Aquatic Botany 120 (2014) 346–351

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Variability of carbon content in mangrove species: Effect of species, compartments and tidal frequency

Daniela Pelluso Rodrigues[a], Cláudia Hamacher[b], Gustavo Calderucio Duque Estrada[a], Mário Luiz Gomes Soares[a,*]

[a] Universidade do Estado do Rio de Janeiro, Faculdade de Oceanografia, Núcleo de Estudos em Manguezais, Rua São Francisco Xavier, 524, sala 4023-E, Maracanã, 20550-013 Rio de Janeiro, RJ, Brazil
[b] Universidade do Estado do Rio de Janeiro, Faculdade de Oceanografia, Laboratório de Geoquímica Orgânica Marinha, Rua São Francisco Xavier, 524, sala 4026-E, Maracanã, 20550-013 Rio de Janeiro, RJ, Brazil

ARTICLE INFO

Article history:
Received 9 August 2013
Received in revised form 11 October 2014
Accepted 14 October 2014
Available online 24 October 2014

Keywords:
Mangrove
Physiographic type
Gradient
Plant compartment

ABSTRACT

As mangroves become recognized as important carbon storages, the need for quantifying and reducing the uncertainty of carbon inventories, such as those arising from specific carbon contents, becomes increasingly emphasized. In this sense, the present study tests the influence of plant parts, species (*Avicennia schaueriana*, *Rhizophora mangle*, *Laguncularia racemosa*) and tidal flooding frequency (physiographic types) on the carbon content ($n = 510$) of mangroves from Southeast-Brazil, using factorial ANOVA and Tukey post-hoc tests. Based on these tests, the impact of the using generic instead of specific carbon contents on the accuracy of carbon stock inventories was assessed. The results show that plant parts and species control, to a certain extent, the carbon content variability. However, we did not detect a clear pattern of influence of the physiographic types on the carbon content. The tests also indicated that woody parts (trunk, branches and prop roots), green parts (leaves and reproductive parts) and roots formed highly distinct groups. Based on the results of the third order interaction test, we propose the following specific carbon contents: woody parts for all species = 44.1 ± 1.4%; green parts of *A. schaueriana* and *L. racemosa* = 42.6 ± 1.4% and of *R. mangle* = 44.9 ± 4.5%; roots of *A. schaueriana* and *L. racemosa* = 42.6 ± 2.2% and of *R. mangle* = 40.0 ± 2.1%. It was estimated that the deviation resulting from the use of generic instead of specific carbon contents to convert biomass into carbon stock may reach undesirable levels: up to 13.6% for aboveground biomass and up to 25% for root biomass.

1. Introduction

Mangroves are globally recognized for their ecological and socio-economic importance (Ewel et al., 1998; Mazda et al., 2006; Nagelkerken et al., 2008). In the last decade, several studies have highlighted the role of mangroves for carbon storage (e.g. Bouillon et al., 2008; Donato et al., 2011; McLeod et al., 2011), showing that considerably more carbon is sequestered than in terrestrial forests, especially in the soil and in the belowground biomass.

The major sources of uncertainty of carbon stock inventories in mangroves are species-specific differences in carbon content and the variability caused by forest age, species composition, intertidal location, soil fertility and community structure (IPCC, 2014). Several authors have shown that the carbon content in mangroves varies according to species and compartment (Alongi et al., 2003; Khan et al., 2007; Ren et al., 2010; Ray et al., 2011). However the effect of ecological factors, such as those caused by different tidal flooding frequencies, on the carbon contents remains as an important gap.

Despite the importance that the carbon content may have on the degree of uncertainty of carbon inventories in mangroves, the difficulty and cost of obtaining specific carbon contents lead several authors to use generic carbon contents, which are based on averages from global data compilations (e.g. Twilley et al., 1992—45%; IPCC, 2006—47%; Bouillon et al., 2008—44%). However, the assessment of the impact caused by the use of generic instead of specific carbon contents on the uncertainty of carbon stock inventories, such as in Martin and Thomas (2011) for terrestrial tropical forests, has not yet been performed for mangroves.

