Mangrove forests associated with salt flats: a case study from southeast Brazil

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ABSTRACT

In this study, forest structure variability of a mangrove associated to a salt flat in Sepetiba Bay (SE-Brazil) was assessed. Forest structure and interstitial water salinity were measured in 32 plots established along three transects ranging from the margin of the estuary to the transition with the salt flat. Structural development was shown to be highly variable, with mean height ranging from 0.54 m to 7.96 m, mean diameter ranging from 1.58 cm to 9.46 cm and trunk density ranging from 2,733 live trunks.ha^{-1} to 106,667 live trunks.ha^{-1}. Forest structure variability responded to the gradient of increasing interstitial water salinity towards the salt flat, with mean height and diameter decreasing and trunks density increasing progressively in the same direction. The following pattern of species dominance was observed: *Rhizophora mangle* near the estuary margin; *Laguncularia racemosa* at the transition with the salt flat; and *Avicennia schaueriana* on intermediate zones. The assessment of structural characteristics of mangrove forests and their relationships with natural stressors (e.g., salinity) contribute to better understand the dynamics of the species along coastal plains associated with preserved salt flats, such as the one found in Guaratiba.

Descriptors: Mangrove, Phytosociology, Salt Flats, Ecological Gradients.

RESUMO

No presente estudo, a variabilidade estrutural de uma floresta de mangue associada a uma planície hipersalina na Baía de Sepetiba (SE-Brasil) é analisada. A estrutura vegetal e a salinidade da água intersticial foram medidas em 32 parcelas estabelecidas ao longo de 3 transectos localizados desde a margem do estuário até a transição com a planície hipersalina. O desenvolvimento estrutural foi altamente variável, com altura média variando entre 0,54 m e 7,96 m, diâmetro médio entre 1,58 cm e 9,46 cm e densidade de troncos entre 2.733 troncos vivos.ha^{-1} e 106.667 troncos vivos.ha^{-1}. A variabilidade da estrutura vegetal respondeu ao gradiente de aumento da salinidade da água intersticial à planície hipersalina, com a altura e o diâmetro médios diminuindo e a densidade de troncos aumentando no mesmo sentido. O seguinte padrão de dominância de espécies foi observado: *Rhizophora mangle* nas proximidades da margem do estuário; *Laguncularia racemosa* na transição com a planície hipersalina; e *Avicennia schauerianna* nas zonas intermediárias. O entendimento das características estruturais das florestas de mangue e suas relações com estressores naturais (ex. salinidade) contribuirá para a melhor compreensão da dinâmica das espécies ao longo de planícies costeiras associadas à planícies hipersalinas bem preservadas como em Guaratiba.

Descritores: Manguezal, Fitossociologia, Planícies hipersalinas, Gradientes ecológicos.

INTRODUCTION

Mangroves are coastal ecosystems located in intertidal zones of tropical and subtropical regions around the world. According to WALSH (1974), mangroves occur and are more developed in sites where the average minimum temperature of the coldest month of the year is higher than 20°C and the annual temperature range is lower than 5°C. They typically occur on muddy substrates protected from wave action and subjected to large tidal amplitudes.

Although these factors generally control the occurrence of mangroves worldwide, the structural and functional characteristics of each mangrove forest are regulated by an interaction of factors that act at the regional scale ("the energy signature"), as described by SCHAEFFER-NOVELLI et al. (1990) and TWILLEY (1995), and the local scale (e.g., factors associated with the frequency of tidal flooding) (SOARES et al., 2003). SOARES et al. (2003) further observed that the structure of mangroves reflects an overlay of characteristics associated with disturbances, namely: (1) type (chronic or acute); (2) spatial variability; (3) variable action over time; (4) variable frequency (recurrence); and (5) the system's capacity to recover after disturbances. OLIVER; LARSON (1990), HUSTON (1996), and FRELICH (2002) have described the mosaic pattern of several plant communities. SMITH (1992), SOARES (1999), SOARES et al. (2003), and BERGER et al. (2008) addressed this mosaic structure more specifically for mangrove forests.

Because mangroves occur in intertidal zones, soil salinity is a key environmental factor controlling the structure, function and distribution of this ecosystem. Mangrove species are generally adapted to survive under high salinity conditions (WALSH, 1974; LUGO; SNEDAKER, 1974; CHAPMAN, 1976). CINTRON et al. (1978) have proposed the upper limit of tolerance for mangrove species as being 2.5 times higher than the average salinity of sea water (35), a level that would allow plants to extract fresh water from saline water.

Although mangrove species have morphological and physiological adaptations for occurring in saline soils, growth and survivorship decline with increasing salinity. BALL (1980) have shown that salinity acts on the inter- and intraspecific competitive abilities of mangrove species and that salt stress limits growth and reproduction of plants. Extremely high salt concentrations in tropical salt flats are responsible for the absence of macrophytes (RIDD; SAM, 1996).

Some studies have characterized the structure of mangrove forests in the state of Rio de Janeiro (Southeast Brazil), such as Paraíba do Sul River (BERNINI; REZENDE, 2004), Guanabara Bay (SOARES et al., 2003; CAVALCANTI et al., 2009), Tijuca Lagoon (SOARES, 1999) and Sepetiba Bay (SILVA et al., 1991; ESTRADA et al., 2013), but adequate characterization of mangroves in some key regions is still lacking. This is the case of Guaratiba (located in Sepetiba Bay), one of the most important remnants of this ecosystem in the state of Rio de Janeiro. The same is true for mangrove forests associated with salt flats throughout the Brazilian coast.

