "(1 − b) * 100". Considering that it is possible to see that the woody parts (trunks = 42%; branches = 44%; twigs = 52%) present lower moisture content than leaves (68%). The values of the moisture content of *A. schaueriana* are similar to those observed by Soares & Schaeffer-Novelli (2005) for *R. mangle* and *L. racemosa* in Guaratiba (leaves and reproductive parts: *R. mangle* = 65%, *L. racemosa* = 70%; twigs: *R. mangle* = *L. racemosa* = 49%; branches and main branches: *R. mangle* = *L. racemosa* = 42%; trunk: *R. mangle* = 34%, *L. racemosa* = 39%). Slim & Gwada (1993) also found similar results for *R. mucronata*, with moisture contents of 66% (leaves), 44% (branches), and 41% (trunk). This trend of higher moisture content in green tissues (leaves and reproductive parts) relative to woody parts is also observed for species from other forest systems. For example,

moisture contents were 62 and 51% for leaves and woody parts, respectively, from Atlantic forest tree species (Moreira-Burger & Delitti, 1999).

Allometric equations

The lower precision of the equations generated from the compartments related to the crown (branches, twigs, and leaves) most likely reflects the more variable nature of these parts compared to the trunk. According to Kuuluvainen (1991), the biomass of crown parts is more susceptible to biotic (e.g., forest density) and abiotic changes, reflecting the current conditions of plant growth, while trunk biomass reflects the portion of organic matter allocated to this compartment throughout the lifetime of the tree. The pattern of greater biomass variability in the compartments associated with the crown was also observed for other mangrove species (Imbert & Rollet, 1989; Clough et al., 1997; Sherman et al., 2003; Soares & Schaeffer-Novelli, 2005; Smith & Whelan, 2006). The use of crown measurements (e.g., volume, area and average diameter), both in isolation as independent variables in simple regressions and in conjunction with other variables in multiple regressions, can improve the estimation of crown biomass (Woodroffe, 1985; Ross et al., 2001; Soares & Schaeffer-Novelli, 2005). However, such measurements are difficult to perform and significantly increase the time spent to perform a forest inventory and are thus rarely used.

The variables DBH and DBH^2 * height alternated to generate the more precise allometric equation for each compartment or total AGB. In fact, both variables have been the most widely used in the development of allometric equations not only for mangrove species (Komiyama et al., 2008) but also for terrestrial tropical rainforest species (Chave et al., 2005). However, the latter authors call attention to the more practical and accurate measurement of DBH in relation to height in forest inventories, especially in tall forests, which would explain the preference for DBH as an independent variable, even in the cases in which such a comparison is not performed. Nelson et al. (1999) showed that even in cases where the inclusion of height as an independent variable, associated or not with DBH, promotes allometric equations with lower SEE, its application should be conditional upon accurate height measurements which are not always possible. It is, therefore, necessary to evaluate the

cases in which the variable DBH^2 * height promoted more precise equations than DBH parsimoniously, because, in practice, the use of height may result in less-precise estimates of biomass. In other words, the error associated with the measurement of height may generate a less-precise biomass estimate even if the SEE of the allometric equation is lower when associated to DBH^2 * height than when associated to DBH. As mentioned in the Materials and methods section, tree heights of *A. schaueriana* measured with and optical rangefinder deviated $7.2 \pm 4.5\%$ from the actual heights. This deviation is low compared to the threshold value determined by Williams & Schreuder (2000), who estimated at 40% the maximum error that the height measurement can reach to compensate for its inclusion (in association with DBH) in volume models of temperate forest species, with the height-measurement accuracy defined by the interaction among the instrument, observer and forest-structure conditions. They opposed the use of allometric models that include height when height has been estimated visually, without the aid of any instrument or calibration method or when the tree crowns cannot be easily observed in dense forests. In the case of *A. schaueriana*, this evaluation needs further studies that accounting for the balance between the precision of height measurements, the precision of the models that include height (DBH^2 * height) and the precision of the DBH models.

