Above-ground biomass of mangrove species.
I. Analysis of models

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Abstract

This study analyzes the above-ground biomass of *Rhizophora mangle* and *Laguncularia racemosa* located in the mangroves of Bertioga (SP) and Guaratiba (RJ), Southeast Brazil. Its purpose is to determine the best regression model to estimate the total above-ground biomass and compartment (leaves, reproductive parts, twigs, branches, trunk and prop roots) biomass, indirectly. To do this, we used structural measurements such as height, diameter at breast-height (DBH), and crown area. A combination of regression types with several compositions of independent variables generated 2.272 models that were later tested. Subsequent analysis of the models indicated that the biomass of reproductive parts, branches, and prop roots yielded great variability, probably because of environmental factors and seasonality (in the case of reproductive parts). It also indicated the superiority of multiple regression to estimate above-ground biomass as it allows researchers to consider several aspects that affect above-ground biomass, specially the influence of environmental factors. This fact has been attested to the models that estimated the biomass of crown compartments.
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1. Introduction

Mangroves have been the focus of attention since studies of the role of their detritus in the food web of the estuarine-coast zone (Heald, 1969; Odum, 1970; Odum and Heald, 1972). Several studies have approached the different stages of organic matter cycling in the mangroves (Soares, 1997), examining litter production and decomposition, export of dissolved and/or particulate organic matter, consumption by the mangrove resident fauna, incorporation of organic matter into the substratum, and its export through the assimilation and feeding by organisms that spend part of their life cycle in the mangroves, which, when they leave the ecosystem, become export agents of assimilated matter.

To better understand the dynamics of organic matter cycling in the mangroves, it is important to know the amount of biomass that is present in the vegetation covering at a given time.

Through the analysis of existing studies on the biomass of mangrove species, Soares (1997) describes some uses for biomass data: (1) estimation of primary productivity of mangroves, taking into account data on litter production; (2) determination of storage and cycling of elements in this ecosystem—for example, organic matter, nutrients and heavy metals; (3) measurement of the conditions of the system (degree of maturity, structural development, and stress levels) to determine the degree of restoration in degraded areas; (4) indication of the

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response of mangroves to several experiments; and (5) evaluation of commercial-valued biomass for companies involved in wood exploitation and silvicultural practices.

According to Soares (1997), the variability of environmental conditions, such as climate, geomorphology, edaphic factors, tides, age, and the history of the forest reflect on the structural characteristics of mangrove forests. After Lugo and Snedaker (1974), Woodroffe (1982) and Mall et al. (1991), the observed variability on mangrove forests biomass is a function of the history of the forest and the structural variability. This makes comparison among biomass data and equations from areas which are geographically different very difficult, discouraging their indiscriminate application.

Saenger and Snedaker (1993) have further concluded that the pattern of organic matter partition also varies according to latitude, in their revision of data about mangrove biomass worldwide. These authors have noted a significant relationship between biomass, forest development (expressed in height), and latitude, the latter being directly related to environmental characteristics (mainly solar radiation, temperature, and water availability). Similarly, Tam et al. (1995) have also highlighted how mangrove biomass increases towards low latitudes and Day et al. (1987), in their study of the Mexican mangroves, have emphasized the errors that were introduced by applying regressions obtained for mangroves other than the one they were working with. Saintilan (1997) describes that mangroves of wide girth in tropical estuaries grow taller than their subtropical counterparts, which may show substantial variation in girth once maximum height is reached. Fromard et al. (1998) also describe the general model established by Saenger and Snedaker (1993). However, they also pointed out factors that limit mangrove development (e.g. the occurrence of hurricanes, low temperatures, low annual rainfall, the presence of a well-marked dry season and high salinity). Lugo and Snedaker (1974), Lugo (1980) and Mall et al. (1991) describe that the maximum potential biomass of mangroves forests in Florida and Puerto Rico are not reached as a result of hurricanes influence. Berger and Hildenbrandt (2000) stressed that the mangrove tree architecture and maximum trunk diameter are highly variable, and depend on several stress factors such as pore water salinity or water logging. Saintilan (1997) also found a decrease of above-ground biomass with increasing substratum salinity for *Avicennia marina* and *Aegiceras corniculatum*. On the other hand, Sherman et al. (2003) found an increase of above-ground biomass across the tidal gradient, which was negatively correlated with porewater salinity, however the authors stress that the cause–effect relationships between soil porewater salinity and forest biomass must remain tentative because salinity often covaries with other potentially stressful factors in the soil environment, such as hydrogen sulfide concentrations, soil redox, and flooding frequency.

Therefore, the need to obtain specific data for each geographical area has led to an increase in studies on the biomass of mangroves. To exemplify this surge, Soares (1997) listed a series of studies on the biomass of mangroves worldwide. For the Atlantic coast of the American continent (including North and South America and the Caribbean) we can mention the studies developed by Golley et al. (1962, 1969, 1971, 1978), Lugo and Snedaker (1974), Cintrón and Schaeffer-Novelli (1985), Day et al. (1987), Imbert and Rollet (1989), Fromard et al. (1998), Ross et al. (2001) and Sherman et al. (2003). We also have to mention the studies developed at the Indo-Pacific region, such as De la Cruz and Banaag (1967), Aksornkoae (1975), Clough and Attiwill (1975), Briggs (1977), Christensen (1978), Ong et al. (1979, 1980, 1984), Suzuki and Tagawa (1983), Boto and Wellington (1984), Gong et al. (1984), Murray (1985), Woodroffe (1985), Putz and Chan (1986), Tamai et al. (1986), Tri (1986), Chakrabarti (1987), Clough and Scott (1989), Gong and Ong (1990, 1995), Lee (1990), Lin and Lu (1990), Choudhuri (1991), Mall et al. (1991), Amarasinghe and Balasubramanian (1992a, 1992b), Sukardjo and Yamada (1992), Mackey (1993), Singh et al. (1993), Tam et al. (1995), Clough et al. (1997), Saintilan (1997) and Komiyama et al. (2000, 2002). For Africa we found studies developed by Slim and Gwada (1993) and, Steinke et al. (1995).

From the above description we confirm the observation made by Fromard et al. (1998) that most of the data published so far concern the mangrove forests of south east Asia and Australia and the species native to those areas and that few data are available for western mangroves (including the South American continent).

We must stress the scarcity of studies that have addressed mangroves in Brazil. The only research on the biomass of Brazilian mangroves is Silva (1988), which considered only one species (*Rhizophora mangle*) and Silva et al. (1993), which presents an indirect study on mangrove biomass, through the development of a volume equation for mangrove trees in northeast Brazil. The shortage of specific studies on the biomass of Brazilian mangroves fully justifies studies of this kind in different areas of the Brazilian coast, especially if we consider its extent and latitudinal range. This is the endeavor this study undertook.

Specifically, we studied *Laguncularia racemosa* and *Rhizophora mangle* in Bertioga (São Paulo) and Guaratiba (Rio de Janeiro) mangroves, Southeast Brazil. By means of regression curves, we related structural measurements such as height, DBH, crown diameter and area to the total above-ground biomass and the biomass per tree compartment (leaves, reproductive parts, twigs, branches, trunks and prop roots). To

determine the model that would be the best estimator of total and per compartment biomass for both species, the study tested several regression models and combinations of independent variables.

2. Materials and methods

2.1. Study area

The study was conducted in the mangroves of Guaratiba (Rio de Janeiro) and Bertioga (São Paulo), Southeast Brazil. The mangroves of Guaratiba (Fig. 1a) are located in the Sepetiba/Guaratiba coastal plain, defined to the north and east by the Pedra Branca mountains and to the south and west by the Sepetiba Bay, about 70 km from downtown Rio de Janeiro. The climate of the area, according to the Koppen classification, may be divided into Aw, tropical hot and humid with dry months in winter, which is typical of the plains, and Af, tropical hot and humid without a dry season, which is typical of the adjacent slope (Ferreira and Oliveira, 1985). Data from the Marambaia Meteorological Station, collected from 1984 to 1992, indicate an average temperature of 23.5 °C and an average rainfall of 1032 mm. They also indicate that rainfall in January and March is higher than that of June and August, the driest months.

In addition, the studied mangroves are located in the interior of Sepetiba Bay, between the Piraquê River and the Guaratiba Hill, integrating a system of islands, rivers and channels. This region is characterized by a micro-tidal regime, with a tidal range below 2 m. The structural characterization of mangroves has been addressed by only a few studies (Dansereau, 1947; Bronnimann et al., 1981) that have diagrammed the distribution of the species in zones.

The margin of the Piraquê River is dominated by *Rhizophora mangle* with an average height of 7.63 m and a density of 4100 trunks ha^{-1}. A detailed characterization of mangrove forests is presented in Table 1. The physiographic type of these stands has been classified as the riverine forest type, according to the classification proposed by Lugo and Snedaker (1974). The second zone may be characterized as a basin forest that possesses an outer strip dominated by *R. mangle* and a significant presence of *Avicennia schaueriana* and *Laguncularia racemosa*, with an average height of 7.05 m and a density of 3900 trunks ha^{-1}.