To fill this gap, a case study from a well-preserved mangrove located in Sepetiba Bay is presented, describing the structural variability and its relationship with environmental gradients and, more specifically, the relationship between low structural development with environmental severity at the transition zone between the mangrove forest and the salt flat. Three hypotheses were defined in order to meet this objective: 1) Structural development of the mangrove forest decreases as the environmental severity towards the salt flat increases; 2) Relative dominance of species change in response to the increase in environmental severity; 3) Space is not optimally occupied in sites with extreme environmental severity for mangrove species.

MATERIAL AND METHODS

STUDY AREA

The study area is located at the Sepetiba/Guaratiba coastal plain, on the west side of the city of Rio de Janeiro, SE-Brazil. According to Köppen's classification, the climate in this region's coastal plain is Aw – tropical, hot and humid, with dry winters – and in its adjacent mountain slopes is Af, tropical, hot and humid, without dry seasons. The annual mean temperature is 23.5° C and the annual mean rainfall reaches 1,067 mm (ESTRADA et al., 2008). January and March are the wettest months and June and August the driest. The potential evapotranspiration in the region is higher from February to April and lower from June to September. The region is characterized by a micro-tidal regime. Groundwater from the Guaratiba Aquifer flows at shallow depths (1.5 m) from the adjacent higher lands to the coastal plain, reaching the estuarine system (VICENTE et al., 2010).

The mangroves of Guaratiba are located on the east side of Sepetiba Bay, between the Piraquê River and the

Guaratiba Mountain. They integrate a system of islands, rivers and channels that constitute the Guaratiba Biological Reserve (Figure 1A, B). Three typical mangrove species occur on the site: *Avicennia schaueriana* Stapf & Leechm. ex Moldenke, *Laguncularia racemosa* (L.) C.F. Gaertn., and *Rhizophora mangle* L. The most inner parts of the intertidal zone are only reached by spring tides, leading to the formation of salt flats: high-intertidal sites occurring in arid or seasonally dry regions (evapotranspiration higher than precipitation) and subjected to low tidal flooding, driving hypersaline conditions in the soil (HUTCHINGS; SAENGER, 1987). There is a continuum of features in Guaratiba that belong to the mangrove ecosystem, as described by HUTCHINGS; SAENGER (1987): (a) mud flats in the zones below mean sea level; (b) mangrove forests in the zones above mean sea level and below the highest neap tides level; and (c) salt flats, located in areas above the zone reached by the highest neap tides and up to the average high spring tides level. The mangrove forests of Guaratiba occupy an area of 20.9 km^2 and the salt flats 7.4 km^2. Previous studies describing the forest structure of the Guaratiba mangroves were undertaken by DANSEREAU (1947) and ESTRADA et al. (2013). The former was strictly descriptive and only provided general distribution diagrams of mangrove species, while the later analyzed the structural properties in order to test suitability of the concept of physiographic types.

SAMPLING DESIGN

The present study was developed in the mangroves occurring in the Piracão River, one of the three rivers that flow onto the Guaratiba coastal plain (Figure 1A, B). In the middle stretch of this river, 32 plots were established. They were positioned along three transects (A, B, and C), from the margin of the river to the interface between the mangrove forest and the salt flat. Plots inside the transects were distributed as follows: 8 at transect A, 10 at B e 14 at C.

CINTRON; SCHAEFFER-NOVELLI (1984) provided a general overview of the method used to characterize the structure of mangrove forests. To sample a representative number of individuals (trees), plots ranging from 15 to 150 m^2, depending on the forest density, were delimited at each sampling site. In addition, homogeneity of structural characteristics (species composition and structural development of individuals) was also taken into consideration. At each plot, all individuals were identified to the species level, had their height and trunk diameter

measured, and were classified according to the condition of their trunks (live or dead). Trunk diameter was measured at 1.30 m from the ground and denoted by D_{130} (BROKAW; THOMPSON, 2000). However, in plot A7, located at the transition zone between the forest and the salt flat, the trees were shorter and shrubby, and hence the diameter was measured at the trunk base.

Once field data had been collected, mean height, mean D_{130}, basal area, relative basal area dominance and density of trunks were calculated. Basal area (g, in m^2.ha^{-1}) was calculated by the formula g = 0.00007854*(D_{130})^2. Mean D_{130} represents the diameter (in cm) of the tree with the mean basal area. Note that this parameter differs from the arithmetic mean of D_{130}'s. Mean D_{130} was calculated by applying live basal area data to the formula:
= [(g)*12732.39/n]$^{1/2}$, where n = the number of trunks per hectare and g = basal area.

Using the Statistica 6.0® package, a cluster analysis (UPGMA) was applied to the data to analyze the relationships between the structural parameters of forests and the position along the tidal gradient. The parameters adopted for these analyses were mean D_{130} and the mean height. A second cluster was run using the relative contribution (%) of each species' live basal area. A regression analysis was run to assess the relationship between trunk density and mean height.

Based on the position of each plot along the transects and on a micro-topographic assessment previously presented by ESTRADA et al. (2013) for the mangroves of Guaratiba, the sampling plots were classified in terms of physiographic types, using the approach proposed by the same authors: fringe forests (sites at the low intertidal zone, with high tidal flooding frequency); basin forests (sites at the intermediate intertidal zone, with intermediate tidal flooding frequency); and transition forests (sites at the transition of the forest and the salt flat, at the high intertidal zone and presenting very low tidal flooding frequency). Plots grouped as physiographic types were compared for trunk density, mean height and mean D_{130} using ANOVA and Tukey post-hoc test (p < 0.05).