The choice of SEE_c as a criterion for selecting the best model appeared strong. Although we observed a coincidence between lower $\%SEE_c$ and greater R_a^2 in most of the compartments (Trunk, Twigs, and Leaves), total AGB showed an inverse pattern (Table 3). In this case, the variable with the greatest R_a^2 (DBH^2 * height) did not show the lowest $\%SEE_c$. That is, if the criterion for choosing the best model was based on R_a^2 or R^2, a model with 23% more SEE_c would have been selected. This difference underscores the importance of using the SEE_c as a criterion for choosing the independent variable that promotes the best estimate, a procedure that is suggested by Draper & Smith (1981) and Zar (1996). Despite this finding, R_a^2 or R^2 has been used as the only selection criterion in most studies of mangrove species (Woodroffe, 1985; Imbert & Rollet, 1989; Tam et al., 1995; Smith & Whelan, 2006; Medeiros & Sampaio, 2008; Kairo et al., 2009; Ray et al., 2011), whereas only Ross et al. (2001), Chave et al. (2005), Soares & Schaeffer-

Novelli (2005) and Siddique et al. (2012) included the SEE as a selection criterion.

Accordingly, the calculation of SEE_c for equations based on log-transformed variables is also highly recommended, because the difference between SEE and SEE_c can be quite large when the untransformed dependent variable shows a sharp deviation from the normal distribution (Baskerville, 1972; Sprugel, 1983; Wood, 1986). This difference may result in the incorrect selection of the most precise model when it is based only on SEE, which is demonstrated in the present study by total AGB, for which the model with the lowest SEE_c did not present the lowest SEE.

Table 4 shows a comparison of the most precise allometric equation to estimate total biomass among those tested in the present study with equations previously developed for genus *Avicennia*, including multispecies equations. The specific equations include 3 of the 8 species of the genus *Avicennia*: *A. schaueriana*, *A. germinans*, and *A. marina*. The multispecies equations include *A. marina*, *A. alba*, and *A. officinalis* in Ray et al. (2011), *A. germinans* in Chave et al. (2005) and *A. alba* in Komiyama et al. (2005).

Although they were developed for species of the same genus, the specific equations show differences in the intercept and the regression coefficient, which were best noted when only the equations for total biomass that consider the DBH as an independent variable are analyzed. Such differences may be partially determined by the architecture of each species, determined by genetics or phenotypically. In addition to this factor, the latitude of tree sampling, which was extremely variable across the compiled studies, certainly influenced the architecture of the trees, as well as the variability of the sample number and range of diameters. Regarding R^2, the worst-fitting equations (<0.90) were those that include only small trees, which are naturally more variable, because they occur at different shading levels in the forest.

Because the best equation developed in the present study uses DBH as the independent variable, comparison with other existing equations concerning the deviation from true measurements was limited to those that also use DBH as the independent variable (Fig. 2; Table 5). Analysis of the average deviation confirms the equation developed in the present study as that with the lowest deviation ($13.5 \pm 10.4\%$) compared to the true data used. The other existing equations can

be divided into three groups based on the average deviation: 1—deviation between 15 and 25%; 2—deviation between 26 and 35%; and 3—deviation >36%.

The group of equations with the lowest deviation includes two multi-specific equations (Chave et al., 2005; Komiyama et al., 2005), and the specific equations developed for *A. germinans* that have a better balance between sample size and the diameter range (Imbert & Rollet, 1989; Fromard et al., 1998), and features that were demonstrated by Chave et al. (2004) as crucial for the precision and accuracy of an allometric model. Furthermore, the fact that these equations were developed for *A. germinans*, a species that is phylogenetically closer to *A. schaueriana* within the genus *Avicennia* (Tomlinson, 1986), suggests greater similarity in terms of architecture and appears to explain their presence in this group. The only exception in this group is the equation of Day et al. (1987), which has the third-lowest average deviation ($17.0 \pm 9.5\%$) despite having been developed from a low sample size ($n = 10$) and a low diameter range (1–10 cm). The presence of multispecies equations in this group, with the average deviation from Komiyama et al. (2005) being the second lowest ($16.3 \pm 11.8\%$) among all of the equations analyzed, is explained in part by the large sample size, and diameter range used to create the equations (Table 4). However, the use of wood density as an additional independent variable in these equations appears to be another factor that increases the precision of the estimates in these equations. This reasoning is consistent with the tests promoted by Breugel et al. (2011) who demonstrated that the inclusion of wood density as an independent variable increases the precision of multi-specific equations.

Group 2 (Amarasinghe & Balasubramaniam, 1992; Clough et al., 1997; Comley & McGuiness, 2005), with average deviations between 26 and 35%, includes equations developed for *A. marina*, an Indo-Pacific species with less phylogenetic similarity to *A. schaueriana*, which were based on intermediate sample sizes and diameter ranges (Table 4). These factors explain the larger deviation compared to the equation developed in the present study and the equations of group 1. Group 3, which showed the greatest average deviations, includes equations developed for *A. marina*, *A. schaueriana*, and *A. germinans* presenting a low sample size and/or reduced diameter range (Table 4).