The other research area (Fig. 1b) is located in the municipality of Bertioga, on the margins of the Bertioga Channel, in the Santos Coastal Plain, being about 100 km from the city of São Paulo. Specifically, the area lies between the Bertioga Channel and the Serra do Mar Mountain. The proximity to the Serra do Mar Mountain, associated with the influence of cold fronts, is responsible for the high pluviometric indexes observed in this area (Martin and Suguio, 1989). The annual rainfall averages 2240 mm. The wet season extends from January to March (summer) and the dry season from July to August (winter). The average monthly temperatures oscillate between 20 and 26 °C.

A transect from this research area has already been studied by Peria et al. (1990), one that goes from the Bertioga Channel to its transition to land, the same area where we have conducted the present study. According to these authors, the mangrove is a mixed forest of *Laguncularia racemosa*, *Rhizophora mangle* and *Avicennia schaueriana*, with a slight dominance of *R. mangle*, with an average height of 7.7 m and density of 2560 trunks ha^{-1}. The structural characteristics of these forests are presented in Table 1. It could be classified as a basin forest in the light of the Lugo and Snedaker (1974) physiographic types.

2.2. Methods

Sampling methods are described in Newbould (1967), Golley et al. (1978), Cintron and Schaeffer-Novelli (1984, 1985), Schaeffer-Novelli and Cintron (1986), Clough and Scott (1989), Imbert and Rollet (1989), and Amarasinghe and Balasubramaniam (1992a). To adapt them to our specific objectives and to the peculiarities of the studied mangrove stands, we modified them somewhat.

A total of 143 individuals were collected, 64 in Guaratiba (32 *Rhizophora mangle* and 32 *Laguncularia racemosa*) and 79 in Bertioga (33 *R. mangle* and 46 *L. racemosa*). Both individual groups were chosen according to their diameter at breast height (DBH), so that all diameter classes in the two study areas, for both species (maximum dbh around 22.0 cm), were represented.

For each sampled tree, DBH, height and crown diameters (based on their projection onto the soil) were registered. To calculate the crown area, crown diameters were used and the crown area was considered an ellipse. The harvested trees were subdivided into the following compartments: leaves (including buds), reproductive parts (flowers, fruits and propagules), twigs (smaller than 2.5 cm in diameter), branches (larger than 2.5 cm in diameter), main branches (originated from the bifurcation of the trunk), trunk and prop roots. Twigs and branches have been distinguished following Cintron and Schaeffer-Novelli (1985).

In the case of the *Rhizophora mangle*, prop roots were collected and its segments (arches) separated whenever present. They were woody (rigid like the trunk), not woody (spongy consistency) and emergent (those that have not reached the substratum yet) structures, or aerial roots (those arising from the lower branches and not from the trunk).
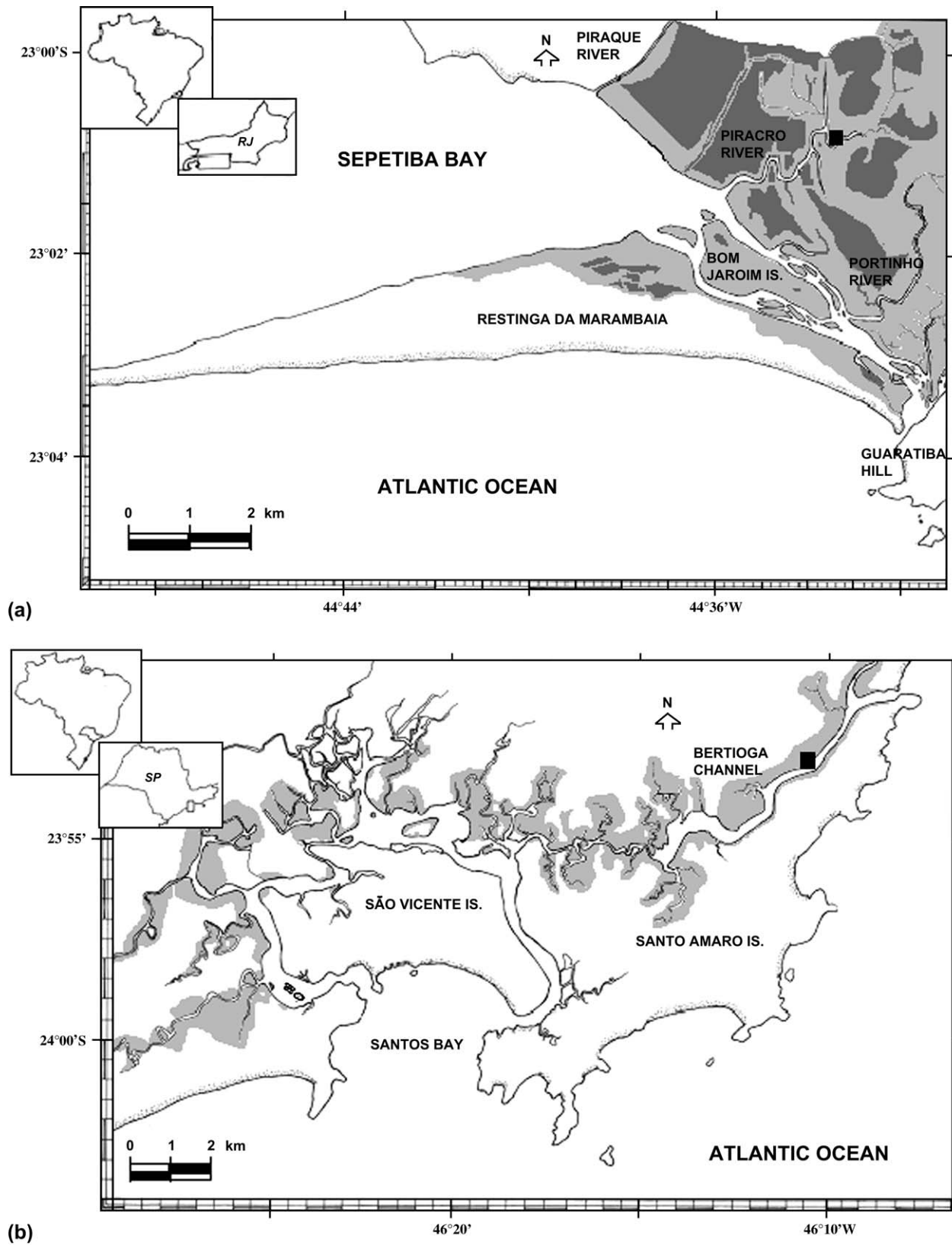
Fig. 1. Maps showing the two studied sites (black squares) in Southeastern Brazil. (a) Guaratiba (Rio de Janeiro). (b) Bertioga (São Paulo). Mangrove forests are presented in light gray and areas in dark gray (at Guaratiba) represent salt-flats.

Table 1
Structural characteristics of the studied mangrove forests at Guaratiba (Rio de Janeiro) and Bertioga (São Paulo)

Parameter	Guaratiba (Rio de Janeiro)	Bertioga (São Paulo)[a]
Mean height $\pm$ SD (m)	7.63 ± 2.86	7.70 ± 0.70
Trunk density (trunk ha^{-1})	4100	2560
Mean DBH (cm)	8.8	7.5
Basal area (m^2 ha^{-1})	24.74	11.30
Relative density (%)		
Rhizophora mangle	74.5	20.0
Avicennia schaueriana	10.6	25.4
Laguncularia racemosa	2.1	26.8
Dead	12.8	27.8
Relative dominance (basal area) (%)		
Rhizophora mangle	43.3	36.6
Avicennia schaueriana	45.1	28.6
Laguncularia racemosa	6.5	16.7
Dead	5.1	18.0

[a] After Peria et al. (1990).

After sorting out the segments, we weighed all the compartments in the field on dynamometer scales and, whenever possible, took all the material for treatment in the laboratory. When it was not possible, freshly weighed sub-samples were collected for later treatment in the laboratory. To determine the total and by-compartment dry weight for each sampled individual, simple linear regressions of dry weight on fresh weight were run, beginning with the sub-sample dry weights. These statistical procedures may be found in Sokal and Rohlf (1979), Wonnacott and Wonnacott (1980), Draper and Smith (1981), and Zar (1996).

The obtained regressions were grouped by compartments: leaves and reproductive parts (8 regressions); twigs (4 regressions); branches, main branches and trunks (10 regressions); roots (7 regressions); and trunks and woody roots (6 regressions). To test them for similarity, the regressions of each of their groupings were compared in terms of slopes (coefficient *b*) and elevations (coefficient *a*).

An analysis of variance (ANOVA), following Byrne and Wentworth (1988), and Zar (1996), and a Student's *t*-test, following Day et al. (1987), Amarasinghe and Balasubramaniam (1992a), and Turner et al. (1995), guided the comparisons. After comparing slopes (*b*) and elevations (*a*), we pooled the data from the various regressions to compute common regressions based on the comparison results.

Biologically, regression curves should go through the origin (elevation equal to zero). Consequently, constant "*a*" was tested through a Student's *t*-test. For each value of "*a*" not significantly different from zero, a new linear regression was calculated, by forcing through the origin ($a = 0$). In cases where the procedure yielded $a \neq 0$, the original regressions were maintained.

Then, an ANOVA and a Student's *t*-test were applied to test all the regressions for significance. In addition, the adjusted coefficient of determination predicted by the regression (R^2a) and the standard error of estimate for the slope (Sb) (this one according to the estimated value for the slope *b*) were examined. An analysis of residuals (Draper and Smith, 1981; Zar, 1996) tested all regressions for assumptions of normality and constant variance.