Assessment of interstitial water salinity was conducted at eight different sites along the tidal flooding gradient inside the mangrove forest (transect A), the first site located near the river margin and the last one at the interface between the mangrove forest and the salt flat. In each of the sampling points, holes were dug in the sediment to the depth where water seeped in. Salinity was assessed in triplicate (three different holes) using an optical
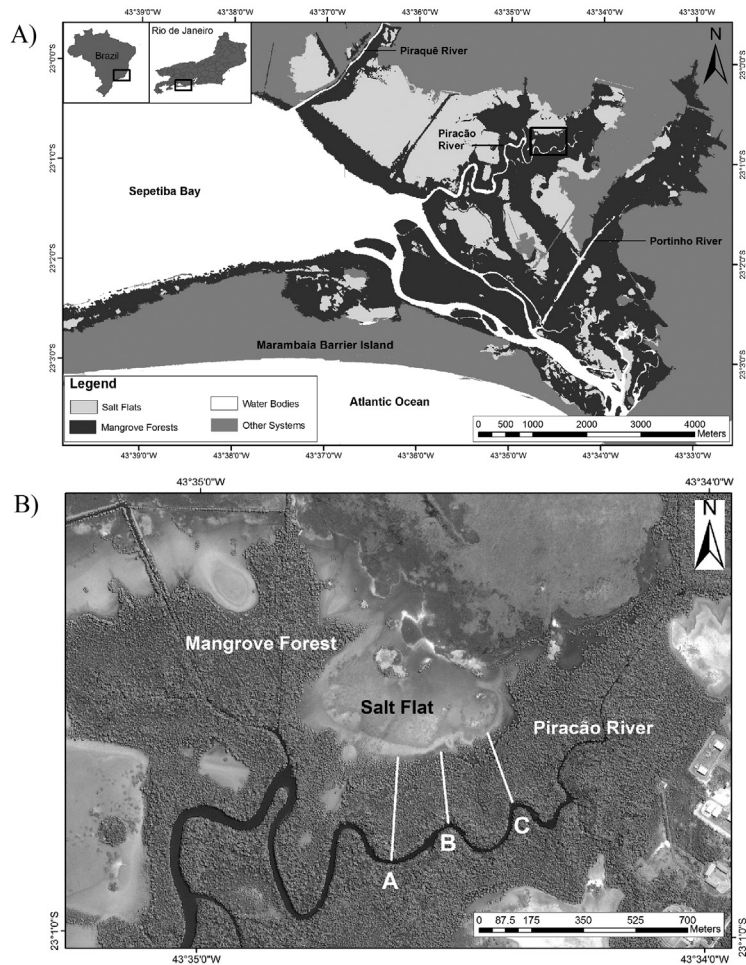
Figure 1. (A) Map showing the study area, with sampling location indicated (black square). Mangrove forests are presented in dark gray and areas in light gray represent salt-flats. (B) Aerial photograph (1:6,000) of the sampling site (black square in figure 1A) indicating the position of transects A, B and C.

refractometer model A366ATC (American Optical), with maximum range of 160 and accuracy of 1 unit.

Differences in the salinity of interstitial water between the eight sites were assessed by the Kruskal-Wallis test.

RESULTS

Mean salinity ranged from 28 at point two to 44 at point eight. There were significant differences in interstitial salinity among sites (KW = 280.35; p < 0.01). Salinity of the interstitial water increased landward and was correlated with the distance from the river (p < 0.05; R^2 = 0.768; Figure 2). In the present study, points one to six were regularly flooded by neap tides and points seven and eight were flooded only during spring tides. The duration of flooding was greater at sites closer to the river. Higher

salinity at point eight is probably due to the combined effect of lower frequency of tidal flooding and evaporation of standing water. On the other hand, lower salinity at point two is explained by higher frequency of tidal flooding.

The distribution of mangrove species along the transects reveals a pattern of zonation, inferred from the relative contribution of each species to the basal area (Tables 1, 2, and 3). This pattern is characterized by a general tendency toward dominance of *R. mangle* near the margin of the Piracão River, *A. schaueriana* between the margin and the salt flat, and *L. racemosa* closer to the salt flat. However, some exceptions to this pattern occurred in transect A, such as the co-dominance of *A. schaueriana* and *R. mangle* at plot one, and the dominance of *A. schaueriana* at plot eight.
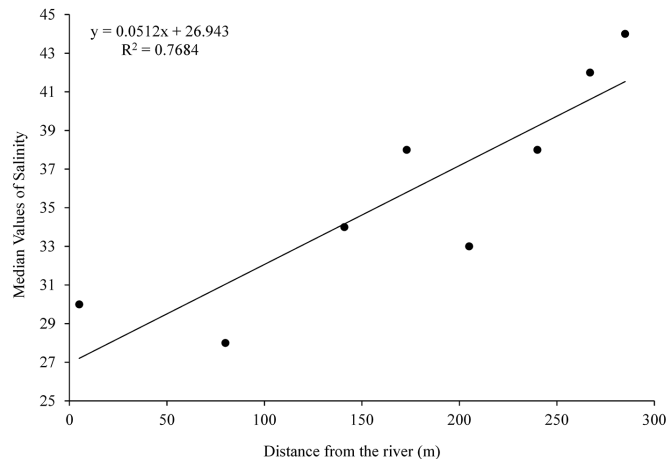
Figure 2. Regression analysis relating interstitial water salinity and distance from Piracão River.