Table 4 Allometric equations for the estimative of aboveground biomass (AGB) of *Avicennia* species

Species	Equation	R^2	n	DBH	Height	Location	Author
A. schaueriana	ln(AGB) = 4.8017 + 2.5282 * ln(DBH)	0.99	53	0.7–37.3	1.2–18.7	Brazil[a]	This study
Multispecific	ln(AGB) = 5.1218 + ln(ρ) + 2.4700 * ln(DBH)	0.99	84	4.0–42.0	–	French Guiana[b] and Guadalupe[c]	Chave et al. (2005)
Multispecific	ln(AGB) = 5.5255 + ln(ρ) + 2.4600 * ln(DBH)	0.98	104	5.0–48.9	4.5–34.3	Thailand and Indonesia[d]	Komiyama et al. (2005)
A. germinans	ln(AGB) = 4.9416 + 2.4000 * ln(DBH)	0.97	25	4.0–42.0	–	French Guiana[b]	Fromard et al. (1998)
A. germinans	ln(AGB) = 4.5455 + 2.5367 * ln(DBH)	0.98	21	6.7–40.7	8.3–18.1	Guadalupe[c]	Imbert & Rollet (1989)
A. germinans	ln(AGB) = 5.3226 + 2.3023 * ln(DBH)	0.97	10	1.0–10.0	–	Mexico[e]	Day et al. (1987)
A. marina	ln(AGB) = 5.1794 + 2.2990 * ln(DBH)	0.97	23	5.5–20.4	–	Australia[f]	Clough et al. (1997)
A. marina	ln(AGB) = 5.5510 + 2.1530 * ln(DBH)	0.92	29	2.0–12.5	–	Sri Lanka[g]	Amarasinghe & Balasubramaniam (1992)
A. marina	ln(AGB) = 5.7311 + 2.1130 * ln(DBH)	0.97	22	1.0–30.0	–	Australia[h]	Comley & McGuiness (2005)
A. germinans	ln(AGB) = 5.3003 + 2.1000 * ln(DBH)	0.82	45	1.0–4.0	–	French Guiana[b]	Fromard et al. (1998)
A. schaueriana	ln(AGB) = 5.4420 + 2.0685 * ln(DBH)	0.78	23	3.4–10.2	–	Brazil[i]	Medeiros & Sampaio (2008)
A. germinans	ln(AGB) = 5.9982 + 1.9340 * ln(DBH)	0.95	8	0.7–21.5	–	USA[j]	Smith & Whelan (2006)
A. schaueriana	ln(AGB) = 4.8881 + 0.8298 * ln(DBH² × Height)	0.84	23	3.4–10.2	3.1–7.5	Brazil[i]	Medeiros & Sampaio (2008)
A. germinans	ln(AGB) = 5.4698 + 1.0515 * ln(DBH² × Height)	0.99	21	6.7–40.7	8.3–18.1	Guadalupe[c]	Imbert & Rollet (1989)
A. germinans	ln(AGB) = 6.0544 + 1.0620 * ln(Parabolic volume)	0.99	7	14.2–26.3	–	Dominican Republic[k]	Sherman et al. (2003)
A. marina	ln(AGB) = 4.2713 + 1.7930 * ln(Height) + 0.7770 * ln(DBH)	0.54	16	10.4 ± 5.2	3.18 ± 0.42	Saudi Arabia[l]	Abohassan et al. (2012)
A. germinans	ln(AGB) = 4.3197 + 2.6410 * ln(Height)	0.92	8	0.7–21.5	–	USA[j]	Smith & Whelan (2006)
A. germinans	ln(AGB) = 2.1340 + 0.8950 * ln(DBH²) + 0.1840 * ln(Crown volume)	0.99	21	–	0.4–6.0	USA[m]	Ross et al. (2001)
Multispecific	ln(AGB) = 6.9538 + 0.8640 * ln(DBH) + 0.6350 * ln(Height) – 1.3700 * ln(ρ)	0.99	100	0.5–20.6	2.2–10.7	India[n]	Ray et al. (2011)

Intercepts and regression coefficients were ln-transformed when the original data were not presented in such scale. The unities of the regression variables were standardized in g (AGB), cm (DBH), m (Height), g cm^{-3} (ρ, wood density), dm^3 (Parabolic volume), cm^3 (Crown volume)