The subsequent procedure determined the total dry weight by compartment, for each sampled individual. The final regression equations were applied to fresh weights obtained in the field, except for individuals for which there had been total sampling of some compartments. In these cases, the corresponding dry weight was directly obtained from the dry weight of the material in the laboratory.

Table 2 presents the regression equations for the total and by-compartment estimates of biomass for the two species, in the two research areas. It also illustrates the several combinations of regression models and independent variables (Soares, 1997) we have drawn on. The units considered for each variable were DBH (centimeters), height (meters), wood density (g cm^{-3}), basal area (m^2), crown area (m^2), and mean crown diameter (meters), respectively.

An ANOVA ($\alpha = 1\%$) tested the significance of the regressions and an analysis of the adjusted standard error of estimate (SEEa) identified the best biomass estimator for each location, species, and, compartment, following Zar (1968, 1996), Draper and Smith (1981), Payandeh (1981), and Soares (1997).

3. Results

Table 3 shows the regressions that relate dry weights and fresh weights by compartment, for both species, in both locations, Guaratiba and Bertioga mangroves. In the case of material that has been partially sampled in the field, we obtained the total and by-compartment dry weights for each tree of the two species in Bertioga and Guaratiba, by applying the regressions in Table 3, as Tables 4–7 clarify.

We tested a total of 182 models, if the combination of regression models and independent variables presented in the methodology is considered. Many of these models were initially assessed, in terms of fittings and estimates (parameters R^2a, F and SEEa). Because the use of variables presupposes their simplicity, we eliminated models that yielded the same fittings and errors of estimate of the biomass. Consequently, a total of 85 models were considered and completely evaluated. Of these, 53 models were applied to all compartments and 32 exclusively to compartments of the crown. Given that *Laguncularia racemosa* had a total of 7 compartments, 5

Table 2
Regression models and independent variables tested for the development of models for the estimation of mangrove species biomass (Soares,1997).
Y = Biomass; a, b, c, d, e, f = constants. Parabolic volume = (basal area × height)/2 (Whittaker, 1961; Newbould, 1967; Whittaker and Marks, 1975)

Models	Independent variables (X, Z, W)
$\ln Y = \ln a + b \ln X$	DBH; height; DBH^2; DBH^2×height; DBH^2×height×wood density; DBH^2+height+(DBH^2×height); basal area; basal area×height; crown area; mean crown diameter; parabolic volume; DBH×height; (basal area)^2×height; (height)^2; (DBH×height)^2; (crown area)^2; (mean crown diameter)^2; DBH×height×wood density; basal area×height×wood density; (DBH×height×wood density)^2; cone volume; cylinder volume
$\ln Y = \ln a + b$ $\ln X + c \ln Z$	DBH and height; DBH and crown area; DBH and mean crown diameter; height and crown area; height and mean crown diameter; basal area and height
$\ln Y = \ln a + bX$	DBH; height; DBH×height; crown area; mean crown diameter; parabolic volume; cone volume; cylinder volume; basal area; DBH^2×height; (basal area)^2×height; DBH^2; height^2; (DBH×height)^2; (crown area)^2; (mean crown diameter)^2; DBH×height×wood density; basal area×height×wood density; (DBH×height×wood density)^2
$Y = a + bX$	DBH; height; basal area; parabolic volume; cone volume; cylinder volume; basal area×height×wood density; DBH×height×wood density; DBH×height; basal area×height; DBH^2×height; DBH^2×height×wood density; crown area; mean crown diameter; DBH^2; height^2; (DBH×height)^2; (parabolic volume)^2; (cone volume)^2; (cylinder volume)^2; (basal area)^2; (DBH×height×wood density)^2; (basal area×height×wood density)^2; (DBH^2×height)^2; (crown area)^2; (mean crown diameter)^2
$\ln Y = a + b \ln (X)^{1/2}$ $\ln Y = a + b \ln X + cX$ $(Y)^{1/3} = a + bX$ $(Y)^{-1/3} = a + bX$	DBH; height; basal area; parabolic volume; cone volume; cylinder volume; DBH×height×wood density; basal area×height×wood density; DBH×height; basal area×height; DBH^2×height; DBH^2×height×wood density; crown area; mean crown diameter
$Y = a + bX + cZ + dW$	DBH^2, Height, DBH^2×Height.
$Y = a + bX + cZ$	DBH and height; DBH×height and height; DBH×height and DBH; basal area and height; basal area×height and height; basal area×height and basal area; DBH^2×height and DBH; DBH^2×height and height; DBH×height×wood density and DBH; DBH×height×wood density and height; basal area×height×wood density and height; basal area×height×wood density and basal area; DBH^2×height×wood density and DBH; DBH^2×height×wood density and height; DBH and crown area; DBH and mean crown diameter; height and crown area; height and mean crown diameter; DBH×height and crown area; DBH×height and mean crown diameter; DBH^2×height and crown area; DBH^2×height and mean crown diameter; basal area and crown area; basal area and mean crown diameter; basal area×height and crown area; basal area×height and mean crown diameter; DBH×height×wood density and crown area; DBH×height×wood density and mean crown diameter; basal area×height×wood density and crown area; basal area×height×wood density and mean crown diameter; DBH^2×height×wood density and crown area; DBH^2×height×wood density and mean crown diameter; DBH^2 and height; DBH^2 and DBH×height; DBH^2 and DBH^2×height; DBH^2 and DBH×height×wood density; DBH^2 and DBH^2×height×wood density; DBH^2 and basal area×height×wood density; DBH^2 and crown area; DBH^2 and mean crown diameter
$Y = a + bX + cX^2 + dX^3$ $+ eX^4 + fX^5$	DBH; height; basal area; basal area×height; parabolic volume; cone volume; cylinder volume; basal area×height×wood density; DBH×height×wood density; DBH×height; crown area; mean crown diameter

of them part of the crown, and *Rhizophora mangle* 9 compartments, 4 of which part of the crown, we ran and analyzed a total of 2272 regressions for the two species, in the two locations.

To obtain the best estimator of the total and by compartment biomass for both species, in each of the study sites (Tables 8 and 9), we analyzed the SEEa of each one of the generated regressions.

Most selected models are multiple regression models and their main representative is the group "Biomass" (without transformation), mainly in the Bertioga area. In Guaratiba, there was a larger division between the groups "Biomass" and "ln (Biomass)" (with logarithmic transformation). In only one case, the best estimator was "(Biomass)$^{1/3} = a + bX$" and in only two cases "(Biomass)$^{-1/3} = a + bX$". The models that best estimated the biomass of each compartment revealed considerable

variability. In none of the cases was same model the best estimator for a given compartment for both areas, Bertioga and Guaratiba. The regression fittings (R^2a) were robust for trunks and the total biomass (R^2a > 0.95). They were weak for some models of the reproductive parts and quite weak for the emergent prop roots and non-woody prop roots (R^2a < 0.50). The regression fittings for the other compartments were good, most of them yielding R^2a greater than 0.80.

4. Discussion

The analysis of the R^2 allowed the linear relationship between the dry weight and the fresh weight of the compartments of sampled trees to become clear (see Table 3). This parameter describes the general fitting of

Table 3

Regressions ($Y = a + bX$) relating dry weights (g) and fresh weights (g) by compartments, region and species (n = sample size; R^2 = coefficient of determination; Y = dry weights; X = fresh weights; Sa = standard error of intercept "a"; Sb = standard error of regression coefficient "b"; Rh, *Rhizophora mangle*; Lg, *Laguncularia racemosa*)

Compartments – species – region	n	R^2	a	b	Sa	Sb
Leaves and reproductive parts – Rh – Guaratiba	53	0.995	0	0.348526	–	0.003
Leaves and reproductive parts – Rh – Bertioga	51	0.999	0	0.328651	–	0.002
Leaves and reproductive parts – Lg – Guaratiba	54	0.995	0	0.298848	–	0.003
Leaves and reproductive parts – Lg – Bertioga	73	0.996	0	0.317777	–	0.002
Twigs – Lg and Rh – Guaratiba and Bertioga	144	0.998	0	0.512287	–	0.002
Branches and main branches – Lg and Rh – Guaratiba and Bertioga	101	0.988	0	0.580636	–	0.006
Trunks – Lg – Guaratiba and Bertioga	248	0.996	−5.706510	0.611510	1.856	0.003
Trunks – Rh – Guaratiba	88	0.997	−18.941037	0.656459	3.372	0.004
Trunks – Rh – Bertioga	145	0.985	0	0.596870	–	0.006
Prop roots (emergent) – Guaratiba and Bertioga	41	0.993	−1.801900	0.393290	0.534	0.005
Prop roots (woody) – Guaratiba	201	0.996	−39.752860	0.591587	3.613	0.003
Prop roots (woody) – Bertioga	296	0.990	−20.869840	0.533205	2.578	0.003
Prop roots (not woody) – Guaratiba	138	0.992	0	0.380604	–	0.003
Prop roots (not woody) – Bertioga	258	0.995	−2.867915	0.391706	2.578	0.002
Prop roots (aerial) – Bertioga	7	0.994	0	0.432780	–	0.014

the model for the selected cases, and, in most cases, yielded a value greater than 0.99. The values of the regression coefficients (b) indicate the relationship between dry weight/fresh weight and roughly reveal the proportion of organic matter for each compartment. In other words, the value "$1 - b$" is equal to the amount of water in the compartment. The larger the "b" value, the smaller the amount of water in the compartment. Such a tendency became clear when we noticed values of "b" of approximately 0.30 for compartments such as leaf and reproductive parts, of approximately 0.50 for twigs and branches, and of 0.60 for trunks. These values indicate a reduction in the amount of water from the green parts to the woody parts of the plant. The same tendency has been observed in the case of the *Rhizophora mangle* prop roots; its emergent and non-woody prop roots (with "spongy" structure) yielded "b" values between 0.30 and 0.40 while the woody prop roots yielded "b" values between 0.50 and 0.60. These results fully agree with Slim and Gwada (1993) findings about *Rhizophora mucronata*. According to them, *R. mucronata* shows 66% (leaves), 44% (branches), 41% (trunk), and 53% (roots) for the amount of water in the several compartments.