The structural development of the three transects showed high variability. Mean height ranged from 0.54 ± 0.46 to 7.96 ± 1.73 m and mean D_{130} from 1.58 to 9.46 cm (Tables 1, 2, and 3). Trunk density also reflected this high variability, ranging from 2,733 to 106,667 live trunks.ha^{-1}. When each transect is analyzed individually, a tendency of decreasing structural development is evident from the margin of the Piracão River to the transition zone, at the interface between the mangrove forest and the salt flat. Hence, as mean height and D_{130} decrease, trunk density increases progressively (Tables 1, 2, and 3).

The tendency of structural development decrease towards the transition zone was also confirmed by changes in basal area. The distribution of basal area by D_{130} classes (Tables 4, 5, and 6) revealed that trunks above 10 cm are concentrated at sites closer to the river and are replaced by intermediate and smaller classes toward the transition zone.

The regression between trunk density and mean height for these forests showed an inverse relationship (Figure 3A; $R^2 = 0.69$; $p < 0.05$). It means that density decreases and size increases as forest development takes place. However, there was also a group of plots with low mean height (0.54 ± 0.46 to 1.58 ± 0.98 m) and low trunk density (12,667 to 45,714 live trunks.ha^{-1}): A5, A6, A7, A8, B10, C12, C13, and C14. These plots are located at the transition with the salt flat. When these plots were excluded from the analysis, this relationship became even stronger (Figure 3B; $R^2 = 0.81$; $p < 0.05$).

A cluster analysis considering mean D_{130} and height revealed four groups (Figure 4A). Group (A) represents

sampling sites located close to the margin of the Piracão River, where tidal flooding frequency is higher. These sites showed higher structural development, mean D_{130} above 7.0 cm, and mean height above 7.0 m. These sites are dominated by *R. mangle*, with a considerable contribution of *A. schaueriana* and the presence of few *L. racemosa* individuals (Tables 1, 2, and 3). Group (B) represents sampling sites near the Piracão River, with D_{130} between 4.5 and 7.0 cm and a mean height lower than 7.0 m. Hence, plots in Group (B) show intermediate structural development. These forests are dominated by *A. schaueriana* but have considerable contribution of *R. mangle* (Tables 1, 2, and 3). Groups (C) and (D) represent forests with lower structural development, with mean D_{130} lower than 4.5 cm (Tables 1, 2, and 3). Plots in Group (C) are located at intermediate distance between the Piracão River and the salt flat. Although they present low mean D_{130}, mean height is above 2.0 m, as opposed to plots in Group (D), located closer to the salt flat, where mean height is below 2.0 m (Tables 1, 2, and 3). Both groups are dominated by *L. racemosa* and/or *A. schaueriana*. However, Group (C) shows the occurrence of few *R. mangle* trees in some plots. As presented earlier by the regression analysis (Figure 3A) plots A5, A6, A7, A8, B10, C12, C13, and C14 do not follow the general relationship between mean height and trunk density. According to the cluster analysis, these plots fall into Group (D). The only exception is plot A7, which is isolated in Group (B), probably because diameter was measured at the trunk base in this plot, as described in the Methods section, leading to an overestimated average.

Table 1. Structural parameters of transect A.

Plot	Density (live trunks.ha⁻¹)	Mean D_{130} (cm)	Mean Height (m)	Basal Area (m².ha⁻¹)	Basal Area Contribution (%)		
					Species	Live	Dead
1	4,100	8.77	7.63±1.41	26.11	*R. mangle*	43	2
					L. racemosa	6	2
					A. schaueriana	45	1
2	2,733	9.46	7.40±1.97	20.15	*R. mangle*	62	2
					L. racemosa	18	2
					A. schaueriana	16	1
3	9,800	5.16	4.19±1.77	25.13	*R. mangle*	28	3
					L. racemosa	6	1
					A. schaueriana	48	14
4	13,400	3.57	3.28±1.76	15.14	*R. mangle*	7	0
					L. racemosa	18	5
					A. schaueriana	63	6
5	34,400	2.3	1.34±0.86	15.03	*R. mangle*	0	0
					L. racemosa	55	4
					A. schaueriana	40	1
6	45,714	4.15	1.07±0.45	62.14	*R. mangle*	0	0
					L. racemosa	86	0
					A. schaueriana	13	1
7	12,667	7.23	1.24±0.19	51.96	*R. mangle*	0	0
					L. racemosa	100	0
					A. schaueriana	0	0
8	33,667	3.74	0.80±0.29	37.24	*R. mangle*	0	0
					L. racemosa	0	0
					A. schaueriana	99	1

Cluster analysis considering species contribution to live basal area (Figure 4B) followed the same general pattern obtained in the structural development analysis. Group (I) includes plots with more than 20% of *R. mangle*. These plots are all included in Groups (A) and (B). Group (II) constitutes forests dominated by *A. schaueriana* and is almost identical to Group (C). Finally, Group (III) is characterized by forests with contribution of *L. racemosa* higher than 55%, no *R. mangle* individuals, and is equivalent to Group (D).

Considering the criteria described in the methods section, plots were grouped as physiographic types as follows: Fringe forests –A1, A2, B1, B2, B3, C1 and C2; Basin Forests – A3, A4, B4, B5, C3, C4, C5, C6, C7, C8, C9 and C10; Transition Forests – A5, A6, A7, A8, B6, B7, B8, B9, B10, C11, C12, C13 and C14. The results confirm significant differences for all the parameters: Trunk density (F = 44.98; p < 0.01); Mean D_{130} (F = 313.85; p < 0.01); and Mean height (F = 499.58; p < 0.01).Tukey test confirmed significant differences between fringe and transition forests for all parameters. However, this was the only significant difference for trunk density (p = 0.001), while for mean D_{130} only basin versus transition had no difference (p < 0.721). Mean height was significantly different in all cases (p < 0.01).