[a] 23.2°S, [b] 4.87°–5.50°N, [c] 16.17°N, [d] 1.17°–12.20°N, [e] 18.67°N, [f] 20.48°–21.97°S, [g] 8.25°N, [h] 12.42°–12.75°S, [i] 7.82°S, [j] 25.15°–25.50°N, [k] 19.17°N, [l] 20.77°N, [m] 25.45°N, [n] 21.53°–22.67°N

Fig. 2 Comparison of the allometric models developed in the present study for *A. schaueriana* (*line*) and in other studies for several species of the genus *Avicennia* in relation to the observed weight of trees from different DBH classes. The equations are presented in Table 5. Fromard et al. (1998)[1,2] refer to models published in the same article but based on large (dbh: 4–42 cm) and small (dbh: 1–4 cm) trees, respectively
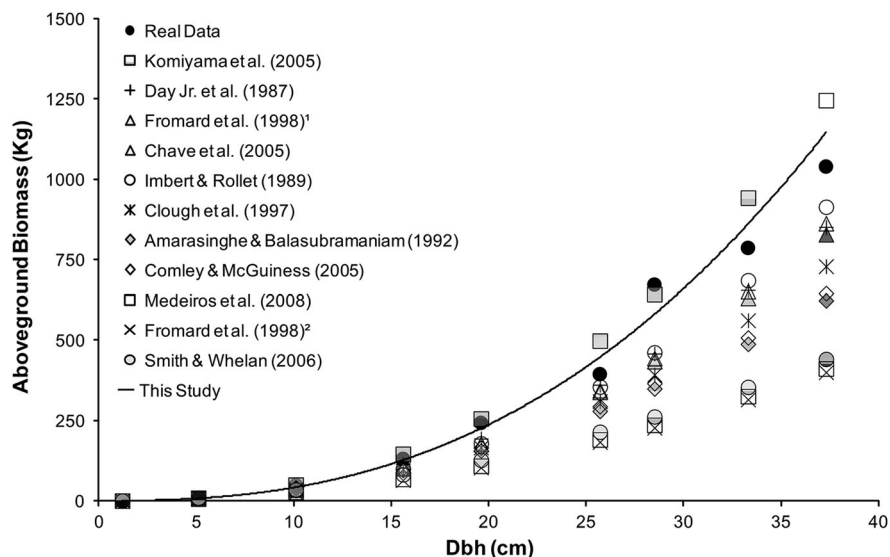
The inclusion of these equations in Group 3 shows that these features can be as or more important in choosing a model than the specific nature. This pattern is the case for the equation of Medeiros & Sampaio (2008), which, despite having been developed for *A. schaueriana*, had the third-highest average deviation ($43.1 \pm 23.8\%$), which is most likely explained by the reduced diameter range (3.4–10.2 cm) used in that study. This result also confirms the exceptional nature of the model of Day et al. (1987), which can be explained by a good choice of trees for their model construction or by a simple coincidence.

In respect to groups 2 and 3, the equations exhibited high negative deviations for all of the classes above 10 cm DBH (Table 5), reaching -66.1% in the equation of Fromard et al. (1998) for 28.5 cm. Considering that, along the succession of mangrove forests, density decreases (after the colonization phase) and tree size increases (Jimenez et al., 1985), the application of these equations to calculate the aboveground biomass of the Guaratiba's mangroves dominated by *A. schaueriana* would cause a large underestimation of the biomass of mature forests (with large trees at low density).

When the average deviation was calculated excluding the 1-cm class, the equation developed in the present study had an even lower mean deviation ($10.2 \pm 3.7\%$). This difference is due to the large deviation (-39.5%) observed for this class in this equation, which shows that the use of the equation for young trees requires caution. In mature and healthy

forests, where the contribution of young trees to the total forest biomass is low, the use of this model ensures the highest possible precision for estimating the aboveground biomass. However, in regenerating forests, where the contribution of young trees to the total forest biomass is high, the use of this model would result in a large underestimation of biomass. In this particular case, for the estimate of forests dominated by young or small (<4 cm DBH) *A. schaueriana* trees, the use of the models of Day et al. (1987), Medeiros & Sampaio (2008) or Fromard et al. (1998), which were generated based on low-DBH trees, may be the most appropriate alternative. Another alternative would be to develop a new model focused only on young or small trees, which could provide better results for the estimation of the biomass of these trees. This procedure was adopted previously by Fromard et al. (1998), who divided the development of allometric models of *A. germinans* between trees of 1–4 cm and trees of 4–42 cm. As shown in Table 5, the model of these authors based on larger trees showed high deviation (-32.1%) in relation to the 1.2-cm tree, whereas the model developed for smaller trees presented one of the lowest deviations (-7.9%) compared to the same tree. Among the equations in group 1, this limitation related to the estimation of the 1-cm class was also observed for the equations of Imbert & Rollet (1989) and Chave et al. (2005), showing even greater underestimation (-44.4 and -53.1%) compared to the equation developed in the present study, which may be related to the fact that