In this sense, the present study tests the influence of compartments (leaves, reproductive parts, branches, trunks, roots, and prop roots), species (*Avicennia schaueriana*, *Rhizophora mangle*,

---

[*] Corresponding author. Tel.: +55 21 2234 0765; fax: +55 21 2234 0591.
E-mail addresses: dani.pelluso@gmail.com (D.P. Rodrigues), claudia.hamacher@gmail.com (C. Hamacher), gustavo.estrada@uerj.br (G.C.D. Estrada), mariolgs@uerj.br (M.L.G. Soares).

http://dx.doi.org/10.1016/j.aquabot.2014.10.004

Laguncularia racemosa), tidal flooding frequency (physiographic types: fringe, basin, and transition with salt flats) and the interactions of these factors on the carbon content of mangrove forests. Based on the results of these tests, the impact of using generic instead of specific carbon contents on the accuracy of carbon stock inventories is assessed.

2. Material and methods

2.1. Study area

The study area is located in Guaratiba region, in the eastern portion of Sepetiba Bay, Rio de Janeiro, Brazil, and is part of the Guaratiba Biological Reserve (Fig. 1). The average annual temperature in Guaratiba is 23.5 °C, and the average annual precipitation is 1067 mm. Rainfall is higher in summer, and lower in winter (Estrada et al., 2013). The region is under a microtidal regime with an amplitude of less than 2 m. The inner parts of the intertidal zones are reached only by the high spring tides, resulting in salt flats. Almeida (Unpublished results) estimated a total area of 43 km^2 of mangroves in Guaratiba, with 33.6 km^2 of forests, and 9.3 km^2 of salt flats. Three typical mangrove species occur in the study area: *A. schaueriana* Stapf & Leechm. ex Moldenke, *L. racemosa* (L.) C.F. Gaertn., and *R. mangle* L. Because of the existence of an extensive coastal plain, the structure of the mangrove forests in Guaratiba varies according to the frequency of tidal flooding and to the relative position of the sources of continental drainage (river and groundwater). These factors enable the identification of three physiographic types: fringe (high frequency of tidal flooding); basin (intermediate-to-low frequency); and transition with salt flats, where the trees assume a shrub architecture due to the conditions imposed by the low frequency of tidal flooding (Estrada et al., 2013). According to these authors, such forests are characterized by a gradient of reduction of the structural development from the fringe to the transition forests (Table 1). In the same direction, interstitial water salinity increases (Table 1) as a response to a gradually lower tidal flooding frequency. Among the species found in this region, *R. mangle* and *A. schaueriana* alternate as dominants, or co-dominants, in the fringe, basin, and transition forests, depending on the prevailing environmental conditions and the successional stage of the forest.

2.2. Methods

Samples from the following compartments of the three species were collected: trunks, branches, roots, prop roots (spongy and woody, as defined by Soares and Schaeffer-Novelli, 2005), leaves, and reproductive parts. For each compartment, 10 samples were collected from distinct, randomly chosen individuals, for each of the three species, and in each physiographic type (fringe, basin, and transition forest). Therefore, samples were collected from 90 individuals, for a total of 510 samples. The sampling procedure consisted of extracting at least the sufficient mass to allow the carbon quantification in an elemental analyzer. However, to increase the precision of the analysis, the collected material was at least ten times higher than the sufficient mass. This material was then mixed to make a compounded sample.

In general, the method of carbon quantification followed Hedges and Stern (1984) with minor adaptations. After sampling, the plant material was dried in an oven at temperatures lower than 70 °C. Subsequently, the samples were ground in a crusher. Approximately 2 mg of this dried material was taken to a Carlo Erba EA 1110 elemental analyzer. Carbon quantification was performed through a cystine calibration curve. For each batch of 10 samples, the accuracy of carbon measurements was checked with a PACS-2 (NRCC) standard marine sediment.