Although the statistical comparison of the regression coefficients from the leaves and reproductive parts of the two species, both in Bertioga and Guaratiba, indicated similarity, *Rhizophora mangle* tends to yield slightly higher coefficients for leaves. This suggests its leaves carry a smaller amount of water than those of *Laguncularia racemosa*.

The same result has been found by Lamberti (1969), when studying the succulence (mass of water/leaf area) of leaves of mangrove species in Itanhaém (São Paulo, Southeast Brazil). He observed that the leaves of *Laguncularia racemosa* are more succulent than those

of *Rhizophora mangle*. He cites Biebl and Kinzel (1965), who also found a larger succulence for the leaves of *L. racemosa* in the mangroves of Puerto Rico. Medina (1992) goes further, affirming that succulence is greater in leaves that are exposed to the sun, a condition that is met by the leaves of *L. racemosa* in the stands we have investigated. Because of the low density of its crown, its leaves are more exposed to the sun, and self-shading is hardly observed.

However, the use of regression curves to determine biomass did not go without problems. One of the greatest problems was choosing the best-estimate curve for the biomass. Several authors, in an erroneous way, have been using R^2 as the parameter for this choice. But R^2 simply offers a general idea of the fitting for the model (Payandeh, 1981; West and Wells, 1990; Zar, 1996). Several studies have illustrated this problem, such as Whittaker and Woodwell (1969), Whigham and Simpson (1978), Tanner (1980), Rai (1984a, b), Rai and Proctor (1986), Brown et al. (1989), Imbert and Rollet (1989), Grundy (1995), Steinke et al. (1995), Tam et al. (1995). Others, as for example Payandeh (1981), not only discuss the problem, but also state that such a choice should be based on the standard error of estimate (SEE), which, according to Zar (1968, 1996) and Draper and Smith (1981), is a global indication of precision of regression in predicting the dependent variable. However, only a few studies have adopted this procedure (Rutter, 1955; Rochow, 1974; Byrne and Wentworth, 1988; Schacht et al., 1988; Zak et al., 1989; Busing et al., 1993; Slim and Gwada, 1993; Haase and Haase, 1995; Ibrahim, 1995).

Tables 8 and 9 demonstrate that "Biomass" models were the best estimators for most compartments. Most biomass studies through regressions, in mangroves or in plant communities, do not use linear models. They prefer

Table 4
Total and by-compartments dry weights of each sampled tree: *Laguncularia racemosa*, Bertioga

Tree	DBH (cm)	Height (m)	Crown diameter (m)		Dry weights (g)						
			D1	D2	Leaves	Reproductive parts	Twigs	Branches	Main branches	Trunks	Total
01	4.60	6.90	1.18	1.51	314.62	4.08	563.34	28.55	0	5410.03	6320.62
02	0.80	1.32	0.62	0.79	12.84	0	20.65	0	0	67.74	101.23
03	5.30	7.40	1.30	1.08	130.72	0.07	442.89	0	0	7271.77	7845.45
04	0.60	1.40	0.59	0.56	14.63	0	21.53	0	0	60.84	97.00
05	4.70	7.00	1.60	1.60	249.14	0	346.26	0	0	4796.72	5392.12
06	1.40	2.40	1.40	1.25	82.11	0.47	135.27	0	0	422.78	640.63
07	2.80	2.40	0.70	0.65	65.99	0	45.38	0	0	731.27	842.64
08	6.50	9.50	1.86	1.70	241.09	3.18	949.87	140.38	0	11 845.85	13 180.37
09	1.30	1.90	–	–	11.27	0	32.95	0	0	173.42	217.64
10	10.00	9.10	2.20	1.65	744.41	0.05	2450.67	9390.20	0	17 374.79	29 960.12
11	3.10	2.40	1.48	1.46	185.85	0.75	377.32	338.47	0	819.00	1721.39
12	8.80	8.70	2.71	1.70	1271.57	23.12	2659.01	8654.51	0	12 882.80	25 491.01
13	1.60	1.86	0.57	0.22	12.08	0	19.06	0	0	162.59	193.73
14	10.00	10.70	3.15	1.70	738.62	0	2267.58	1778.96	9920.41	20 848.35	35 553.92
15	2.50	1.20	1.15	0.95	33.67	0	82.28	0	0	66.10	182.05
16	6.40	7.70	1.86	1.95	587.81	61.32	1163.58	1200.77	0	10 520.01	13 533.49
17	2.80	2.15	1.56	1.00	125.62	0	146.70	0	0	631.11	903.43
18	3.10	3.50	1.53	1.04	175.82	1.31	164.22	0	0	1125.17	1466.52
19	5.80	9.10	1.37	1.15	234.03	0.18	776.64	0	0	9700.15	10 711.00
20	3.90	5.90	1.31	0.98	70.46	0.30	230.45	0	0	2404.84	2706.05
21	1.20	2.30	1.00	0.55	16.55	1.05	23.20	0	0	73.95	114.75
22	6.40	10.30	0.70	0.63	347.75	0	657.00	139.09	0	10 157.05	11 300.89
23	1.30	1.25	0.75	0.45	14.05	0	33.74	0	0	57.08	104.87
24	2.40	2.50	1.65	1.48	89.67	3.01	157.32	0	0	542.02	792.02
25	4.70	7.00	1.17	1.30	335.79	0.50	721.13	0	0	5868.66	6926.08
26	5.10	7.30	0.58	0.66	311.39	8.67	732.83	120.49	0	6166.06	7339.44
27	7.40	7.90	2.18	2.25	215.80	4.57	816.67	1393.86	0	14 079.56	16 510.46
28	7.30	9.70	1.83	0.99	982.64	0.72	1902.54	3301.94	0	17 623.63	23 811.47
29	3.00	2.90	1.40	2.10	160.08	2.04	397.18	0	0	885.03	1444.33
30	9.40	9.40	4.20	2.70	762.63	0.13	2582.22	2560.54	4374.08	25 027.16	35 306.76
31	11.20	9.10	2.50	2.30	613.10	0	3477.34	4228.30	0	33 435.17	41 753.91
32	10.10	8.70	2.60	1.74	840.85	0	2577.16	3509.00	0	29 687.29	36 614.30
33	9.30	8.00	2.68	2.35	1168.32	0	2578.85	1530.60	0	23 038.97	28 316.74
34	7.50	7.40	1.90	2.40	679.60	0	1746.46	1455.72	0	14 168.02	18 049.80
35	8.00	9.20	2.00	1.50	671.25	0	2065.60	2055.84	0	18 709.61	23 502.30
36	9.30	8.60	1.94	1.37	991.25	0	2590.59	5459.04	3648.91	23 462.06	36 151.85
37	8.30	7.80	3.50	2.85	2165.78	0	3535.28	3723.65	0	19 455.49	28 880.20
38	15.60	10.40	3.95	3.60	3266.93	0	6076.90	18 997.83	15 967.49	50 808.55	95 117.70
39	18.60	10.80	3.70	5.10	2236.59	0.17	4756.89	17 009.49	0	99 256.79	1 23 259.90
40	13.40	10.00	5.60	5.35	4141.00	333.60	9202.00	11 514.44	22 732.74	42 339.51	90263.29
41	16.30	8.60	4.33	4.25	5254.33	332.60	10 268.63	32 790.27	0	74 149.81	1 22 795.60
42	12.90	10.40	4.00	4.70	4297.56	455.62	7773.54	7157.73	12 170.36	48 042.19	79897.00
43	14.00	10.20	4.70	4.50	5217.05	718.50	9524.32	18 254.61	0	58 834.10	92548.58
44	20.00	10.70	4.90	4.51	4455.37	526.11	10 146.07	14 375.95	64 131.25	99 617.84	1 93 252.60
45	17.20	12.10	3.80	4.30	6709.80	889.96	11 236.47	17 437.50	20 199.64	80 301.03	1 36 774.40
46	12.30	9.80	3.60	3.67	3385.87	965.94	6218.53	12 789.48	0	47 970.44	71 330.26

logarithmic transformations (Soares, 1997). The problem is that such studies do not test other models. They simply adopt models that had already been used in other studies and that are not the best estimators, although they yield acceptable results such as the models of the type "ln (Biomass) = $a + b$ ln (DBH)" or "ln (Biomass) = $a + b$ ln (DBH^2 × height)". For mangrove communities we can describe some studies that adopt logarithmic transformations: Golley et al. (1962), Ong et al. (1979, 1980, 1984, 1985), Suzuki and Tagawa (1983), Cintron and Schaeffer-Novelli (1984, 1985), Putz and Chan (1986), Schaeffer-Novelli and Cintron (1986), Silva (1988), Clough and Scott (1989), Imbert and Rollet (1989), Lee (1990), Silva et al. (1991), Amarasinghe and Balasubramaniam (1992a, 1992b), Sukardjo and Yamada (1992), Mackey (1993), Slim and Gwada (1993), Chen et al. (1995), Gong and Ong (1995), Steinke et al. (1995), Tam et al. (1995), Turner et al. (1995) and Ross et al. (2001).