Table 5 Percentage deviation of the estimates produced by the equation developed in this study, and equations produced by other authors (see Table 4) in relation to the real weight of trees with different DBH values

DBH (cm)	This study	Komiyama et al. (2005)	Day et al. (1987)	Fromard et al. (1998)[c]	Chave et al. (2005)	Imbert & Rollet (1989)	Clough et al. (1997)	Amarasinghe & Balasubramaniam (1992)	Comley & McGuiness (2005)	Medeiros & Sampaio (2008)	Fromard et al. (1998)[d]	Smith & Whelan (2006)
Deviation (%)												
1.2	−39.5	−16.9	−2.3	−32.1	−44.4	−53.1	−15.4	19.4	42.0	5.5	−7.9	79.5
5.1	11.7	39.2	30.1	4.3	−5.5	−12.3	12.2	28.2	43.8	0.2	−8.5	40.4
10.1	−13.3	3.1	−13.5	−25.9	−29.6	−31.6	−25.6	−23.0	−15.9	−43.2	−47.0	−27.4
15.6	−3.1	11.9	−12.3	−21.6	−23.2	−23.2	−24.7	−26.9	−21.5	−48.0	−50.8	−37.3
19.6	−7.2	5.5	−20.2	−27.1	−27.4	−26.3	−31.6	−35.7	−31.7	−55.2	−57.3	−47.6
25.7	13.3	26.5	−8.4	−14.0	−12.8	−9.8	−21.4	−29.1	−25.4	−51.7	−53.5	−45.5
28.5	−13.7	−4.4	−31.8	−35.4	−33.9	−31.3	−41.6	−48.0	−45.6	−64.9	−66.1	−61.0
33.3	9.4	19.9	−16.6	−19.7	−17.1	−12.8	−28.6	−37.9	−35.4	−58.6	−59.9	−54.9
37.3	10.2	19.9	−18.1	−20.3	−17.0	−12.0	−29.9	−40.0	−37.9	−60.4	−61.5	−57.5
Mean[a]	13.5 ± 10.4	16.3 ± 11.8	17.0 ± 9.5	22.3 ± 9.4	23.4 ± 11.8	23.6 ± 14.0	25.6 ± 8.8	32.0 ± 9.1	33.2 ± 10.4	43.1 ± 23.8	45.8 ± 22.1	50.1 ± 15.2
Mean[b]	10.2 ± 3.7	16.3 ± 12.6	18.9 ± 8.3	21.0 ± 9.3	20.8 ± 9.5	19.9 ± 9.2	26.9 ± 8.5	33.6 ± 8.3	32.2 ± 10.6	47.8 ± 20.4	50.6 ± 18.1	46.5 ± 11.3

The means (±standard deviation) were calculated from the modules of the deviations

[a] Based on all DBH classes, [b] based on the classes 5.1 a 37.3 of DBH, [c] based on large trees (dbh: 4–42 cm), [d] based on small trees (dbh: 1–4 cm)

these authors did not include small trees (<4 cm) to develop their models (Table 4).

The results of this comparison show, on one hand, the importance of developing species and site-specific equations, because the equation developed in the present study has the lowest mean deviation in comparison with other equations previously developed for the genus *Avicennia*. On the other hand, the results, particularly regarding the equation of Komiyama et al. (2005), also indicate that multi-specific equations may be the best option when there are no equations available that are specific or that have satisfactory precision, as long as the sample size is large, and the diameter range is compatible (Komiyama et al., 2008; Breugel et al., 2011).