The results obtained for the organic carbon content in the different compartments, species, and physiographic types were tested using a factorial analysis of variance (ANOVA) and the Tukey post-hoc test (both in the Statistica 6.0 StatSoft), to identify differences

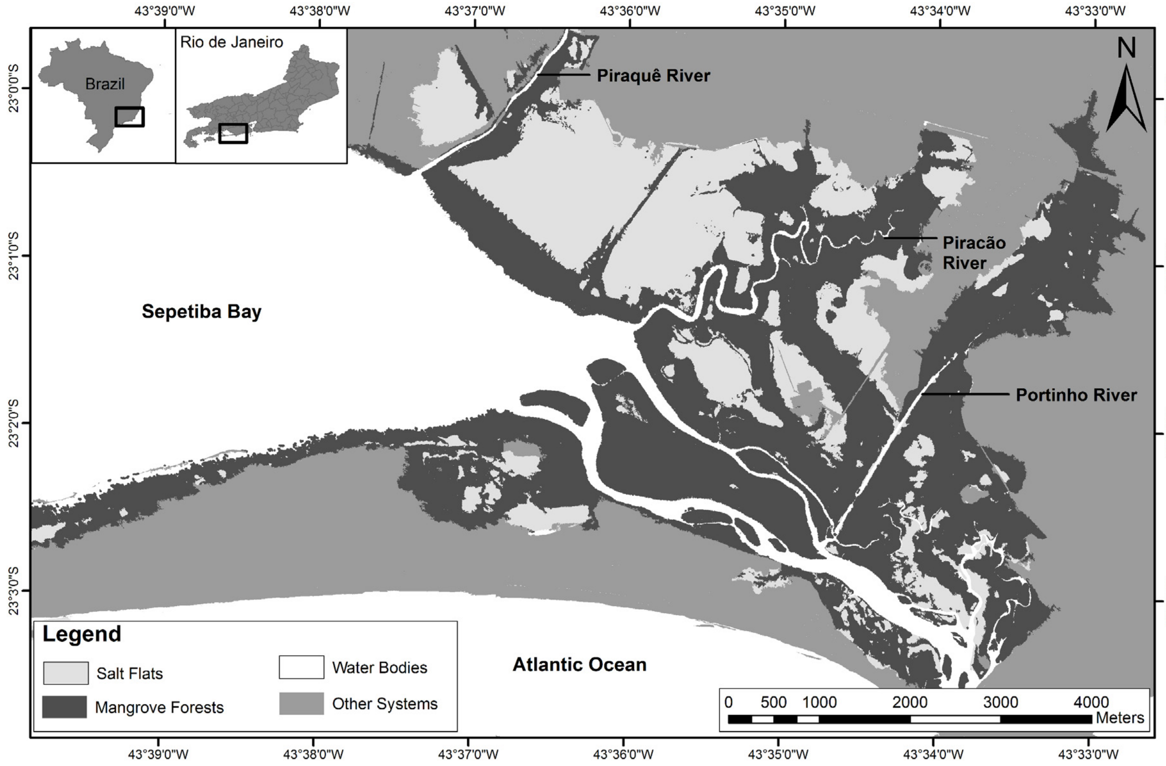

Fig. 1. Map showing the study area in Guaratiba region (Rio de Janeiro, Brazil).

Table 1
Mean (±standard deviation) structural parameters and mean interstitial water salinity of the mangrove forests of Guaratiba (Rio de Janeiro, Brazil) per physiographic type. Data from Estrada et al. (2013).

Physiographic Type	Density[a]	Mean dbh[b]	Mean height[c]	Mean salinity
Fringe	5895 ± 9399	10.1 ± 3.8	7.4 ± 2.3	35.3 ± 7.3
Basin	10,260 ± 8554	5.8 ± 2.0	5.0 ± 1.8	40.9 ± 7.5
Transition	19,001 ± 14,426	3.0 ± 1.6	2.0 ± 1.2	42.2 ± 10.1

[a] Trunks ha^{-1}.
[b] cm.
[c] m.

between each treatment ($p < 0.05$). The same statistical tests mentioned above were conducted for the prop roots. In this case, only the comparison between the organic carbon content from prop roots, branches and trunks of *R. mangle* was made. This procedure was adopted to ensure an equal sample number for all treatments (Zar, 1996).

3. Results

Carbon content was found to vary between 34.1% and 47.3%, with an overall mean of 43.4 ± 2.0%. The factorial ANOVA test revealed the existence of significant differences for all factors and interactions (Table 2). Due to the complexity of the results of the Tukey post-tests, we chose to first examine the interaction between species and compartment (Table 3) and then examine the interaction between the three factors in each group separately (Tables SM1–SM3).