Fromard et al. (1998, 2004) studied the mangroves of French Guinana, which have a floristic composition similar to the Brazilian forests (they estimated the total biomass, leaf biomass, branch and trunk biomass of

Table 5
Total and by-compartments dry weights of each sampled tree, *Laguncularia racemosa*, Guaratiba

Tree	DBH (cm)	Height (m)	Crown diameter (m)		Dry weights (g)						
			D1	D2	Leaves	Reproductive parts	Twigs	Branches	Main branches	Trunks	Total
1	6.10	5.70	1.40	1.65	390.26	9.82	1116.30	377.78	0	6657.62	8551.78
2	6.40	6.10	1.85	1.26	359.59	7.77	1349.80	816.98	2082.02	8219.61	12 835.77
3	4.20	5.60	2.10	1.40	173.12	2.90	532.80	0	0	4538.63	5247.45
4	8.60	7.30	1.85	2.20	692.16	8.50	2779.98	2996.52	5483.97	14 518.88	26 480.01
5	7.90	8.60	3.68	3.25	1420.80	443.14	4035.60	2080.76	0	18 477.11	26 457.41
6	7.70	6.40	1.30	1.70	340.19	3.59	1095.20	709.20	0	11 070.37	13 218.55
7	5.20	6.00	1.37	1.15	169.20	0.17	455.38	162.96	0	6924.67	7712.38
8	4.30	5.55	1.36	1.76	103.15	0	520.86	275.16	1335.46	2465.20	4699.83
9	3.50	5.45	1.28	1.09	91.15	0	250.10	460.50	0	2383.59	3185.34
10	10.50	9.60	3.70	3.70	1970.12	18.53	5731.91	6270.83	10947.61	28 044.93	52 983.93
11	7.10	7.12	3.90	3.40	992.92	6.24	2408.75	1218.24	2587.04	13 453.82	20 667.01
12	6.80	7.60	2.11	2.42	964.20	1.70	2058.32	3890.02	0	10 162.68	17 076.92
13	13.40	10.60	3.12	2.31	877.20	0	3304.24	5750.50	0	48 293.67	58 225.61
14	4.50	6.80	1.15	1.30	92.79	0	728.50	0	0	4320.52	5141.81
15	15.30	9.00	−	−	2961.34	6.95	7229.40	10 244.50	0	52 864.14	73 306.33
16	17.50	10.20	−	−	2254.85	0.30	7079.98	14 922.96	21956.22	68 931.71	1 15 146.00
17	1.40	2.30	1.20	1.08	44.07	0	132.26	0	0	331.46	507.79
18	1.80	1.94	2.20	1.10	59.27	0	124.24	0	0	470.48	653.99
19	8.10	8.60	3.93	2.80	1114.30	49.00	3123.93	4811.68	0	19 071.87	28 170.78
20	11.40	9.60	3.75	4.45	2266.60	129.60	5521.08	8825.67	0	48 475.86	65 218.81
21	22.20	10.80	5.90	4.50	3587.26	878.77	10 067.82	30 569.92	0	1 45 935.20	1 91 039.00
22	9.40	9.60	2.92	3.20	1285.63	246.60	3804.70	5429.41	0	29 123.26	39 889.60
23	7.50	8.60	2.20	2.20	228.00	3.40	802.15	1858.49	0	15 700.73	18 592.77
24	3.10	3.70	1.42	0.52	64.20	0	382.52	0	0	1217.31	1664.03
25	2.10	3.60	0.93	0.94	81.20	1.00	233.53	0	0	911.56	1227.29
26	2.40	4.65	0.74	0.55	35.90	0	311.65	0	0	1033.86	1381.41
27	19.60	10.60	6.17	6.59	5875.43	4318.92	20 407.23	43 344.48	0	13 8905.10	212 851.20
28	5.80	6.70	1.60	1.40	254.57	0.50	1409.90	0	0	9021.82	10 686.79
29	2.80	4.60	1.05	1.25	48.80	0	147.90	0	0	1400.77	1597.47
30	1.10	2.30	0.70	0.55	9.10	0	92.70	0	0	178.30	280.10
31	5.00	5.50	1.28	1.10	139.60	3.50	608.90	693.16	0	4783.23	6228.39
32	3.80	5.15	1.80	1.40	146.70	6.00	695.30	424.60	0	2587.50	3860.10

Avicennia germinans, *Rhizophora* spp., and *Laguncularia racemosa*). The authors tested various forms of regression through the analysis of correlation coefficients and residuals distribution and found that the logarithmic model gave the best description of the relationships between biomass and diameter.

The use of logarithmic transformation is motivated by its capacity to simplify calculations (Zar, 1968; Payandeh, 1981; Sprugel, 1983; Brown et al. 1989). We start to adjust a straight line through the method of the least squares, when the original data led us to work with a nonlinear model. This transformation guarantees homogeneity to the variance for a whole interval of data. In fact, the originally linear models offer the advantage of having been developed as relationships based on original variables, without transformation. On the other hand, logarithmic transformation deforms these variables, potentially introducing bias in the estimate when we go back to the original unit (Beauchamp and Olson, 1973). Similarly, Baskerville (1972) states that one of the most common

problems associated with logarithmic transformation in the analysis of regressions to estimate biomass is the biased-estimate. According to him, the origin of the error is the transformation of the results obtained from a logarithmic unit into the original arithmetic unit. Another problem is that the logarithmic transformation does not reach the same results as the original nonlinear model does. In other words, although they are mathematically equivalent, statistically, they are not so equivalent (Zar, 1968; Payandeh, 1981). Even so, Zar (1968) considers the logarithmic transformation approach satisfactory.

To solve the biased-estimate controversy, Sprugel (1983) developed a correction factor. Similarly, several other authors discussed the problem of logarithmic transformation and the use of correction factors, among them Baskerville (1972, 1974), Munro (1974), Madgwick and Satoo (1975) and Whittaker and Marks (1975). While Sprugel (1983) says the non-use of this factor results in a small error of estimate, about 10% or less, Baskerville (1972) says the error is approximately 10–20%.

Table 6
Total and by-compartments dry weights of each sampled tree. *Rhizophora mangle*, Bertioga