Conclusion

The equations developed in the present study to estimate the total AGB and biomass per compartment of *A. schaueriana* trees showed high R_a^2 values (0.9415–0.9949; not considering branches, whose equations were forced through the origin). DBH was the variable that provided the lowest %SEE_c in the regressions related to total AGB and leaves, while $DBH^2 * height$ provided the most precise regressions for woody compartments (trunk, branches, and twigs). Considering only the independent variable that provided the greatest precision among the regressions tested for each compartment, total AGB and trunk biomass had the lowest %SEE_c values (23.75 and 21.01%, respectively) and are therefore the most reliable. In comparison with other equations previously developed for the genus *Avicennia,* the most precise equation for the estimation of the total biomass among those developed in the present study showed the lowest mean deviation (13.5 ± 10.4%) compared to trees with known biomass, which confirms the importance of developing species- and site-specific equations. However, the low deviations shown by multi-specific equations that use wood density as an additional variable also indicate that such equations may be the best choice if there are no equations available that are both specific and have satisfactory precision, as long as their sample size is large, and the diameter range is compatible.

References

Abohassan, R. A. A., C. A. Okia, J. G. Agea, J. M. Kimondo & M. M. McDonald, 2012. Perennial biomass production in arid mangrove systems on the Red Sea coast of Saudi Arabia. Environmental Research Journal 6: 22–31.

Alongi, D. M., B. F. Clough, P. Dixon & F. Tirendi, 2003. Nutrient partitioning and storage in arid-zone forests of the mangroves *Rhizophora stylosa* and *Avicennia marina*. Trees 17: 51–60.

Amarasinghe, M. D. & S. Balasubramaniam, 1992. Net primary productivity of two mangrove forest stands on the North-western coast of Sri Lanka. Hydrobiologia 247: 37–47.

Baskerville, G. L., 1972. Use of logarithmic regression in the estimation of plant biomass. Canadian Journal of Forest Research 2: 49–53.

Breugel, M., J. Ransijn, D. Craven, F. Bongers & J. S. Hall, 2011. Estimating carbon stock in secondary forests: decisions and uncertainties associated with allometric biomass models. Forest Ecology and Management 262: 1648–1657.

Brown, S., 2002. Measuring carbon in forests: current status and future challenges. Environmental Pollution 116: 363–372.

Chave, J., R. Condit, S. Aguilar, A. Hernandez, S. Lao & R. Perez, 2004. Error propagation and scaling for tropical forest biomass estimates. Philosophical Transactions of the Royal Society B: Biological Sciences 359: 409–420.

Chave, J., C. Andalo, S. Brown, M. A. Cairns, J. Q. Chambers, D. Eamus, H. Fölster, F. Fromard, N. Higuchi, T. Kira, J. P. Lescure, B. W. Nelson, H. Ogawa, H. P. B. Riéra & T. Yamakura, 2005. Tree allometry and improved estimation of carbon stocks and balance in Tropical Forests. Oecologia 145: 87–99.

Cintron, G., A. E. Lugo & R. Martinez, 1985. Structural and functional properties of Mangrove Forests. In D'Arcy, W. G. & M. D. Correa (eds), The Botany and Natural History of Panama. Missouri Botanical Garden, Saint Louis: 53–66.

Clough, B., 1998. Mangrove forest productivity and biomass accumulation in Hinchinbrook Channel, Australia. Mangroves and Salt Marshes 2: 191–198.

Clough, B. F., P. Dixon & O. Dalhaus, 1997. Allometric relationships for estimating biomass in multi-stemmed mangrove trees. Australian Journal of Botany 45: 1023–1031.

Cole, T. G., K. C. Ewel & N. N. Devoe, 1999. Structure of mangrove trees and forests in Micronesia. Forest Ecology and Management 117: 95–109.

Comley, B. W. T. & K. A. McGuiness, 2005. Tree allometry and improved estimation of carbon stocks and balance in Tropical Forests. Australian Journal of Botany 53: 431–436.

Day Jr., J. W., W. H. Conner, F. Ley-Lou, R. H. Day & A. M. Navarro, 1987. The productivity and composition of mangrove forests, Laguna de Terminos, Mexico. Aquatic Botany 27: 267–284.

Donato, D. C., J. B. Kauffman, D. Murdiyarso, S. Kurnianto, M. Stidham & M. Kanninen, 2011. Mangroves among the most carbon-rich forests in the tropics. Nature Geoscience 4: 293–297.

Draper, N. R. & H. Smith, 1981. Applied Regression Analysis. Wiley Series in Probability and Mathematical Statistics. Wiley, New York.

Eisenhauer, J. G., 2003. Regression through the origin. Teaching Statistics 25: 76–80.