The results of the Tukey test for the interaction between species and compartments (Table 3) indicate, with minor exceptions, the formation of three groups of similarity: (1) leaves and reproductive parts (green parts); (2) branches and trunks (woody parts); and (3) roots. The exceptions are the significantly lower carbon content in the roots of *R. mangle* and the significantly higher carbon contents in the leaves and reproductive parts of the same species in comparison with *A. schaueriana* and *L. racemosa* (Table 3). Therefore, we decided to analyze the third order interactions (between species, compartments and physiographic types) separately per each group: woody parts, green parts and roots.

Table 2
Results of the factorial ANOVA test comparing carbon contents (%C) for each factor and interactions between factors. %SS = percentual sum of squares; df = degrees of freedom.

Factors	%SS	df	*F*	*p*
Species (SP)	2.6	2	9.0	<0.01
Physiographic type (PT)	6.6	2	23.3	<0.01
Compartment (COMP)	37.7	4	66.1	<0.01
SP × PT	4.9	4	8.6	<0.01
SP × COMP	33.1	8	29.0	<0.01
PT × COMP	7.0	8	6.1	<0.01
SP × PT × COMP	8.2	16	3.6	<0.01

Table 3
Mean values of carbon content (%) for each combination of plant compartment and species. Letters represent similarities among results ($\alpha = 0.05$).

Species	Compartments	Carbon content (%)
A. schaueriana	Roots	43.0 ± 2.1^{b,c}
	Leaves	42.0 ± 2.0^{b}
	Reproductive parts	42.7 ± 1.0^{b}
	Branches	44.5 ± 1.1^{d,e}
	Trunks	45.1 ± 0.9^{d,e}
L. racemosa	Roots	42.1 ± 2.2^{b}
	Leaves	42.7 ± 0.8^{b}
	Reproductive parts	43.0 ± 1.1^{b,c}
	Branches	43.1 ± 0.9^{b,c}
	Trunks	44.4 ± 1.1^{d,e}
R. mangle	Roots	40.0 ± 2.1^{a}
	Leaves	45.1 ± 1.8^{e}
	Reproductive parts	44.7 ± 1.2^{d,e}
	Branches	44.0 ± 1.5^{c,d}
	Trunks	44.6 ± 1.1^{d,e}

3.1. Woody parts

There were no significant differences between the carbon contents determined in trunks and branches, considering the interactions between physiographic types and species (Table SM1). Spongy and woody roots also showed no significant difference from trunks and branches of *R. mangle*, except for spongy prop roots in the transition forests (Table SM1). Based on these results, we suggest the adoption of a single carbon content for the conversion of the biomass of woody parts into carbon stock: 44.1 ± 1.4% (Table 4), calculated from the overall mean of carbon content in trunks, branches, and prop roots of the three species in the different physiographic types.

3.2. Roots

There was no clear pattern of carbon content variation in roots in relation to physiographic types (Table SM2). The carbon content in roots basically showed an overall pattern of significantly higher values in *A. schaueriana* and *L. racemosa* in comparison to *R. mangle* (Table SM2). The only clear exception to this pattern was the carbon content of *A. schaueriana* roots from basin forests, which was significantly higher than all other combinations. Based on this general pattern, it is suggested the use of a single carbon content for both *A. schaueriana* and *L. racemosa* (42.6 ± 2.6%) and another one for *R. mangle* (40.0 ± 2.1%).

3.3. Green parts

The results indicated no effect of physiographic types and compartments on the carbon content of green parts, except for *A. schaueriana* leaves from transition forests, which were significantly lower than all other combinations of species, physiographic type and compartment (Table SM3). However, the results indicate a clear pattern of significantly higher values in *A. schaueriana* and *L. racemosa* in comparison to *R. mangle* (Table SM3). Therefore, we suggest that the conversion of green parts biomass into carbon stock follow the same procedure described for roots: a single carbon content for *A. schaueriana* and *L. racemosa* (42.6 ± 1.4%) and a different one for *R. mangle* (44.9 ± 4.5%).