Tree	DBH (cm)	Height (m)	Crown diameter (m)		Dry weights (g)									
			D1	D2	Leaves	Reproductive parts	Twigs	Branches	Trunks	Woody roots	Not woody roots	Emergent roots	Aerial roots	Total
1	3.20	4.30	2.00	1.47	270.00	0	699.52	0	1797.77	411.22	56.18	0	0	3234.69
2	1.80	2.00	–	–	18.39	0	85.85	0	310.43	0	9.21	0	0	423.88
3	8.40	10.10	1.70	1.75	1412.32	33.82	4066.65	2704.96	18 338.83	976.60	0	0	0	27 533.18
4	3.20	4.90	1.68	1.67	259.65	0	711.98	0	1793.00	288.59	23.71	1.26	0	3078.19
5	4.70	6.50	2.74	1.87	698.42	1.00	1153.35	870.79	4245.75	1156.04	24.42	12.67	0	8162.44
6	1.70	1.95	1.80	0.90	67.24	0	244.99	0	557.08	136.47	0	0	0	1005.78
7	2.30	2.20	0.95	0.77	10.88	0	96.70	0	576.68	136.47	0	0	0	820.73
8	4.60	4.40	2.95	1.46	143.06	0	784.39	0	5233.06	611.47	26.66	0	0	6798.64
9	7.80	8.50	2.74	2.90	994.87	56.10	2128.69	2980.43	14 921.75	6679.62	231.62	0	0	27 993.08
10	5.60	6.40	1.29	1.21	272.02	0	671.58	0	7488.04	1226.37	0	0	0	9658.01
11	5.50	7.70	2.00	1.59	551.63	6.72	1130.39	1197.48	7860.47	1022.80	297.34	0	0	12 066.83
12	9.30	10.50	3.05	3.70	2356.11	98.98	6762.19	6967.63	24 173.24	9567.53	376.46	0	0	50 302.14
13	3.80	5.40	1.15	1.80	450.43	3.74	998.26	0	3414.80	515.74	10.20	0.74	0	5393.91
14	2.20	2.22	1.15	0.91	28.85	0	176.55	91.93	359.80	0	16.29	0	0	673.42
15	2.20	2.25	1.70	1.30	79.14	0	330.88	0	541.01	78.51	1.65	0	0	1031.19
16	2.60	2.25	2.00	2.30	132.51	0	712.56	0	797.94	135.96	0	0	0	1778.97
17	2.30	1.80	1.90	1.55	152.11	0	461.93	0	371.79	11.46	69.77	0	0	1067.06
18	1.30	2.23	1.00	0.70	26.25	0	34.03	0	227.57	0	28.99	0	0	316.84
19	4.10	5.35	1.75	2.40	591.29	0	1510.86	0	3925.11	306.09	296.91	9.72	0	6639.98
20	5.20	5.90	1.98	2.60	745.46	0	1905.57	0	4804.80	974.45	365.78	0	0	8796.06
21	16.30	8.00	8.20	5.80	7799.95	1428.97	17 272.19	60 159.91	60 060.04	48 677.52	1332.57	0	1453.12	1 98 184.30
22	6.70	8.00	2.60	2.20	738.06	0	2769.81	51.80	13 778.73	1920.75	139.65	0	0	19 398.80
23	7.10	8.20	1.90	2.60	783.66	37.87	2322.30	853.12	15 488.78	3899.29	17.25	0	0	23 402.27
24	6.20	8.00	1.50	1.35	346.18	8.81	1259.22	0	11 131.63	3439.12	28.83	0	0	16 213.79
25	12.00	10.80	4.20	3.40	3664.42	233.40	10 213.48	11 340.84	49 062.71	17 793.78	816.79	0	0	93 125.42
26	10.50	9.00	3.70	4.60	1330.23	146.95	8324.34	5453.29	32 510.44	11 460.89	2104.62	0	0	61 330.76
27	13.10	10.60	4.53	4.76	5153.45	330.79	12 521.98	9816.77	59 582.55	23 741.86	1130.27	0	0	1 12 277.70
28	15.10	11.00	4.40	5.00	6566.91	379.10	13 449.14	32 155.99	81 010.18	32 583.86	2058.28	0	0	1 68 203.50
29	11.40	9.40	4.70	4.10	4858.83	790.34	9570.26	12 008.39	40 393.18	14 368.80	1808.46	47.45	0	83 845.71
30	14.60	11.20	5.00	6.10	7712.34	548.77	15 266.44	27 152.91	61 149.33	19 756.53	6604.39	0	0	1 38 190.70
31	17.00	11.40	–	–	8776.74	1753.32	24 456.02	60 288.42	85 484.02	51 247.37	3453.72	5.32	0	2 35 464.90
32	18.00	10.80	5.20	5.70	6590.12	1065.20	20 230.29	1 07 301.50	90 142.29	37 242.33	658.09	194.36	0	2 63 424.20
33	19.40	7.60	6.70	7.10	9120.75	4141.91	22 665.31	1 11 533.30	96 633.25	65 244.55	894.32	0	0	3 10 233.30

Table 7
Total and by-compartments dry weights of each sampled tree, *Rhizophora mangle*, Guaratiba

Tree	DBH (cm)	Height (m)	Crown diameter (m)		Dry weight (g)								
			D1	D2	Leaves	Reproductive parts	Twigs	Branches	Trunks	Woody roots	Not woody roots	Emergent roots	Total
1	3.30	6.00	1.83	1.85	185.93	0	463.53	0	3139.71	225.23	0	5.52	4019.92
2	2.70	4.46	1.13	1.24	161.79	0	372.29	0	1734.11	98.01	0	0	2366.20
3	2.90	4.80	1.20	1.37	86.11	0	303.49	0	2074.26	103.23	0	0	2567.09
4	3.50	5.20	−	−	240.68	0	809.19	0	2941.85	95.41	6.41	0.96	4094.50
5	1.80	2.50	0.90	1.00	28.51	0	113.74	0	592.06	77.82	4.55	0	816.68
6	1.60	1.96	0.75	1.14	66.41	0	193.47	0	323.72	71.42	21.81	0	676.83
7	1.50	1.90	0.60	1.05	38.89	0	115.46	0	186.56	0	4.97	0	345.88
8	2.70	3.88	2.10	1.40	99.99	0	251.86	0	1293.98	296.07	29.81	0	1971.71
9	4.60	5.60	2.00	1.80	666.93	0	1605.82	0	5153.41	2118.63	303.51	0	9848.30
10	6.00	6.70	2.11	2.93	859.48	1.56	2943.59	332.72	10 527.27	5793.82	228.42	0	20 686.86
11	5.10	6.00	2.07	2.40	533.71	0	1764.85	138.35	6242.65	2253.74	262.02	0	11 195.32
12	7.00	8.60	1.70	1.50	1189.79	3.20	2315.25	0	15 598.43	5226.92	526.06	0	24 859.65
13	6.40	7.10	2.28	2.17	986.62	1.19	2773.87	827.90	12 206.31	5578.58	214.93	0	22 589.40
14	4.20	5.10	1.40	1.56	430.88	4.75	1484.06	0	4718.92	1231.75	248.38	0	8118.74
15	8.00	9.20	2.55	2.35	1910.44	16.27	4859.30	561.31	21 482.56	10 301.28	2053.73	0	41 184.89
16	7.30	9.20	2.45	2.80	2106.75	62.68	5129.60	526.65	18 549.96	9216.51	345.01	0	35 937.16
17	5.40	5.90	3.00	2.30	592.29	0	1872.20	0	7914.09	3270.91	266.27	0	13 915.76
18	4.80	6.20	2.30	1.90	623.80	1.09	1996.70	0	6226.24	2858.93	136.17	0	11 842.93
19	5.80	7.10	1.50	2.10	735.68	179.92	1330.60	577.74	9897.35	1261.95	165.16	23.23	14 171.63
20	3.90	5.70	1.80	1.60	515.27	111.76	1005.20	0	4407.10	1150.99	116.14	40.80	7347.26
21	6.80	7.00	1.88	1.90	871.87	148.99	2991.10	0	16 583.12	1237.22	50.86	15.11	21 898.27
22	10.00	10.00	2.25	3.45	2558.50	971.14	4987.92	4925.41	42 119.45	11 126.34	205.89	57.71	66 952.36
23	9.50	8.00	2.75	2.55	2661.27	346.41	9240.22	1683.37	30 709.57	22 445.48	2252.01	597.87	69 936.20
24	11.50	11.00	4.55	4.95	3712.77	4186.27	11 459.74	8709.54	54273.86	21 474.57	533.91	297.18	1 04 647.80
25	15.20	13.10	4.00	3.85	6531.90	418.00	15 652.43	8564.38	1 04 320.50	36 405.17	1334.65	412.57	1 73 639.60
26	13.90	11.60	3.10	3.90	4068.80	70.50	10 394.33	8775.36	83 900.27	28 800.61	493.69	49.20	1 36 552.80
27	17.90	14.10	4.65	4.02	4521.16	178.98	18 451.40	61 102.86	1 12 987.60	36 470.83	913.29	56.40	2 34 682.60
28	22.00	15.10	5.20	5.25	6165.40	176.52	20 175.46	36 991.79	1 69 376.10	31 084.13	909.53	0	2 64 878.90
29	10.80	9.60	4.00	3.20	2175.42	21.03	6070.48	4180.56	39 425.30	6489.39	628.94	6.72	58 997.84
30	8.70	9.20	3.27	2.65	1225.00	3.30	5446.60	2672.85	26 743.05	4033.36	142.50	0	40 266.66
31	7.40	7.80	2.90	1.68	820.70	5.10	2948.60	929.69	17 450.40	2908.15	162.59	0	25 225.23
32	19.50	14.60	5.00	5.10	5265.94	110.94	15 923.90	34 713.46	1 50 205.00	72 506.13	985.83	0	2 79 711.20

Table 8

Final models for the estimation of total and by-compartments biomass (g) for *Laguncularia racemosa* in Bertioga and Guaratiba

Compartments		R^2a	SEEa	F
Bertioga				
Leaves	Biomass $= -87.75333 + 0.54642$ (DBH^2 × height) $+ 181.59020$(crown area)	0.818	735.844	99.595
Reproductive parts	Biomass $= -39.83038 + 28.38034$ (crown area)	0.451	177.799	37.153
Twigs	Biomass $= -474.58417 + 21.24002$ (DBH × height) $+ 337.13616$ (crown area)	0.895	1051.385	188.448
Branches	Biomass $= -497.11886 + 232.50267$ (DBH)^2 $- 298.50812$(height) $- 15.08719$ (DBH^2 × height)	0.801	3195.271	61.267
Main branches	(Biomass)$^{-1/3} = 0.08494 - 0.00303$ (DBH)	0.755	6461.185	22.612
Trunks	Biomass $= -590.18014 + 266.81851$ (DBH)^2	0.978	3894.605	2012.069
Total	Biomass $= -441.05021 + 464.47815$ (DBH)^2 $- 645.89716$ (height)	0.975	7032.947	874.551
Guaratiba				
Leaves	ln(biomass) $= 2.79278 + 1.11395$ ln (height) $+ 0.90691$ ln (crown area)	0.929	201.227	189.735
Reproductive parts	ln(biomass) $= -1.45023 + 1.53975$ (mean crown diameter)	0.734	115.771	53.480
Twigs	(Biomass)$^{1/3} = 3.22566 + 3.65288$ (mean crown diameter)	0.889	785.512	233.246
Branches	ln(biomass) $= 3.15091 + 1.70106$ ln (DBH) $+ 0.65406$ ln (crown area)	0.868	2250.217	63.259
Main branches	ln(biomass) $= 1.74443 + 1.18296$ ln (DBH) $+ 2.08874$ ln (height)	0.956	823.548	55.123
Trunks	ln(biomass) $= 4.15617 + 0.00377$ (DBH × height) $+ 1.26092$ ln (DBH × height)	0.987	6441.192	1183.582
Total	Biomass $= 1645.12584 + 40.09963$ (DBH^2 × height)	0.951	1.148E+04	600.368

This author defends the adoption of the correction factor because known errors can be minimized.