Table 7 compares the results of the present study to the ones presented previously to other mangroves from the state of Rio de Janeiro, which are located in a narrow latitudinal range, between 21°18' and 23°23'S, and in the same coastal segment (Schaeffer-Novelli et al., 2000). In terms of mean D_{130} and height, mangrove forests in the Piracão River vary from low to intermediate structural development compared to other mangroves in the state. Basal area is within range found for other forests in this regions. The exceptions are sampling plots 6 and 7 of transect A and plot 8 of transect C, where basal area is much larger.

DISCUSSION

The pattern of species distribution observed in Guaratiba is typical of mangrove forests located in south and southeast Brazil (SCHAEFFER-NOVELLI et al., 1990), where only *R. mangle*, *L. racemosa*, and *A. schaueriana* occur. A similar pattern has been described by SHERMAN et al. (2000), LARA; COHEN (2006), and PIOU et al. (2006) for other regions where *R. mangle*, *L.*

Table 2. Structural parameters of transect B.

Plot	Density (live trunks.ha^{-1})	Mean D$_{130}$ (cm)	Mean Height (m)	Basal Area (m^2.ha^{-1})	Basal Area Contribution (%)		
					Species	Live	Dead
1	5,100	7.37	7.71±1.48	26.62	*R. mangle*	48	7
					L. racemosa	0	3
					A. schaueriana	34	8
2	5,700	6.31	5.61±2.26	21.11	*R. mangle*	33	6
					L. racemosa	0	3
					A. schaueriana	51	7
3	6,400	5.86	5.04±1.14	25.83	*R. mangle*	32	1
					L. racemosa	7	1
					A. schaueriana	28	30
4	15,143	4.56	3.05±1.75	27.35	*R. mangle*	25	4
					L. racemosa	8	2
					A. schaueriana	58	3
5	15,143	4.56	3.05±1.75	27.35	*R. mangle*	15	0
					L. racemosa	21	9
					A. schaueriana	44	11
6	23,250	3.62	2.88±1.51	27.08	*R. mangle*	0	0
					L. racemosa	16	5
					A. schaueriana	72	7
7	41,250	2.5	2.46±1.23	23.12	*R. mangle*	0	0
					L. racemosa	25	6
					A. schaueriana	63	7
8	69,714	2.25	1.55±0.94	29.43	*R. mangle*	0	0
					L. racemosa	63	4
					A. schaueriana	32	2
9	85,333	1.61	1.57±0.46	21.17	*R. mangle*	0	0
					L. racemosa	71	18
					A. schaueriana	11	0
10	36,000	3.15	0.60±0.34	28.08	*R. mangle*	0	0
					L. racemosa	99	0
					A. schaueriana	1	0

racemosa, and *A. germinans* occur, and by SCHAEFFER-NOVELLI et al. (1990), and SANTOS et al. (1997) for regions where mangrove forests are associated with salt flats. According to JIMENEZ; SAUTER (1991), the high salinity levels found in the most inner sites of the mangrove forests they have studied constrain the development of *Rhizophora racemosa*, in contrast to *Avicennia bicolor* which tolerates higher salinities. A similar relationship has been described by LARA; COHEN (2006) and PIOU et al. (2006) for *Rhizophora mangle* and *Avicennia germinans*.

The interstitial salinity increases with increasing distance from the river, contradicting the pattern reported previously by JOSHI; GHOSE (2003). The initial low salinities can be explained by the higher frequency and duration of tidal flooding after point one. Low frequency and duration of tidal flooding, in a seasonally dry climate such as in the Guaratiba region, are probably the driving factors for the observed high salinity in the landward

areas of the intertidal zone. This pattern is responsible for the formation and maintenance of salt flats associated with mangrove forests, as previously described by HUTCHINGS; SAENGER (1987). Results of the direct-gradient analysis show that different mangrove species have different distributions along the salinity gradient. *A.schaueriana* and *L. racemosa* are found in wide ranges of soil salinity, whereas *R. mangle* is restricted to lower salinity levels.

The distribution of mangrove species associated with a gradient of frequency of tidal flooding has been reported by many authors, and may be a response to a salinity gradient (CINTRON et al., 1978; TOMLINSON, 1986; JOSHI; GHOSE, 2003). Despite the importance of salinity control of the mangrove species distribution, we must consider the importance of many other physico-chemical factors (NICKERSON; THIBODEAU, 1985; EWEL et

Table 3. Structural parameters of transect C.