Table 4
Suggested carbon (C) contents to be used in the conversion of biomass into carbon stock of the studied species.

Compartment	Species	C content (%)
Woody parts	All species	44.1 ± 1.4
Roots	*A. schaueriana* and *L. racemosa*	42.6 ± 2.6
Roots	*R. mangle*	40.0 ± 2.1
Green parts	*A. schaueriana* and *L. racemosa*	42.6 ± 1.4
Green parts	*R. mangle*	44.9 ± 4.5

Table 5
Biomass allocation in woody and green parts of *A. schaueriana*, *L. racemosa* and *R. mangle* in the mangroves of Guaratiba and the resulting balanced AGB (aboveground biomass) C content calculated from Eq. (1).

Species (*n*)[b]	DBH range (cm)	Biomass allocation[a] (mean ± SD)		Balanced AGB
		Woody parts (%)	Green parts (%)	C content (%)
A. schaueriana (50)	1.2–37.3	93.9 ± 2.1	6.1 ± 2.1	44.0
L. racemosa (32)	1.1–22.2	96.3 ± 1.9	3.7 ± 1.9	44.0
R. mangle (32)	1.5–22.0	95.0 ± 5.0	5.0 ± 2.1	44.1

[a] Calculated from the data presented in Soares and Schaeffer-Novelli (2005) and Estrada et al. (2014).
[b] Number of trees used to calculate de mean allocation.

Table 6
Deviations (%) resulting from the use of generic instead of specific carbon contents to convert aboveground biomass (AGB) of a tree and forest belowground biomass (BGB) into carbon stock.

Specific carbon contents	Deviation from the specific carbon contents (%)				
	Bouillon et al. (2008) (44%)	Twilley et al. (1992) (45%)	IPCC (2014) (45.1%)	IPCC (2006) (47%)	IPCC (2003) (50%)
AGB					
Trees of *A. schaueriana* and *L. racemosa* (44.0%)	0.0	2.3	2.5	6.8	13.6
Trees of *R. mangle* (44.1%)	−0.2	2.0	2.3	6.6	13.4
BGB					
Monoespecific or mixed forests with *A. schaueriana* and/or *L. racemosa* (42.6%)	3.3	5.6	5.9	10.3	17.4
Monoespecific forests of *R. mangle* (40.0%)	10.0	12.5	12.8	17.5	25.0

4. Discussion

The carbon contents obtained in the present study (Table 4) are within the range found in the literature for other mangrove species: 42–49% in woody parts; 38–47% in green parts; and 34–45% in roots (Alongi et al., 2003; Khan et al., 2007; Ren et al., 2010; Kauffman et al., 2011; Ray et al., 2011).

The pattern of lower carbon contents in roots in comparison with woody parts was also observed for other mangrove species (Alongi et al., 2003; Khan et al., 2007; Ren et al., 2010). However, the lack of information on carbon contents of tropical tree roots (Martin and Thomas, 2011) prevents the understanding of whether or not this is a typical pattern and which factors would explain it. The results also revealed differences among species in regard to the carbon contents in roots and green parts (Table 4). In the case of roots, the difference between *R. mangle* and *A. schaueriana* follows the pattern observed by Alongi et al. (2003) for Indo-Pacific species of the same genus (*Rhizophora stylosa* and *Avicennia marina*). However, the phytochemical characteristics that explain this difference are yet to be understood. In the case of green parts, the higher carbon contents in *Avicennia* and *Laguncularia* in comparison with *Rhizophora* may be explained by their differences in terms of structural compounds, since the species of the latter genus present higher concentration of tannins and lignins (Smith, 1987; Mckee, 1995).