Estrada, G. C. D., C. H. Callado, M. L. G. Soares & C. S. Lisi, 2008. Annual growth rings in the mangrove *Laguncularia racemosa* (Combretaceae). Trees 22: 663–670.

Estrada, G. C. D., M. L. G. Soares, F. O. Chaves & V. Fernandez, 2013. Analysis of the structural variability of mangrove forests through the physiographic types approach. Aquatic Botany 111: 135–143.

Fromard, F., H. Puig, E. Mougin, G. Marty, J. L. Betoulle & L. Cadamuro, 1998. Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. Oecologia 115: 39–53.

Fromard, F., C. Vega & C. Proisy, 2004. Half a century of dynamic coastal change affecting mangrove shorelines of French Guiana. A case study based on remote sensing data analyses and field surveys. Marine Geology 208: 265–280.

Gibbs, H. K., S. Brown, J. O. Niles & J. A. Foley, 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. Environmental Research Letters 2: 1–13.

Gordon, H. A., 1981. Errors in computer packages. Least squares regression through the origin. The Statistician 30: 23–29.

Healy, M. J. R., 1984. The use of R^2 as a measure of goodness of fit. Journal of the Royal Statistical Society 147: 608–609.

Imbert, D. & B. Rollet, 1989. Phytomasse aerienne et production primaire dans la mangrove du Grand Cul-De-Sac Marin (Guadeloupe, Antilles Francaises). Bulletin d'Ecologie 20: 27–39.

Jimenez, J. A., A. E. Lugo & G. Cintron, 1985. Tree mortality in mangrove forests. Biotropica 17: 177–185.

Kairo, J. G., J. Bosire, J. Langat, B. Kirui & N. Koedam, 2009. Allometry and biomass distribution in replanted mangrove plantations at Gazi Bay, Kenya. Aquatic Conservation: Marine and Freshwater Ecosystems 19: S63–S69.

Kauffman, J. B. & T. G. Cole, 2010. Micronesian Mangrove Forest structure and tree responses to a severe typhoon. Wetlands 30: 1077–1084.

Komiyama, A., V. Jintana, T. Sangtiean & S. Kato, 2002. A common allometric equation for predicting stem weight of mangroves growing in secondary forests. Ecological Research 17: 415–418.

Komiyama, A., S. Poungparn & S. Kato, 2005. Common allometric equations for estimating the tree weight of mangroves. Journal of Tropical Ecology 21: 471–477.

Komiyama, A., J. E. Ong & S. Poungparn, 2008. Allometry, biomass, and productivity of mangrove forests: a review. Aquatic Botany 89: 128–137.

Kuuluvainen, T., 1991. Relationships between crown projected area and components of above-ground biomass in Norway spruce trees in even-aged stands: empirical results and their

interpretation. Forest Ecology and Management 40: 243–260.

Lovelock, C. & I. Feller, 2003. Photosynthetic performance and resource utilization of two mangrove species coexisting in a hypersaline scrub forest. Oecologia 134: 455–462.

Lugo, A. E. & S. C. Snedaker, 1974. The ecology of mangroves. Annual Review of Ecology, Evolution and Systematics 5: 39–64.

Medeiros, T. C. C. & E. V. S. B. Sampaio, 2008. Allometry of aboveground biomasses in mangrove species in Itamaracá, Pernambuco, Brazil. Wetlands Ecology and Management 16: 323–330.

Moreira-Burger, D. & W. B. C. Delitti, 1999. Fitomassa epigéa da mata ciliar do Rio Mogi-Guaçu, Itapira—SP. Revista Brasileira de Botânica 22: 429–435.

Nelson, B. W., R. Mesquita, J. L. G. Pereira, S. G. A. Souza, G. T. Batista & L. B. Couto, 1999. Allometric regressions for improved estimate of secondary forest biomass in the central Amazon. Forest Ecology and Management 117: 149–167.

Payandeh, B., 1981. Choosing regression models for biomass prediction equations. Forestry Chronicle October: 229–232.

Peel, M. C., B. L. Finlayson & T. A. McMahon, 2007. Updated world map of the Koppen-Geiger climate classification. Hydrology and Earth System Sciences 11: 1633–1644.

Pellegrini, J. A. C., M. L. G. Soares, F. O. Chaves, G. C. D. Estrada & V. F. Cavalcanti, 2009. A method for the classification of mangrove forests and sensitivity/vulnerability analysis. Journal of Coastal Research SI56: 443–447.