Plot	Density (live trunks.ha⁻¹)	Mean D$_{130}$ (cm)	Mean Height (m)	Basal Area (m².ha⁻¹)	Basal Area Contribution (%)		
					Species	Live	Dead
1	6,900	5.66	4.50±3.07	20.83	R. mangle	60	16
					L. racemosa	0	0
					A. schaueriana	24	0
2	3,800	8.87	7.96±1.73	33.99	R. mangle	47	5
					L. racemosa	2	0
					A. schaueriana	20	26
3	16,286	5.43	2.90±1.23	37.9	R. mangle	22	0
					L. racemosa	2	0
					A. schaueriana	76	0
4	47,143	1.69	1.87±0.78	11.96	R. mangle	5	0
					L. racemosa	24	7
					A. schaueriana	59	4
5	19,429	3.06	2.07±1.07	15.36	R. mangle	2	0
					L. racemosa	28	6
					A. schaueriana	64	1
6	31,143	2.25	2.34±1.01	14.0	R. mangle	44	0
					L. racemosa	39	11
					A. schaueriana	6	1
7	14,400	3.48	3.35±1.40	23.95	R. mangle	13	0
					L. racemosa	8	8
					A. schaueriana	36	35
8	55,600	2.35	2.77±0.85	44.18	R. mangle	0	0
					L. racemosa	22	10
					A. schaueriana	32	36
9	27,600	3.97	2.75±1.73	35.35	R. mangle	3	0
					L. racemosa	6	1
					A. schaueriana	88	3
10	31,200	2.76	3.64±1.76	21.8	R. mangle	0	0
					L. racemosa	29	3
					A. schaueriana	56	11
11	106,667	1.58	1.74±0.66	26.32	R. mangle	0	0
					L. racemosa	38	10
					A. schaueriana	42	10
12	28,000	1.95	1.58±0.98	8.52	R. mangle	0	0
					L. racemosa	59	2
					A. schaueriana	39	0
13	21,600	2.86	1.06±0.56	14.27	R. mangle	0	0
					L. racemosa	71	3
					A. schaueriana	26	0
14	22,400	1.67	0.54±0.46	5.04	R. mangle	0	0
					L. racemosa	70	1
					A. schaueriana	28	1

al., 1998; FELLER et al., 2003; LOVELOCK et al., 2007), which and are also regulated by tidal flooding.

The progressive decrease of structural development towards the transition zone between the forest and the salt flat observed in Guaratiba has also been reported previously for other dry or seasonally dry regions (BALL, 1980; SCHAEFFER-NOVELLI et al., 1990; CINTRON-MOLERO, 1993; SANTOS et al., 1997). However, such a structural decrease may also occur where the mangrove forest is associated with a terrestrial ecosystem (DAHDOUGH-GUEBAS, 2004; LARA-DOMÍNGUEZ et al., 2005; KRAUSS et al., 2006).

Such a pattern reflects the environmental severity in the transition zones, which derives from a gradient of tidal

Table 4. Basal area, live and dead, by D_{130} class (cm) on transect A.

Plot	Live basal area ($m^2.ha^{-1}$)			Dead basal area ($m^2.ha^{-1}$)		
	$D_{130} < 2.5$	$2.5 \leq D_{130} < 10.0$	$D_{130} \geq 10.0$	$D_{130} < 2.5$	$2.5 \leq D_{130} < 10.0$	$D_{130} \geq 10.0$
1	0	9.86	14.88	0	1.37	0
2	0.05	6.46	12.72	0.04	0.88	0
3	0.75	9.77	9.98	0.39	1.58	2.65
4	1.57	8.23	3.65	0.72	0.98	0
5	4.76	8.58	0.95	0.48	0.26	0
6	4.23	57.5	0	0.17	0.23	0
7	0	51.96	0	0	0	0
8	3.6	26.27	7.13	0	0.24	0

Table 5. Basal area. live and dead. by D_{130} classes (cm) at transect B.

Plot	Live basal area ($m^2.ha^{-1}$)			Dead basal area ($m^2.ha^{-1}$)		
	$D_{130} < 2.5$	$2.5 \leq D_{130} < 10.0$	$D_{130} \geq 10.0$	$D_{130} < 2.5$	$2.5 \leq D_{130} < 10.0$	$D_{130} \geq 10.0$
1	0	13.76	7.98	0	3.04	1.84
2	0.32	8.86	8.61	0.12	3.19	0
3	0.12	10.17	6.97	0.15	1.16	7.26
4	2.02	10.37	12.37	0.75	1.84	0
5	2.8	8.78	0	1.64	1.16	0
6	3.49	10.18	10.28	1.5	1.62	0
7	6.17	11.44	2.64	2.03	0.83	0
8	9.98	17.79	0	1.52	0.15	0
9	14.09	3.32	0	3.37	0.38	0
10	1.58	26.51	0	0	0	0

Table 6. Basal area. live and dead. by D_{130} class (cm) on transect C.

Plot	Live basal area ($m^2.ha^{-1}$)			Dead basal area ($m^2.ha^{-1}$)		
	$D_{130} < 2.5$	$2.5 \leq D_{130} < 10.0$	$D_{130} \geq 10.0$	$D_{130} < 2.5$	$2.5 \leq D_{130} < 10.0$	$D_{130} \geq 10.0$
1	0.71	6.78	9.84	0.15	0.39	2.96
2	0	12.39	11.09	0	0.86	9.65
3	2.0	10.93	0	0.16	0	0
4	7.79	2.81	0	1.36	0	0
5	2.99	4.34	0	0.52	0.55	0
6	5.16	7.26	0	1.17	0.4	0
7	1.46	12.2	0	1.09	3.22	5.99
8	9.62	14.42	0	4.25	8.91	6.97
9	3.32	11.98	0	0.77	0	0
10	4.12	14.52	0	2.92	0	0
11	14.35	6.65	0	4.99	0	0
12	5.09	3.26	0	0.09	0	0
13	2.24	11.63	0	0.04	0	0
14	4.04	0.88	0	0.12	0	0