4.1. Practical use of the proposed carbon contents

As the results indicated the use of different carbon contents for woody and green parts and, for the latter compartment, the use of different levels for *R. mangle*, it is necessary to assess how they can be used together to transform the total aboveground biomass (woody + green parts) of a tree into carbon stock. When specific models to estimate the aboveground biomass of each species and compartment are available, the biomass of a tree can be estimated individually for green and woody parts and subsequently converted to carbon stock through the specific carbon content. However, most existing studies present only models for total aboveground biomass (Chave et al., 2005; Komiyama et al., 2008). In this case, a weighted average between the two specific carbon contents can be made, considering the relative allocation of biomass of each species in woody and green parts, as follows:

$$\text{Balanced AGB [C]} = \frac{[(\text{Wood [C]} \times \text{Wood\%}) + (\text{Green [C]} \times \text{Green\%})]}{100}, \tag{1}$$

where AGB [C] = carbon content in the aboveground biomass of a tree, Wood [C] = carbon content of woody parts, Wood% = percentage of biomass allocation on woody parts, Green [C] = carbon content of green parts, Green% = percentage of biomass allocation on green parts.

Using Eq. (1), balanced carbon contents were obtained for Guaratiba (Table 5). As the biomass allocation in woody parts is greater than 90% in Guaratiba, the balanced carbon contents obtained are very close (*A. schaueriana* and *L. racemosa*) or equal (*R. mangle*) to the specific carbon content of woody parts (44.1%). Considering that the biomass allocation in Guaratiba is similar to that observed for the same species in other mangroves of the Americas (Lugo and Snedaker, 1974; Fromard et al., 1998; Coronado-Molina et al., 2004; Medeiros and Sampaio, 2008) it is possible to suggest that balanced carbon contents found in this study can be widely used. However, forests dominated by young individuals (e.g. in regenerating forests) may have lower biomass allocation in woody parts (e.g. Ross et al., 2001). In such cases, specific balanced carbon contents should be obtained.

In the case of root biomass, the estimation of root biomass is made for the forest as a whole and not by individual (see Komiyama et al., 2008). Therefore, in mixed forests composed by the three species, none of the specific carbon contents (Table 4) can be used. A simple way of solving this problem would be to use the average carbon content among the three species (41.7 ± 2.5%). However, this approach could generate undesirable deviations in forests with high dominance of one of the species. In this sense, we propose that the conversion of root biomass to carbon stock in mixed forests that include *R. mangle* is made from a balanced carbon content based on the weighted average of the specific carbon contents, considering the relative dominance on basal area of each species, as follows:

$$\text{Balanced BGB [C]} = \frac{[(\text{Sp1 BGB [C]} \times \text{Sp1 Dominance\%}) + (\text{Sp2 BGB [C]} \times \text{Sp2 Dominance\%}) + (\text{Sp3 BGB [C]} \times \text{Sp3 Dominance\%})]}{100}, \tag{2}$$

Table 7
Deviations (in tC ha^{-1}) resulting from the use of generic instead of specific carbon contents to convert the aboveground biomass (AGB) of eight plots into carbon stock. The plots are located in the mangroves of Guaratiba and their data were originally presented in Estrada et al. (2014).

Plot	C stock in AGB (tC ha^{-1})[a]	Deviation from C stocks obtained from specific C contents (tC ha^{-1})				
		Bouillon et al. (2008) (44%)	Twilley et al. (1992) (45%)	IPCC (2014) (45.1%)	IPCC (2006) (47%)	IPCC (2003) (50%)
1	99.0	−0.1	2.2	2.4	6.7	13.4
2	119.8	−0.1	2.7	2.9	8.1	16.3
3	100.4	−0.2	2.1	2.3	6.6	13.5
4	92.7	−0.2	1.9	2.1	6.1	12.4
5	121.0	−0.2	2.6	2.8	8.0	16.3
6	84.8	−0.1	1.8	2.0	5.7	11.5
7	120.6	−0.1	2.7	2.9	8.1	16.3
8	76.3	0.0	1.7	1.9	5.2	10.4
Mean ± SD	101.9 ± 17.2	−0.1 ± 0.1	2.2 ± 0.4	2.4 ± 0.4	6.8 ± 1.2	13.8 ± 2.3

[a] Calculated from the balanced carbon contents presented in Table 7.

where BGB [C] = carbon content in the belowground biomass, Sp BGB [C] = specific carbon content in BGB, Sp Dominance% = relative dominance of basal area (%).