The great diversity of selected models with best estimators for each compartment, species and location give us the impression of confusion and lack of pattern. However, we should keep in mind that such models are best-found estimators and probably reflect subtleties in the relationship between the biomass and the considered variables. The subtleties express variations that have not been considered by other models, such as variability of environmental characteristics or characteristics which are typical of the species and sampled individuals in the two research locations. Most models that were selected as best estimators (Tables 8 and 9) are composed of multiple regressions, which demonstrates that the inclusion of variables can improve the estimate of

Table 9

Final models for the estimation of total and by-compartments biomass (g) for *Rhizophora mangle* in Bertioga and Guaratiba

Compartments		R^2a	SEEa	F
Bertioga				
Leaves	Biomass $= -161.37278 + 1.37202$ (DBH^2 × height) $+ 142.51237$ (crown area)	0.957	580.417	335.797
Reproductive parts	Biomass $= 73.09127 + 20.46809$(DBH)$^2 - 65.45230$ (height) $- 1.30051$ (DBH^2 × height)	0.884	257.191	82.618
Twigs	Biomass $= -112.82205 + 4.13105$ (DBH^2 × height) $+ 260.84352$ (crown area)	0.990	661.977	1493.026
Branches	Biomass $= -1372.12535 + 133714071.04$ (basal area)^2	0.963	5598.541	837.710
Trunks	Biomass $= -1586.62311 + 131.45408$ (DBH)$^2 + 421.67081$(height) $+ 14.50127$ (DBH^2 × height)	0.985	3804.836	679.707
Emergent roots	Biomass $= -2.12100 + 0.00001$(DBH^2 × height)^2	0.291	29.048	14.130
Woody roots	Biomass $= -434.21140 + 224.68206$ (DBH)$^2 - 123.30217$(DBH × height)	0.958	3543.494	369.322
Not woody roots	(Biomass)$^{-1/3} = 0.51821 - 0.04019$ (height)	0.496	947.947	27.613
Total	ln(biomass) $= 4.89219 + 2.61724$ ln (DBH)	0.991	4161.693	3462.828
Guaratiba				
Leaves	ln(biomass) $= 2.15738 - 0.00012$ (DBH^2 × height) $+ 0.83094$ ln (DBH^2 × height)	0.953	495.053	312.950
Reproductive parts	Biomass $= -414.60279 - 11.32908$ (DBH)$^2 + 274.80040$ (crown area)	0.616	470.717	25.096
Twigs	ln(biomass) $= 14.67539 - 25.88961$ (basal area) $+ 1.16464$ ln (basal area)	0.966	1223.648	439.748
Branches	Biomass $= 5116.04009 - 3338.23769$ (DBH) $+ 342.03486$ (DBH × height)	0.768	6477.952	52.428
Trunks	ln(biomass) $= 4.16291 - 0.00060$ (DBH^2 × height) $+ 0.93200$ ln (DBH^2 × height)	0.996	3904.646	3803.200
Emergent roots	Biomass $= -57.88544 + 5.33219$ (DBH)$^2 - 0.34468$ (DBH^2 × height)	0.224	117.482	5.463
Woody roots	ln(biomass) $= 17.96919 - 45.69003$ (basal area) $+ 1.68949$ ln (basal area)	0.891	7063.611	124.208
Not woody roots	Biomass $= -76.86273 + 19.92975$ (DBH)$^2 - 1.18598$ (DBH^2 × height)	0.351	453.648	9.390
Total	ln(biomass) $= 17.79752 - 20.74652$ (basal area) $+ 1.34908$ ln (basal area)	0.993	9839.505	2307.984

biomass. Following this line of reasoning, Wonnacott and Wonnacott (1980) confirm that the use of multiple regressions improve the estimate of a dependent variable, decreasing random error. Payandeh (1981) corroborates this idea, stating that the use of multiple linear models constitutes a good alternative to avoid logarithmic transformation. This is what we obtained with the data collected at Bertioga and Guaratiba. The procedure led us to obtain an expressive number of multiple linear models as best-found estimators. Ross et al. (2001), as in the present study, developed allometric equations for the estimation of total above-ground biomass of *Rhizophora mangle*, and *Laguncularia racemosa*, as well as, *Avicennia germinans*, using multiple regression models.

Several studies that have used regressions to investigate biomass adopt the DBH or the perimeter at breast height as the independent variable (Soares, 1997). For mangrove communities we can describe some studies that adopt these independent variables: Ong et al. (1980, 1984); Cintron and Schaeffer-Novelli (1985); Putz and Chan (1986); Silva (1988); Clough and Scott (1989); Imbert and Rollet (1989); Amarasinghe and Balasubramaniam (1992); Sukardjo and Yamada (1992); Slim and Gwada (1993); Gong and Ong (1995); Steinke et al. (1995); Tam et al. (1995); Fromard et al. (1998). However, some studies used equations based on height and DBH for the estimation of above-ground biomass of mangrove species (Suzuki and Tagawa, 1983; Cintron and Schaeffer-Novelli, 1985; Imbert and Rollet, 1989; Lee, 1990; Saintilan, 1997).

Mackey (1993) calculated the biomass of individuals using predictive regression of biomass on height or girth. In the same way, Sherman et al. (2003) found high significant allometric relationships between tree parabolic volume (which is based on height and DBH) and above-ground biomass components (total, leaf, trunk, branch and prop roots).

Ross et al. (2001) studying American mangroves, used both simple and multiple regression models for the estimation of above-ground biomass of *Avicennia germinans*, *Laguncularia racemosa* and *Rhizophora mangle*. They developed models for stem, branch, leaf, proproot and total biomass estimation, based on diameter at 30 cm above-ground, height and crown volume. Fromard et al. (1998) also estimated the biomass of *A. germinans*, *L. Racemosa* and *Rhizophora* spp. through the use of DBH as independent variable.

Komiyama et al. (2002) describe that the allometric relationship for stem weight is usually expressed as a function of stem diameter and height, such as dbh^{2}H, which differs between tree species, forcing the determination of a series of allometric equations for all tree species. After the authors the species segregation in the dbh^{2}H–weight relationship occurred because of the difference in the specific gravity of stem. In this way the authors took into consideration the specific gravity of

stem and established a common equation for the five mangrove species they studied. They analyzed species-specific allometric relationships based on the specific gravity of stem, with the aim of establishing a common equation for predicting the stem weight of mangroves.

After Cintron and Schaeffer-Novelli (1985) and Steinke et al. (1995) the inclusion of height do not improve the models for the estimation of mangrove above-ground biomass, as the relation between DBH and height is very variable.

Generally, in the case of *Laguncularia racemosa* in this study, the crown compartments (leaves, reproductive parts, twigs, branches) show variables that relate to the crown measurements (crown area or mean crown diameter) separately or jointly with other variables. By inference, we may say that these models involve two aspects: the first one deals with variables such as DBH and height. This component would then express the relationship between the biomass of the crown compartments and the plant development (structural variable).

On the other hand, the measurements of the crown might be the projection of environmental variables on the biomass, in other words, the reflex of environmental characteristics on branching and tree architecture. This effect may be explained by Kuuluvainen's reasoning (1991): the trunk biomass reflects the portion of organic matter allocated to the trunk during the life-time of the tree (structural variable), and the biomass of the crown compartments (branches and leaves, mainly), in a more direct way, reflects the current conditions of growth of a tree (environmental effect). In a similar way, Ross et al. (2001) describe that the inclusion of a term for crown volume improved diameter-based predictions (equations) of branch, leaf, and total biomass for *Avicennia germinans*, *Laguncularia racemosa*, and *Rhizophora mangle*. They attribute this to the wide range of crown shapes included in their sample, which ranged from dwarf trees 45 cm tall to fast-growing individuals nearly 7 m in height. Ross et al. (2001) chose a model based on trunk diameter (they used the diameter at 30 cm above ground, as they studied dwarf mangroves) and crown volume, which, as described by Kuuluvainen (1991) reflects both the biomass allocated to the trunk and the biomass associated to the crown. On the other hand, for the estimation of trunk biomass alone the selected model was based on diameter and height and for the estimation of prop-root biomass they used a model based on the diameter. Ross et al. (2001) also emphasize that while the models based on height and crown dimensions generally provided a better fit than models based on stem diameter alone, models based on the latter may provide useful biomass estimates for studies in which those variable were not measured.

Woodroffe (1985) highlights the importance of crown measurements as independent variables in the regressions. This is why he finds a highly significant correlation

between the mean crown diameter and the total above-ground biomass. Kuuluvainen (1991) also estimates the biomass of a species by using regressions based on the crown area. Likewise, Kittredge (1945) adopts models based on crown measurements when the studied community includes individuals with ramifications close to the soil, preventing thus the use of the diameter of the trunk as an independent variable. Catchpole and Wheeler (1992), for their turn, state that the use of measurements of trunk diameter is unreasonably difficult for forests where great ramification of the trunks occurs at soil level. According to these authors, crown diameter is the best measurement in these cases.