frequency (KRAUSS et al., 2008), leading to gradients of salinity (SAM; RIDD, 1998; ELLISON et al., 2000), nutrients concentration and availability (NICKERSON; THIBODEAU, 1985; EWEL et al., 1998) and concentration of H_2S (FELLER et al., 2003; LOVELOCK et al., 2007). As a result, the space tends to be sparsely occupied by individuals of low structural development in the transition zones. In other words, under adverse conditions, the available space is not fully occupied, contrary to what occurs in forests under better environmental conditions. This confirms the third hypothesis of this study. This hypothesis is in accordance with ODUM (1985), who stated
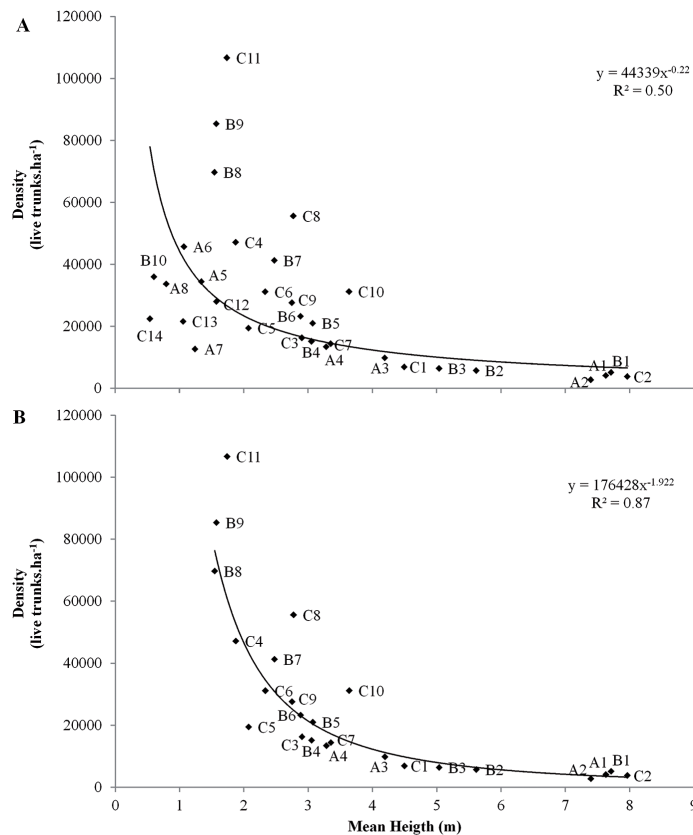
Figure 3. Regression analysis relating density and mean height (A) including all plots studied and (B) excluding plots located at the transition between mangrove forests and the salt flat (A5, A6, A7, A8, B10, C12, C13 and C14).

that in ecosystems under stress, organisms become smaller in size and resource utilization becomes less efficient, such as the case of space in the present study.

The occurrence of a zone with reduced mean height and trunk density at the transition between mangroves and salt flats has been reported by SOARES et al. (2008) in NE-Brazil, where only individuals of *A. schaueriana* were found and had a dead basal area of 45%. Landward from this zone, 99% of the individuals were dead. GORDON (1993) has previously shown that shrub-like forests, characterized by low structural development and density, occur at transition zones between mangroves and salt flats. These findings have been reinforced by MEDINA et al. (2001) as well, who have described the occurrence of shrub-like, sparse forests of *A. germinans* in sites where salinity levels were higher than 60.

BALL (1980) observed that zones with low tidal flooding frequency are subjected to extreme conditions, such as substrate dehydration and wide variability

in salinity levels, as opposed to areas with high tidal frequency, and more stable environmental conditions. Discussing the same topic, JIMENEZ (1990) showed that high rates of mortality of low-size classes associated with environmental severity (water stress) leads to low density of trees.

In the light of these facts, the relationship between density and mean height (Figure 3A) does not clearly describe the complex relationship between density and structural development (represented by mean height), since it includes sampling sites subjected to different regimes of tidal flooding and levels of stress. As shown in the results section, Figure 3A includes zones where the relationship between density and height is inverse (different maturation phases) and zones where this relationship does not occur (sites under high environmental severity). ARREOLA-LIZÁRRAGA et al. (2004) described a similar pattern for mangroves in the Gulf of California, where hypersalinity limits forest development. These forests have low density,
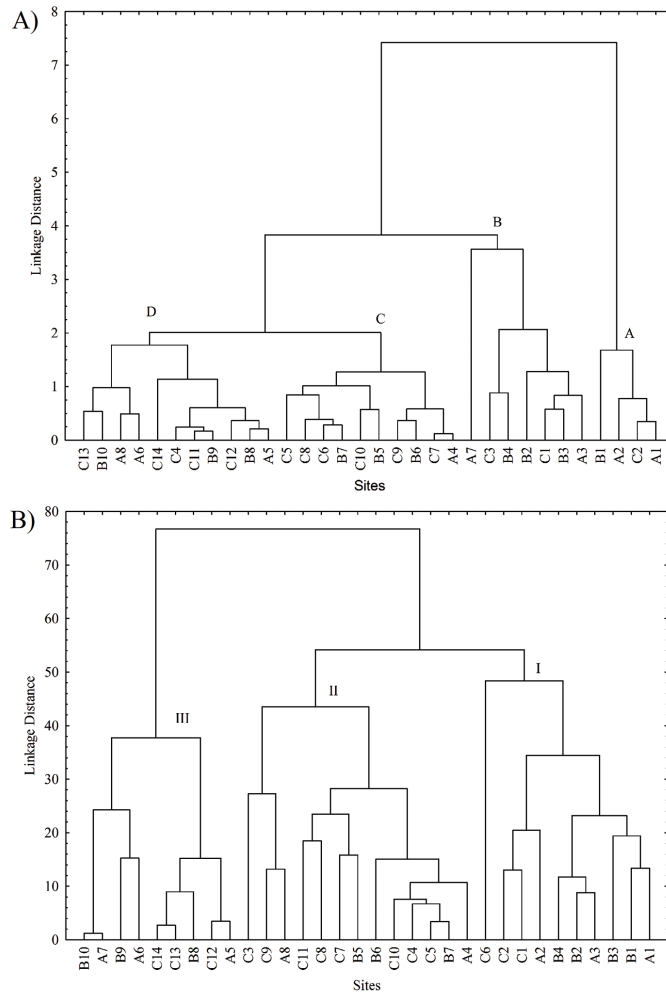
Figure 4. Cluster analysis (UPGMA) of sites studied (A) considering mean D_{130} and mean height and (B) considering live basal area contribution (%) of each species.