4.2. *Impact of the use of generic against specific carbon contents*

In regard to aboveground biomass, the generic carbon contents developed for mangrove species (Twilley et al., 1992; Bouillon et al., 2008; IPCC, 2014), presented lower deviations in relation to the specific carbon contents than the other ones (Table 6). It is noteworthy that the carbon content proposed by Bouillon et al. (2008) does not generate significant deviations, and can be a safe alternative for the conversion of biomass into carbon. However, considering that the uncertainty of a carbon stock inventory is a result of various aspects (e.g. sample size, plot size, precision and accuracy of allometric models) including carbon content, even the lower deviations from the carbon contents proposed by Twilley et al. (1992) and IPCC (2014) should not be disregarded. The carbon contents proposed by the IPCC as default (50%—IPCC, 2003) and for tropical/subtropical forests (47%—IPCC, 2006) cause even greater deviations, that reach up to 13.6%. In terms of absolute deviations, the use of generic carbon contents (excluding Bouillon et al., 2008) would cause an increase of 2.2 ± 0.4 to 13.8 ± 2.3 tC ha^{-1} in the carbon stock of the mangroves of Guaratiba, where the mean stock in the aboveground biomass is 101.9 ± 17.2 tC ha^{-1} (Table 7).

In the case of root biomass, even the generic carbon contents for mangrove species cause high deviations (Table 6), especially in monoespecific forests of *R. mangle* (10.0 to 12.8%). The other generic carbon contents cause deviations that reach up to 25% for *R. mangle*. This impact is further amplified by the fact that mangrove forests have, in general, a higher ratio of BGB:AGB than terrestrial forests (Komiyama et al., 2008; Donato et al., 2011; IPCC, 2014).

5. Conclusion

In the present study, carbon content in the biomass of mangrove trees was shown to be controlled by species and compartment, but not by tidal frequency (physiographic types). While carbon content in woody parts was similar among the three species, *R. mangle* differed from both *A. schaueriana* and *L. racemosa* for green parts and roots. Therefore, five specific carbon contents were proposed. For the cases when only allometric models for total aboveground biomass are available and no specific carbon content can be applied, we developed the 'balanced carbon content method', based the species-specific biomass allocations of woody and green parts. A similar method was developed for the conversion of roots biomass into carbon stock in mixed forests, in which a balanced carbon content is calculated from the relative dominance of basal area of each species. The present study has also demonstrated that the deviation resulting from the use of generic instead of specific carbon contents to convert biomass into carbon stock may reach undesirable levels: up to 13.6% for aboveground biomass and up to 25% for root biomass.

Acknowledgements

We thank two anonymous reviewers and the editor for their careful reading and thoughtful comments on the manuscript. We also thank FAPERJ (Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro) for the scholarship granted for the first author (Grant no. E-26/100.938/2011) and fundação SOS Mata Atântica for providing financial support. This study was authorized by the administration of the Guaratiba Biological Reserve (Instituto Estadual do Ambiente—INEA).

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.aquabot.2014.10.004.

References

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

Bouillon, S., Borges, A.V., Moya, E.C., Diele, K., Dittmar, T., Duke, N.C., Kristensen, E., Lee, S.Y., Marchand, C., Middelburg, J.J., Rivera-Monroy, V.H., Smith III, T.J., Twilley, R.R., 2008. Mangrove production and carbon sinks: a revision of global budget estimates. Aquat. Bot. 89, 128–137.

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

Coronado-Molina, C., Day Jr., J.W., Reyes, E., Perez, B.C., 2004. Standing crop and aboveground biomass partitioning of a dwarf mangrove forest in Taylor River Slough, Florida. Wetlands Ecol. Manage. 12, 157–164.

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

Estrada, G.C.D., Soares, M.L.G., Chaves, F.O., Cavalcanti, V.F., 2013. Analysis of the structural variability of mangrove forests through the physiographic types approach. Aquat. Bot. 111, 135–143.

Estrada, G.C.D., Soares, M.L.G., Santos, D.M.C., Fernandez, V., Almeida, P.M.M., Estevam, M.R.M., Machado, M.R.O., 2014. Allometric models for aboveground biomass estimation of the mangrove *Avicennia schaueriana*. Hydrobiology 734, 171–185.