Ray, R., D. Ganguly, C. Chowdhury, M. Dey, S. Das, M. K. Dutta, S. K. Mandal, N. Majumder, T. K. De, S. K. Mukhopadhyay & T. K. Jana, 2011. Carbon sequestration and annual increase of carbon stock in a mangrove forest. Atmospheric Environment 45: 5016–5024.

Rezende, A. V., A. T. Vale, C. R. Sanquetta, A. F. Figueiredo & J. M. Felfili, 2006. Comparação de modelos matemáticos para estimativa do volume, biomassa e estoque de carbono da vegetação lenhosa de um cerrado sensu stricto em Brasília, DF. Scientia Forestalis 71: 65–76.

Ross, M. S., P. L. Ruiz, G. J. Telesnicki & J. F. Meeder, 2001. Estimating above-ground biomass and production in mangrove communities of Biscayne National Park, Florida (USA). Wetlands Ecology and Management 9: 27–37.

Saintilan, N., 1997. Above- and below-ground biomasses of two species of mangrove on the Hawkesbury River estuary, New South Wales. Marine & Freshwater Research 48: 147–152.

Schaeffer-Novelli, Y., G. Cintron-Molero, R. R. Adaime & T. M. Camargo, 1990. Variability of mangrove ecosystems along the Brazilian coast. Estuaries 13: 204–218.

Schaeffer-Novelli, Y., G. Cintrón-Molero, M. L. G. Soares & M. M. T. De-Rosa, 2000. Brazilian mangroves. Aquatic Ecosystem Health & Management 3: 561–570.

Sherman, R. E., T. J. Fahey & P. Martinez, 2003. Spatial patterns of biomass and aboveground net primary productivity in a mangrove ecosystem in the Dominican Republic. Ecosystems 6: 384–398.

Siddique, M. R. H., M. Hossain & R. K. Chowdhury, 2012. Allometric relationship for estimating above-ground biomass of Aegialitis rotundifolia Roxb. of Sundarbans mangrove forest, in Bangladesh. Journal of Forestry Research 23: 23–28.

Slim, F. J. & P. Gwada, 1993. Primary producers—the mangrove vegetation. In Woitchik, A. F. (ed.), Dynamics and Assessment of Kenyan Mangrove Ecosystems. Belgium-Kenya Marine & Fisheries Research Institute, Brussels: 6–34.

Smith, T. J. & K. R. T. Whelan, 2006. Development of allometric relations for three mangrove species in South Florida for use in the Greater Everglades Ecosystem restoration. Wetlands Ecology and Management 14: 409–419.

Soares, M. L. G. & Y. Schaeffer-Novelli, 2005. Above-ground biomass of mangrove species. I. Analysis of models. Estuarine, Coastal and Shelf Science 65: 1–18.

Sobrado, M. A. & S. M. L. Ewe, 2006. Ecophysiological characterisics of Avicennia germinans and Laguncularia racemosa coexisting in a scrub mangrove forest at the Indian River Lagoon, Florida. Trees 20: 679–687.

Spalding, M., M. Kainuma & L. Collins, 2010. World Atlas of Mangroves. Earthscan, London.

Sprugel, D. G., 1983. Correcting for bias in log-transformed allometric equations. Ecology 64: 209–210.

Suwa, R., K. Analuddin, N. I. Khan & A. Hagihara, 2008. Structure and productivity along a tree height gradient in a Kandelia obovata mangrove forest in the Manko Wetland, Okinawa Island, Japan. Wetlands Ecology and Management 16: 331–343.

Tam, N. F. Y., Y. S. Wong, C. Y. Lan & G. Z. Chen, 1995. Community structure and standing crop biomass of a mangrove forest in Futian Nature Reserve, Shenzhen, China. Hydrobiologia 295: 193–201.

Tomlinson, P. B., 1986. The Botany of Mangroves. Cambridge University Press, Cambridge.

Williams, M. S. & H. T. Schreuder, 2000. Guidelines for choosing volume equations in the presence of measurement error in height. Canadian Journal of Forest Research 30: 306–310.

Wood, A. G., 1986. A potential bias in log-transformed allometric equations. Wader Study Group Bulletin 47: 17–19.

Woodroffe, C. D., 1985. Studies of a mangrove basin, Tuff Crater, New Zealand. III. The flux of organic and inorganic particulate matter. Estuarine, Coastal and Shelf Science 20: 447–461.

Zar, J. H., 1996. Biostatistical Analysis. Prentice Hall, New Jersey.