but also low height and basal area, exactly as plots A5, A6, A7, A8, B10, C12, C13 and C14, at the transition zone, do. As described earlier, by excluding these plots from the analysis, the effects of maturation of the selected forests could be demonstrated without the "noise" from the variability inserted by stress (Figure 3B; $R^2 = 0.87$; $p < 0.05$).

With some few exceptions, plots classified as fringe forests were defined as Groups A and B in the cluster analysis, while plots classified as basin and transition forests were defined as Groups C and D, respectively. This pattern highlights the relationship between structural development and tidal flooding frequency, which is in agreement with the findings of previous studies, such as CINTRON et al. (1978); SCHAEFFER-NOVELLI et al. (1990); JIMENEZ; SAUTER (1991); EWEL et al. (1998);

FELLER et al. (2003); DAHDOUH-GUEBAS et al. (2004); LARA-DOMÍNGUEZ et al. (2005); KRAUSS et al. (2006); LARA; COHEN (2006) and ESTRADA et al. (2013). The mangrove forests of Guaratiba, located in a protected area (Biological Reserve of Guaratiba), undergo little human interference. Consequently, the low structural development found at some sites reflects the influence of natural factors associated with environmental severity caused by low frequency of tidal flooding at the interface between mangrove forests and the salt flat. In contrast, mangrove forests with low structural development in the Guanabara Bay (Table 7), for example, are under strong human pressure (SOARES et al., 2003; CAVALCANTI et al., 2009).

Although some plots in Guaratiba showed low structural development as demonstrated by mean height parameters,

Table 7. Structural parameters for other mangrove forests in Rio de Janeiro state, between 21°18' and 23°23'S.

Study Area	Mean Diameter (cm)	Mean Height (m)	Basal Area (m².ha⁻¹)	Reference
Itacuruçá	7.80	6.10±1.20	21.6	SILVA et al. (1991)
Tijuca Lagoon	4.80 - 16.67	3.37 - 11.58	14.25 - 41.37	SOARES (1999)
Itabapoana River	3.70 - 13.50	4.00 - 10.10	13.50 - 48.30	BERNINI; REZENDE (2010)
Paraíba do Sul River	7.44 - 13.40	6.30 - 9.90	14.50 - 35.30	BERNINI; REZENDE (2004)
Suruí River	5.16 - 7.11	4.90 - 6.58	0.61 - 17.17	SOARES et al. (2003)
Nova Orleans	4.31 - 6.49	4.31 - 6.49	12.91 - 20.00	SOARES et al. (2003)
Piedade	1.73 - 7.83	2.40 - 6.72	9.84 - 18.16	SOARES et al. (2003)
Duque de Caxias	1.33 - 7.42	1.80 - 6.20	1.10 - 24.02	SOARES et al. (2003)
São Gonçalo I	3.65 - 5.56	3.33 - 6.37	11.72 - 17.78	SOARES et al. (2003)
São Gonçalo II	4.22 - 6.56	3.86 - 7.27	9.45 - 15.74	SOARES et al. (2003)
Guanabara Bay PA[1]	8.38±1.96	7.46±1.96	16.04±3.92	CAVALCANTI et al. (2009)
Guanabara Bay[2]	5.07±1.53	4.86±1.38	13.20±4.87	CAVALCANTI et al. (2009)
Piracão River	1.61 - 9.46	0.54 - 7.96	4.92 - 62.74	Present study

Footnotes: 1. Parameters calculated from 43 plots located in two Protected Areas; 2. Parameters calculated from 30 plots.

their live basal areas reflect the degree of conservation. Forests in degraded areas, such as those described by SOARES et al. (2003) for Guanabara Bay, contain less than 20.0 m².ha⁻¹ of basal area. On the other hand, 72% of the forests studied in Guaratiba have more than 20.0 m².ha⁻¹ of basal area, and about 22% of them have more than 30.0 m².ha⁻¹.

In summary, the analysis of the forest structure in the selected region allowed us to describe the structural variability of a mangrove forest associated to a gradient of tidal flooding frequency. Along this gradient, soil environmental severity increases and reaches maximum levels in the salt flat, where no mangrove plant occur. On one end of this gradient, the forest is well developed and dominated by *R. mangle*; whereas on the other end the forest is characterized by low structural development and dominated by *A. schaueriana* and *L. racemosa*. This pattern is similar to other mangroves from dry or seasonally dry regions where a gradient of tidal frequency toward the transition zone is observed. Low structure development found at the transition between the forest and the salt flat is probably determined by natural stressors, such as hypersalinity, nutrient depletion, and high H_2S concentration. These stressors are associated with low tidal frequency, and must not be confused with anthropogenic disturbances that lead to similar structural characteristics.

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