Tam et al. (1995) did not find significant regressions when they used models based on DBH and/or height to estimate the biomass of *Avicennia marina*. According to them, the architecture of the species in the studied location, irregular and with ramifications below breast height (often close to the substratum), was responsible for the insignificant results. This type of architecture is the same as we observed for *Avicennia schaueriana* in Bertioga and Guaratiba. In these cases, Tam et al. (1995) suggest the development of models based on crown measurements. However, Saintilan (1997) used the height to estimate the weight, through the use of a height/weight relationship, for smaller trees and shrubs of *A. marina* and *Aegiceras corniculatum*, which have numerous stems, often not reaching breast height. Fromard et al. (1998) describe that the most frequently used predictive variable for the estimation of mangrove above-ground biomass is the DBH, either alone or associated with the height and rarely, with the diameter of the crown. To generate regressions that would yield a good estimate for the biomass of the *Avicennia* species, we would have had to use elaborate models, combining independent variables and/or using a quite high sample size. Fromard et al. (1998) describe that the tip of *Avicennia germinans* often breaks off and apical growth is replaced by that of axillary branch, changing the diameter/height correlation. In this way they used the diameter as predictive variable, as it can be accurately measured. Similarly, Cintron and Schaeffer-Novelli (1985) highlight the variability in the diameter/height relationship for *A. germinans*. Because of variability in the individual forms of this species, it is difficult to estimate its biomass by means of regressions. Likewise, Clough and Attiwill (1975) describe a great ramification of trunks below 0.5 m above the surface of the sediment for *A. marina*, not to mention the great variability of leaf distribution. According to these authors, these facts hinder individual grouping in classes of DBH to elaborate allometric relationships. Christensen (1978), for his turn, describes the case of a *Rhizophora apiculata* forest that was cut down. Its re-growth originated trees with quite an irregular structure, which made it impossible to divide it into DBH classes.

Fromard et al. (1998) found for *Avicennia germinans* pioneer population and adult populations regression equation for total biomass estimation with R^2 values of 0.82 and 0.97, respectively. For *Laguncularia racemosa* they found a R^2 value of 0.97 and for *Rhizophora* spp. a R^2 value of 0.92. Putz and Chan (1986) found a R^2 of 0.98 for the regression model for the estimation of total above-ground biomass of *Rhizophora apiculata*. Clough and Scott (1989) found, for six mangrove species studied in Australia, a good fit (R^2 generally greater than 0.9) for all the compartments, except for leaves, which yielded more variable data. Because of the seasonal variation of the compartment, this result was already expected. Studies by Cintron and Schaeffer-Novelli (1985), Amarasinghe and Balasubramaniam (1992a, b), Sukardjo and Yamada (1992), and Tam et al. (1995) also reveal that the leaf compartment yields lower results than the others. Sukardjo and Yamada (1992) attribute these lower fittings to seasonal variability, wind action and, in the specific case of their study, to differences in crown architecture. Our data yielded similar results, that is, relatively low fittings for the leaf compartment. However, it is difficult to attribute such a fact to a seasonal variation, given other possible interference on biomass partition and tree architecture. Ross et al. (2001) studied the same species considered in this study, as well as *A. germinans*. These authors found R^2 greater than 0.9 for all compartments (total, stem, branch and leaf) except for prop-roots ($R^2 = 0,74$). For leaves they obtained R^2 greater than 0.95. Sherman et al. (2003) also found good fits (R^2 greater than 0.94) for all compartments (total, leaf, trunk, branch and prop-roots) of the studied species (*Rhizophora mangle*, *L. racemosa* and *A. germinans*). However for leaf of *R. mangle* the R^2 was 0.86. For *Avicennia marina* Mackey (1993) found R^2 values of 0.93 (trunk), 0.88 (stem), 0.99 (leaf), and 0.84 (leaf).

With regards to the main branches of *Laguncularia racemosa*, higher values of R^2a for Guaratiba have originated from a model with logarithmic transformation that did not take into consideration cases in which the compartment biomass was zero. Consequently, the variability of the sampled population was reduced and hid the biomass variability of that compartment by biotic characteristics (growth form, architecture and density) and abiotic characteristics (light availability, for example). Imbert and Rollet (1989) also observed such a behavior for *Rhizophora mangle*, *Laguncularia racemosa*, and *Avicennia germinans* branches, where values of R^2 were below 0.90 for the three species, in regressions of the type "log (Biomass) $= a + b$ log (DBH)" and "log (Biomass) $= a + b$ log (DBH$^2 \times$ height)". These values were always lower than those obtained for other compartments. Newbould (1967) also gives an account of a larger variability (error) in the estimate of branch production.

Table 10
Alternative models (not based on variables related to the crown), for the estimation of the biomass (g) of crown compartments

Species / local / compartment	Model	R^2a	SEEa	F
Laguncularia racemosa				
Bertioga				
Leaves	$(Biomass)^{1/3} = 2.0769 + 0.85346 \, (DBH)$	0.865	998.586	289.480
Reproductive parts	$(Biomass)^{1/3} = 0.44646 + 22.43945 \, (basal \ area \times height)$	0.388	218.388	29.541
Twigs	$\ln (biomass) = 1.97689 + 0.8619 \ln (DBH^2 + height + DBH^2 \times height)$	0.937	1473.151	666.714
Guaratiba				
Leaves	$\ln(biomass) = 2.77575 + 2.36706 \ln (DBH) - 0.62266 \ln (height)$	0.888	661.752	123.620
Reproductive parts	$(Biomass)^{1/3} = 0.83016 + 24.16175 \, (basal \ area \times height)$	0.462	687.628	27.610
Twigs	$\ln(biomass) = 3.87569 + 1.81169 \ln (DBH)$	0.909	2085.927	309.580
Branches	$(Biomass)^{1/3} = -2.29285 + 1.71256 \, (DBH)$	0.878	4082.067	223.295
Rhizophora mangle				
Bertioga				
Leaves	$(Biomass)^{1/3} = 2.12257 + 1.06499 \, (DBH)$	0.943	971.194	525.607
Twigs	$\ln (Biomass) = 3.67671 + 2.18622 \ln (DBH)$	0.938	1389.617	482.491
Guaratiba				
Reproductive parts	$(Biomass)^{1/3} = -2.00246 + 0.65284 \, (height)$	0.373	765.509	19.410

Reproductive parts yielded weak fittings, perhaps because the biomass of this compartment does not only depend on the development of the tree. That is, the biomass of reproductive parts does not adjust well to measurements related to structural development, such as DBH, height and measurements of the crown. This fact may be explained by the variable production and development of these components throughout the year.

Non-woody prop roots and emergent prop roots yielded weak fittings too. According to Soares (1997), their case may be explained by the dependence of their production on specific environmental factors. That is, the production of roots (which here may have reflected on the biomass of emergent and non-woody roots) does not only depend on the structural development of the forest, but also on environmental factors which are site specific; for example microtopography, salinity, flood frequency by the tides, nature of the substratum, stress, among others. The development of these roots (woody prop roots) may also have been affected by these factors. However, there may have been a larger influence of forest structural variables. That is, in addition to external factors (abiotics), part of the variability in the biomass could be explained by the development of the tree, if we take into consideration how the plant needs mechanical support. Fittings of biomass curves for the woody prop roots may confirm this conclusion, if we compare them with fittings from emergent and non-woody prop roots. Woody prop roots yielded better fittings (higher values of R^2a) because of their higher relationship with structural characteristics. However, because of the influence of external factors such as the ones already mentioned, these values are not so high. The same result has been found by Day et al. (1987), in their study of prop roots of *Rhizophora mangle*, in Mexico, by Ross et al. (2001), for *R. mangle* in Florida,

and by Amarasinghe and Balasubramaniam (1992a), in their study of prop roots of *Rhizophora mucronata*, in Sri Lanka. In these studies the fittings were not good. Silva et al. (1993) did not find a good correlation between prop roots biomass with DBH and tree height. On the other hand Sherman et al. (2003) found a good fit ($R^2 = 0.97$) for a model based on the parabolic volume for the estimation of *R. mangle* prop roots biomass.

If we consider the weak fittings of regressions that estimated the biomass of emergent and non-woody prop roots and those of reproductive parts, an alternative to the estimate of a more variable compartment biomass would be to group these compartments with others, forming units with a less variable biomass and a more accurate estimate, as for example total roots and green parts. Table 10 illustrates this idea, introducing some alternative models to estimate the biomass of crown compartments. Such models are the best estimators for these compartments and are not based on crown-related variables.

To estimate the above-ground biomass of *Rhizophora mangle* and *Laguncularia racemosa*, in the two study locations, we recommend the use of the models presented in Tables 8, 9, and 10. In the case of common regressions, to estimate both the biomass of the same and different species in both locations, further studies are necessary to generate regressions with wider application, thus minimizing the estimate error. With regard to the most variable compartments (reproductive parts, emergent prop roots, and non-woody prop roots), the grouping of the regressions of these compartments into total roots and green parts still needs to be tested.

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