Ewel, K.C., Zheng, S., Pinzón, Z.S., Bourgeois, J.A., 1998. Environmental effects of canopy gap formation in high-rainfall mangrove forests. Biotropica 34, 510–518.

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

Hedges, J.I., Stern, J.H., 1984. Carbon and nitrogen determinations in carbonate-containing solids. Limnol. Oceanogr. 29, 20–34.

IPCC, 2003. Good Practice Guidance for Land Use, Land-Use Change and Forestry. Intergovernmental Panel on Climate Change (IPCC), Hayama.

IPCC, 2006. Forest lands. In: Guidelines for National Greenhouse Gas Inventories. Intergovernmental Panel on Climate Change (IPCC), Hayama.

IPCC, 2014. 2013 Supplement to the 2006 IPCC Guidelines for National Greenhouse Gas Inventories. Intergovernmental Panel on Climate Change (IPCC), Switzerland.

Kauffman, J.B., Heider, C., Cole, T.G., Dwire, K.A., Donato, D.C., 2011. Ecosystem carbon stocks of micronesian mangrove forests. Wetlands 31, 343–352.

Khan, N.I., Suwa, R., Hagihara, A., 2007. Carbon and nitrogen pools in a mangrove stand of *Kandelia obovata* (S., L.) Yong: vertical distribution in the soil–vegetation system. Wetlands Ecol. Manage. 15, 141–153.

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

Lugo, A.E., Snedaker, S.C., 1974. The ecology of mangroves. Annu. Rev. Ecol. Evol. Syst. 5, 39–64.

Martin, A.R., Thomas, S.C., 2011. A reassessment of carbon content in tropical trees. PLoS One 6, e23533.

Mazda, Y., Kobashi, D., Okada, S., 2006. Tidal-scale hydrodynamics within mangrove swamps. Wetlands Ecol. Manage. 13, 647–655.

Mckee, K.L., 1995. Interspecific variations in growth, biomass, partitioning, and defensive characteristics of neotropical mangrove seedlings: response to light and nutrient availability. Am. J. Bot. 82, 299–307.

Mcleod, E., Chmura, G.L., Bouillon, S., Salm, R., Björk, M., Duarte, C.M., Lovelock, C.E., Schlesinger, W.H., Silliman, B.R., 2011. A blueprint for blue carbon: toward an improved understanding of the role of vegetated coastal habitats in sequestering CO_2. Front. Ecol. Environ. 9, 552–560.

Medeiros, T.C.C., Sampaio, E.V.S.B., 2008. Allometry of aboveground biomasses in mangrove species in Itamaracá, Pernambuco, Brazil. Wetlands Ecol. Manage. 16, 323–330.

Nagelkerken, I., Blaber, S.J.M., Bouillon, S., Green, P., Haywood, M., Kirton, L.G., Meynecke, J.O., Pawlik, J., Penrose, H.M., Sasekumar, A., Somerfield, C.J., 2008. The habitat function of mangroves for terrestrial and marine fauna: a review. Aquat. Bot. 89, 155–185.

Ray, R., Ganguly, D., Choudhury, C., Dey, M., Das, S., Dutta, M.K., Mandal, S.K., Majumdar, N., De, T.K., Mukhopadhyay, S.K., Jana, T.K., 2011. Carbon sequestration and annual increase of carbon stock in a mangrove forest. Atmos. Environ. 45, 5016–5024.

Ren, H., Chen, H., Li, Z., Han, W., 2010. Biomass accumulation and carbon storage of four different aged *Sonneratia apetala* plantations in Southern China. Plant Soil 327, 279–291.

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

Smith III, T.J., 1987. Seed predation in relation to tree dominance and distribution in mangrove forests. Ecology 68, 266–273.

Soares, M.L.G., Schaeffer-Novelli, Y., 2005. Above-ground biomass of mangrove species. I. Analysis of models. Estuarine Coast. Shelf Sci. 65, 1–18.

Twilley, R.R., Chen, R.H., Hargis, T., 1992. Carbon sinks in mangrove forests and their implications to the carbon budget of tropical coastal ecosystems. Water Air Soil Pollut. 64, 265–288.

Zar, J.H., 1996. Biostatistical Analysis. Prentice Hall, Upper Saddle River, NJ.